INVESTIGATING THE CONSERVATION VALUE OF LEOPARD POPULATION INDICES OBTAINED THROUGH CAMERA TRAPS IN THE GREATER KRUGER REGION OF SOUTH AFRICA

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FOR THE LEOPARDS

I grew up listening to stories about how the leopard got its spots and have now included that exact question in my doctoral thesis. Thank you to these special creatures for instilling in me such a love for the natural world. I really hope that this work will help to secure their future on our shared planet.

ABSTRACT

Leopards (*Panthera pardus*) are one of the most widespread large felids, historically ranging across much of Africa, the middle east and Asia. Their solitary and elusive nature has allowed them to persist in many areas where other members of the large carnivore guild have been extirpated. However, the combined effects of habitat loss, reduced prey abundance, unsustainable trophy hunting, negative interactions with humans and a growing demand for body parts are taking their toll on the species. Leopards now occupy between 25 and 37% of their historic range, and population densities are decreasing across many small reserves in South Africa. Modifications to current management regimes, informed by monitoring programs, are thus crucial to the persistence of the species. Kruger National Park (KNP) is the largest protected area in South Africa and has thus been assumed to be an inviolate refuge for leopards, despite a lack of data on key leopard population parameters. In this thesis I provide crucial density estimates for leopards in different regions of KNP and adjacent privately managed areas. Additionally, I explore other often neglected data routinely recorded by camera traps that are potentially important to refining population monitoring efforts. Specifically, I investigate temporal leopard activity quantified using time stamps on photographs of individuals and the potential drivers of activity patterns across different sites as well as the relationship between phenotypic similarity derived from photographs of known individuals and relatedness estimates from pedigree data. Multisession spatial capture-recapture (SCR) models proved useful in estimating density across sites and looking at drivers of density. Leopard density ranged from 2.6 ± 0.6 to 13.2 ± 2.6 leopards/100km^2 across the sites surveyed. Differences in reserve management appear to be having a substantial effect on the density of leopard populations, providing cause for concern that leopards are being negatively affected by anthropogenically driven mortalities and populations are thus failing to reach their carrying capacity. Normalised Difference Vegetation Index (NDVI) was also an important driver of density, showing a strong interaction with Reserve Type. Higher NDVI was more strongly positively correlated with leopard density in better protected reserves. Leopard activity was predominantly nocturnal with crepuscular peaks and diel activity patterns that differed between sites. These differences were driven mainly by seasonal variation in temperatures and not the relative abundance of humans, potential competitors, or prey. Leopard activity also varied on a lunar scale, with leopards showing higher activity levels with greater lunar illumination, possibly in response to decreased hunting success at higher light levels. I quantified phenotypic similarity in leopards from the Sabi Sand Game Reserve (SSGR) by measuring the resemblance of flank rosette patterns using Hotspotter and ImageJ software and manually recording the resemblance of whisker spot markings. I then compared these metrics to relatedness scores obtained from a pedigree derived from known maternal relationships with offspring. Despite six of 15 phenotypic metrics showing significant heritability, this relationship was noisy at the population level and thus phenotypic resemblance measures derived from photographic data could not provide information on the level of relatedness between leopard individuals from within populations. The data collected throughout this study provides a comprehensive baseline of leopard population status in KNP and select adjacent and contiguous private protected areas. Density remains highest in the SSGR which invests heavily in preventing negative anthropogenic impacts, is intermediate in KNP where there is concern over the potential for some human induced mortality and is lowest in Karingani Game Reserve (KGR), a protected area in its infancy where the effects of protection have not yet had time to materialise. This study also provides an indication of the uses and limitations of camera trap data, and how it can be helpful in informing leopard conservation and management.

DECLARATION

I, Lucy Kay Smyth, hereby declare that this doctoral thesis was carried out in accordance with the regulations and expectations set out by the University of Cape Town. Everything contained in this thesis is my own original work, except where explicitly stated otherwise. No part of this work is being submitted for another degree at any other university. I grant the university free license to reproduce any part of this work for research purposes. I also acknowledge that this work was carried out as part of a larger, ongoing collaboration between the Institute for Communities and Wildlife in Africa (iCWild) and Panthera, that data collection involved many other partners, and that some data was collected by Panthera before my involvement in the project. I began this work in February 2018 as an MSc, and it was upgraded to a PhD in February 2019 by the Doctoral Degrees Board. I am presenting this work to the University of Cape Town for examination towards the degree of Doctor of Philosophy in Conservation Biology in the Department of Biological Sciences and the Faculty of Science. This thesis has been submitted to the Turnitin module and I confirm that my supervisors have seen my report and that any concerns raised therefrom have been resolved between myself and my supervisors.

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CHAPTER 1

GENERAL INTRODUCTION

Figure 1.1: A camera trap photograph of a young leopard in Kruger National Park, the largest state run park in South Africa, which is widely believed to be a stronghold for the species.

1.1 Context

In the last 200 years the human population has increased sevenfold, from 1 billion to over 7.6 billion people (Mogelgaard, 2019). Human population growth is inextricably tied to land use change, resource extraction and climate change (McKee et al., 2004). These activities have had overwhelmingly negative consequences for a wide range of organisms (McKee et al., 2013). More than 75% of the world's land is currently classified as degraded and is therefore no longer available to wildlife as it once was (Kotiaho and Halme, 2018). Not only is wild land being replaced with human modified landscapes but weather patterns are changing and pollutants are being introduced throughout terrestrial and aquatic ecosystems (Vitousek et al., 1997; McKee et al., 2004; Tilman et al., 2017). It is therefore not surprising that during the Anthropocene the background rate of extinction has increased to such an extent that we are currently experiencing what is now referred to as the sixth extinction (McCallum, 2015).

1.2 Large carnivore conservation

Large carnivores have been particularly badly impacted by anthropogenic activity (Vitousek et al., 1997). There are a multitude of reasons for this: they are wide ranging, they can be dangerous and they sometimes prey on domestic animals or other animals of sentimental or financial importance to humans (Ripple et al., 2014; Swanepoel et al., 2014; Balme et al., 2014; Rosenblatt et al., 2014). For example, lions frequently attack humans in Tanzania (Packer et al., 2005) and wolves routinely prey on livestock in Canada (Treves et al., 2004). Negative perceptions of the impacts of large carnivores are however often inflated, and large carnivores have historically been persecuted to such an extent that they have repeatedly been driven to local extinction (Breitenmoser, 1998; Fortin et al., 2005). This happens most commonly through retaliatory shooting, snaring and poisoning (Nyhus, 2016). Other major threats to large carnivores include habitat loss, reduced prey availability, targeted poaching and unsustainable hunting practices (Lindsey et al., 2013; Jorge et al., 2013; Ripple et al., 2014; Swanepoel et al., 2014; Balme et al., 2014; Rosenblatt et al., 2014). The conservation of large carnivore populations is therefore important for their survival, and aims to ensure the persistence of viable, stable, self-sustaining populations of sufficient abundance to maintain genetic diversity and ecological function (Balme et al., 2014).

One of the most common approaches to managing the potential danger imposed by the presence of large carnivores is the erection of fences either around private farms or around protected areas as part of the fortress conservation model (Packer et al., 2013a). These Protected areas therefore currently form the cornerstone of most large carnivore conservation strategies (Caro, 2015). However, there is increasing evidence that even protected areas may not effectively conserve carnivores (Creel et al., 2013). Poaching of carnivores inside protected areas is widespread and may reach levels that drive population declines of both prey and predator populations (Becker et al., 2013; Rosenblatt et al., 2016; Johnson et al., 2016). Such poaching can be deliberate, when carnivores are targeted for their body parts (Williams et al., 2017), or incidental, when carnivores are caught in snares intended for other species (Lindsey et al., 2011; Becker et al., 2013).

Not only are carnivores themselves poached, but so is their prey. Bushmeat poaching, while sometimes a low-impact subsistence level activity occurring on land adjacent to protected areas, is becoming increasingly commercialised (Lindsey et al., 2013; Rogan et al., 2019). The depletion of prey populations, an inevitable consequence of the bushmeat trade, is widely regarded as an increasing threat to large carnivore populations, and a driver behind their widespread declines (Stein et al., 2016; Wolf and Ripple, 2016). Reduced prey availability has been correlated with lower densities in a number of felid species including lions, leopards and tigers (Karanth and Nichols, 1998; Fuller and Sievert, 2001; Henschel et al., 2011; Bauer et al., 2014; Rosenblatt et al., 2014; Rosenblatt et al., 2016).

Poaching further affects large carnivore populations through the destabilisation of ecosystem level processes (Balme et al., 2009). Thus while infanticide is relatively common among large carnivores, rates increase substantially when dominant males are removed through activities such as trophy hunting or poaching (Wolff and Macdonald, 2004; Balme et al., 2013; Balme and Hunter, 2013a). Higher than usual rates of infanticide can be of particular importance to populations already exposed to other threats, such as targeted poaching and hunting (Whitman et al., 2004; Balme et al., 2009; Packer et al., 2009; Balme et al., 2012; Wolf and Ripple, 2016).

Given their size, charisma and power, large carnivores are often the target of hunting endeavours. Some of these are legal and others not. Illegal hunting invariably has negative consequences for populations of wild animals (Jorge et al., 2013). Unfortunately however legal hunting activities also often have more negative consequences on populations than anticipated (Whitman et al., 2004; Balme et al., 2012; Braczkowski et al., 2015). That is because hunting regulations are often based on sparse or unreliable datasets, and not updated regularly enough (Balme et al., 2010a). Enforcement is also a major problem, and the line between legal and illegal hunting has on occasion become far too blurred (Balme et al., 2012; Johnson et al., 2016; Loveridge et al., 2017). However, when managed properly, trophy hunting can have a net benefit to biodiversity conservation through income generation and the protection of wild lands (Di Minin et al., 2016; Dickman et al., 2019). While trophy hunting remains a topic of much debate, many believe that banning trophy hunting altogether will negatively affect conservation, and that instead it needs to be more carefully managed (Di Minin et al., 2016; Dickman et al., 2019).

The persecution of carnivores in the areas immediately adjacent to protected areas can also threaten the persistence of protected populations (Woodroffe and Ginsberg, 1998). Due to their wide-ranging behaviour, carnivores frequently move beyond the boundaries of protected areas, where their risk of persecution increases because of the risks they pose to human lives and livelihoods (Balme et al., 2010b; van der Meer et al., 2013; Loveridge et al., 2017). The peripheries of protected areas can thus function as population sinks and, if mortality in border regions is not balanced by reproduction in core areas, the resulting edge effect can cause the decline or even extinction of carnivore populations in protected areas (Woodroffe and Ginsberg, 1998; Balme et al., 2009; Rosenblatt et al., 2014).

Large carnivores have particularly high space requirements, and smaller protected areas are often not large enough to support self-sustaining, genetically diverse populations (Funston, 2011; Fattebert et al., 2013). Consequently many large carnivore populations from different protected areas need to be managed as a metapopulation (Creel et al., 2013). This involves moving certain individuals between reserves to maintain sufficient genetic diversity and hence prevent the deleterious impacts of inbreeding (Buk et al., 2018). While crucial to maintaining the integrity of small populations, this kind of management intervention is invasive, costly, risky and time consuming, and acquiring the required resources is often a challenge (Creel et al., 2013; Dolrenry et al., 2014). Therefore, where there is debate between the benefits and drawbacks of having fewer larger protected areas versus more smaller ones, arguments for large carnivores tend to favour the former. Larger protected areas also decrease the perimeter to area ratio of reserves, reducing the impacts of edge effects (Woodroffe and Ginsberg, 1998; Balme et al., 2010b).

Large carnivores play a critical part in ecosystem function through their role as apex predators. They act as agents of top-down control, affecting both prey numbers and behaviour (Ripple et al., 2014). A lack of apex predators typically results in a cascade of negative consequences at the scale of entire ecosystems (Estes et al., 2011). Arguably one of the most commonly documented examples of this occurred in Yellowstone National Park where the extirpation of wolves allowed the elk population to balloon with cascading adverse ecological effects (Ripple et al., 2001; Fortin et al., 2005; Ripple and Beschta, 2012). While the magnitude of the impact of the reintroduction of wolves and mechanisms behind consequent increases in aspen regeneration has been debated in recent years, with questions on whether the impact of top-down control by large carnivores has been overstated, the presence of top-down control remains (Kauffmanet al., 2010; Mech, 2012; Brice et al., 2021). The critical role which apex predators play in maintaining ecosystem function makes many large carnivores keystone species: species which have a disproportionately large impact on their surrounding environment relative to their abundance across the landscape (Dalerum et al., 2008).

In addition to their important role in ecosystem functioning, large carnivores are also regarded as umbrella species, meaning that their conservation frequently leads to the indirect conservation of other species (Simberloff, 1998; Roberge and Angelstam, 2004). This is because they require large tracts of protected land, which is available to other animals too. Also, the charismatic nature and familiarity of large carnivores to the general public means that they often attract disproportionate amounts of conservation concern, tourist revenue and research funding, making them flagship species as well (Dalerum et al., 2008). Both flagship and umbrella species represent single-species approaches to conservation, which are sometimes criticised in favour of ecosystem level conservation approaches (Simberloff, 1998; Roberge and Angelstram, 2004). However, ecosystem management is equally criticised for its focus on processes over species, meaning that the consideration of flagship and umbrella species is not useless, but should be done in conjunction with the consideration of species from other taxa as well as landscape level processes (Simberloff, 1998; Roberge and Angelstram, 2004). There is no unfortunately no magic bullet in the world of conservation.

Given their important role in ecosystem functioning, the conservation of large carnivore populations is critical not only for the persistence of the species themselves, but also at a landscape level. Protected areas however do not cover nearly enough ground, nor provide sufficient connectivity between populations to singlehandedly conserve large carnivores globally (Stein et al., 2016; Pitman et al., 2017). Other forms of conservation, including community-based conservation endeavours as well as human-wildlife coexistence models are critical for successful large carnivore conservation. With increases in awareness regarding the negative consequences of excluding humans from wild lands, particularly for communities who have historically relied on resources from those lands, has come a growing interest in linking conservation and local development objectives, resulting in models that aim to ensure the sustainability and longevity of biodiversity protection by ensuring that local communities participate in, benefit from and ideally manage natural resources themselves (Berkes, 2004; Berkes, 2007; Suich, 2010). Even with such initiatives in place though, there remains a strong need for human-wildlife coexistence initiatives, which help to allow humans and wildlife to share land that is becoming increasingly scarce (Nyhus, 2016; Pooley et al., 2021). Such initiatives help to buffer protected areas from detrimental edge effects and increase levels of connectivity, and consequently wildlife movement and genetic exchange between otherwise isolated systems (Di Minin et al., 2013; Havmøller et al., 2019). There is evidence that large carnivore populations do recover with changes in policies and attitudes, and that such changes can allow for populations to return to or expand in areas where they had previously been locally extinct, or only transient (Chapron et al., 2014).

1.3 Leopard ecology

Leopards, *Panthera pardus*, are the second largest cat in Africa (Bailey, 1993) and the most widely distributed wild felid, with their range extending throughout most of Africa and large portions of Asia and the middle east (Stein et al., 2016). As their broad range suggests leopards are habitat generalists, ranging from dense forests to open grasslands and deserts (Nowell and Jackson, 1996). Leopards are also dietary generalists, consuming a wide variety of species from small insects, rodents and birds to large antelope (Hayward et al., 2006). They have however been found to show a preference for medium to large sized herbivores (Hayward et al., 2006). Leopards are ambush hunters, showing the greatest hunting success in areas of relatively dense cover, where they can stalk and then pounce upon prey (Bailey, 1993). Their particular affinity for areas with relatively high levels of tree cover is thought to be a driver behind their flank rosette markings, which help improve camouflage in dappled light (Allen et al., 2011). A higher proportion of melanistic individuals are found in areas with denser, darker forests (da Silva et al., 2017).

Within South Africa, leopards were historically found in all non-urban areas except the greater Karoo basin where there was insufficient prey or water to allow for their survival (Friedmann and Daly, 2004). Leopards living in more productive regions in the north-east of the country (mainly Mpumalanga, Limpopo and KwaZulu-Natal) are substantially larger in size, averaging almost double the weight of their counterparts in the Western and Eastern Cape (Martins and Martins, 2006). These are however not classified as separate subspecies.

Leopards are solitary, territorial felids with a polygynous mating system (Bailey, 1993). Male home ranges are typically larger than those of females, and encompass parts of multiple females' territories (Fattebert et al., 2016; Balme et al., 2019). Both sexes defend territories against conspecifics. Given the diversity of landscapes in which leopards occur, home range size varies substantially depending on resource availability, ranging from 9km^2 in southeast Asian jungles to over 2 000km^2 in African deserts (Bothma et al., 1997; Grassman, 1999; Martins and Harris, 2013). Females typically reach sexual maturity at 3.8 years, and breed throughout the year (Balme and Hunter, 2013a). The gestation period of females is between 90-106 days and litters range in size from 1-3 cubs (Hunter et al., 2013). Cubs are altricial and are kept in den sites in rocky or thickly vegetated areas for their first 6-8 weeks of life (Roux and Skinner, 1989). They are cared for exclusively by their mother, and usually establish their own territories at 18 months of age, although this has been found to vary from 9-31 months (Balme et al., 2013). Female leopards are philopatric, establishing territories adjacent to that of their mother, while males disperse to establish their territories away from their site of birth (Fattebert et al., 2013; Fattebert et al., 2015). Male dispersal helps to maintain the genetic diversity of populations but the removal of adult males through legal or illegal harvesting can greatly reduce dispersal distances of young males and lead to localised inbreeding (Naude et al., 2020a). The furthest recorded distance travelled by a dispersing young male is 352.8km (Fattebert et al., 2013). Cub survival in leopards is low with only 37% of cubs surviving to adulthood even within well protected sites (Balme et al., 2013). Low cub survival is due to a multitude of factors including inter-specific and intra-specific competition, disease, malnutrition and natural events such as floods and fires. Despite being a solitary species, infanticide rates for leopards are some of the highest recorded for any species (Balme and Hunter, 2013a).

1.4 Monitoring leopard populations

Leopards have undergone a marked reduction in numbers and range, yet the species is often assumed to warrant little conservation concern (Stein et al., 2016; Jacobson et al., 2016). This is due partly to a paucity of reliable population estimates both within and outside of protected areas. Accordingly, relatively few leopard populations are actively monitored and population health or status is often informed more by anecdote than science (Balme et al., 2014). The monitoring of populations, particularly long-term monitoring, is crucial to our ability to detect changes within populations and react through adaptive management to prevent further detrimental changes, or recognise management interventions with positive outcomes that could be replicated in other systems (Witmer, 2005; Marsh and Trenham, 2008). This differs from pure research in its end goal of detecting change within populations over time, and direct impact on management decisions and consequently conservation actions. In order to provide reliable information, it is important that monitoring efforts provide accurate, precise, unbiased data (Witmer, 2005). This is a major challenge in the face of conservation, as sample sizes are often small, and time scarce (Robinson, 2006). Therefore, finding the best possible ways of analysing available data is of utmost importance.

Large carnivore populations are notoriously difficult to monitor as they exist across landscapes at relatively low densities (Ray et al., 2005). Leopards are particularly difficult given their shy, elusive and solitary nature, and are thus understudied relative to the rest of their guild (Martins and Martins, 2006; Stein et al., 2016; Balme et al., 2019). Historically, large carnivore populations have commonly been monitored using spoor surveys (Stander, 1998). These methods are still used today, but are reliant on certain environmental variables which impact detectability, and can be difficult to use for individual identification and consequently density estimation (Pirie et al., 2016; Torrents-Ticó et al., 2017). Recent advances in technology and statistical analyses have overcome some of the challenges inherent in monitoring cryptic carnivores such as leopards. Remotely triggered camera traps are now widely used in combination with spatial capture-recapture (SCR) modelling to estimate leopard population densities (Rowcliffe and Carbone, 2008; Goldberg et al., 2015; Swanepoel et al., 2015; Ramesh et al., 2017a).

SCR models rely on two processes to estimate the density of individually recognisable individuals within populations. The first is the observation/detection model, which describes the decaying probability of detection as a function of the distance between a trap and an animal's putative home-range center. The second is the state model, which uses a spatial Poisson point process to describe the intensity of home-range centers in space (Royle et al., 2009; Efford, 2017). The observation/detection model estimates the lambda naught parameter which provides an indication of detectability while the state model estimates the sigma parameter which provides an indication of the size of activity centers (Efford, 2017). Station specific covariates, relating to the environment of individual stations, and capture specific covariates, relating to the characteristics of animals responsible for camera trap triggers, can be added to these models (Efford, 2017). The use of SCR methods as opposed to traditional capture-recapture methods is of great benefit to improving the accuracy of density estimates. The inclusion of spatial information allows for density to be directly estimated without having to first estimate the effective trapping area, which is required for traditional capture-recapture methods and is widely recognised as being problematic (Royle et al., 2009).

Information on density is key to informing leopard conservation status and assessing the effectiveness of conservation management decisions and policies (Balme et al., 2014). However, camera trap arrays currently used for leopard monitoring are resource intensive. Individual identification, required by SCR models, is most reliable with data from paired cameras. SCR also requires the possibility of recapturing individuals at multiple stations, meaning that stations need to be positioned close enough together that multiple stations are located within the home range of a single individual. In the case of leopards therefore stations need to be 2-3km apart, making this approach impractical for monitoring large protected areas (Tobler and Powell, 2013; Efford, 2017). This technique is however practical in the many small reserves common throughout South Africa and has been used by Panthera to conduct annual camera trap surveys in the country since 2013. These surveys are being used to understand leopard population trends within protected areas and to inform national leopard population management policy. Currently this survey design and approach is being expanded by Panthera to numerous other southern and central African countries, as well as Asia and the middle east. However, recent advances in SCR modelling have provided more stringent survey design recommendations to help reduce the chances of low detectability levels influencing density estimates (Efford and Boulanger, 2019; Durbach et al., 2021; Dupont et al., 2021). These recommendations are even more resource intensive, recommending that inter-trap distances be reduced, and surveys be left out for longer to allow for an increased number of recaptures of known individuals and hence greater precision in density estimates.

The use of camera traps for monitoring wild animals provides information at the scale of populations rather than individuals, which is beneficial when making decisions regarding the conservation of a species within a particular area (O'Connell et al., 2010; Trolliet et al., 2014). Additionally, camera traps are non-invasive, meaning that they have only a relatively small effect on the individuals involved, reducing the impact which monitoring efforts can have on populations (McCallum, 2013; Newey et al., 2015). It has been suggested that white flashes may deter some individuals from revisiting sites where camera traps are present, however this has not been observed with leopards (Meek et al., 2016, G. Balme pers. comm.). Otherwise, camera traps have no known fitness costs to study populations.

In cases where research has required fine scale information with regards to individual leopard activity, Global Positioning System (GPS) or radio-collars have been used to track movement and activity patterns or help locate individuals (Bothma and Bothma, 2006; Balme et al., 2009; Odden et al., 2014). The use of collars however is substantially more expensive than the use of camera traps, and is also more invasive (Balme et al., 2014). Trapping and darting leopards to fit collars is risky for the individuals both during capture and handling and for the duration of the time the animal is wearing the collar

(Proulx et al., 2012). Furthermore, although technological advances are allowing for the creation of smaller, lighter collars, these still have the potential to impact animal movement and health (Coughlin and van Heezik, 2014). While collar data is still of great use to conservation and remains the best way of answering questions about fine-scale movement, there has been a strong move towards non-invasive methods like camera trapping for monitoring large carnivore species worldwide.

Another important aspect of monitoring animal populations relates to their genetic health, in an effort to ensure that they do not succumb to the negative effects of inbreeding (Frankham, 2005; Ropiquet et al., 2015). This involves the collection of animal material, the extraction of Deoxyribonucleic Acid (DNA), the amplification of DNA through polymerase chain reactions and the sequencing of the genetic information (Taberlet et al., 1999). Nuclear or mitochondrial sequences can then be compared between individuals to determine the genetic diversity of a population (Taberlet et al., 1999). Traditionally genetic monitoring was an invasive procedure, requiring the collection of animal blood or tissue samples usually collected from darted individuals (Taberlet et al., 1999). Recent technological advances however have allowed for the extraction of DNA from a broader range of animal material, including scat (Taberlet et al., 1999). This has proved useful for the monitoring of leopards as it allows for the non-invasive monitoring of population genetics (Naude et al., 2020a).

Additionally, building on the premise that the genotype of an individual has a direct effect on its phenotype, recent work has found that genetic information may be obtained from measurable phenotypic characteristics. The phenotype of an organism is affected by a combination of genotype and environment, and characteristics that are more affected by genetics than environmental effects are known as heritable (Cheverud, 1988). When heritable characteristics are quantifiable they can be compared between individuals, producing similarity scores. Both giraffes and cheetahs have shown a greater degree of resemblance with regards to coat patterning among more closely related individuals (Balme and Hunter, 2013b; Lee et al., 2018). Given that leopard coat patterns vary between individuals (Miththapala et al., 1989), it is possible that differences in rosette patterns may be able to provide an indication of genetic similarity, allowing for a move away from genetic sampling altogether.

While monitoring efforts are crucial to conservation, too often they fail to effectively influence management decisions, and therefore represent an inefficient use of effort and funds (Nichols and Williams, 2006). In order to effectively influence management decisions, monitoring programs need clearly stated objectives and hypotheses, and a careful consideration of potential sources of error that will influence the outcomes of monitoring programs and how these can be dealt with (Yoccoz et al., 2001). Adaptive management approaches provide an effective use of monitoring data as they include it in a feedback loop, whereby monitoring efforts are used to evaluate the impact of management decisions, and inform future changes that could benefit the ecosystem (Lyons et al., 2008). Monitoring efforts also provide a better use of effort and funds when the data they produce is used frequently, and for as many purposes as possible (Lindenmayer and Likens, 2010).

1.5 Conservation status of the leopard

Leopards are classified as Vulnerable on the IUCN Red List of Threatened Species due to decreasing numbers and substantial range loss (Figure 1.2) (Stein et al., 2016). There are many drivers behind the decrease in leopard population size, a number of which are common to most large carnivores: habitat loss and fragmentation, persecution due to human wildlife conflict, increased illegal wildlife trade, badly managed trophy hunting and prey base declines (Ray et al., 2005; Balme et al., 2009; Packer et al., 2009; Swanepoel et al., 2014; Pitman et al., 2015; Fattebert et al., 2016; Wolf and Ripple, 2016). Leopards have been extirpated from approximately 61% of their historic global range, with half of this having occurred in the last 100 years (Stein et al., 2016). Not only have leopards lost large tracts of their range, but what remains of their habitat has also been severely fragmented (Naude et al., 2020a). Fragmentation is a significant threat to populations as natural movement patterns are interrupted, limiting the spread of genetic diversity and threatening the integrity and persistence of populations (Tilman et al., 2017; Naude et al., 2020a).

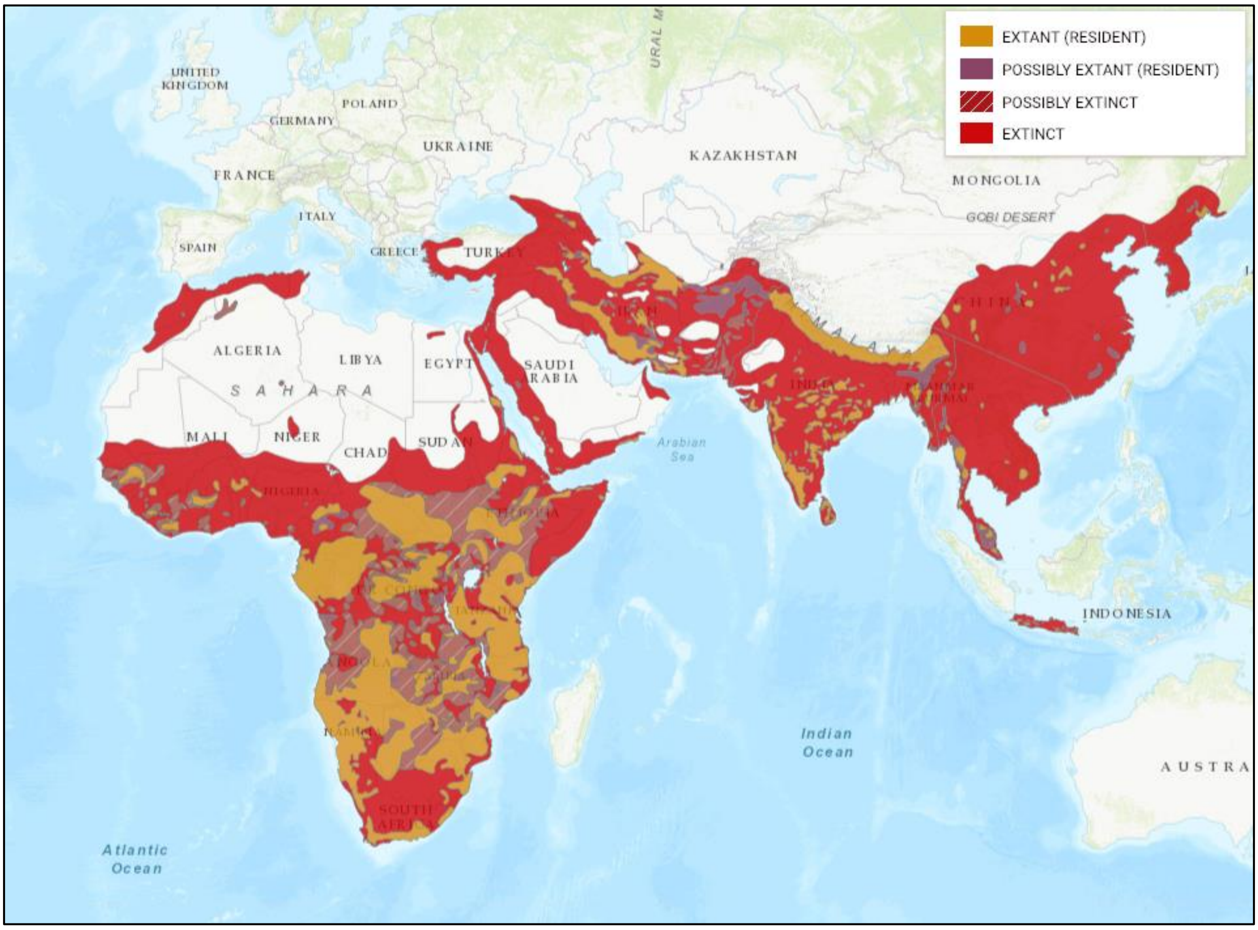

Figure 1.2: Current and historical leopard range, taken from the IUCN Red List of Threatened Species (Stein et al., 2016).

The southern African leopard population consists of a single continuous population structured by isolation by distance, meaning that genetic variation throughout leopard range is explained by the geographic distance between populations (Uphyrkina et al., 2001; Ropiquet et al., 2015). Therefore, within the broader population there are a number of distinct, geographically isolated groups, with groups that are further apart showing greater genetic differences than those that are closer together. There is thus a spatial structure to genetic markers within the population (Ropiquet et al., 2015). Recent genetic work has shown that inbreeding is an area of concern for low density populations, and should be considered when looking at the health of leopard populations (Naude et al., 2020a).

In response to anthropogenic pressures species have been classified into three broad categories based on their response to urbanisation: urban exploiters, urban adapters and urban avoiders. Urban exploiters are species able to draw benefit from land transformation and anthropogenic activity through increases in foraging opportunities, decreases in predation risk and increases in roosting, nesting, denning or sleeping sites (Blair, 1996; McKinney, 2002). These species are usually generalist and opportunistic, and may reach high population densities in human modified or dominated landscapes (Adams, 1993). Urban adapters generally exploit a range of food sources, both natural and human-derived, and often benefit from a reduced presence of predators or competitors in urban settings (Blair, 1996; McKinney, 2002). They tend to continue with life in a similar manner as in undisturbed areas, unlike urban avoiders which struggle to exist in human dominated areas, or even areas of human presence (Blair, 1996; McKinney, 2002). While most predators are classified as urban avoiders, leopards are best described as urban adapters, capable of exploiting human derived food resources within and adjacent to urban areas (Athreya et al., 2013). However, while leopards are able to tolerate human modified landscapes this tolerance is seldom reciprocated, and the potential threat which they pose to humans, livestock and domestic animals means that they are often the target of preemptive retaliatory killings in areas of human activity (Swanepoel et al., 2014). Over the course of a 25 year period, from 1975 to 2000, there was a 57% increase in the conversion of potential leopard habitat to agricultural areas (Stein et al., 2016). Deforestation is another cause of land degradation affecting leopards, particularly the increasing size of rubber and palm oil plantations in south-east Asia (Stein et al., 2016).

Given their solitary and elusive behaviour, leopards have managed to remain present in certain regions of high human population density, particularly in areas in and around select cities in India (Athreya et al., 2013). While leopards do exist in developed areas, these areas are generally not able to sustain the densities of leopards found in more natural habitats, particularly in an African context where leopard densities are substantially lower in non-protected areas (Balme et al., 2010b; Pitman et al., 2015; Rosenblatt et al., 2016). Leopard population density often tracks the biomass of available wild prey species (Marker and Dickman, 2005; Henschel et al., 2011), which are under increasing pressure from both land transformation and an increase in and commercialisation of unsustainable bushmeat trading (Wolf and Ripple, 2016). The commercial bushmeat trade has led to the collapse of prey populations in many areas across Africa, and an estimated concomitant 59% reduction in the population size of leopard prey across 78 protected areas in western, eastern and southern Africa between 1970 and 2005 (Craigie et al., 2010; Stein et al., 2016). Poaching pressure on leopard prey species in Asia is also extensive and has led to prey base declines and threats of local extinction for certain leopard prey species (Corlett, 2007; Stein et al., 2016). However, reduced prey stocks in India appear to be having less of an impact on leopard population densities than in Africa, as densities appear to remain high in highly urbanised areas such as regions surrounding Mumbai, which are virtually devoid of natural prey species (Athreya et al., 2013). Leopards existing in these areas appear to have unusually small home ranges, and subsist almost entirely on consuming domestic animals, particularly dogs (Odden et al., 2014). One of the main differences between the situation in India and Africa is that the retaliatory killing of large felids is severely prohibited in India, and this law is strictly adhered to (Odden et al., 2014).

Not only are leopards affected indirectly by various human activities but direct impacts, including targeted poaching, appear to be increasing, driven primarily by the demand for skins (Swanepoel et al., 2016). Several ethnic groups in southern Africa use leopard skins for ceremonial attire. Foremost amongst these is the Nazareth Baptist or Shembe Church, a 100-year-old religious sect best defined as an amalgamation of traditional Zulu and Christian beliefs (Papini, 2004). The broader Shembe community has adopted the Zulu custom of chiefs and royals wearing leopard skins as symbols of prestige, and modified it to entail all men wearing leopard skins, as the chiefs of their households (Kumalo and Mujinga, 2017). Preliminary capture-recapture surveys undertaken at Shembe gatherings suggest that between 4500-7000 leopards are harvested every year to fuel this demand for skins, and that there may be as many as 15000 leopard skins currently distributed among Shembe followers (Naude et al., 2020b). Many of these skins originate from leopards killed in protected areas (Naude, 2020). Targeted leopard poaching is also a reality in Asia, where a regional study conducted in the south eastern part of India found that leopards are poached at a rate of approximately four individuals per week (Raza et al., 2012). However, only an average of 3.5 leopard seizure cases have been reported annually in India since 2000, meaning that most cases of leopard poaching remain undetected by the authorities (Nowell and Pervushina, 2014). This poaching rate is specific to of a certain part of India, and may well be lower in other areas as leopard populations appear to exist at surprisingly high densities near certain urban areas in the country, particularly Mumbai (Athreya et al., 2013). However, the magnitude of the illegal trade in leopard parts appears to be similar to that of the tiger, boding badly for the future of leopards (Nowell and Pervushina, 2014).

The killing of leopards by humans is not always illegal however: trophy hunting adds further pressure to leopard populations. Overharvesting through trophy hunting is a major driver of leopard declines in both the KwaZulu-Natal and Limpopo provinces of South Africa (Balme et al., 2009; Balme et al., 2010b; Braczkowski et al., 2015; Pitman et al., 2015). Even good hunting regulations are difficult to police and enforce, and the historical issuing of hunting licenses to hunting outfitters rather than specific areas has resulted in uneven pressure on populations, sometimes beyond what is sustainable (Balme et al., 2010a). Trophy hunting of leopards can be a sustainable activity when only older males (> 7 years) are hunted out of otherwise well managed and protected populations (Balme et al., 2012). The success of such regulations however relies in part on the hunter's ability to reliably age an animal, often under difficult observational conditions. A moratorium was placed on leopard hunting in 2016 following evidence of the detrimental effects that trophy hunting has been found to have on leopard populations in South Africa and a concern over incomplete record keeping. However hunting quotas were reinstated the following year albeit with reduced numbers (Stein et al., 2016). Leopards are also listed by CITES as an appendix I species, regulating the trade in live individuals as well as body parts (Stein et al., 2016).

The harvesting of leopards and their prey occurs both inside and outside protected areas. Land outside protected areas is however more risky for leopards due to high human presence and retaliatory killings for perceived and actual livestock losses (Balme et al., 2009; Balme et al., 2010b; Pitman et al., 2015; Braczkowski et al., 2015). Elevated human presence around protected areas invariably increases the rate at which protected source populations sink into neighbouring human modified landscapes, limiting both emigration and immigration. Unlike most other large carnivore species that are more easily contained within fenced areas, leopards routinely cross boundary fences making them particularly prone to edge effects (Woodroffe and Ginsberg, 1998; Balme et al., 2010b). Consequently, unless protected areas are sufficiently well resourced to effectively combat poaching and maintain leopard-proof fences, leopard populations may only be stable in the few large, protected areas of South Africa in which core areas are adequately buffered from edge effects. While it is not practical to rely solely on such large protected areas for the conservation of leopards and other large carnivores, they are currently a cornerstone of their protection in the Anthropocene.

1.6 Indicators of population status

Maintaining or improving population status is the desired outcome of most population monitoring efforts for vulnerable species (Marsh and Trenham, 2008). Both goals demand a clear understanding of the term 'population status' which commonly refers to both the size or density of the current population relative to the size of the population that could be supported by the environment in question if it were undisturbed by anthropogenic activity, and also to population trend, meaning whether it is stable, increasing or decreasing (Buckland et al., 2000; Marsh and Trenham, 2008). Essentially measures of population size or density consider the density of the animal in question relative to the carrying capacity of the area but without any certainty on what baselines of 'natural' should be used. One of the major benefits considering population trend is that it is immune to questions about what baseline to use for comparison and the potential fluidity of baselines, however measuring population trend requires repeated sampling over relatively long time periods.

Calculating density for individually recognisable species such as leopards is relatively straightforward given the recent advances in SCR models (Rowcliffe and Carbone, 2008; Royle et al., 2009; Efford, 2017), however there are two problems implicit in the role of density in the above definition of population status. Firstly, determining the carrying capacity of a landscape is challenging, particularly given that all landscapes have been disturbed in many ways, few of which are quantifiable and many of which happened before written records were kept (Hayward et al., 2007). Ecosystems are naturally dynamic, and separating change as a result of anthropogenically driven activity as opposed to naturally occurring change is difficult (Nelson et al., 2006). To include the naturally cyclic, or fluid nature of many environmental variables, the idea of thresholds of potential concern has been developed. This allows variables to respond to certain normal changes within ecosystems and self-regulate within pre-defined bounds: when variables exceed these limits, management is called into action (Gillson and Duffin, 2007). Secondly, the integrity of a population is not solely reliant on the number of individuals present, but also on a number of other characteristics generally measured through indices or metrics such as reproductive rates, mortality rates, sex ratios and age structure (Marsh and Trenham, 2008).

Some of these indices or metrics, crucial to the trajectory of a species, fall within the realm of population dynamics. Together these variables influence the density of a species in a particular area, which explains the ubiquity of this variable's use when monitoring population status within specific areas (Balme et al., 2009). Variables relating to population dynamics can help to provide reasons for decreases in density: whether reproductive rates are low, and few individuals are entering the population, or mortality rates are high and too many individuals are leaving the population. Also crucial to the status of a population is population structure and demographics, which are emergent properties of rates of fecundity, survival, emigration and immigration. The most important aspects of demographics affecting the integrity of populations are sex ratios and age structure (Fuller and Sievert, 2001; Robinson et al., 2008; Jones et al., 2018; Anile and Devillard, 2018). These are integral to the persistence of populations, and changes in density are often preceded by changes in these metrics. They can therefore be of great use to wildlife managers by serving as early warning signs of pending shifts in densities, allowing for interventions to dampen extreme shifts in numbers that may demand more costly interventions if not attended to. These metrics are also relatively easy to obtain from camera trap data, which is already being collected for leopards in many South African reserves, as photographs of individual leopards reveal both age and sex traits (Balme et al., 2012). Demographic metrics such as age and sex ratios are best investigated using SCR models as these can account for differences in detectability between groups, and therefore need to be looked at in addition to, and not instead of, density. Similar abnormal age and sex structures within populations can however arise from different demographic processes and external stressors, and therefore warrant deeper investigation into population dynamics in the area.

The behaviour of individuals within populations can also have substantial effects on population integrity. Behaviour influences inter and intra-specific relationships which can feed back into population dynamics through effects on mating success, competition and survival, and also as an indicator of general stressors to which the population is exposed (Monterroso et al., 2013; Palmer et al., 2017). For example, general activity patterns of a species have been found to change in response to environmental and anthropogenic cues. Temperature (Ruf and Geiser, 2015), light (Gaston et al., 2013) and lunar cycles (Prugh and Golden, 2013; Palmer et al., 2017) have all been shown to play an important role in influencing animal activity. While fine scale animal activity is usually monitored using data from GPS collars, camera trap data also provides an indication of population level activity patterns when the number of captures of a species throughout the day is used as a proxy for activity (Palmer et al., 2017).

Anthropogenic activity is a major source of light and noise, both of which are crucial to animal sensory ecology and behaviour: obtaining information about the surrounding environment, as well as sharing information between individuals and species (Stevens, 2013). The emission of light and noise by humans are therefore referred to as forms of sensory pollution, and can negatively impact animal communication and the detection of signals essential for survival and reproduction (Halfwerk and Slabbekoorn, 2015). Recent findings have shown that while species react differently to anthropogenic pressures in many ways, there is a common trend towards a greater proportion of nocturnal activity in animal populations exposed to higher levels of human disturbance (Gaynor et al., 2018). This was found across a broad range of mammalian taxa, ranging from rodents to antelope. The reasons for this are presumably based around animals attempting to avoid human disturbance through shifting their activity to times when humans are least active.

Moving to a finer scale both individual and population level genetics may be used to provide indicators of health and viability (Lande, 1988; Frankham, 2005). The importance of maintaining genetic diversity is one of the primary drivers behind the metapopulation management of many isolated large carnivore populations (Dolrenry et al., 2014; Buk et al., 2018). A metapopulation is a wide-ranging population existing within a framework of habitat patches separated by less suitable environments (Dolrenry et al., 2014). Naturally, long-distance dispersal helps to retain genetic diversity within metapopulations through genetic exchange (Fattebert et al., 2013), however impenetrable artificial barriers in the form of fences and urban land cause the isolation of habitat patches, which subsequently require metapopulation management through the translocation of individuals (Di Minin et al., 2013; Buk et al., 2018; Pretorius et al., 2021). Ideally metapopulation management is guided by prior genetic knowledge of individuals, however it sometimes relies on predictions regarding genetics instead. Isolation of large predators in protected areas has been linked to reduced fertility rates (Packer et al., 1991), reduced disease resistance (Kissui and Packer, 2004; Cleaveland et al., 2007) and morphological abnormalities (Roelke et al., 1993; Purchase et al., 2007). While little genetic work has been done on leopards, the recent link found between unsustainable anthropogenically driven mortality and inbreeding suggests that more research is required on other populations to fully understand the relationship between genetic health and various population parameters (Naude et al., 2020a). Currently genetic research is largely done using genetic material extracted from scat samples (Naude et al., 2020a), however the use of phenotypic characteristics, such as flank rosette patterns, could provide a more efficient and accessible metric or proxy of genetic health.

To effectively conserve wild animals it is important that population status is monitored regularly and repeatedly, detecting changes and subsequently searching for drivers of change to assist in adapting management approaches (Marsh and Trenham, 2008). For this to be feasible, robust, objective, precise, accurate and repeatable methods for measuring population status are required. Estimates with high levels of precision are particularly important in allowing for changes to be detected (Gerrodette, 1987). Spatially explicit density estimates using camera traps satisfy all of these criteria when camera trap arrays are appropriately deployed, but establishing camera trap arrays and processing the images for analyses is costly, time consuming and requires considerable expertise. If the data from camera trap surveys can be used to provide additional parameters for the target population with only additional analytical time, then the initial costs of establishing a camera trap monitoring program may be more easily justified. Additionally, if they provide an improved understanding of potential threats to populations then they may be used instead of other more invasive or labour intensive methods in certain cases. In this thesis I firstly derive density estimates for leopards at a number of sites both within Kruger National Park (KNP) and in neighbouring privately managed protected areas and I then explore the potential of this camera trap data to provide information on both activity patterns and genetic diversity as proxies for population health and the extent of anthropogenic impacts. Through these investigations I also aim to determine whether differences between sites can be linked to drivers of change, therefore providing indications of underlying variables or process that are causing differences between populations, and should be considered in management interventions.

1.7 Thesis outline

The primary aim of my thesis is to conduct a population assessment of leopards in and around southern and central KNP, the largest protected area in South Africa. Thereafter I explore new ways in which camera trap data could potentially be used to help gain a more holistic view of anthropogenic and environmental impacts on the behaviour and genetic status of leopards within protected areas.

In **chapter 1** I provide a general overview of leopard ecology, conservation and monitoring.

In **chapter 2** I introduce the greater KNP system and my camera trapping methodology.

In **chapter 3** I estimate leopard population densities at camera trap sites located in and around central and southern KNP and determine the relative importance of biological and anthropogenic factors as drivers of density in the area.

In **chapter 4** I consider the impact of anthropogenic disturbances and environmental factors on the activity patterns of leopards to establish whether changes in activity patterns can provide an indication of the type or intensity of stressors to which a population is exposed.

In **chapter 5** I investigate the possibility of using phenotypic similarity measured from flank rosette markings as an indication of genetic relatedness and extrapolating that as a measure of the genetic heath of the population.

Finally, in **chapter 6** I summarise my findings in the context of leopard population status, carnivore conservation more generally and the monitoring of rare and elusive species in large protected areas.

CHAPTER 2
GENERAL METHODS

Figure 2.1: A camera trap photograph of an adult leopard showing a distinct pelage pattern which can be used for individual identification.

2.1 Study site

South Africa has the second highest gross domestic product (GDP) in Africa: an indication of relative financial wealth (International Monetary Fund., 2019). By and large however, with increased wealth comes increased urbanisation, resource extraction and land transformation. Of particular importance to the South African economy are natural resources (mainly diamonds, gold and coal) and agriculture (most importantly corn, wheat and fruit), both of which result in the loss of large tracts of wild land (Stats SA., 2020). South Africa covers an area of 1.2 million km^2 with a human population of approximately 59 million, equating to a population density of roughly 49 people/km^2 (World Population Review., 2020). Over 50% of the population lives below the poverty line, and South Africa has been classified as the country with the most unequal distribution of wealth in the world according to its Gini coefficient (Francis and Webster, 2019).

High rates of poverty and inequality undeniably complicate conservation, as social and ecological factors are inextricably linked. A total of 8% of South African land currently falls within protected areas, 3% (n=21 protected areas) of which is owned by the national government (Government of South Africa, 2008; South African National Parks., 2016). While some of the remaining protected areas are provincially owned, conservation through private land plays an important role in South Africa's protected area network (Clements et al., 2019). Although protected areas are not the sole means of conservation in the country, they are particularly important for the persistence of large carnivore populations. Given the susceptibility of large carnivores to edge effects, defined as the detrimental effects caused by increased levels of anthropogenic mortality near reserve edges, the bigger the protected area the better (Woodroffe and Ginsberg, 1998; Balme et al., 2010b). Implementing strategies for the coexistence of humans and large carnivores on neighbouring land is also an important management objective, and one with the potential to help reduce harmful edge effects (Di Minin et al., 2013).

Kruger National Park (KNP) is the biggest protected area in South Africa by almost an order of magnitude: it covers 19 485km^2 and extends for 360km from north to south and 65km from east to west (South African National Parks., 2016). The next largest tract of protected land in South Africa is the Kalahari Gemsbok National Park which covers 9 591km^2 – less than half the area covered by KNP (South African National Parks., 2016). The rest of South Africa's 400 protected areas are classified as small protected areas. A total of 21 protected areas in the country belong to the national government (South African National Parks), while a number of others are managed by provincial authorities such as CapeNature or Ezemvelo KZN Wildlife (Paterson, 2009). KNP was established as South Africa's first National Park in 1926 through the fusion of the Sabi Game Reserve and the Shingwedzi Game Reserve, both of which were established and owned by the national government (Carruthers, 1995; du Toit et al., 2003). KNP is situated in the northeast of South Africa, in the Limpopo and Mpumalanga provinces and borders Zimbabwe to the north and Mozambique to the east. While fences and rivers still separate KNP from Gonarezhou National Park in Zimbabwe and Limpopo National Park in Mozambique, these three reserves now together form the Greater Limpopo Transfrontier Park. There are 12 tourist camps and several satellite camps and private lodges distributed throughout KNP with one main camp, Skukuza, acting as the park's headquarters. While the park as a whole is managed by South African National Parks (SANParks), certain concessions are leased to private high-end tourism companies, who are bound by SANParks management guidelines (South African National Parks., 2016). These private concessions are not fenced off from the rest of the park. Hunting is illegal in the park, and revenue is generated through tourism (du Toit et al., 2003). Anti-poaching activities are undertaken by field-ranger teams (South African National Parks., 2016) but poaching remains a problem with high numbers of bushmeat snares as well as snares and cage-traps specifically targeting large carnivores having been found within the park (C. Williams pers. comm.). Despite this, most human activity in the park is non-consumptive and while vehicle traffic can be heavy it is largely constrained to a relatively sparse road network. Off road driving is not permitted.

KNP has seven major rivers: the Limpopo and Luvuvhu rivers in the north, the Olifants and Letaba rivers in the center and the Sabie, Sand and Crocodile rivers in the south. Vegetation within KNP all falls within the savanna biome, although it varies substantially along a rainfall gradient from north to south and a soil gradient from east to west (du Toit et al., 2003). The driest regions of the park are in the north, while the southern section receives more precipitation. Mean annual rainfall ranges from 375-400mm in the north of the park to 901-925mm in the south (Scientific Services., 2020). The park experiences summer rainfall, with most precipitation occurring between November and March, and the dry season running from April through to October (du Toit et al., 2003). Soils in the western section of KNP are granitic, whereas the eastern regions of the park are characterised by basaltic plains, which are high in nutrients and retain more water (Scientific Services., 2020). KNP has a number of large rivers and a variety of habitat types ranging from open grasslands to mopane thicket to Afromontane forest. Given the size of the park and the variety of ecosystems it encompasses, I could not cover the entire area and thus focused my research on the central and southern regions of the park, where leopard (*Panthera pardus*) densities are highest, and where anthropogenic threats are greatest (Maputla, 2014).

KNP is not an isolated system. The southern-central section of its western edge is open to several privately owned reserves adjacent to the park, and animals roam freely between these areas. Additionally, the fence separating KNP from outside communities along the western and southern boundaries is relatively porous, allowing for the occasional passage of both animals and people. The fence separating KNP from Mozambique along the eastern boundary is similar in some sections but there are also sections with no fencing at all. It therefore follows that animal populations in KNP are contiguous with those in surrounding reserves where management and levels of disturbance differ. For this reason, I extended my surveys into private reserves bordering KNP: the Sabi Sand Game Reserve (SSGR) on the western boundary of KNP, and Karingani Game Reserve (KGR) in Mozambique on its eastern boundary.

The SSGR is a block of three high-end private game reserves geared towards photographic tourism: Sabi Sand Game Reserve, Mala Mala Game Reserve and Sabie Game Reserve. These reserves have no internal fences and together contain 21 commercial lodges. The SSGR was established in 1950 through the fusion of a number of privately owned farms, and Mala Mala Game Reserve subsequently split off from the main reserve, followed by Sabie Game Reserve (Schmidtz and Willott, 2012). The SSGR includes sections of two major rivers: the Sabie and the Sand rivers. Vegetation and climate are similar to southern KNP, being dominated by semi-wooded savanna with warm dry winters from April to October and hot humid summers from November to March (Balme et al., 2019). While hunting is illegal in the SSGR just as it is in KNP, management differs (Balme et al., 2019). Unlike in KNP where self-drive tours are permitted, all guests are driven by qualified guides (Balme et al., 2013). The road network is substantially denser than in KNP to allow better game viewing for guests, and off-road driving is permitted. Although still wild, animals inhabiting the SSGR are more habituated to the presence of vehicles than in KNP or KGR (Balme et al., 2013). Additionally, the SSGR has a high density of artificial water holes, which provision water year-round. While KNP does have some artificial water holes, many have been closed in recent years in order to allow the system to return to a more natural state (South African National Parks., 2016).

Given the higher income of the SSGR, their budget differs by orders of magnitude (per area) to KNP (Schmidtz and Willott, 2012). This allows the SSGR to be bordered on its western edge by one of the only fences in Africa known to prohibit leopard movement (Balme et al., 2019), while it is open to KNP to the south and east, and to the Manyeleti Private Game Reserve to the north. The impenetrable fence on the western edge of the SSGR is three meters high with an overhang at the top, dug one meter underground and electrified. Additionally, all trees overhanging the fence have been cleared, and all rivers and drainage lines are adequately fenced. The fence is patrolled daily and monitored by security cameras, meaning that both animals and humans are unable to cross it. Additionally, the inside of the reserve is constantly patrolled by anti-poaching units. Given the environmental similarity of the SSGR to KNP, but the hard boundary it presents to outside communities and thus the low risk of anthropogenically driven wildlife mortality, the SSGR provides an ideal comparison to the more porous and hence human-impacted KNP.

KGR on the other hand is found in Mozambique along the central section of the eastern boundary of KNP. While the long-term plan for this reserve is similar to that of the SSGR, its current status is vastly different. This reserve was only established in 2008 and has been expanded since then to reach its current size of 1 416km^2. A section of the northern half of KGR was previously an unfenced protected area known as Xonghile Game Reserve which contained a few small privately owned camps but had relatively low levels of tourism and low game densities as a consequence of armed conflict in the area between 1964 and 1992 (Strampelli et al., 2018a). The southern section of KGR was communal land until it was included within the reserve. The community was moved off the land and all structures removed to restore the natural habitat. At the time of my study the fences surrounding the reserve had still not been completed, and both humans and animals could therefore move between the reserve and surrounding community land. While KGR is also patrolled by anti-poaching units, poaching remains a major concern, particularly given the proximity of impoverished local communities and relatively porous boundaries. This area is therefore potentially at an even greater risk of anthropogenically driven animal mortality than KNP. Given that KGR was still being established as a reserve and it was not yet open to tourism the road networks were sparse and human activity levels were low and mostly associated with management and anti-poaching patrols at the time of this study.

2.2 Camera trapping

I deployed a total of 10 camera trap arrays in the greater Kruger region (Figure 2.2). The locations of camera trap arrays were selected to represent variation in environmental and anthropogenic variables across reserves, while also re-surveying sites where camera trapping had already occurred to allow for temporal comparisons. Four of these arrays were located in KNP, four were in the SSGR and two were in KGR. Of the four sites in KNP, two were in the southern (Pretoriuskop and Skukuza/Lower Sabie) and two in the central (N'wanetsi and Houtboschrand) sections of the park. Pretoriuskop and Nwanetsi both lie along the boundaries of KNP, making them more accessible to poachers and also more susceptible to edge effects. Pretoriuskop is located along the south-western boundary of KNP which is bordered by dense human settlements, while N'wanetsi is on the eastern boundary, which borders KGR in Mozambique. Accordingly, Pretoriuskop may be more vulnerable to edge effects than N'wanetsi. The other two sites, Skukuza/Lower Sabie and Houtboschrand, were located further inside the park, potentially buffering them from anthropogenic drivers of mortality and edge effects. All four sites within KNP were surveyed by Maputla (2014) between 2008 and 2011 allowing for a direct comparison with the results from this study. Rainfall and consequently vegetation characteristics differ substantially between the central and southern sections of KNP, and for this reason I spread my arrays evenly between these two regions, allowing for both to be represented and for these environmental variables to be taken into consideration during analyses to prevent them confounding anthropogenic variables. Camera trap arrays in the SSGR served as a control region with virtually no anthropogenically driven leopard mortalities, and covered the entire reserve. Arrays deployed in KGR aimed to provide more insight into the situation outside the park, with one located in the north of the reserve and the other in the south, to allow for representation of environmental differences across the reserve. The area covered by KGR is however substantially smaller than that covered by KNP, and environmental differences within KGR are thus smaller than those present between the central and southern sections of KNP. Unfortunately empirical data on levels of human disturbance, particularly those related to poaching, are difficult to gather at best, and when gathered are usually kept private by management authorities. I was thus unable to use empirical data to support the gradient in anthropogenic disturbance illustrated here, but feel that it is nonetheless representative of the actual situation, as is reflects the opinions of park management authorities, and rangers on the ground. In summary, I placed one array of camera traps at each of 10 sites in the greater Kruger region. Each camera trap array, or site, is referred to as an independent session in the SCR models of Chapter 3.

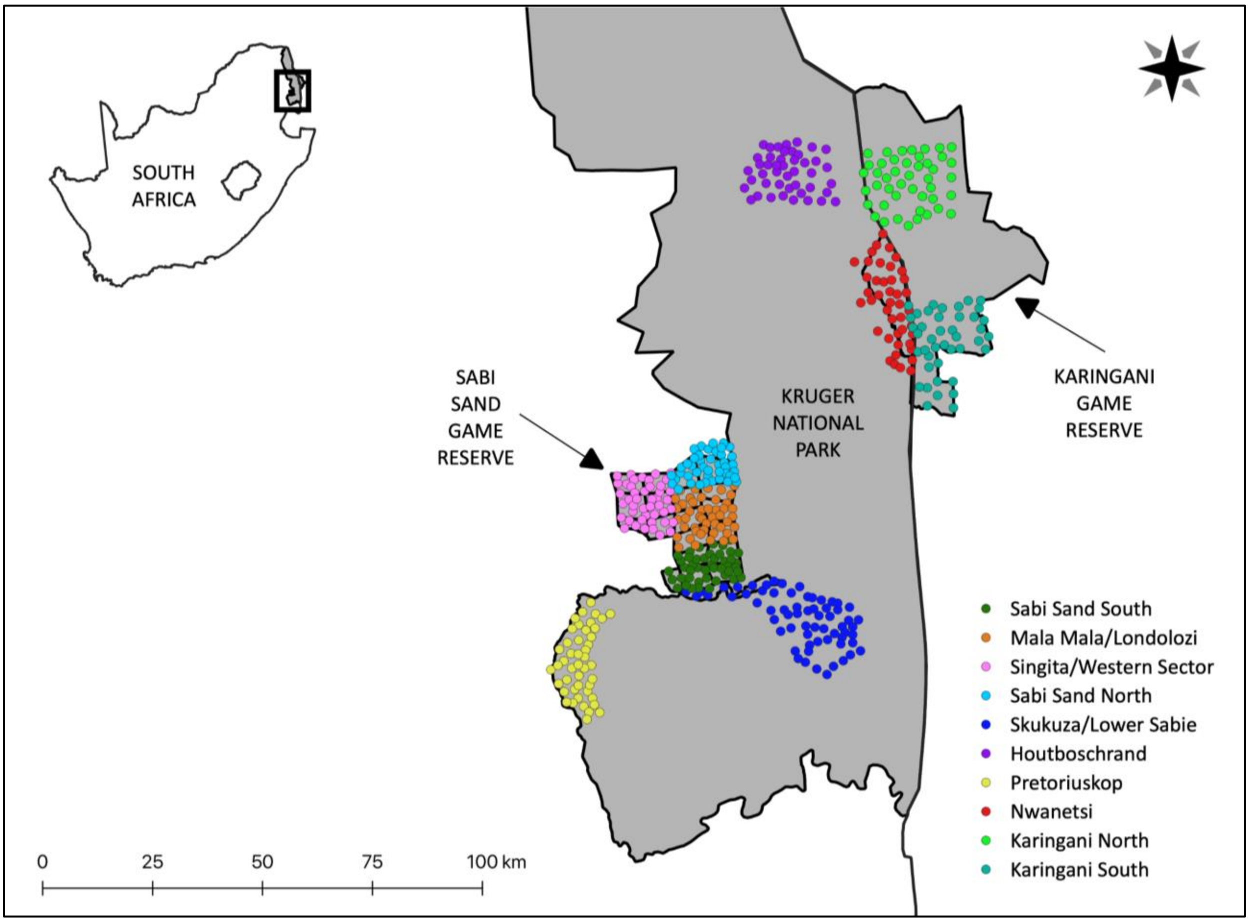

Figure 2.2: Locations of paired camera trap arrays in and around Kruger National Park in South Africa.

At each site, I deployed 80-90 Panthera V4, V5 or V6 digital camera traps at 40–45 paired stations, except at Skukuza/Lower Sabie where I deployed 64 stations. The camera trap array at Skukuza/Lower Sabie was extended to make it contiguous with the SSGR arrays. Preliminary camera trap locations were marked on a map beforehand, to ensure that stations were evenly spread across the landscape and appropriately spaced. Camera trap stations were placed 1–3km apart, meaning that the total area covered by cameras at each site, calculated as the size of the minimum convex polygon covering the entire area containing camera trap stations, was >100km^2. This is more than double the mean home range size of male leopards in KNP (Bailey, 1993), and thus adequately large for spatial capture-recapture (SCR) density estimation (Tobler and Powell, 2013). This spacing also has cameras spaced at ideally 3km, and a maximum of 4km apart (including the 500m buffer allowed), which is approximately double the sigma estimate for female leopards in SCR models, further discussed in Chapter 3 (Dupont et al., 2021). However, in visiting these preliminary waypoints during survey setup I allowed actual station locations to vary by up to 500m from each preliminary point, so that cameras could be deployed in areas where leopard movement was likely. They were therefore set alongside management tracks, drainage lines and well-used animal paths with most stations located at intersections of two or more movement corridors to maximise leopard detections. Cameras were fixed to trees or poles with cable ties and placed approximately 40cm above the ground. Paired cameras were placed approximately 10m apart to maximise the chances of obtaining photographs of both the left and right sides of each leopard. Six AA alkaline or rechargeable batteries powered each camera. Stations were checked at least every 10 days when rechargeable batteries were used and after approximately 25 days for cameras with alkaline batteries. Cameras all used 4GB micro SD cards for image storage. Each camera also contained two sachets of silica to act as a desiccant. To satisfy the SCR model assumption of population closure, the surveys at each site ran for between 46 and 60 days (Royle et al., 2013). Although this is slightly longer than the more conservative approach of a maximum of 45 days, recent work has shown that in slow-living species, the benefits accrued by leaving camera traps out for longer outweigh the potential costs of a violation of population closure over periods of up to 5 months (Dupont et al., 2019). Apart from young dispersing males, leopards generally display relatively stable home ranges, and thus rates of immigration and emigration are unlikely to have caused a violation of the assumption of population closure over the period that camera traps were active (Odden et al., 2014; Van Cleave et al., 2018; Snider et al., 2021).

The camera traps deployed use white flashes to capture images at night, and an automatic sensor activates the flash when light levels become sufficiently low. The flash takes 8 seconds to recharge at night, and therefore the minimum time interval between successive triggers was set to 8 seconds to keep this consistent between day and night. Cameras were programmed to take only one photograph per trigger. Camera sensitivity was set to medium, the flash brightness to 10m and image compression to medium. These settings were configured using Camera Trap File Manager (CTFM) software.

Table 2.1: Details of the 10 camera trap arrays deployed throughout this study.

Site	Number of Stations	Average Inter-Trap Distance (km)	Area (km^2)	Start Date	End Date	Survey Length (days)	Level of Human Disturbance
Sabi Sand South	45	1.6	147.1	11-04-2018	09-06-2018	60	Control
Mala Mala/Londolozi	46	1.7	183.0	03-07-2018	24-09-2018	53	Control
Singita/Western Sector	44	1.7	171.0	13-10-2018	30-11-2018	49	Control
Sabi Sand North	43	1.4	121.7	18-05-2019	05-07-2019	49	Control
Skukuza/Lower Sabie	64	1.9	481.3	12-04-2018	04-06-2018	54	Low
Houtboschrand	45	2.1	253.6	26-10-2018	11-12-2018	47	Low
Pretoriuskop	44	1.8	252.1	29-06-2018	14-07-2018	47	Medium
Nwanetsi	43	2.0	270.2	31-07-2018	16-10-2018	47	Medium
Karingani North	45	2.5	339.3	15-03-2019	01-05-2019	48	High
Karingani South	42	2.2	363.9	20-03-2019	04-05-2019	46	High

2.3 Data processing

All images collected were classified using PantheraIDS software. Wild mammals were classified to species level with the remaining images categorised as domestic animals, humans, vehicles or blank images. PantheraIDS software has a machine learning algorithm that performed the first round of classification. All classifications were then manually checked for accuracy and corrected, except in cases where there were more than 5000 images of a taxon from one site, in which case a subset consisting of half of the images was checked.

Subsequent to classification individual leopards were identified based on their unique pelage patterns using Hotspotter pattern recognition software (Crall et al., 2013a). This software generates a similarity score for all pairwise combinations of images based on a nearest neighbour search and indicates which images are most similar (Crall et al., 2013b). Leopard images matched to a unique individual were confirmed with a visual check. Time stamps and Global Positioning System (GPS) coordinates were then used to match left and right side images of the same individual. Images of opposite sides of a leopard taken by different cameras at the same station within a period of 30 seconds were considered to be of the same individual, unless specific visual features, such as external genitalia, suggested otherwise. The sex of individuals was determined based on the presence or absence of testes, as well as other phenotypic features including body size, dewlap development, lactation and the presence of dependent cubs (Balme et al., 2012). Dependent cubs (typically <1-years-old) were excluded from all analyses due to their non-independent capture probabilities (Karanth and Nichols, 1998). Only images of individuals that could be identified were used in density analyses, however all independent captures were included in activity pattern analyses.

2.4 Statistical analyses

All statistical analyses were carried out in R version 3.5.2 (R Core Team, 2017), and spatial analyses were carried out using a combination of R version 3.5.2 (R Core Team, 2017) and QGIS version 3.6 (QGIS Development Team, 2019).

CHAPTER 3

COUNTING SPOTS: DRIVERS OF LEOPARD DENSITY IN THE KRUGER-LIMPOPO ECOSYSTEM

Figure 3.1: A camera trap photograph of a pregnant female leopard passing a camera trap station in Kruger National Park.

3.1 Abstract

Leopards (*Panthera pardus*) are widely distributed throughout Africa, Asia and the middle east, but have suffered substantial population declines. The combined effects of targeted poaching, by-catch in bushmeat snares, retaliatory killing, prey depletion and habitat loss mean that populations rarely reach carrying capacity in protected areas. While populations are decreasing in most small reserves across South Africa, concern over the future of leopards in the country, now listed as Vulnerable on the IUCN Red List, has been moderated with an underlying but unsupported assumption that the stronghold of the South African leopard population lies within Kruger National Park (KNP). I have assessed the status of leopard populations in and around the central and southern sections of KNP using 10 camera trap arrays: four inside KNP, four in the Sabi Sand Game Reserve (SSGR) along the western boundary of KNP and two in Karingani Game Reserve (KGR) along the eastern boundary of KNP. There is substantial variation in the potential for human offtake across these sites, creating a gradient of threat levels. Using multisession spatial capture-recapture (SCR) models I tested the impacts of a range of biological and anthropogenic covariates on leopard population density estimates in this region. Leopard density was best explained by Reserve Type and Normalised Difference Vegetation Index (NDVI) modelled as main effects with an interaction term. Density varied substantially between sites and reserves, ranging from 2.6 ± 0.6 leopards/100km^2 in Karinagni South to 13.2 ± 2.6 leopards/100km^2 in Sabi Sand North. NDVI was positively associated with leopard densities in KNP and SSGR, and more strongly so in SSGR, but was negatively associated with leopard density in KGR. This suggests that in well protected areas leopard density is more influenced by biological, bottom-up processes with NDVI serving as a proxy for prey catchability. By contrast in more impacted areas such as KGR the impact of anthropogenically driven mortality may override bottom-up variables such as NDVI. Providing density estimates for leopards within protected areas is a fundamental step in the long-term goal of monitoring leopard populations and ensuring that conservation authorities and reserve managers can respond to chronic threats to the persistence of this species within the private and public protected areas of South Africa.

3.2 Introduction

Leopard populations in southern Africa have shown a substantial decrease in recent years (Stein et al., 2016). This has been attributed to a variety of factors including, but not limited to, habitat loss and fragmentation, reduced abundance of natural prey, negative interactions with humans over livestock losses, unsustainable hunting practices and the illegal harvesting and trade of leopard skins and other body parts (Balme et al., 2010a; Lindsey et al., 2013; Braczkowski et al., 2015; Pitman et al., 2015; Pitman et al., 2017; Naude et al., 2020a). While populations are decreasing in most small reserves across South Africa (Stein et al., 2016; Rogan, 2021), concern over the future of leopards in the country, now listed as Vulnerable on the IUCN Red List, has been moderated with an underlying but unsupported assumption that an important stronghold of the South African leopard population lies in the greater KNP region (Stein et al., 2016).

Leopards are apex predators and thus naturally exist at relatively low densities across the landscape (Bailey, 1993; Pitman et al., 2017). This means that large tracts of natural habitat are helpful in sustaining viable populations. While protected areas are only one of many approaches to conservation, they have been deemed particularly useful to large carnivore conservation efforts in Africa (Packer et al., 2013a; Caro, 2015). This is chiefly because the presence of large carnivores in human inhabited landscapes can threaten both human safety as well as livestock and other domestic animals, and often results in retaliatory killings (Balme et al., 2009; Swanepoel et al., 2014; Pitman et al., 2015; Nyhus, 2016). Ultimately this cascades into conflict amongst stakeholders regarding how best to reduce losses to farmers and limit leopard killings (Redpath et al., 2015). However, given their agility, leopards cross artificial and geographic boundaries with relative ease and are therefore exposed to a range of threats outside of protected areas (Fattebert et al., 2013) which makes them particularly prone to edge effects (Balme et al., 2010b). Leopards with home ranges along the edges of protected areas are likely to cross out of the protected areas and encounter and kill livestock and then become subject to retaliatory killings (Balme et al., 2010b; Thorn et al., 2012; Swanepoel et al., 2014). Leopards living near the edge of reserves are also more likely to be negatively affected by poachers coming into the reserve from outside (Balme et al., 2010b). This creates a source-sink dynamic within the protected area, where anthropogenically driven mortality near edges opens up territories and other leopards move into available habitat, particularly young dispersing males, and then fall victim to the same threats that took out the previous leopard in that same territory. Larger protected areas are less vulnerable to edge effects, because an increase in size decreases the perimeter to area ratio of a reserve, meaning that a greater proportion of animals will have home ranges falling entirely within the reserve, and are therefore less likely to venture into the surrounding areas or encounter humans within the reserve harvesting natural resources (Woodroffe and Ginsberg, 1998). Leopard populations are more likely to lie below carrying capacity, defined as the natural population density that can exist across a landscape given the availability of environmental resources such as food, water and space, outside of protected areas (Balme et al., 2010b; Havmøller et al., 2019; Searle et al., 2021b). Protected areas therefore provide important refuges for the species.

KNP is the largest protected area in South Africa, and one of the few protected areas in the country considered large enough to be invulnerable to detrimental edge effects (South African National Parks., 2016). This park however does not exist in isolation, as it is open to several private reserves along its western boundary, and also forms part of the Greater Limpopo Transfrontier Park given its connectivity to Mozambique’s Limpopo National Park, and to other national parks and game reserves in the region. Due to its size it is assumed to be an inviolate refuge for leopards, and a source of dispersing individuals that can supplement nearby, more threatened populations (Bailey, 1993; Maputla, 2014). However, this assumption has not been rigorously tested. Moreover, there have been an increasing number of anecdotal reports of targeted leopard poaching incidents inside KNP, particularly near its south-western border. This has been seen through the presence of baited cage-traps specifically targeting large carnivores (G. Balme, pers. comm.).

The majority of targeted leopard poaching incidents appear to be efforts to obtain leopard skins used in traditional gatherings by members of the Shembe or Nazareth Baptist church (Swanepoel et al., 2016). The Shembe church follows a combination of traditional Zulu and Christian principles, and believes that all men are the chiefs of their households, and should therefore wear leopard skins during traditional rituals as a symbol of power and good fortune (Papini, 2004; Kumalo and Mujinga, 2017). Traditionally, skins have been passed down from one generation to the next, however a large increase in the number of Shembe Church members has resulted in an unsustainable demand for new leopard skins (Papini, 2004; Kumalo and Mujinga, 2017). Genetic assignment tests confirm that some Shembe-owned leopard skins originate from in and around KNP (Naude, 2020).

Not only does targeted poaching threaten leopard populations within protected areas, leopards and other large carnivores are also vulnerable to the effects of non-targeted bushmeat poaching (Lindsey et al., 2011; Lindsey et al., 2013; Balme and Hunter, 2013b). This involves wire snares set in large numbers by community members who typically live in areas bordering the park, in an attempt to acquire meat used for subsistence or trade (Lindsey et al., 2013). Over 100 wire snares have been removed in a single day from sections along the edge of KNP that border rural communities (C. Williams pers. comm.). While mainly aimed at antelope, these snares catch any animal that walks into them, including large carnivores (Noss, 1998). Sometimes large carnivores caught in snares remain there until dead, and in other instances they are able to break the snare off the tree to which it was attached, and escape with the wire around their neck (Noss, 1998). Sightings of hyenas, wild dogs and leopards with snares or snare scars are therefore not uncommon in areas along the edges of KNP. In addition to directly threatening carnivores of all sizes, bushmeat snaring also threatens carnivore populations indirectly by decreasing prey abundances (Henschel et al., 2011). Abundant and accessible prey is beneficial for leopard populations as it increases rates of fecundity and survival, helping to keep densities high and reduce the effects associated with population instability and high turnover rates (Balme et al., 2013).

KNP covers 19 485km^2, and is surrounded by a range of land use types, from impoverished communities to high end private reserves (South African National Parks., 2016). The severity of anthropogenic disturbance seen through edge effects therefore varies throughout the park. The southwestern section of the park is bordered by Mbombela and Bushbuckridge municipalities, and a multitude of low-income and relatively high density communities lie along the park fence in these areas. These are the areas where most incidents of targeted large carnivore poaching have been recorded and where bushmeat poaching and snaring is rife, providing an indication of the permeability of the fences in the area, and the accessibility of wildlife populations to poachers (C. Williams pers. comm.). Currently, most of the park's conservation efforts are focused on interrupting complex criminal syndicates involved in rhino poaching which is most severe in this section of the park as well (Ferreira and Okita-Ouma, 2012; South African National Parks., 2016). While cage-traps and snares are removed when found, large carnivore and bushmeat poaching remain a lower priority than curbing rhino poaching and therefore are not as well resourced, monitored or managed.

Despite assumptions that KNP is the stronghold of South Africa's leopards, little work has been done on leopards in the park. Without long-term monitoring of the KNP leopard population we cannot know whether the park is indeed home to a stable, abundant population of leopards as would be required of a population stronghold. The leopard population of KNP is thought to have varied non-directionally over the course of the 40 years preceding the first population assessment (Bailey, 1993; Maputla, 2014). Maputla (2014) undertook a density-focused assessment of the KNP leopard population between 2008 and 2011, reporting a wide range in leopard densities across the park. These estimates however have high levels of uncertainty due to limited sampling efforts, particularly in the southern regions of the park. Spatial variations in leopard density within the park were not found to be associated with prey biomass or with densities of other carnivore species and were therefore assumed to be environmentally driven (Maputla, 2014). However, no further status assessment has been conducted, and it is difficult to gauge the impact of the emerging threat of poaching. Concern exists over leopard populations in some reserves bordering the park, particularly those on the eastern side that are plagued by high levels of bushmeat poaching linked to greater poverty in the area (Everatt et al., 2014; Strampelli et al., 2018a; Strampelli et al., 2018b). By contrast both SSGR and Timbavati Game Reserve on the western edge have high recorded leopard densities, due to favourable habitat and negligible levels of human induced mortality (Balme et al., 2019; Rogan, 2021).

As a general rule, top-down regulation tends to be less important than bottom-up factors for animals higher up the food chain (Carbone and Gittleman, 2002). The relatively recent appearance of the human 'super predator' however has changed the delicate balance between bottom-up and top-down control for many species, as humans can and do threaten all species, from herbivores to apex carnivores (Darimont et al., 2015; Smith et al., 2017). Therefore, while large carnivore populations have repeatedly been found to be at least partially driven by habitat variables and prey stocks, they are showing an increasing dependence on anthropogenic impacts and reserve management (Kiffner et al., 2009; Balme et al., 2010b; Riggio et al., 2013; Havmøller et al., 2019; Searle et al., 2020).

Anecdotal evidence of increased poaching pressure on leopards in the KNP region and the need for a follow up to the first density estimates provided in 2011 (Maputla, 2014) have called for a greater understanding of the health of leopard populations in and around KNP. I aim to assess the density of leopard populations in the central and southern regions of KNP and to compare these with private reserves neighbouring the park which have different historical and current management practices. Additionally, I explore the drivers of density in the area. I focused my efforts on the southern half of the park as it is more likely to be affected by anthropogenically driven mortality than the north because it has naturally higher leopard densities and greater proximity to more low income communities (Maputla, 2014).

Given the growing impact of the illegal skin trade, and anecdotal evidence of poaching in and around KNP, I predict that leopard densities in the area will be driven by a combination of habitat and anthropogenic variables. I predict that the Sabi Sand Game Reserve (SSGR), on the southwestern boundary of KNP, is likely to have the highest leopard densities given its favourable habitat and high levels of security which minimize anthropogenically induced mortalities. Sites within KNP which are buffered from anthropogenic activity due to their distance from the edge of the park (Schmidtz and Willott, 2012; Balme et al., 2019) will likely have intermediate densities while sites in KGR, on the Mozambican side of KNP's central eastern boundary, will likely have the lowest densities given they have only recently attained protected status and are both close to and accessible to impoverished local communities. I further predict that greater tree cover in southern sites, which provides more favourable habitat for leopard hunting, will be a driver of higher densities than the more open grasslands characteristic of the central sites.

3.3 Methods

This chapter uses camera trap data from 10 sites spread between three reserves: four from within the southern and central regions of KNP, four from the SSGR on the western boundary of KNP and two from KGR on the eastern boundary of KNP (see Chapter 2 for descriptions of reserves). Camera trap surveys at these sites took place in 2018 (n=7) and 2019 (n=3). Four of the 10 sites that I surveyed were in and around the central region of KNP (Houtboschrand, Nwanetsi, Karingani North, Karingani South) and six were in and around the southern region of KNP (Sabi Sand South, Mala Mala/Londolozi, Singita/Western Sector, Sabi Sand North, Skukuza/Lower Sabie and Pretoriuskop). Two sites were surveyed predominantly during the wet season (Singita/Western Sector and Houtboschrand), and the rest were surveyed during the dry season (Table A5.1). Each camera trap survey consisted of approximately 45 paired stations set up at a site, with two cameras placed opposite each other at each station to capture images of both sides of leopards passing by. Camera trap stations within sites were placed 1-3km apart, ensuring that the total area covered by cameras at each site was >100 km^2, which is more than double the mean home range size of male leopards in KNP (Bailey, 1993). This layout also has spacing between camera trap stations equal to approximately double the sigma estimate for female leopards in SCR models from the region, and helps to ensure the accuracy of density estimates (Dupont et al., 2021). Each survey, representative of a site, and in the case of multisession models a session as well, was active for approximately 45 days to ensure that the assumption of population closure, required by SCR models, was met (Royle et al., 2013). Due to equipment limitations the sampling was done in an iterative manner with a maximum of two camera trap surveys operational at one time. Detailed camera trapping protocols are described in Chapter 2.

Data were analysed using SCR models in the 'secr' package (Efford, 2017) within the R statistical environment (R Core Team, 2017) to determine drivers of density and provide density estimates. SCR requires the identification of individuals. Paired stations are crucial for this as they allow for the matching of left and right flanks to a particular individual. It was however not always possible to match left and right flanks for all individuals. To avoid replicating individuals for which I was unable to match left and right flanks, I used either all unpaired left flank images or all unpaired right flank images from each site (whichever category contained the most images) in addition to all paired images. Captures were recorded as a count of the number of independent observations of each individual at each station, where independent observations were defined as either non-consecutive observations or consecutive observations recorded more than eight hours apart (Rogan et al., in press). The total trapping effort per station was calculated as the total number of trap nights that at least one of the two cameras per station was active.

SCR relies on two conditionally related models: the observation/detection model, which describes the decaying probability of detection as a function of the distance between a trap and an animal's putative home-range center and the state model, which uses a spatial Poisson point process to describe the intensity of home-range centers in space (Royle et al., 2009; Efford, 2017). These models assume that individuals all have activity centers distributed throughout space, and that the likelihood of encountering an individual decreases with distance from its activity center following a detection function. I used a hazard half-normal detection function to model the baseline detection rate of individuals. I also used a hybrid mixture model to model differences between males and females, given that home range size and movement patterns have been found to vary according to sex in leopards (Fattebert et al., 2016; Balme et al., 2019; Searle et al., 2021b). Sex was therefore included as an individual specific covariate, along with several trap specific covariates. SCR models estimate a lambda naught (λ_0) parameter which provides an indication of detectability and a sigma (σ) parameter which provides an indication of the spatial decay in detection as distance from a camera trap increases, and derive density estimates from estimates of these two parameters (Efford, 2017). The SCR methods implemented here follow the approach of Rogan et al. (in press) and Havmøller et al. (2019).

Trap specific covariates were measured either at the scale of an entire site, or at the scale of each habitat pixel within a site and fell into one of two categories: biological or anthropogenic. Regarding spatially continuous variables which needed to be extracted from raster layers, I used inverse distance weighted means which accounted for the fact that activity centers are representative of the central point of each animal's home range or area of use, and that this central point is used more frequently than regions further out from the central point (Chandler and Hepinstall-Cymerman, 2016). Values for covariates varying continuously across the landscape were therefore given a higher weighting in pixels closer to the center of the area of use. The use of inverse distance weighted means benefits from a prior understanding of the space usage of a leopard, most importantly size of the area of use, and the spatial decay parameter associated with that (Rogan et al., in press). These were derived from a preliminary SCR model run with density varying per session and detection parameters (σ and λ_0) held constant. The radius of the area of use, r_{AU}, was then calculated according to the formula $r_{AU} = 2.447\sigma$ (Royle et al., 2013). Covariate values were calculated as the mean of all raster pixels within the area of use, with each pixel weighted according to a half normal function with a spatial decay parameter of σ. The use of distance weighted means addresses the problem associated with unweighted means, caused by a greater number of pixels occurring further away from the center of an animal's area of use, and the corresponding covariate therefore being more strongly influenced by values of the covariate in areas where the animal is assumed to spend less time.

I included a range of biological covariates all of which were scaled within sites. At the scale of sites, rather than individual camera trap stations, I derived the relative abundance index (RAI) for nine potential prey species detected across all stations at each site as a proxy for the abundance of prey. I used the number of independent captures in the calculation of RAIs, with an independence threshold of 30 minutes between successive photographs of the same species (O'Brien, 2011). Prey RAI was calculated as the total number of independent captures of prey species relative to the total number of days at least one camera per station was active. The nine prey species consist of all locally present herbivores within the leopard's preferred weight range of 10-70kg and included bushbuck (*Tragelaphus scriptus*), grey duiker (*Sylvicapra grimmia*), grysbok (*Raphicerus sharpei*), impala (*Aepyceros melampus*), klipspringer (*Oreotragus oreotragus*), nyala (*Tragelaphus angasii*), reedbuck (*Redunca arundinum*), steenbok (*Raphicerus campestris*) and suni (*Neotragus moschatus*) (Hayward et al., 2006; Pitman et al., 2012; Pitman et al., 2014; Schwarz and Fischer, 2017). RAIs obtained from camera traps, particularly in the case of arrays tailored to a specific species, are generally not comparable between species and ecosystems due to differences in detection as well as random station-specific effects (Treves et al., 2010; Sollmann et al., 2013). They have however been shown to be sufficiently accurate to draw broad inferences at the population level (Carbone et al., 2001; O'Brien et al., 2003; Kelly, 2008; Rovero and Marshall, 2009; Palmer et al., 2018). It is for this reason that Prey RAI was included in models at the scale of sites rather than stations. However, the abundance of prey does not guarantee ample feeding opportunities for large carnivores, as prey vulnerability, or catchability, has been found to play an equally, if not more important role in driving large carnivore predation events (Hopcraft et al., 2005;

Balme et al., 2007; Coon et al., 2020). Leopards are ambush hunters and thus rely on either rugged terrain (Martins and Harris, 2013) or vegetation to provide sufficient cover to allow them to get close to prey (Balme et al., 2007). Leopards have been found to have the highest levels of hunting success in moderately dense vegetation (Balme et al., 2007). I have included two environmental covariates to account for this, both measured across all habitat pixels: normalised difference vegetation index (NDVI) and Distance to River. NDVI values were obtained from Landsat imagery (30m resolution), sampled at the median month of all surveys (September 2018) (Vermote et al., 2016). A map of major rivers was obtained from the FAO geonetwork, and Distance to River was calculated as the Euclidian distance between the central pixel of each habitat cell within the state space and the nearest major river (FAO GeoNetwork, 2014). While not all rivers flowed at all times of year, they were included primarily because of the riparian habitat they are associated with that provides opportunities for ambush hunting. Artificial water sources such as dams were not included in analyses, as they do not affect surrounding vegetation to the same extent as rivers.

I selected two variables to represent anthropogenic pressure: Reserve Type at site level, and Distance to Edge measured across habitat pixels. With regards to Reserve Type, sites were classified according to whether they were managed by Sabi Sand Game Reserve (SSGR), Sanparks (KNP) or Karingani (KGR), as available resources and management regimes differ substantially between these three reserves. The main differences between the management of these three reserves include access to financial resources, fence quality, incidence of poaching activities, time since protection and active management of resources (pumping of water, vegetation control). Distance to Edge was measured as the Euclidian distance between the centroid of each habitat cell within the state space and the nearest protected area boundary, and represents proximity to potentially deleterious edge effects (Woodroffe and Ginsberg, 1998; Balme et al., 2010b). In the case of the SSGR however, deleterious edge effect are unlikely given the impenetrable nature of the fence, and instead home-range pile up resulting in increased leopard density is a more likely effect of Distance to Edge. I therefore also considered whether the effects of Distance to Edge on leopard density interacted with Reserve Type. I defined the state space using a habitat mask that extended 12km beyond the edges of each camera trap array, with the exception of the western boundary of the SSGR which is considered impenetrable to leopards and was considered a hard boundary (Balme et al., 2019). This 12km distance was large enough to ensure that animals with activity centers at the far edge of the buffer would not be captured by the camera trap array. The habitat mask discretized the state space into 1km-by-1km cells and excluded all cells with their centroids located in non-habitat (urban areas or water).

Prey RAI and Reserve Type were highly correlated (r=0.821, Table A3.2) and Prey RAI and Distance to River showed some degree of correlation (r=-0.262, Table A3.2). A principal component analysis (PCA) also revealed that variation in Prey RAI and Distance to River was aligned along a single axis (Figure

A3.1). Thus, to avoid problems associated with collinearity, I excluded Prey RAI in models that included Reserve Type or Distance to River, and considered these correlations in subsequent interpretations.

Prey RAI showed a high level of variation between sites, ranging from 0.96 (Karingani North) to 7.06 (Singita/Western Sector) captures per trap night (Table 3.1). Prey RAI was low in KGR (0.96-2,12), medium in KNP (2.09-3.84) and high in SSGR (3.76-7.06) (Figure 3.2). Mean NDVI was relatively similar between sites, ranging from 0.24 in Houtboschrand to 0.30 in Pretoriuskop (Table 3.1). Overall, mean NDVI was highest in KGR, medium in KNP and lowest in SSGR (Figures 3.2 and 3.3). NDVI showed very little variation within the SSGR, as all four sites in that reserve had a mean NDVI of 0.26, with minimum and maximum values ranging from 0.24 to 0.30. Minimum NDVI values of 0.20 were recorded in Houtboschrand, and maximum NDVI values of 0.55 were obtained in Pretoriuskop. Like mean NDVI, mean Distance to River was also highest in KGR, medium in KNP and lowest in SSGR (Figures 3.2 and 3.3). There was however more variation in mean Distance to River than in NDVI values between reserves. All sites had habitat cells that were next to a river, however the maximum Distance to River was highest in Karingani North, at 20150m (Table 3.1). Mean Distance to Edge was higher in KNP than in KGR or SSGR (Figures 3.2 and 3.3). The habitat cell with the greatest Distance to Edge was in Houtboschrand, at 41114m (Table 3.1).

Table 3.1: Session level covariates and mean ± standard deviation (SD), minimum and maximum values for station level covariates at the 10 camera trap arrays deployed, measured across all habitat pixels of the state space for each site, including the 12km buffer.

Session	Veg Type	Season	Reserve Type	Prey RAI	NDVI			Distance to River (m)			Distance to Edge (m)		
					Mean (± SD)	Min	Max	Mean (± SD)	Min	Max	Mean (± SD)	Min	Max
Sabi Sand South	Southern	Dry	SSGR	3.76	0.26 (0.01)	0.24	0.29	3125 (2344)	10	9679	10851 (6874)	11	25754
Mala Mala/Londolozi	Southern	Dry	SSGR	5.73	0.26 (0.01)	0.24	0.30	4031 (2845)	1	11461	9819 (6673)	7	24941
Singita/Western Sector	Southern	Wet	SSGR	7.06	0.26 (0.01)	0.24	0.30	3300 (2408)	19	9944	4476 (3033)	18	12457
Sabi Sand North	Southern	Dry	SSGR	4.51	0.26 (0.01)	0.24	0.29	4158 (2868)	0	11333	10255 (6173)	8	23304
Skukuza/Lower Sabie	Southern	Dry	KNP	3.84	0.27 (0.01)	0.24	0.31	3866 (2828)	14	12147	14023 (7286)	43	27664
Houtboschrand	Central	Wet	KNP	2.10	0.24 (0.03)	0.20	0.33	4445 (3349)	4	13629	23867 (9200)	2532	41114
Pretoriuskop	Southern	Dry	KNP	2.09	0.30 (0.05)	0.23	0.55	6102 (3622)	10	18498	5705 (3932)	2	16454
Nwanetsi	Central	Dry	KNP	3.51	0.27 (0.03)	0.22	0.36	4618 (3411)	0	13747	15401 (9325)	11	37228
Karingani North	Central	Dry	KGR	0.96	0.27 (0.03)	0.21	0.33	6904 (4094)	17	20150	11386 (8479)	12	33255
Karingani South	Central	Dry	KGR	2.12	0.29 (0.04)	0.22	0.38	5359 (3419)	13	13861	6891 (5283)	4	23180

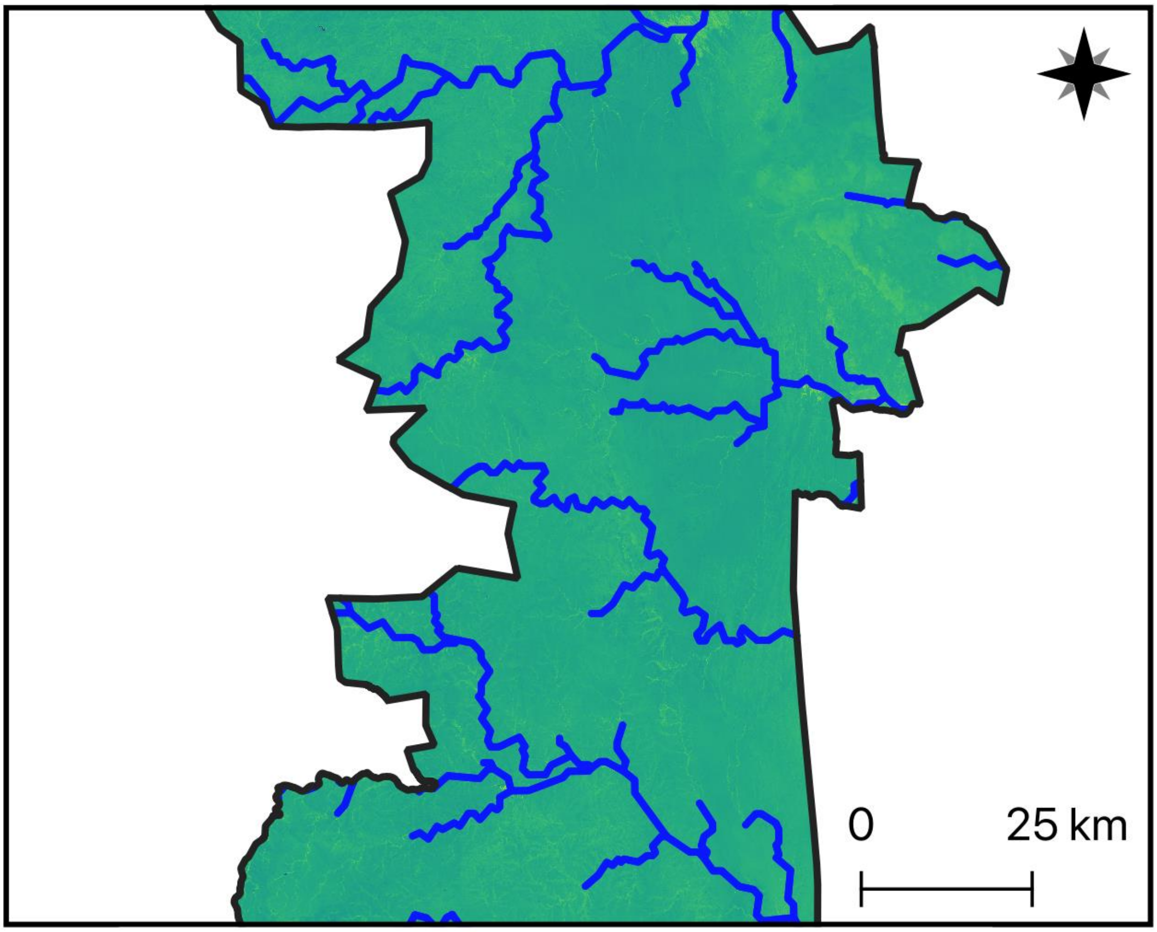

Figure 3.2 Map of study region showing variation in NDVI (lighter green represents higher NDVI), major rivers (in blue), and reserve boundary (in black).

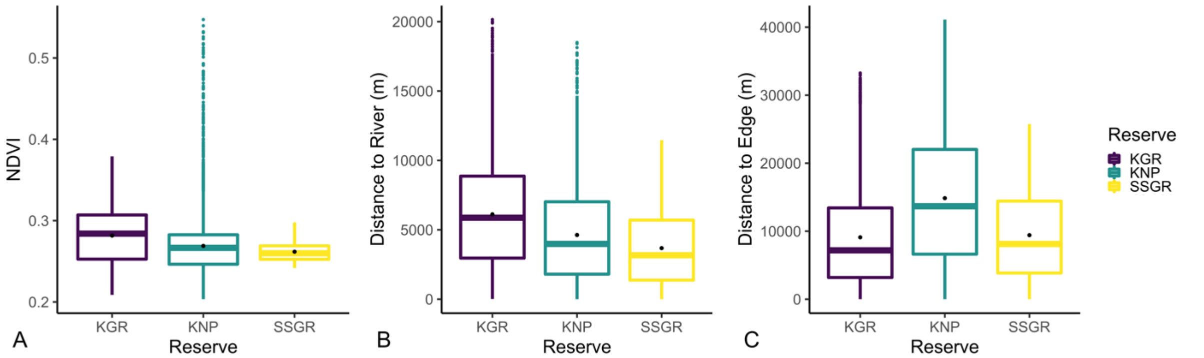

Figure 3.3: Boxplots showing how station specific covariates (NDVI, Distance to River, Distance to Edge) vary between reserves. Mean values are shown with black dots.

It has been well established in the literature that the parameters σ and λ_0 differ with sex, with female leopards having smaller home ranges and lower detectability than males (Havmøller et al., 2019; Rogan et al., 2019). Environmental covariates also affect these parameters (Havmøller et al., 2019). More open habitats provide camera traps with an increased field of view and therefore an increased chance of detection, but also make it easier for animals to move through the landscape without relying on movement corridors such as game trails. It is therefore useful to include these covariates in the detection model. However, sharing detection parameters between sites helps to smooth the stochasticity involved in the detection process and also increases the robustness of detection parameters estimated from sites with fewer captures (Rogan et al., in press). To balance the benefits of sharing detection parameters between sites and the need to account for variation in environmental factors between sites, I divided the 10 sites into two broad vegetation categories: central KNP and southern KNP. Central KNP receives less rainfall than southern KNP and is therefore characterised by a more open, grassy savanna landscape, in contrast to the more heavily wooded savanna landscape found further south in the park. I also categorised sites by whether camera trapping took place during the dry (April – September) or wet (October – March) season, as vegetation changes associated with rainfall also have the potential to impact leopard movement and detection (Balme et al., 2013; Loock et al., 2018). I then fitted a series of models with homogenous, session specific density and different parameterisations of the detection model, to choose the best way of incorporating environmental, seasonal and sex-based variability into the detection function. I compared these models using AICc scores and selected the model with the most support to inform my choice of appropriate detection parameters. I used these detection parameters in a series of inhomogeneous density models where density was related to predictor variables using a linear model with a natural log link function. Firstly, I ran a model with session as a covariate on density to derive session specific density estimates. Then, I compared and selected using AICc, the best performing of a series of models derived from *a priori* hypotheses of possible drivers of leopard density (Table 3.2). Models were run by maximising the full likelihood optimised using the Nelder-Mead estimator (Borchers and Efford, 2008).

Table 3.2: Hypotheses of potential drivers of leopard population density across the southern and central portion of Kruger National Park and neighbouring reserves. Associated density models show covariates relevant to the hypotheses. The density model refers to the linear predictor using a log link function (ln(D)). Colons represent interaction terms and asterisks represent interaction terms plus the main effect of each variable in the interaction.

ID	Hypothesis	Density Model	N Parameters
M0	Leopard density remains consistent across all sites	D ~ Intercept	1
M1	Leopard density increases with NDVI and proximity to rivers	D ~ Intercept + NDVI + Distance to River	3
M2	Leopard density increases with the abundance of prey	D ~ Intercept + Prey RAI	2
M3	Leopard density increases with prey abundance and vulnerability	D ~ Intercept + Prey RAI + NDVI	3
M4	Leopard density increases with proximity to rivers	D ~ Intercept + Distance to River	2
M5	Leopard density is limited by the proximity of human settlements	D ~ Intercept + Distance to Edge	2
M6	Leopard density is dependent on reserve management	D ~ Intercept + Reserve Type	2

M7	Leopard density is limited by the proximity of human settlements, but this can be mitigated by reserve management	D ~ Intercept + Distance to Edge: Reserve Type	3
M8	Leopard density increases with NDVI and proximity to rivers, but is limited by proximity to human settlements	D ~ Intercept + NDVI + Distance to River + Distance to Edge: Reserve Type	5
M9	Leopard density increases with NDVI and prey abundance, but is limited by proximity to human settlements	D ~ Intercept + NDVI + Prey RAI + Distance to Edge: Reserve Type	5
M10	Leopard density increases when prey is both more abundant and more vulnerable, with an interaction between these variables	D ~ Intercept + Prey RAI + NDVI + Prey RAI: NDVI	5
M11	Leopard density increases with increasing NDVI	D ~ Intercept + NDVI	2
M12	Leopard density increases with NDVI, but is limited by proximity to human settlements	D ~ Intercept + NDVI + Distance to Edge: Reserve Type	4
M13	Leopard density increases with proximity to rivers, but is limited by proximity to human settlements	D ~ Intercept + Distance to River + Distance to Edge: Reserve Type	4
M14	Leopard density increases with prey abundance, but is limited by proximity to human settlements	D ~ Intercept + Prey RAI + Distance to Edge: Reserve Type	4
M15	Leopard density increases with NDVI and proximity to rivers, but is also affected by management	D ~ Intercept + NDVI + Distance to River + Reserve Type	4
M16	Leopard density increases with NDVI, but is also affected by management	D ~ Intercept + NDVI + Reserve Type	3
M17	Leopard density increases with proximity to rivers, but is also affected by management	D ~ Intercept + Distance to River + Reserve Type	3
M18	The relationship between leopard density and NDVI depends on reserve management	D ~ Intercept + NDVI * Reserve Type	4

3.4 Results

I recorded a total of 1637 independent leopard captures from the 10 camera trap surveys carried out. The number of independent captures per survey ranged from 31 in Houtboschrand to 324 in Sabi Sand South, and the number of individually recognisable leopards ranged from 13 in Houtboschrand to 76 in Skukuza/Lower Sabie (Table 3.3). All sites consisted of approximately 45 camera trap stations (range of 42-46) except for Skukuza/Lower Sabie which had 64. This site was larger than usual because it was expanded to link it onto the Sabi Sand South site, which required some extra cameras. The number of trap nights (one trap night represents at least on camera active per station for a 24 hour period) ranged from 1961 in Karingani South to 4064 in Skukuza/Lower Sabie (Table 3.3). Naïve occupancy of leopards was generally high (>0.7), except for Houtboschrand (0.30) and Karingani South (0.55). Overall, leopard capture rates were highest in the SSGR (Figure 3.4).

Table 3.3: Summary of leopard data collected from camera trap surveys at 10 different sites. The number of trap nights refers to the cumulative number of 24 hour periods over the course of the survey that at least one camera at each station was active. The number of individuals refers to the number of unique leopards identified, and the number of captures refers to the number of independent leopard captures. The number of males and females is not necessarily equal to the total number of individuals because not all individuals could be reliably sexed. Naïve occupancy refers to the proportion of sites at which leopards were captured. The lowest number of individuals with either left side only or right side only captures were excluded from SCR analyses to avoid duplicating IDs.

Site	Year	Stations	Trap Nights	Individuals	Identified Leopard Captures	Males	Females	Naïve Occupancy	Unidentified Leopard Captures	Left/Right Side Only Individuals Excluded
Sabi Sand South	2018	45	2656	42	324	20	18	0.93	35	2 (Right)
Mala Mala/Londolozi	2018	46	2299	35	196	16	19	0.83	38	9 (Right)
Singita/Western Sector	2018	45	2317	22	90	9	11	0.73	7	2 (Right)
Sabi Sand North	2019	43	2168	33	185	14	16	0.98	1	3 (Right)
Skukuza/Lower Sabie	2018	64	4064	76	275	35	38	0.89	30	12 (Left)
Houtboschrand	2018	45	2252	13	31	5	4	0.38	5	2 (Right)
Pretoriuskop	2018	45	2134	31	155	12	15	0.80	21	5 (Right)
Nwanetsi	2018	43	2113	38	103	16	17	0.70	5	11 (Right)
Karingani North	2019	45	2186	35	217	15	16	0.82	17	2 (Right)
Karingani South	2019	42	1961	16	61	9	4	0.55	4	2 (Left)

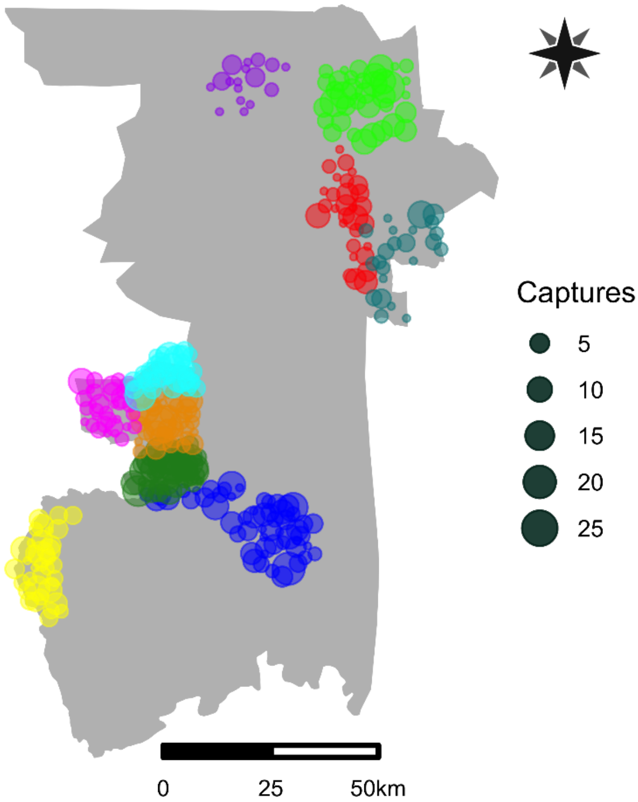

Figure 3.4: Map of independent leopard captures across all camera trap arrays deployed. Different colours represent different sites. See figure 2.2 for site names.

Model selection using AICc indicates that the best detection model is MD2 which includes an interaction between Sex and Vegetation Type on both detection parameters (σ and λ_0) (Table 3.4). Only two of the eight models tested show any support, with MD2 showing eight times more empirical support than MD5 (MD5 includes an interaction between sex and season on λ_0 and sex as a covariate on σ). MD2 had an AICc weight of 0.89, compared to 0.11 (dAIC = 4.268) for MD5.

Table 3.4: Model selection for detection parameters associated with leopard population density across the southern and central portion of Kruger National Park and neighbouring reserves.

ID	Predictor Variables on λ_0	Predictor Variables on σ	N Parameters	AICc	dAICc	AICc Weight	Evidence Ratio
MD2	Vegetation Type: Sex	Vegetation Type: Sex	21	7305.135	0	0.894	1
MD5	Season: Sex	Sex	18	7309.403	4.268	0.106	8.434
MD4	Season + Sex	Sex	16	7322.095	16.96	0	NA
MD6	Season * Sex	Sex	17	7323.295	18.16	0	NA
MD1	Vegetation Type + Sex	Vegetation Type + Sex	17	7368.585	63.45	0	NA
MD3	Vegetation Type * Sex	Vegetation Type * Sex	19	7368.620	63.485	0	NA
MD7	Sex	Sex	15	7369.839	64.704	0	NA
MD0	1	1	13	7486.878	181.743	0	NA

With these detection parameters included in all subsequent inhomogeneous density models, model selection using AICc indicates that M18 was best able to predict leopard density across the study area. M18 includes an interaction between NDVI and Reserve Type as covariates on density, in addition to both variables as fixed effects. M18 is substantially better than all other models, with an AICc weight of 0.91 (Table 3.5). There is some support for three other models: M16, M15 and M6 with dAICc scores of 5.476, 6.863 and 9.746 respectively and AICc weights of 0.06, 0.03 and 0.01 respectively. M16 includes NDVI and Reserve Type as only additive effects, and not interactive effects, M15 includes NDVI, Distance to River and Reserve Type as additive effects and M6 includes only Reserve Type as a predictor of density. Reserve Type is present in all of these models, and three of the four include NDVI. Evidence ratios however indicate that M18 shows 15 times more support than the next best model, indicating that this model performs substantially better than any of the others.

Table 3.5: Model selection for the hypotheses of potential drivers of leopard population density across the southern and central portion of Kruger National Park and neighbouring reserves. Density ~ session performed better than any of these models and has an Akaike weight of 1 when compared to this list of models. Colons represent interaction terms and asterisks represent interaction terms plus the main effect of each variable in the interaction.

ID	Predictor Variables	N Parameters	AICc	dAICc	AICc Weight	Evidence Ratio
M18	NDVI * Reserve Type	17	7322.043	0	0.905	1
M16	NDVI + Reserve Type	15	7327.519	5.476	0.059	15.339
M15	NDVI + Distance to Rivers + Reserve Type	16	7328.906	6.863	0.029	31.207
M6	Reserve Type	14	7331.792	9.749	0.007	129.286
M9	NDVI + Prey RAI + Distance to Edge: Reserve Type	17	7332.914	10.871	0	NA
M14	Prey RAI + Distance to Edg: Reserve Type	16	7333.058	11.015	0	NA
M17	Distance to River + Reserve Type	15	7333.978	11.935	0	NA
M8	NDVI + Distance to River + Distance to Edge: Reserve Type	17	7338.880	16.837	0	NA
M12	NDVI + Distance to Edge: Reserve Type	16	7339.096	17.053	0	NA
M13	Distance to River + Distance to Edge: Reserve Type	16	7339.446	17.403	0	NA
M7	Distance to Edge: Reserve Type	15	7339.527	17.484	0	NA
M2	Prey RAI	13	7342.204	20.161	0	NA
M10	Prey RAI + NDVI + Prey RAI: NDVI	15	7342.831	20.788	0	NA
M3	Prey RAI + NDVI	14	7344.132	22.089	0	NA
M0	1	12	7366.447	44.404	0	NA
M4	Distance to River	13	7366.913	44.87	0	NA
M5	Distance to Edge	13	7367.786	45.743	0	NA
M11	NDVI	13	7368.590	46.547	0	NA
M1	NDVI + Distance to River	14	7369.101	47.058	0	NA

Detection parameters remain similar among all inhomogeneous density models tested. In the southern region males have marginally higher detectability than females, as represented by λ_0, and larger activity centers, as represented by σ (Table 3.6). In the central region however, females are substantially more detectable than males, and have much smaller activity centers (Table 3.6). The proportion of males to females in the population was approximately 0.48 for all models.

Table 3.6: Detection parameter estimates (λ_0 and σ) for individually identifiable male and female leopards in the southern and central Kruger National Park. P_{male} refers to the estimated proportion of males in the population. See table A5.3 for standard errors (SE).

ID	Southern λ_0		Central λ_o		Southern σ		Central σ		P_{male}
	Female	Male	Female	Male	Female	Male	Female	Male	
M18	0.0207	0.0279	0.0568	0.0323	2026	2556	1575	3213	0.486
M16	0.0212	0.0292	0.0627	0.0299	2023	2556	1469	3173	0.485
M15	0.0213	0.0285	0.0615	0.0294	2031	2587	1492	3158	0.483
M6	0.0214	0.0284	0.0614	0.0293	2027	2591	1478	3156	0.479
M9	0.0213	0.0285	0.0621	0.0292	2034	2593	1474	3139	0.481
M14	0.0214	0.0284	0.0615	0.0292	2031	2598	1481	3135	0.481
M17	0.0214	0.0284	0.0615	0.0292	2024	2588	1480	3155	0.479
M8	0.0212	0.0284	0.0613	0.0294	2037	2600	1471	3097	0.479
M12	0.0213	0.0284	0.0612	0.0292	2042	2602	1468	3095	0.477
M13	0.0218	0.0281	0.0644	0.0293	2004	2620	1437	3079	0.486
M7	0.0211	0.0283	0.0628	0.0294	2060	2608	1457	3070	0.491
M2	0.0212	0.0285	0.0620	0.0292	2044	2594	1462	3112	0.481
M10	0.0213	0.0284	0.0616	0.0292	2039	2601	1471	3120	0.479
M3	0.0213	0.0283	0.0612	0.0291	2039	2601	1473	3121	0.478
M0	0.0213	0.0283	0.0607	0.0292	2058	2619	1445	3028	0.475
M4	0.0213	0.0283	0.0604	0.0292	2055	2615	1447	3029	0.475
M5	0.0213	0.0284	0.0605	0.0292	2056	2616	1447	3034	0.475
M11	0.0213	0.0283	0.0609	0.0291	2060	2623	1442	3028	0.476
M1	0.0212	0.0279	0.0618	0.0291	2063	2624	1442	3032	0.479

Reserve Type is present as a predictor of density across the four inhomogeneous density models that showed at least some support (Table 3.7). In all four of these models, leopard densities are predicted to be lowest in KGR, medium in KNP and highest in the SSGR. In models M16 and M15 NDVI has a positive impact on leopard densities, (b = 0.300 ± 0.097 and b = 0.263 ± 0.098 respectively). The impact of NDVI is slightly lower in M15 because Distance to River accounts for some of the variation in density otherwise attributed to NDVI. In M18 however, the best model, the impact of NDVI differs starkly between reserves. In KGR, the baseline in the model parameterisation used, NDVI is negatively associated with leopard density (b = -0.553 ± 0.128) (Figure 3.5). However, NDVI is positively associated with leopard density in both KNP and SSGR with the effect being slightly stronger in SSGR than in KNP (b = 1.261 ± 0.335 and b = 1.158 ± 0.205 respectively).

Table 3.7: Estimated effects of predictor variables in supported models and associated standard errors (SE).

Model	Intercept (SE)	NDVI (SE)	Distance to River (SE)	Reserve KNP (SE)	Reserve SSGR (SE)	NDVI: Reserve KNP (SE)	NDVI: Reserve SSGR (SE)
M18	-7.446 (0.126)	-0.553 (0.128)	-	0.357 (0.147)	0.828 (0.177)	1.158 (0.205)	1.261 (0.335)
M16	-7.959 (0.155)	0.300 (0.097)	-	0.822 (0.181)	1.256 (0.192)	-	-
M15	-7.915 (0.153)	0.263 (0.098)	0.047 (0.072)	0.785 (0.183)	1.210 (0.196)	-	-
M6	-7.794 (0.143)	-	-	0.560 (0.162)	0.987 (0.168)	-	-

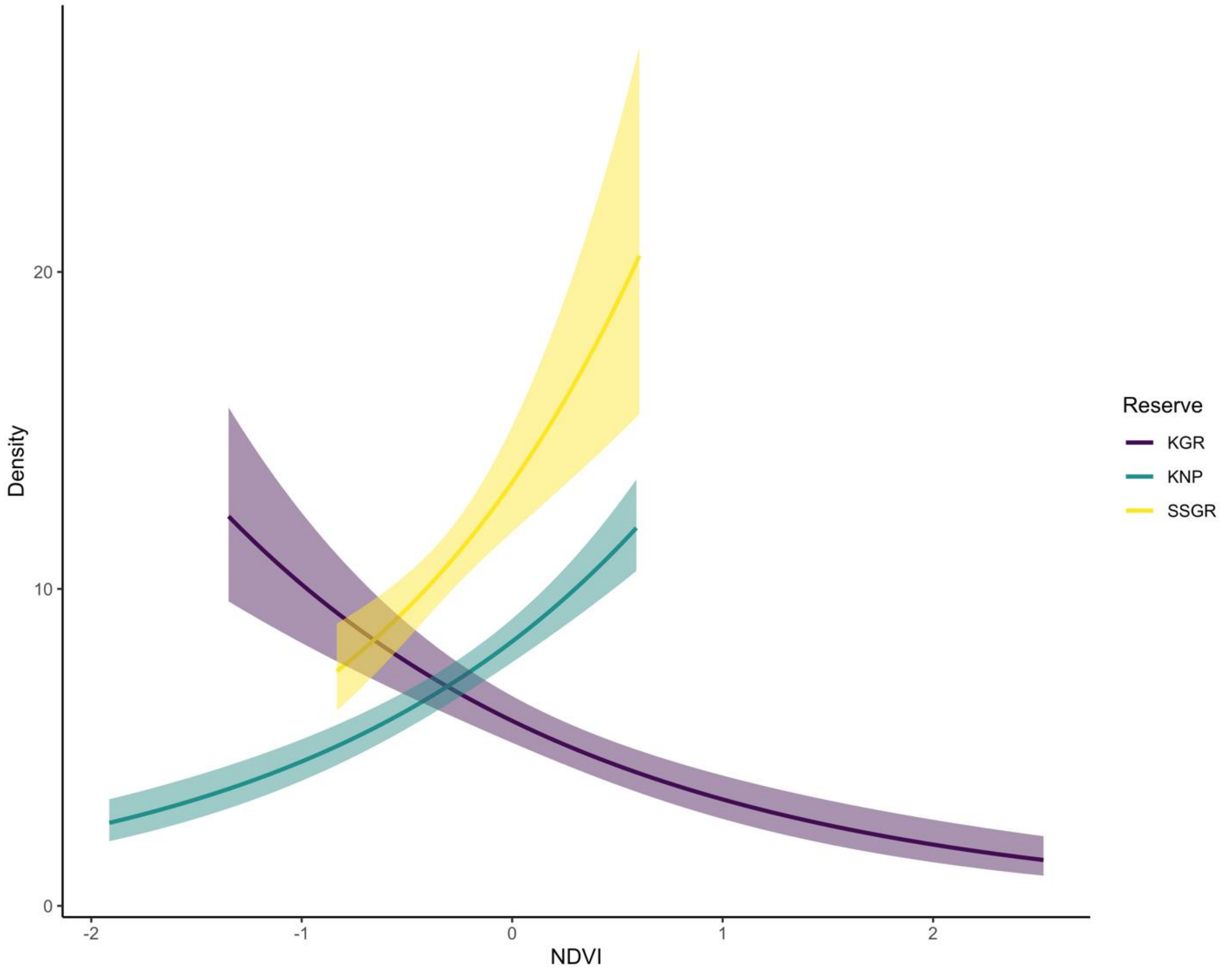

Figure 3.5: Estimated effect of NDVI (scaled) on predicted leopard density (leopards/100km^2) within each of the reserves surveyed, using the best supported model, M18. Confidence intervals (CI) shown by shaded regions were calculated from the relevant beta parameter plus or minus one standard error.

The combined effects of Reserve Type and NDVI across the study areas predict high leopard densities in the SSGR, particularly in the north-western corner of the reserve, where the Singita/Western Sector site is located (Figure 3.6). Densities are predicted to generally decrease moving into KNP, however they rise sharply in the southern section of the Pretoriuskop site, because of a sharp increase in NDVI in that area. Predicted densities are higher in the southern region of KNP than in the central region and are predicted to increase slightly in the far west of the central section as well as along the eastern boundary of KNP close to the Lebombo mountains. Within KGR densities are predicted to be higher in the northern section relative to the southern section.

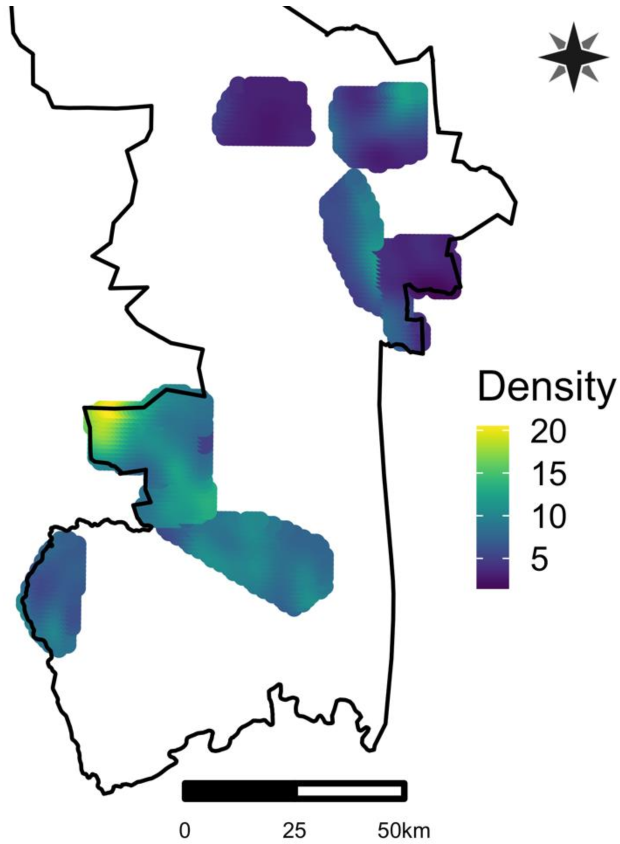

Figure 3.6: Predicted leopard densities (leopards/100km^2) derived from the best model, M18, across all study sites.

However, density predicted using session as a covariate is better able to describe variations in density over the study area than any other inhomogeneous density models tested (AICc weight of 1). A SCR model with density modeled as a function of session predicts that leopard densities are highest in Sabi Sand South and Sabi Sand North, at 13.2 leopards/100km^2 (± 2.0 and 1.3 respectively), and lowest in Karingani South, at 2.6 leopards/100km^2 (± 0.6) (Table 3.8). Generally, densities were highest in the SSGR, ranging from 9.9 (± 1.7) to 13.2 (± 2.3), medium in KNP ranging from 2.9 (± 0.8) to 9.7 (± 1.2) and lowest in KGR, ranging from 2.6 (± 0.6) to 5.9 (±1.0). Of the three reserves, densities showed the most variation in KNP, with densities being higher in the southern region and lower in the central region. These results are relatively consistent with predictions from M18 but differ markedly in their predicted mean density for Houtboschrand and Pretoriuskop. M18 appears to overestimate leopard densities in these areas relative to the session specific model, due to its consideration of NDVI. The difference in estimates between these models is due to the fact that M18 is attempting to model differences across the entire landscape, and consequently sites as well, based on the environmental and anthropogenic variables provided, while the session specific model simply estimates density at each site, without consideration of the variables that cause differences in density. M18 is not able to predict densities at each site as accurately as the session specific model because it is missing some variables that impact density, which I was not able to measure or incorporate into models. It does however provide an indication of which known variables are driving differences in density.

Table 3.8: Session specific density estimates and associated standard errors (SE).

Session	D ~ session Density (SE)	M18 Density (SE)	M16 Density (SE)	M15 Density (SE)	M6 Density (SE)
Sabi Sand South	13.2 (2.0)	11.4 (1.1)	11.5 (1.0)	11.3 (1.0)	11.1 (1.0)
Mala Mala/Londolozi	9.9 (1.7)	10.9 (1.0)	11.3 (1.0)	11.2 (1.0)	11.1 (1.0)
Singita/Western Sector	10.2 (2.1)	11.3 (1.0)	11.5 (1.0)	11.3 (1.0)	11.1 (1.0)
Sabi Sand North	13.2 (2.3)	10.9 (1.0)	11.3 (1.0)	11.3 (1.0)	11.1 (1.0)
Skukuza/Lower Sabie	9.7 (1.2)	8.4 (0.7)	8.0 (0.7)	7.9 (0.7)	7.2 (0.6)
Houtboschrand	2.9 (0.8)	5.2 (0.6)	6.3 (0.6)	6.5 (0.6)	7.2 (0.6)
Pretoriuskop	7.5 (1.4)	13.4 (1.9)	10.0 (1.3)	10.0 (1.5)	7.2 (0.6)
Nwanetsi	7.2 (1.2)	7.7 (0.6)	7.6 (0.6)	7.7 (0.6)	7.2 (0.6)
Karingani North	5.9 (1.0)	5.9 (0.8)	3.5 (0.5)	3.7 (0.6)	4.1 (0.6)
Karingani South	2.6 (0.6)	3.9 (0.7)	4.3 (0.6)	4.4 (0.6)	4.1 (0.6)

3.5 Discussion

The fortress conservation model, where tracts of wild land are fenced off from human communities in an attempt to minimise external anthropogenic impacts, has come under much scrutiny in recent years (Berkes, 2007; Abensperg-Traun et al., 2011; Barrett et al., 2011; Büscher, 2015; Jooste et al., 2018; Dickman et al., 2020; Roe et al., 2020). Opponents prefer a mosaic of natural and anthropogenic land use types in which humans and wildlife share space within a coexistence framework (Berkes, 2004; König et al., 2020; Pooley et al., 2021). While this approach has its merits and clearly works under certain circumstances (Suich, 2010; Abensperg-Traun et al., 2011; Boudreaux and Nelson, 2011; Hazzah et al., 2014; Dolrenry et al., 2016), it is much more difficult to achieve when large carnivores share space with high densities of people and their livestock. Predators may threaten both human safety and that of their livestock, and hence livelihoods (Thorn et al., 2012; Broekhuis et al., 2020; Jordan et al., 2020). Large carnivores are thus often perceived as unwelcome residents in many areas, and may be heavily persecuted even in the absence of direct damage (Balme et al., 2009). Furthermore, when natural resources are continuously and unsustainably harvested by growing human populations within a shared landscape then few wildlife species thrive, and many become locally extirpated (Ceballos and Ehrlich, 2002; Hill et al., 2020). For these reasons, large carnivore conservation in densely populated areas with high levels of poverty currently still relies heavily on protected areas with hard boundaries and anti-poaching activities, that limit external anthropogenic threats (Balme et al., 2010b; Pitman et al., 2015; Stephens, 2015; Ashrafzadeh et al., 2020). This has been extensively documented in the case of lions throughout Africa, where population densities are only able to come close to estimated ecological carrying capacities in intensively managed reserves reliant upon fortress conservation tactics as opposed to unfenced areas (Packer et al., 2013a; Packer et al., 2013b; Bauer et al., 2015). The erection of such fences unfortunately brings with it certain negative consequences, such as the interruption of natural dispersal routes, habitat fragmentation and the genetic isolation of populations (Creel et al., 2013), and these costs need to be weighed against the benefits of fencing in certain protected areas to eliminate anthropogenically driven threats.

It must also be remembered that some carnivores are arguably better than no carnivores. While the fortress conservation model, when stringently implemented, currently appears to retain landscapes with some of the highest densities of large carnivores, density is not the only metric of a viable, resilient and ecologically beneficial population. Community based conservation and coexistence models are undeniably of huge value to conservation efforts (Boudreaux and Nelson, 2011; Pooley et al., 2021), and metrics of success in these cases are not purely population density, but rather population stability (Balme et al., 2009; Snider et al., 2021). This study however focuses on population density, measured within protected areas that aim to eliminate anthropogenically driven mortalities and thus provide tracts of land representative of communities of wild animals living without human impacts. In this case, it is therefore important to assess population density against ecological carrying capacity. If these reserves, which undeniably impact surrounding communities in their attempts to keep harmful human activities at bay (Büscher, 2015), are not achieving their desired outcomes, then management either needs to be adapted so that they do, or they need to revise their approach to conservation entirely.

While protected areas aim to minimise anthropogenic impacts, they are not all equally effective at achieving this (Pitman et al., 2015; Ashrafzadeh et al., 2020; Rogan, 2021) and thus densities may vary substantially between reserves for a variety of natural and anthropogenic reasons. In this study Reserve Type was included in the top four models explaining leopard density across sites. Leopard densities differed markedly between reserves (from 4.1 ± 0.6 leopards/100km^2 in KGR to 11.1 ± 1.0 leopards/100km^2 in SSGR), but still fell within the range of previously recorded densities for this species in protected areas of South Africa (Martins and Martins, 2006; Balme et al., 2009; Balme et al., 2010b; Mann, 2014; Swanepoel et al., 2015; Ramesh et al., 2017b; Strampelli et al., 2018a; Balme et al., 2019; Rogan, 2021). The SSGR, a private reserve with one of the most generous security and maintenance budgets in the country had the highest density (11.1 ± 1.0 leopards/100km^2) of leopards in this study. KNP, which is contiguous with SSGR, is a state-owned reserve with more limited financial resources, particularly when considered on a per area basis, and hosted lower leopard population densities than SSGR but higher than KGR (7.2 ± 0.6 leopards/100km^2). KGR, a private protected area in its early stages of development and protection, held the lowest leopard population density of the three reserves (4.1 ± 0.6 leopards/100km^2).

One important consideration in interpreting the importance of Reserve Type is that this variable was highly correlated to Prey RAI across the 10 sites included in this study, with relative prey abundance being highest in the SSGR, medium in KNP and lowest in KGR. The effects of Reserve Type therefore by default include at least some effect of prey abundance. Interestingly however, Prey RAI and NDVI showed no correlation at all, despite the generally accepted trend of higher herbivore abundances associated with higher primary productivity, and consequently increased NDVI (Pettorelli et al., 2011). Therefore, there appears to be more influencing Prey RAI in this region than simply primary productivity, and I propose that this may be the management regime of the area, reflected in the Reserve Type variable. Prey abundance in this case, although usually considered a bottom-up variable, is itself likely affected by top-down factors. Regardless, it is important to consider that prey abundances did vary substantially between reserves, along with numerous other variables including access to financial resources, anti-poaching activities, quality of fencing, time since protection and water availability. Unfortunately these other variables could not be quantified in this study due to some data being kept confidential by reserves, and other data being impossible to measure with camera traps. The specific components of Reserve Type discussed therefore represent associations between predicted densities and factors that varied observationally between reserves, without these observations having been quantified.

These findings of higher leopard density within a well-established private reserve are consistent with the results from a previous study in the SSGR which estimated 11.8 leopards/100km^2, and another small, fenced, private reserve in Namibia, Okonjima Nature Reserve, with an estimated 14.5 leopards/100km^2 (Balme et al., 2019; Noack et al., 2019). Leopard density is not typically driven by top-down forces including competition with other larger predators (Balme et al., 2017b), however humans do exert measurable effects on large carnivores and have therefore been classified as 'super predators' (Darimont et al., 2015; Clinchy et al., 2016; Smith et al., 2017; Suraci et al., 2019). Thus in Tanzania leopard densities were higher in the core area of a well-established National Park than in a neighbouring community managed area despite both areas having a similar vegetation type, illustrating that ecologically similar protected areas under different management regimes can have starkly different leopard densities (Searle et al., 2021b). Additionally, reducing human persecution has been determined to be more effective at restoring large carnivore populations than restoring prey numbers, illustrating the severity of the consequences associated with anthropogenically driven mortality (Bleyhl et al., 2021). Interestingly, while edge effects have been reported to negatively impact leopard populations in a number of instances, (Balme et al., 2009; Balme et al., 2010b; Havmøller et al., 2019), they do not appear to be significantly impacting populations in this system. A similar finding has been observed across reserves in northeastern South Africa where other aspects of management and human impact were associated with leopard density, without an edge effect (Rogan et al., in press).

The leopard population in the SSGR is one of the best studied and protected in South Africa and is indicative of a leopard population free of anthropogenically driven causes of mortality (Balme et al., 2019). My estimate of leopard density in the SSGR is thus close to the upper limit of expected leopard densities in southern Africa (Balme et al., 2019; Noack et al., 2019) and in stark contrast to the recently protected KGR which had the lowest leopard densities in this study. KGR has a recent history of armed conflict, bushmeat poaching and snaring (Everatt et al., 2014; Strampelli et al., 2018a) and has similar leopard densities to Xonghile Game Reserve (2.60 ± 0.96 leopards/100km^2 at the time it was studied), which was a legally protected but unfenced reserve, before becoming part of KGR (Strampelli et al., 2018a). Follow up density surveys in KGR will provide an important before and after case study for the effects of fortress conservation on leopard densities in protected areas. Based on the findings in this study I predict that leopard densities will increase in KGR provided tourism and hence revenue for improved protection recovers globally following the COVID-19 pandemic (Lindsey et al., 2020; Terraube and Fernández-Llamazares, 2020; Wiedenfeld et al., 2021).

There is a concern that anthropogenically driven leopard mortalities are increasing within the larger state-owned reserve of KNP. Previous leopard density estimates for sites in the southern section of KNP have too much uncertainty (Pretoriuskop confidence interval varied from 1-1318 leopards/km^2) to serve as a robust baseline for a temporal comparison with this study. Despite the high confidence intervals associated with previous density estimates, on a broad scale, 10 years ago leopard density within KNP was estimated to be highest in the southwestern region of the park (Maputla, 2014). Anecdotal evidence points towards an increase in the targeted poaching of large carnivores in the Pretoriuskop area (C. Williams, pers. comm.) and my results reveal that leopard densities are currently higher around the Skukuza/Lower Sabie region than in Pretoriuskop, despite NDVI being higher in Pretoriuskop. The density estimates generated in this study provide a robust baseline, to which future estimates can be compared, allowing for changes in densities to be detected, inferences about population trend to be made and management practises to be adapted. KNP, being a state owned and funded reserve, has more limited resources, and covers a substantially area greater than the SSGR. While larger protected areas are better able to host viable populations of more species, particularly larger ones, they are also more difficult to protect (Woodroffe and Ginsberg, 1998; Balme et al., 2010b; Di Minin et al., 2013; Pitman et al., 2015). Large reserves like KNP have little to no road access in many regions and very long boundary fences. The former may provide some respite from tourism related disturbances (Blickley and Patricelli, 2010; Halfwerk and Slabbekoorn, 2015; Smith et al., 2017;

Oberosler et al., 2017; Suraci et al., 2019), but also limits the efficacy of patrolling for illegal activities. Long boundary fences are expensive to construct, maintain and patrol, and when resources are limited this provides opportunities for incursions from neighbouring communities to both engage in bushmeat harvesting and target valuable species such as leopard (Packer et al., 2013a).

While Reserve Type is a clear driver of leopard density in this study, there was also substantial support for NDVI as a driver of density, which is a relatively coarse proxy for the bottom-up ecological processes that may influence leopard populations (Balme et al., 2007; Mann, 2014) and has been positively linked to higher leopard densities in smaller protected areas of northeastern South Africa (Rogan, 2021). Higher NDVI has previously been associated with higher primary productivity, which on a broad scale is associated with higher prey abundance, and generally thicker vegetation cover (Pettorelli et al., 2011). NDVI and Prey RAI however were not colinear in this study, meaning that these two variables provide different information on the underlying landscape. Leopards have previously been shown to select for hunting grounds with higher NDVI scores, presumably because NDVI provides an index of cover and hence prey catchability, which is seemingly more important for leopard hunting success than prey abundance (Balme et al., 2007). Similar results have been found for lions and pumas, both of which are also ambush hunters (Hopcraft et al., 2005; Coon et al., 2020) although Gaughan et al. (2013) have suggested caution in linking NDVI with vegetation structure in savannas. I therefore also included Distance to River as another covariate linked to vegetative cover, given that rivers in savanna systems are bordered by riparian vegetation. However, NDVI, despite its potential lack of differentiation between tree canopy and grassy or forb layers, was more important in influencing leopard densities than Distance to River.

While NDVI is positively associated with leopard density across the entire study region, there is also a significant interaction between NDVI and Reserve Type, indicating that the impact of NDVI differs between Reserve Types. NDVI has the strongest positive effect on leopard population density in the SSGR, and a lesser but still positive effect in KNP. However, the relationship was negative in KGR, where leopard densities are lowest. It is likely that this reversal is not actually representative of lower NDVI being more favourable for high leopard densities, but rather that other variables not included in the analyses are more important in this reserve. One such variable would be 'time since protection'. I lacked sufficient variation in this variable to include it in models as both KNP and SSGR, representing eight out of the 10 sites surveyed, have been protected for over 50 years (Carruthers, 1995; du Toit et al., 2003; Schmidtz and Willott, 2012). However, the northern section of KGR was protected under the name of Xongile Game Reserve until it became a part of KGR. The southern section of KGR however was only added to the reserve the year before camera trapping took place and had previously been unprotected community land. The importance of 'time since protection' in this reserve may therefore surpass that of NDVI and could explain why leopard densities were higher in the north of the reserve compared to the south. Population recovery following the gazettement of a protected area is a process that takes time, particularly for larger mammals such as leopards with relatively slow recruitment rates (Balme et al., 2009; Fattebert et al., 2016). While many protected areas have a history of disturbance, as is the case for all three of the reserves investigated here, the SSGR and KNP have had over 50 years to recover from the impacts of cattle farming and hunting respectively, while KGR is only just beginning to recover from the impacts of a civil war and the high levels of poaching that followed. The importance of the interaction between Reserve Type and NDVI leads to the conclusion that leopard populations closer to carrying capacity are more strongly regulated by biological, bottom-up forces such as NDVI, while those at low densities such as in KGR are regulated more strongly by anthropogenically driven top-down forces.

While the SSGR is one of the few leopard populations in the country known to be free of anthropogenically driven mortality (Balme et al., 2019) it is arguably not reasonable to expect for such unrestrained budgets and intensive management regimes to be replicated across the region. It does however provide a control site and thus a valuable comparison with KNP due to its similar environmental variables. However, it is not an entirely natural baseline with which to compare other leopard populations. There is a relatively heavy human presence in the SSGR as a result of the photo-tourism based activities that take place, seen through the high road density, frequent game drives and lodges scattered throughout (Balme et al., 2017c; Balme et al., 2019). Large mammals in the SSGR have become habituated to the presence of humans (Balme and Hunter, 2013a; Balme et al., 2017b), and predators have even been observed to make use of game drive vehicles, lodges and swimming pools for stalking and hunting prey. Additionally there are substantial differences in land management between KNP and SSGR: SSGR has been more active in limiting bush encroachment, and certain private properties also mow some grassy areas to make game viewing easier, which in turn attracts certain grazing species (Koelble, 2011). Water is also pumped into artificial water holes, many of which have been discontinued in KNP in an effort to return the land and resulting interspecific interactions to a more natural state (van Wyk, 2010; Koelble, 2011; South African National Parks., 2016). The landscape of the SSGR is thus human modified, and this may artificially elevate the carrying capacity for leopards relative to KNP. Another potential factor resulting in artificially inflated densities includes the potential for ‘home-range pile-up’, whereby the hard boundary presented by the impenetrable fence surrounding the SSGR causes greater home range overlap between territorial animals like leopards, and smaller home ranges (Strasburg, 2006). This has been observed in coyote and bobcat populations inhabiting regions with artificial barriers to movement such as major roads (Strasburg, 2006).

While leopard densities differ between the three connected reserves in this study these differences are not entirely explained by the variables included in the analyses (NDVI, Distance to River, Prey RAI, and Distance to Edge and Reserve Type). It is possible that an unmeasured contributor to this variation is illegal human offtake, a recognised threat to leopards throughout their distribution and a growing concern for leopard populations within South Africa's protected areas (Naude et al., 2020a; Naude et al., 2020b). My only metric for anthropogenic impacts was Distance to Edge which, despite having been shown to adversely impact large carnivores elsewhere, (Woodroffe and Ginsberg, 1998; Balme et al., 2010b; Havmøller et al., 2019) did not appear to explain the variation in leopard density in this study. Distance to Edge ultimately represents both the presumed decrease in human disturbance with increasing distance from protected area boundaries, and also the proportion of protected area included in an animal's home range (except in the case of hard boundaries, such as the SSGR boundary fence) (Havmøller et al., 2019). A similar lack of effect of Distance to Edge, previously found in northeastern South Africa, has been attributed to leopard biology, given that the dispersing of young males results in the rapid filling of territorial gaps in populations, effectively smoothing out densities in protected areas, despite increased mortality rates outside of these protected areas (Rogan et al., in press). Provided the rate of illegal offtake does not exceed the rate of immigration into anthropogenically created territory vacancies, reduced leopard densities near protected area edges will be difficult to detect. However, lower densities of leopards in the recently proclaimed KGR and intermediate levels in areas of KNP with recent evidence for increased poaching (such as Pretoriuskop) suggest that anthropogenic threats may be a concern to leopard populations and that long term monitoring through camera trap surveys should be a management goal even in the conservation stronghold of KNP.

CHAPTER 4

SPOTS OF LIGHT, COLD, FEAR OR OPPORTUNITY: LEOPARD ACTIVITY OVER THE DIEL AND LUNAR SCALES

Figure 4.1: A camera trap photograph of a leopard catching a nyala in broad daylight in the Sabi Sand Game Reserve.

4.1 Abstract

Spatial avoidance is one of the most pervasive responses of wildlife to human disturbance, but new research is increasingly revealing the importance of temporal shifts in activity. Most animal species appear to become more nocturnal in areas with greater levels of human disturbance. Leopards (*Panthera pardus*), being solitary, elusive and behaviourally flexible with a broad diet are one of few large carnivore species that readily persist in human modified landscapes. Here I investigate the relative importance of anthropogenic and ecological factors on the activity patterns of leopards within the greater Kruger National Park (KNP). I use independent captures from camera trap data collected across 10 sites in central and southern KNP as an index of leopard activity, and kernel density models to estimate activity patterns of leopards, humans, potential leopard prey species and potential local competitors of leopards. I explore the relative influence of humans, potential prey, potential competitors and select environmental variables (temperature, season, artificial light at night and distance to human settlements) on the temporal activity patterns of leopards. No differences in overall leopard activity levels were evident between sites but activity patterns within a 24 hour period did differ. These differences were best explained by ambient temperature and not the relative abundance of humans, potential leopard prey or potential competitors. Leopard activity also varied significantly with the lunar cycle, peaking near full moon. Together these results suggest that leopard activity patterns in South Africa's largest protected area are primarily driven by environmental factors and that both anthropogenic effects and the relative abundance of potential prey and potential competitors have only a limited influence. The sensitivity of leopard activity to nocturnal illumination does urge caution regarding the levels of human induced artificial light at night both from settlements within the park and on game drives.

4.2 Introduction

Anthropogenic activities have a broad range of impacts on wildlife communities. Climate change, agriculture, urbanisation and other forms of land use change have removed, altered and fragmented large tracts of wild land, forcing animals to adjust their behaviour and movements (Aspinall and Matthews, 1994; Jepsen et al., 2005; Harper et al., 2007; Ogutu et al., 2014). These changes undeniably impact the ranges of species and include the interruption of migration routes, affecting the ability of individuals and entire populations to perform innate behaviours and movement critical to their survival (Palacín et al., 2017). However, not only are migration routes being interrupted spatially, but also temporally, as increases in temperature linked to global warming affect the timing of migration in a multitude of species (Jenni and Kéry, 2003; Marra et al., 2005).

Animal activity patterns are driven by a complex suite of potentially interacting factors, which can be difficult to identify and measure (Monterroso et al., 2013; Ohashi et al., 2013; Ross et al., 2013; Ordiz et al., 2017; Gaynor et al., 2018; Caravaggi et al., 2018; Havmøller et al., 2020). Changing activity patterns in response to human activity have only been recorded relatively recently, and are considered crucial for many species to both coexist alongside humans, and tolerate human driven environmental changes (Ohashi et al., 2013; Ordiz et al., 2017; Gaynor et al., 2018; Patten et al., 2019; Buchholz et al., 2021). There are three major ways in which animal activity patterns can change in response to humans: overall levels of activity can change, the location of activity can change and the timing of activity can change (Díaz-Ruiz et al., 2016; Dröge et al., 2017). In this study I have focused mainly on the timing of activity, with a secondary assessment of overall activity levels.

Generally speaking, animals do not exert more energy than is required for survival and reproduction (Rizzuto et al., 2017). Overall activity levels are therefore indicative of how much energy an animal needs to exert to survive (Rizzuto et al., 2017). In the case of leopards this will involve, amongst other things, time spent hunting, patrolling territories, avoiding threats, and searching for mates. Changes in overall activity levels are usually indicative of changes in stressors requiring modifications to activity budgets. The directionality of how changes in stress levels affect overall activity budgets varies greatly: reduced prey availability for instance may increase the amount of time and energy an animal needs to exert in order to search for food, but may also cause the animal to reduce overall activity to conserve energy due to the lack of food (Díaz-Ruiz et al., 2016; Van Cleave et al., 2018; Havmøller et al., 2020).

All animal species show some form of activity patterning, expressed as the proportion of time and energy spent on different activities at different times. The activity patterns of animals are driven by a multitude of factors which occur at different scales and are driven by both environmental and biological cues. One of the strongest environmental drivers of activity patterns is light (Foster and Roenneberg, 2008; Gaston et al., 2013). Light affects activity patterns through seasonal changes in day length, monthly changes in the lunar cycle and daily changes in illumination as the earth rotates around the sun (Foster and Roenneberg, 2008; Gaston et al., 2013). While seasonal variation increases with latitude, all parts of the world experience lunar cycles and daily variations in light which result in diel activity patterns among virtually all species (Ashby, 1972).

Light influences the circadian rhythm, which is the endogenous clock of an organism that regulates activity over a 24 hour period, therefore acting as an environmental cue known as a zeitgeber (Takahashi et al., 1984; Arendt and Broadway, 1987). While light is undeniably important in regulating the activity patterns of animals (Gaston et al., 2013), different animal species show different activity levels under different levels of light (Ashby, 1972). This results in temporal niche partitioning which promotes the ecological separation of species, allowing a wide variety of species to exist within the same ecosystem (Gutman and Dayan, 2005; Hayward and Slotow, 2009; Ramesh et al., 2017a). Temporal niche partitioning can be seen through the existence of diurnal, nocturnal and crepuscular species allowing species to coexist within the same environment with reduced competition (Ashby, 1972; Jones et al., 2001).

The amount of light at night varies due to naturally occurring phenomena such as lunar cycles and cloud cover, which have been found to affect the timing of activity across a range of species (Hayward and Slotow, 2009; Kyba et al., 2011; Kronfeld-Schor et al., 2013). However, while the earth's light regimes have remained relatively unchanged over geological timescales, the Anthropocene has seen a sudden and novel rise in artificial lighting at night which is increasing by an average of 6% annually and is now classified as a form of pollution (Hölker et al., 2010b; Gaston et al., 2013). The newly emerging threat to ecosystem integrity produced by artificial light at night is concerning because of the huge distances travelled by light (Gaston et al., 2013; Jechow et al., 2017).

Changes to the earth's natural lighting regime have been found to affect the natural environment at many scales, from changes in the behaviour of individuals through to changes in population dynamics and the structure and composition of communities (Longcore and Rich, 2004; Hölker et al., 2010b; Gaston et al., 2013; Minnaar et al., 2015; Halfwerk and Slabbekoorn, 2015). Activity patterning is intricately linked to timing of food availability, hunting success and concealment and is therefore an important component in predator-prey relationships (Ashby, 1972; Monterroso et al., 2013; Minnaar et al., 2015; Dröge et al., 2017). The presence of artificial light at night has the potential to affect an organism's ability to perceive naturally occurring shifts in light over a 24 hour period, changing their time activity budgets and consequently impacting interspecific relationships (Hölker et al., 2010b; Gaston et al., 2013). In response to artificial light, organisms can lengthen or shorten their activity periods, shift peaks in activity to earlier or later or respond spatially by relocating. All of these changes will however impact other species with which they come into contact, affecting competitive and predator-prey relationships (Gutman and Dayan, 2005; Cozzi et al., 2012; Minnaar et al., 2015; Palmer et al., 2017). The exponential growth in the presence of artificial light at night is therefore reshaping both ecological and evolutionary processes.

The effects of varying levels of light across the nighttime landscape differ on a species-specific basis. Responses to changes in moonlight are most closely related to a species' trophic position, as well as its primary sensory modality (Prugh and Golden, 2013). Prey species relying mostly on vision as their primary sensory system tend to increase activity levels at night during periods of increased illumination (Prugh and Golden, 2013). This response in prey species is likely due to a heightened ability to detect predators in the presence of increased moonlight, resulting in lower vulnerability and swaying the risk reward balance in favour of foraging as opposed to vigilance (Prugh and Golden, 2013). Predatory species however do not appear to show a consistent pattern of changes in activity relative to lunar illumination, regardless of their reliance on vision. Within the suite of African predators, this has been explored most extensively in lions, where conflicting results have been reported, with some studies showing a decrease in activity levels with increased moonlight (Packer et al., 2011) and others finding no change in activity throughout the lunar cycle (Cozzi et al., 2012; Prugh and Golden, 2013). While little consensus has been reached regarding the impact of moonlight on lion activity levels, hunting success in lions is consistently reported as being higher at times of lower moon illumination (Funston et al., 2001; Packer et al., 2011; Kronfeld-Schor et al., 2013). This is presumed to be the result of increased prey vulnerability and leads to the conclusion that lower levels of light lead to greater decreases in predator detection by prey than prey detection by predators. While the impacts of light on leopard activity levels and hunting success are less well understood, data from leopards in the Cedarberg Mountains of South Africa indicates that they too make more kills during periods of lower light (Martins and Harris, 2013). By contrast a study in Kenya revealed that leopard activity levels were highest at times of greater moon illumination, potentially to compensate for lower hunting success (Van Cleave et al., 2018). Both studies used Global Positioning System (GPS) collar data, providing fine scale information on animal movement. When merged together, results from these two studies corroborate one another: greater hunting success during darker nights causes a decrease in overall activity required to catch prey (Martins and Harris, 2013), resulting in higher overall activity required at times of more moonlight to compensate for decreased hunting success (Van Cleave et al., 2018).

Temperature is also important in the timing of animal activity, and is another well established zeitgeber (Kappeler and Erkert, 2003; Lemel et al., 2003; Hart et al., 2021). While temperature extremes are a strong determinant of the species assemblage that can persist in a given region (Hortal et al., 2008), within regions daily temperature variation sets limits on the time periods during which different species can be active (Creel et al., 2016; Hall and Chalfoun, 2019). As temperatures reach more extreme levels for a particular environment an animal's ability to thermoregulate, thereby maintaining its body temperature within the required range, decreases and activity is usually reduced (Khaliq et al., 2014). Broadly, larger animals are more constrained by heat dissipation, meaning that they are more impacted by higher temperatures, while smaller animals are more constrained by heat retention, and therefore are more constrained by colder temperatures (Creel et al., 2016). This impacts interspecific relationships and it has been found that in an African context extreme heat disadvantages wild dog prey more than the wild dogs themselves, resulting in increased hunting success (Creel et al., 2016).

Similar to light, temperature varies across multiple scales: most importantly the annual scale, with changes in season, and the daily scale with changes in sunlight. Temperature is therefore not independent from light, as temperatures are consistently higher during daylight hours than at night (Bennie et al., 2014). However, increased activity when temperatures are extreme can have more severe, and often lethal consequences, relative to the cost of activity at extremes of day and night associated with light (Owen-Smith, 2019; Rabaiotti et al., 2021). This is particularly true for apex predators, who are not at a greater risk of being predated upon at certain times of day. Thus the impact of light, and other factors, on activity must occur within the constraints of that species' intrinsic thermal limits (Bennie et al., 2014). This often results in species showing more nocturnal activity during summer months when mean daily temperatures are higher, and more diurnal activity during winter months when temperatures are lower (Fernandez-Duque, 2003; Theuerkauf, 2009).

In addition to the environmental cues which affect activity patterns, biological factors are also important components of animal activity patterns. These biological factors often relate to predator-prey relationships with predators and prey seeking to maximise and minimise overlap in activity respectively (Ross et al., 2013; de Matos Dias et al., 2018; Viviano et al., 2021). In many ways however, humans are the current 'super predators' of the planet, and a broad array of species, ranging from prey to predators, all appear to be reacting more strongly to human presence than to each other (Lemel et al., 2003; Clinchy et al., 2016; Smith et al., 2017; Gaynor et al., 2018; Johann et al., 2020). Human activity is largely diurnal, particularly in rural and natural areas, although human activity also influences the nighttime landscape through artificial light (Longcore and Rich, 2004; Hölker et al., 2010b; Gaston et al., 2013). A multitude of studies have explored the spatial avoidance of humans by animal species, however only more recently has temporal avoidance been recorded (Kronfeld-Schor and Dayan, 2003; Jepsen et al., 2005; Harper et al., 2007; Ogutu et al., 2014; Gaynor et al., 2018; Searle et al., 2021a). Across a range of 62 mammalian species, from 21 orders and 9 families, increased levels of human disturbance have been linked to a shift towards a greater proportion of nocturnal activity with largely unknown impacts on ecosystem level processes (Gaynor et al., 2018).

Leopard activity patterns have been shown to be primarily nocturnal across a broad range of habitats, however usually still involve some daytime activity (Martins and Harris, 2013; Van Cleave et al., 2018; Searle et al., 2021a). They do however exhibit behavioural flexibility regarding timing of activity, and appear to show a higher proportion of nocturnal activity in areas of greater human activity (Odden et al., 2014). Females in particular have also been shown to increase levels of daytime activity in the presence of nocturnal competitors such as spotted hyenas (Havmøller et al., 2020). The relative importance of environmental, biotic and anthropogenic factors on leopard activity may involve complicated interactions. These variables have the potential to invoke additive or opposing effects, increasing the complexity of understanding the drivers behind activity patterning. In this study I aimed to explore how these covariates influence leopard activity in and around the large, protected area of KNP. I predict that higher levels of human presence will suppress leopard activity levels during the day regardless of the presence of potential prey or potential competitors, but that the magnitude of this impact will be moderated by ambient temperatures. Leopard activity is therefore predicted to be inversely related to human activity which is predominantly diurnal, resulting in a shift towards greater nocturnality as has been shown for other animals (Gaynor et al., 2018). In many cases this shift in activity has been observed regardless of whether human activity is consumptive or not (Gaynor et al., 2018), however given that leopards in the SSGR appear to become habituated to the presence of vehicles, I investigate the effects of humans on foot separately to those in vehicles, predicting that humans on foot will have a stronger effect on leopard activity than those in vehicles. Leopards are also predicted to avoid temperature extremes and be more active in the daytime during winter. On a lunar scale, I predict that leopard activity levels will increase with greater moon illumination, to compensate for decreased hunting success associated with more light (Funston et al., 2001; Packer et al., 2011).

4.3 Methods

In this chapter I use data from 10 camera trap surveys, which collected animal and human activity and relative abundance data across three reserves. Four sites were in the Sabi Sand, Mala Mala and Sabie Private Game Reserves (SSGR), two in Karingani Game Reserve (KGR), and four in KNP (Figure 2.2). Detailed camera trap methodology and site descriptions can be found in Chapter 2.

Capture rate, detected by passive sensors such a as camera traps, has been widely used as a measure of animal activity (Ross et al., 2013; Palmer et al., 2017; de Matos Dias et al., 2018; Caravaggi et al., 2018; Buchholz et al., 2021). I consider captures of the same species as independent if separated by a 15 minute interval because high vehicle volumes on certain roads would be under-represented by a longer interval. I further grouped independent captures into one of four categories: leopards, humans (on foot and in vehicle), potential prey and potential competitors. Humans on foot were further categorised as pedestrian captures to investigate whether these would have a greater impact on leopard activity than humans in vehicles. Potential leopard prey was defined as herbivore species falling within the leopard's preferred weight range of 10-70kg and included nine species present in the study area: bushbuck (*Tragelaphus scriptus*), grey duiker (*Sylvicapra grimmia*), grysbok (*Raphicerus sharpei*), impala (*Aepyceros melampus*), klipspringer (*Oreotragus oreotragus*), nyala (*Tragelaphus angasii*), reedbuck (*Redunca arundinum*), steenbok (*Raphicerus campestris*) and suni (*Neotragus moschatus*). I did not obtain enough captures of each species at all sites to run kernel density models at the level of species, and thus all potential prey species were combined into a single prey category. Similarly, potential leopard competitors include both lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). While these two species pose different threats to leopards, with lions predominantly responsible for direct mortality of leopards and hyaenas for kleptoparasitism of leopard prey, there were insufficient lion captures at all sites to analyse competitor species separately (Balme et al., 2017b; Balme et al., 2017a).

Data analyses were conducted in R version 3.5.2 (R Core Team, 2017). I used the 'activity' package (Rowcliffe, 2019) to fit kernel density models to the time of day data over a 24 hour period and calculate overall activity estimates for leopards at each site. Activity estimates were derived from circular kernel density models, with higher activity estimates representing a greater proportion of the day spent being active. I used the 'overlap' package (Meredith and Ridout, 2020) to compare temporal overlap in leopard activity patterns between sites as well as between leopard and human, potential prey and potential competitor activity patterns within sites over 24 hour periods using the Dhat 4 overlap index.

The Dhat 4 index of overlap provides an estimate of activity pattern overlap, derived from kernel density estimates of each species at the times they were detected. Confidence intervals for Dhat 4 estimates were calculated from 1000 bootstrap samples and were bias corrected.

Day length changes throughout the year at higher latitudes, and the resulting changes in light regimes influence wildlife activity (Caravaggi et al., 2018). I thus calculated time of detection relative to sunrise or sunset to control for day length changes. Time of detection for images from 0:00-11:59 was taken relative to sunrise, and time of detection for images from 12:00-23:59 was taken relative to sunset. Times before sunrise or after sunset were represented by a negative integer, while times after sunrise or before sunset were represented by a positive integer. Sunrise and sunset time specific to each station location and detection date were obtained from the R package 'suncalc' (Thieurmel and Elmarhraoui, 2019). I then modelled the relative time of leopard detection in response to a series of explanatory variables representing human, potential prey and potential competitor activity, anthropogenically driven changes to the landscape and seasonal effects. The explanatory variables used were as follows: distance (meters) from each station to the edge of the reserve or nearest human settlement within the reserve, light pollution level (radiance), relative abundance index (RAI) of all human activity, both in vehicles and on foot (hereafter referred to as human), RAI of humans on foot only (hereafter referred to as pedestrian), potential prey RAI, potential competitor RAI, season, and mean monthly temperature. Light pollution data were obtained for the median month of all surveys (September 2018) from Google Earth Engine's VIIRS Nighttime Day/Night Band Composites Version 1 dataset (Gorelick et al., 2017). This value represents the mean monthly radiance calculated from nighttime data from the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (DNB), measured at a 1km resolution. Human, pedestrian, potential prey and potential competitor RAIs were calculated at the level of each camera trap station for the duration of each survey as the total number of captures relative to the total number of days at least one camera per station was active. Pedestrians were included as a separate variable because while animals are often habituated to the presence of vehicles they typically flee when exposed to people on foot. Mean monthly temperature represents the mean temperature per month throughout the whole of KNP averaged over 29 years, as temperature data specific to each location and year were not available (Zambatis, 2006). Many variables were colinear and thus I ran only univariate models. Models were compared using AIC to determine the best predictor of relative time of leopard detection.

I used cross correlation functions (CCFs) to further investigate the relationship between the timing of leopard detections and detections of humans, potential prey and potential competitors. Detections of each category were binned into 1 hour time slots, creating two sets of time series data. CCFs were then used to determine whether a lag in one variable acts as a predictor of the other variable. CCFs function by searching for a correlation between X_a and Y_{a+l}, where a represents time. A positive lag (represented by a significant correlation between X_a and Y_{a+i}) indicates that X lags Y, while a negative lag (represented by a significant correlation between X_a and Y_{a-i}) indicates that X leads Y. The magnitude of the lag is indicative of the number of time periods that separate the leading and lagging variables. I used the 'CCF' function in R's core library (R Core Team, 2017) to run CCFs, and the 'testcorr' package (Dalla et al., 2021) to check for significance.

While previous analyses have looked exclusively at the temporal aspect of leopard activity, I also used time to event analyses to investigate spatio-temporal leopard activity relative to humans, potential prey and potential competitors. I did this by comparing the observed probability to the expected probability of detecting a leopard at a specific camera trap station in six hour time intervals for the 48 hours before and after a detection of a human, potential prey species or competitor. The observed probability of detecting a leopard in each 6 hour bin was calculated from the minimum time intervals between each human, potential prey or potential competitor detection and the most recent leopard detection at the same camera trap station. The expected probability of detecting a leopard during each time bin was derived from 1000 random simulations of leopard capture times, calculated by randomly assigning detection times to leopard observations while accounting for the observed diel activity pattern of the species, following Cusack et al. (2017). Differences between observed and expected probabilities of detection were tested for significance using a standard permutation test which assessed the probability of the expected value being greater than or less than the observed value at a significance level of 0.05 (Cusack et al., 2017)

The relationship between leopard activity and moonlight and whether this relationship changes based on anthropogenic factors remains poorly understood (Packer et al., 2011; Cozzi et al., 2012; Kronfeld-Schor et al., 2013; Palmer et al., 2017; Van Cleave et al., 2018). To further investigate the relationship between leopard movement and light I modelled the RAI of leopards across all stations per calendar day against the fraction of moon illuminated (Thieurmel and Elmarhraoui, 2019). I used all detections and not only nocturnal detections to provide an indication of overall daily activity over a 24 hour period. I grouped RAIs per moon phase (using 11 phases, from 0-10), and used the mean daily leopard RAI from each moon phase in models. I did this for all stations together, and for stations grouped by reserve (SSGR, KNP or KGR) and by site, to look for possible interactions between moon illumination and reserve or site.

Additionally, I investigated whether moon illumination affects hunting success in leopards using observational data collected by guides in the SSGR. The SSGR, a high end photo-tourism destination, hosts one of the most well documented leopard populations given that guides recognise resident leopards by their spot patterns and collect sightings information (Balme et al., 2013; Balme and Hunter, 2013a; Balme et al., 2017a). This has allowed for the collection of detailed behavioural data which is usually only accessible through the use of collars. In 2013 Panthera released a data collection software program to all lodges in the reserve, allowing for sightings information to be centralised and for records to be checked against one another to remove duplicates. All guides record the time, date and GPS coordinates of all leopard sightings, identify the individual leopard based on its spots and record behavioural observations including whether the leopard was on a kill, and whether the kill was fresh or not. I therefore used all sightings records of leopards collected between 2013 and 2019 to run a logistic regression model investigating whether more leopard kills were observed at times of greater lunar illumination. I did this in a mixed model framework to incorporate individual leopard as a random effect. I excluded all observations of leopards on old or kleptoparasitised kills and modelled whether the leopard in each observation was on a kill or not as a binomial response variable with fraction of the moon illuminated as the explanatory variable.

4.4 Results

In total I collected 1505 independent captures of leopards over 24150 trap nights across all 10 sites. Captures per site ranged from 55 in Karingani South to 294 in Sabi Sand South (Table 4.1). Activity estimates were not significantly different between sites (all combinations $p > 0.05$, exact values in Table A4.1) with the proportion of a 24 hour period spent being active ranging from 0.42 ± 0.10 in Houtboschrand to 0.61 ± 0.05 in Skukuza/Lower Sabie (Table 4.2). The proportion of independent captures taken at night versus during the day did however differ significantly between sites (Pearson's Chi-squared test = 22.474, df = 9, $p < 0.05$) with leopards at Pretoriuskop having the lowest proportion of nighttime captures (56%) and Nwanetsi the highest (78%) (Figure A4.1).

Table 4.1: Summary of data collected from camera trap surveys. The number of trap nights refers to the cumulative number of nights over the course of the survey that at least one camera per station was active. The number of captures refers to the number of independent captures, using a threshold of 15 minutes between successive captures of the same species or target group. Pedestrian captures refer to humans on foot, and human captures refer to both vehicles and humans on foot.

Site	Year	Number of stations	Trap nights	Number of leopard captures	Number of pedestrian captures	Number of human captures	Number of prey captures	Number of competitor captures
Sabi Sand South	2018	45	2656	294	678	2704	1303	644
Mala Mala/Londolozi	2018	46	2299	174	468	1817	1360	555
Singita/Western Sector	2018	45	2317	85	588	2398	1649	597
Sabi Sand North	2019	43	2168	171	613	2192	1318	596
Skukuza/Lower Sabie	2018	64	4064	256	634	1299	1996	865
Houtboschrand	2018	45	2252	30	249	823	861	373
Pretoriuskop	2018	45	2134	148	447	998	956	392
Nwanetsi	2018	43	2113	98	756	1267	1011	533
Karingani North	2019	45	2186	194	244	1015	770	198
Karingani South	2019	42	1961	55	454	1127	684	177

Table 4.2: Activity estimates derived from kernel density models, representing the proportion of the day spent active for leopards at each of the 10 study sites. A Wald test shows no significant differences in overall activity estimates between any of the sites ($p > 0.05$ for all combinations of sites (Table A4.1)).

Site	Activity Estimate	Standard Error
Sabi Sand South	0.51	0.05
Mala Mala/Londolozi	0.55	0.07
Singita/Western Sector	0.46	0.07
Sabi Sand North	0.59	0.06
Skukuza/Lower Sabie	0.61	0.05
Houtboschrand	0.42	0.10
Pretoriuskop	0.53	0.07
Nwanetsi	0.52	0.05
Karingani North	0.48	0.05
Karingani South	0.57	0.08

Kernel density models of activity patterns over a 24 hour period indicate that leopard activity was predominantly nocturnal but with clear peaks at dusk and dawn (Figure 4.3). Variation between sites was apparent with leopards having either greater morning or evening peaks and both distinct (e.g., Pretoriuskop) and vague (e.g., Nwanetsi) bimodal patterns. Despite these slight differences, activity levels were always lowest in the middle of the day at all sites. The overlap in leopard activity patterning between sites measured through the Dhat 4 index was generally high, ranging from 0.73 (Pretoriuskop vs Houtboschrand) to 0.93 (Sabi Sand North vs Karingani South) (Figure 4.2). Activity patterns at Houtboschrand, Pretoriuskop and Nwanetsi were most different from each other and other sites.

Figure 4.2: Overlap index in kernel density estimates of leopard activity (Dhat 4) for all combinations of sites. Darker blue represents more overlap in timing of leopard activity. The observed overlap indices were then compared against a null distribution of overlap indices using data sampled randomly with replacement from the combined datasets. Stars represent the level of significance in the difference between observed overlap and randomised overlap distribution (*** = p < 0.001, ** = p < 0.01, * = p < 0.05).

There is evidence of temporal partitioning between leopard and human activity with leopards being predominantly nocturnal and humans predominantly diurnal (Figure 4.3). Human activity peaked before sunrise and then virtually ceased at sunset across all sites in accordance with the rules restricting movement after sunset within the reserves. Leopard activity began to taper off before sunrise but was not at its lowest point at the time that humans were most active. Dhat 4 overlap estimates ranged from 0.20 at Pretoriuskop to 0.49 at Houtboschrand (Table A4.2). Potential prey showed predominantly diurnal activity, with a peak in activity in the early hours of the morning across all sites (Figure 4.3). Activity levels then showed a gradual decrease throughout the day, with a small peak around dusk and then a sudden decrease around sunset, remaining low throughout the night compared to daytime activity levels. Overlap between leopard and potential prey activity was higher than for leopard and human activity, with Dhat 4 estimates ranging from 0.41 at Pretorisukop to 0.70 at Nwanetsi (Table A4.2). Potential competitors however showed similar activity patterns to leopards, with activity being almost entirely nocturnal, and characterised by crepuscular peaks (Figure 4.3). Potential leopard competitors showed less diurnal activity than leopards, with virtually no activity in the middle of the day at any sites. Dhat 4 overlap estimates show a high proportion of overlap in activity between leopards and their potential competitors, ranging from 0.69 in Pretoriuskop to 0.86 in Singita/Western Sector (Table A4.2).

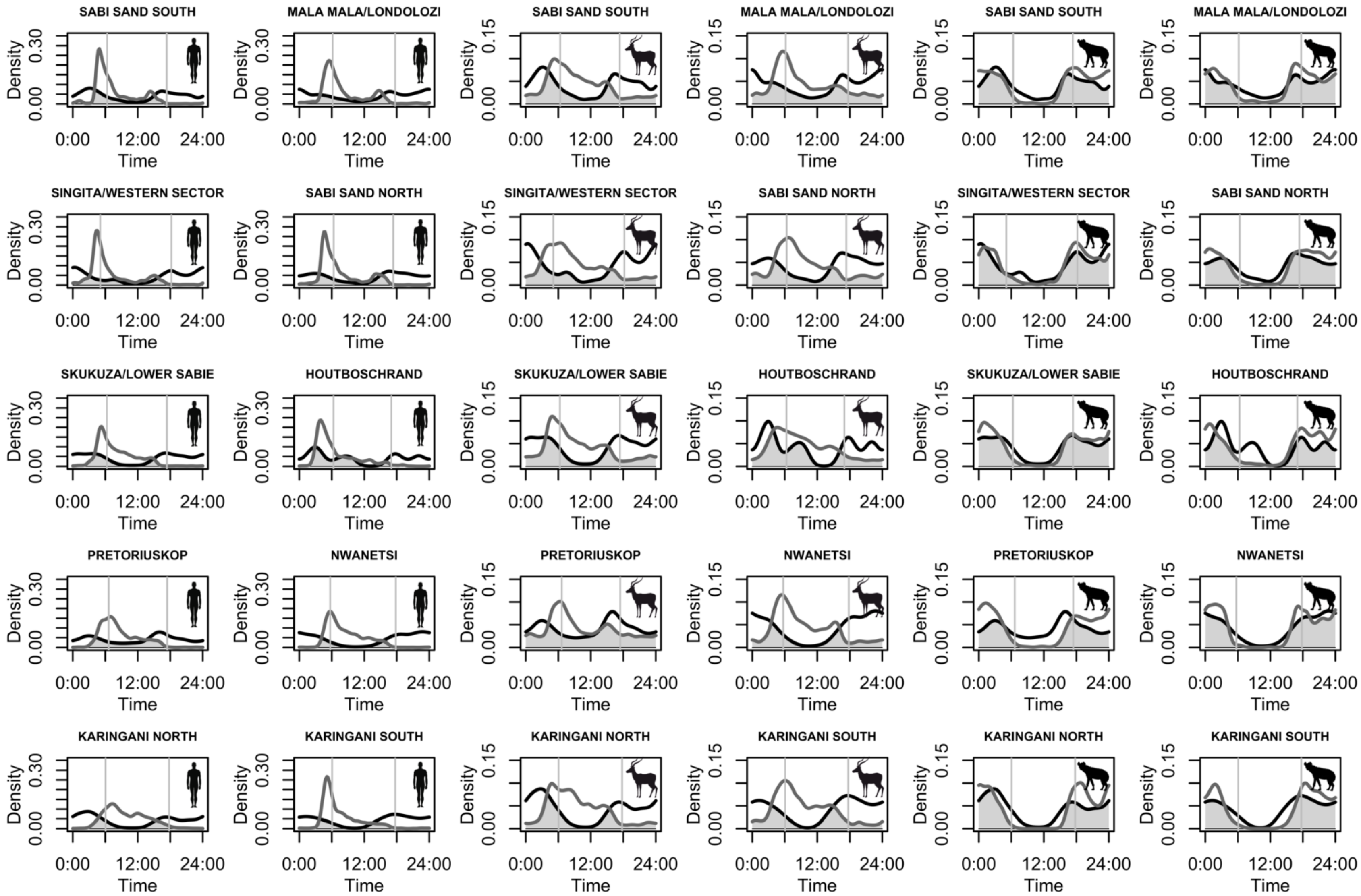

Figure 4.3: Kernel density models showing temporal overlap between the activity of leopard (black) and humans, potential prey species and potential competitor species (grey). Pale grey vertical lines show times of sunrise and sunset.

When leopard captures are scored relative to sunrise or sunset, whichever is nearest to the capture, the mean time of capture for all sites lies between 1 and 3 hours before sunrise or after sunset and is closest to 2 hours for most sites (Figure 4.4). Relative time of capture was closest to sunrise or sunset at Pretoriuskop, and furthest from sunrise or sunset at Nwanetsi. Linear regression and AIC based model selection indicates that the model best able to predict relative time of leopard capture includes temperature as a covariate (Table 4.3). AIC scores between the first and second models differ by only 0.11 indicating that there is almost as much support for the impact of season on the relative time of capture of leopards. The third and fourth models also have dAICs of less than 1 when compared to the best models and include potential prey RAI and distance to human settlement as predictors. These variables however do not show significant relationships with relative time of capture (estimate = 0.10732, t = 1.467, p-value = 0.142 and estimate = -0.10643, t = -1.455, p-value = 0.146, respectively). All four of these models however are better than the null model, confirming that these variables do improve model fit. Temperature, present in the top model, shows a negative relationship with relative time of leopard capture that approaches significance (estimate = -0.129, t = -1.760, p-value = 0.079) and captures during winter months have a significantly higher relative time of capture (closer to daytime) when compared to those occurring in autumn, spring and summer (estimate = 0.433, t = 2.548, p-value < 0.05).

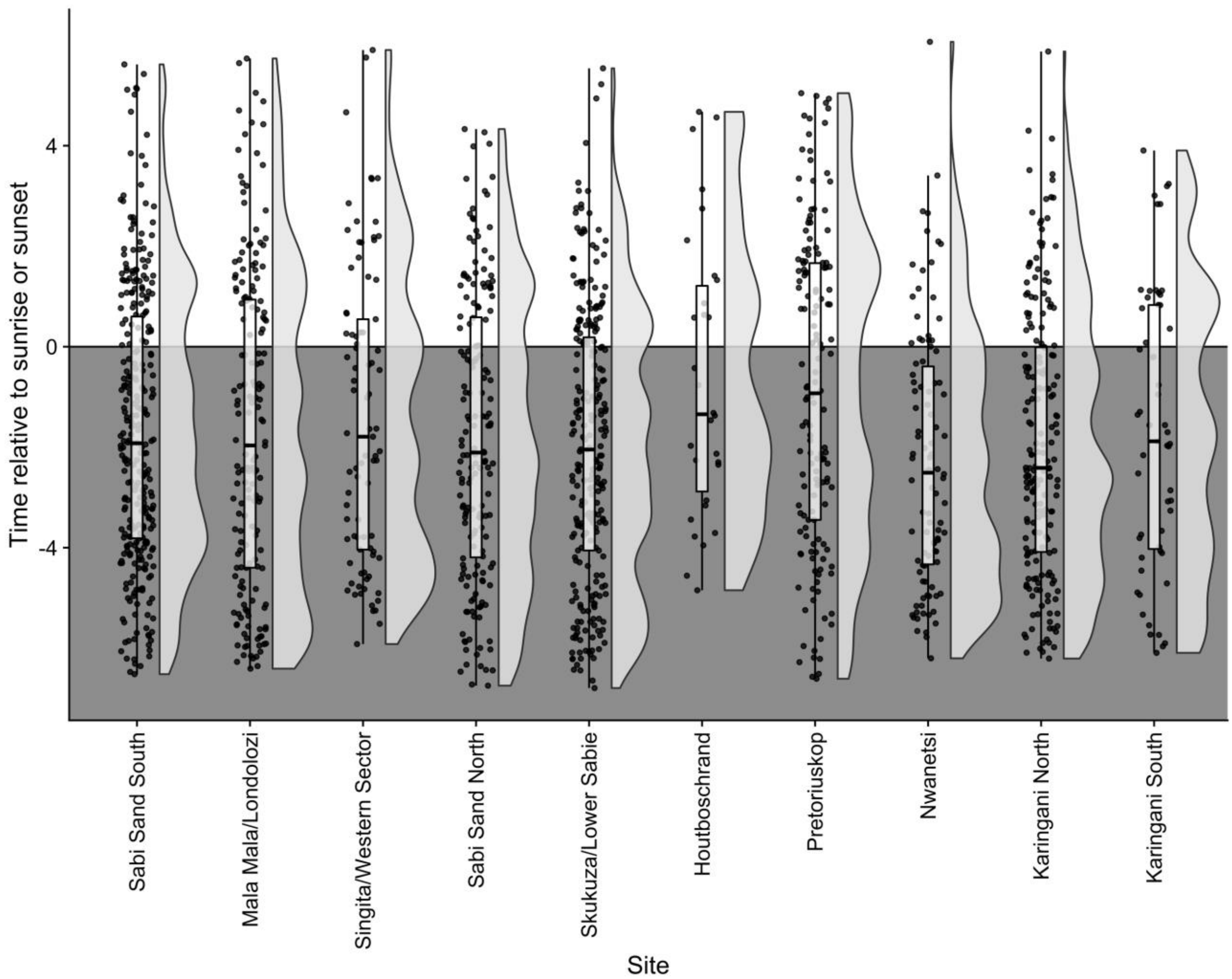

Figure 4.4: Time of detection relative to sunrise or sunset for leopards across 10 sites in and around Kruger National Park. Time of detection for images from 0:00-11:59 was taken relative to sunrise, and time of detection for images from 12:00-23:59 was taken relative to sunset. The lower, shaded area represents images captured at night, and the upper, white area represents images captured in the daytime. Boxplots represent the mean and standard deviation, and raincloud plots, shown in light grey, illustrate the intensity and spread of data points.

Table 4.3: Model selection table investigating variables that could impact the timing of leopard activity. Time refers to time of detection relative to sunrise or sunset for leopards across 10 sites in and around Kruger National Park. Time of detection for images from 0:00-11:59 was taken relative to sunrise, and time of detection for images from 12:00-23:59 was taken relative to sunset.

Model	Number of Parameters	AIC	Delta AIC	AIC Weight
Time ~ Temperature	3	7412.13	0.00	0.19
Time ~ Season	5	7412.23	0.11	0.18
Time ~ Prey RAI	3	7413.07	0.94	0.12
Time ~ Distance to settlement	3	7413.11	0.98	0.11
Time ~ 1	2	7413.22	1.10	0.11
Time ~ Pedestrian RAI	3	7413.43	1.30	0.10
Time ~ Human RAI	3	7413.46	1.34	0.10
Time ~ Light	3	7414.30	2.18	0.06
Time ~ Competitor RAI	3	7415.17	3.04	0.04

Cross Correlation Functions (CCFs) do not provide conclusive evidence of leopard activity being temporally related to that of humans (Table 4.4). Of the 10 sites surveyed two (Singita/Western Sector and Houtboschrand) show maximum lags with positive values, meaning that human captures, in vehicles and on foot, mostly lagged leopard captures, while the other eight sites show negative maximum lags, meaning that leopard captures mostly lagged human captures. The magnitude of the lags also differs substantially, ranging from 1 in Karingani North to 12 in Karingani South. CCFs also do not show conclusive evidence for a consistent relationship between the timing of capture of leopards and their potential prey (Table 4.4). At Houtboschrand the maximum lag is positive, indicating that potential prey captures lagged leopard captures, while at the other nine sites the maximum lag is negative, indicating that leopard captures lagged potential prey captures. The magnitude of these lags differs substantially between sites, ranging from 1 in Karingani South to 10 in Pretoriuskop. CCFs examining leopard and potential competitor captures show that there is not much difference in the timing of activity between these two groups, with lags ranging only from, at maximum, -3 to 3, and peak lags ranging only from -1 to 1 (Table 4.4). There is however no clear consensus on whether competitor captures lead or lag leopard captures.

Table 4.4: Temporal associations between leopards and humans, potential prey and potential competitors across 10 sites calculated using cross correlation functions. Only the peak lag associated with the greatest correlation is shown per site.

Site	From	To	Peak Lag	Correlation	t	p-value
			Leopards and Humans			
Sabi Sand South	-11	-12	-11	0.440	2.158	0.031
Mala Mala/Londolozi	-2	-7	-5	-0.423	-2.072	0.038
Singita/Western Sector	3	4	4	0.457	2.237	0.025
Sabi Sand North	-11	-12	-11	0.510	2.498	0.012
Skukuza/Lower Sabie	-1	-6	-3	-0.607	-2.975	0.003
Houtboschrand	1	2	1	0.510	2.444	0.015
Pretoriuskop	-8	-11	-10	0.522	2.559	0.011
Nwanetsi	1	-5	-2	-0.557	-2.727	0.006
Karingani North	1	-4	-1	-0.707	-3.464	0.001
Karingani South	-12	-12	-12	0.463	2.269	0.023
			Leopards and Prey			
Sabi Sand South	-1	-5	-3	-0.482	-2.364	0.018
Mala Mala/Londolozi	-1	-6	-5	-0.441	-2.162	0.031
Singita/Western Sector	1	-7	-5	-0.491	-2.405	0.018
Sabi Sand North	1	-6	-2	-0.583	-2.857	0.004
Skukuza/Lower Sabie	-1	-6	-4	-0.589	-2.886	0.004
Houtboschrand	5	8	7	0.390	1.909	0.056
Pretoriuskop	-9	-11	-10	0.578	2.832	0.005
Nwanetsi	-1	-5	-2	-0.541	-2.648	0.008
Karingani North	0	-6	-3	-0.568	-2.781	0.005
Karingani South	2	-5	-1	-0.381	-1.865	0.062
			Leopards and Competitors			
Sabi Sand South	2	-2	0	0.770	3.773	0.000
Mala Mala/Londolozi	2	-2	0	0.682	3.343	0.001
Singita/Western Sector	2	-1	0	0.695	3.333	0.001
Sabi Sand North	2	-3	1	0.726	3.555	0.000
Skukuza/Lower Sabie	2	-2	0	0.777	3.647	0.000
Houtboschrand	0	-2	-1	0.418	1.963	0.050
Pretoriuskop	3	0	1	0.442	2.165	0.030

Nwanetsi	0	-1	0	0.716	3.123	0.002
Karingani North	2	-3	-1	0.647	3.035	0.002
Karingani South	2	1	1	0.481	2.040	0.041

Similarly, time to event analyses do not provide any conclusive evidence that leopards avoid stations in the hours following a human detection, in a vehicle or on foot. At two of the sites (Sabi Sand North and Skukuza/Lower Sabie) the observed probability of leopard detection does appear to be lower than what would be expected in the six hours following a human detection, but this is not statistically significant in either case (Figure 4.5). At Skukuza/Lower Sabie however, leopards were significantly more likely to be detected in the six hours preceding the detection of a human (Figure 4.5). Potential prey detections appear to have no influence on the probability of leopard capture, however there is some evidence that the detection of a competitor does impact leopard probability of capture, as in three sites (Sabi Sand South, Singita/Western Sector and Skukuza/Lower Sabie) potential competitors were significantly more likely to be detected in the six hours before a leopard was detected, and the 12 hours before a leopard detection for one site (Sabi Sand South, Figures 4.6 and 4.7). Leopard detections however were not lower than expected in the six hours following a competitor detection (Figure 4.7).

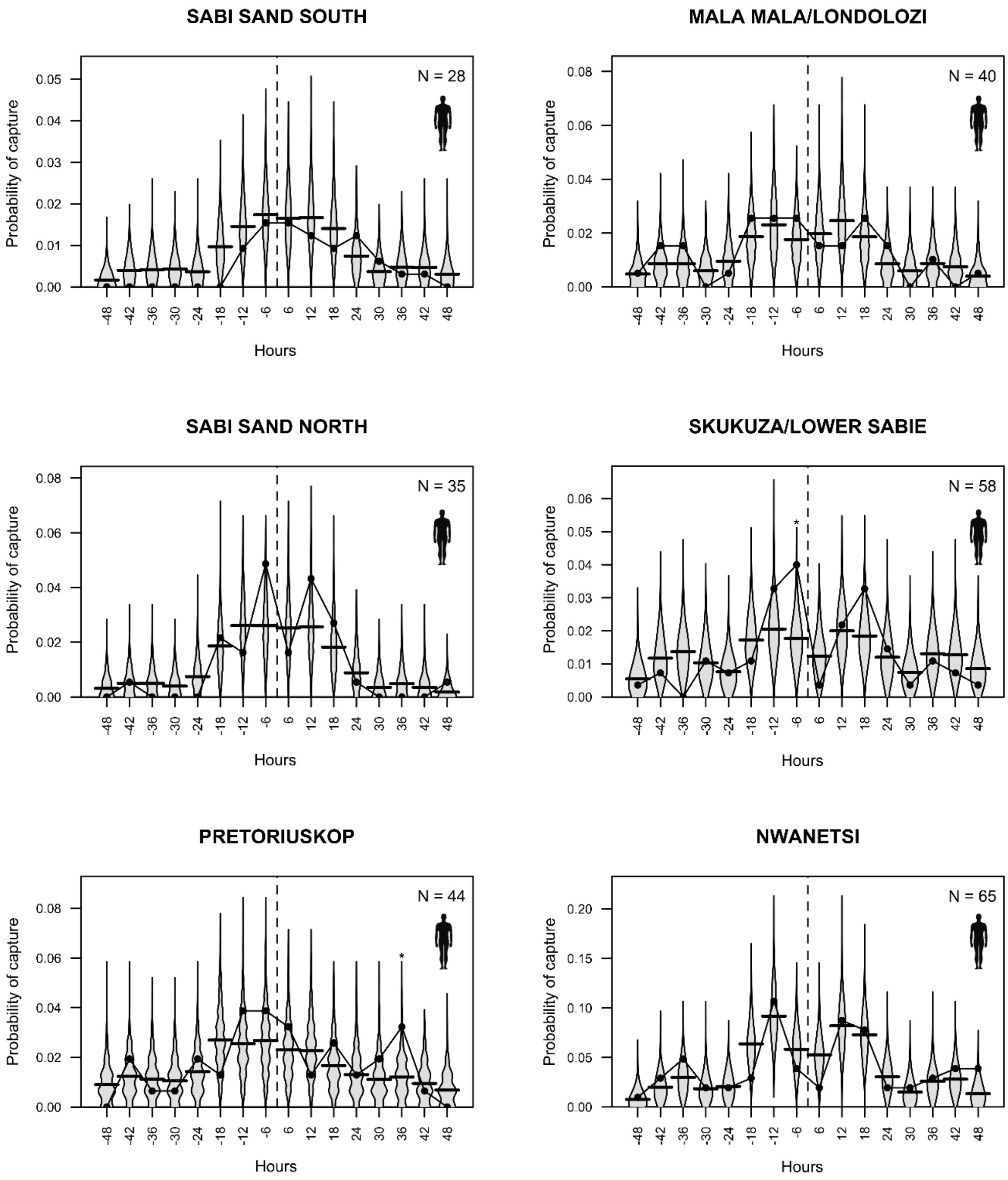

Figure 4.5: Observed probability of capture (black dots) of leopards in six hour intervals for two days before and after the detection of a human in comparison to the expected distribution of leopard sightings at those same intervals (grey bean plots). The expected distribution of leopard sightings in each time bin was derived from 1000 randomly simulated iterations of leopard sightings, which account for the activity pattern of the species. The mean expected probability of capture for each six hour interval is shown on the bean plot with a black line. Asterisks indicate cases where the observed and expected probability of capture are significantly different ($p<0.05$). Four sites have either too few data points or data points that are too sparsely distributed to run time to event analyses (Singita/Western Sector, Houtboschrand, Karingani North, Karingani South).

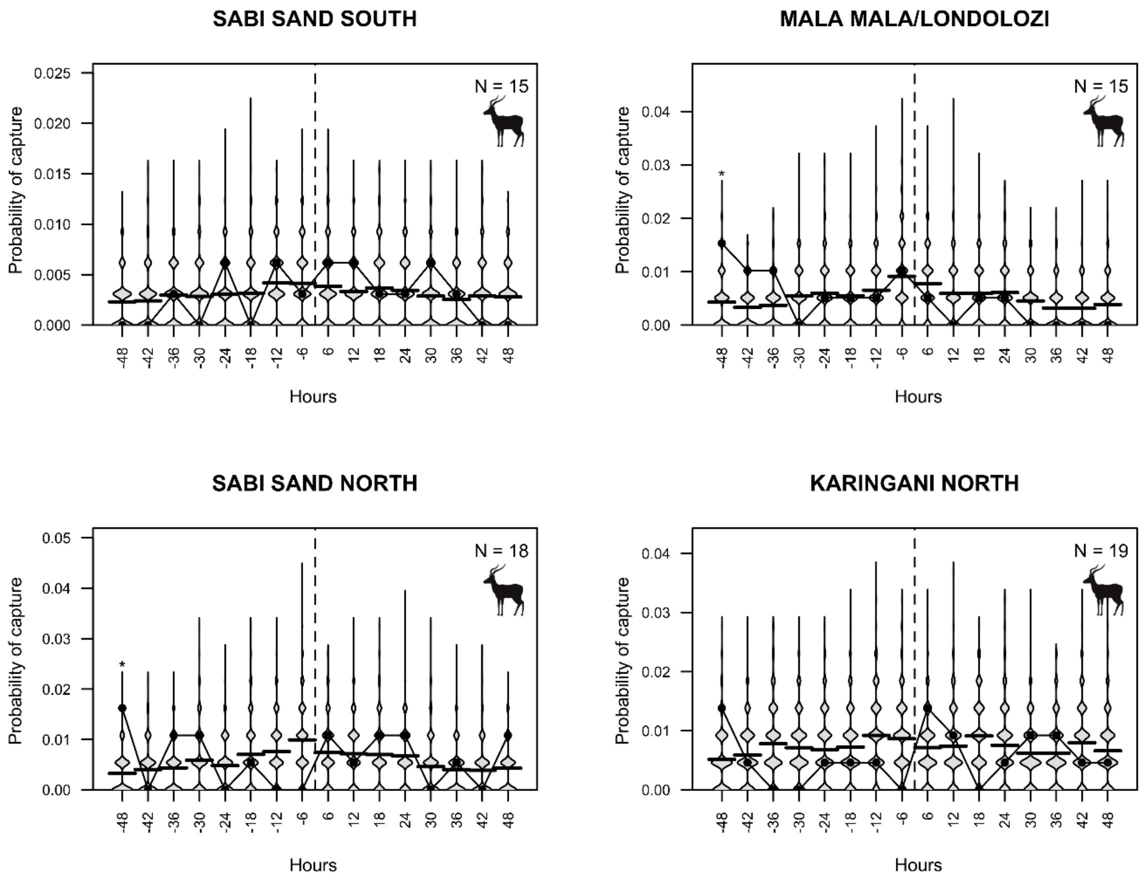

Figure 4.6: Observed probability of capture (black dots) of leopards in six hour intervals for two days before and after the detection of a potential prey species in comparison to the expected distribution of leopard sightings at those same intervals (grey bean plots). The expected distribution of leopard sightings in each time bin was derived from 1000 randomly simulated iterations of leopard sightings, which account for the activity pattern of the species. The mean expected probability of capture for each six hour interval is shown on the bean plot with a black line. Asterisks indicate cases where the observed and expected probability of capture are significantly different ($p<0.05$). Six sites have either too few data points or data points that are too sparsely distributed to run time to event analyses (Singita/Western Sector, Skukuza/Lower Sabie, Houtboschrand, Pretoriuskop, Nwanetsi, Karingani South).

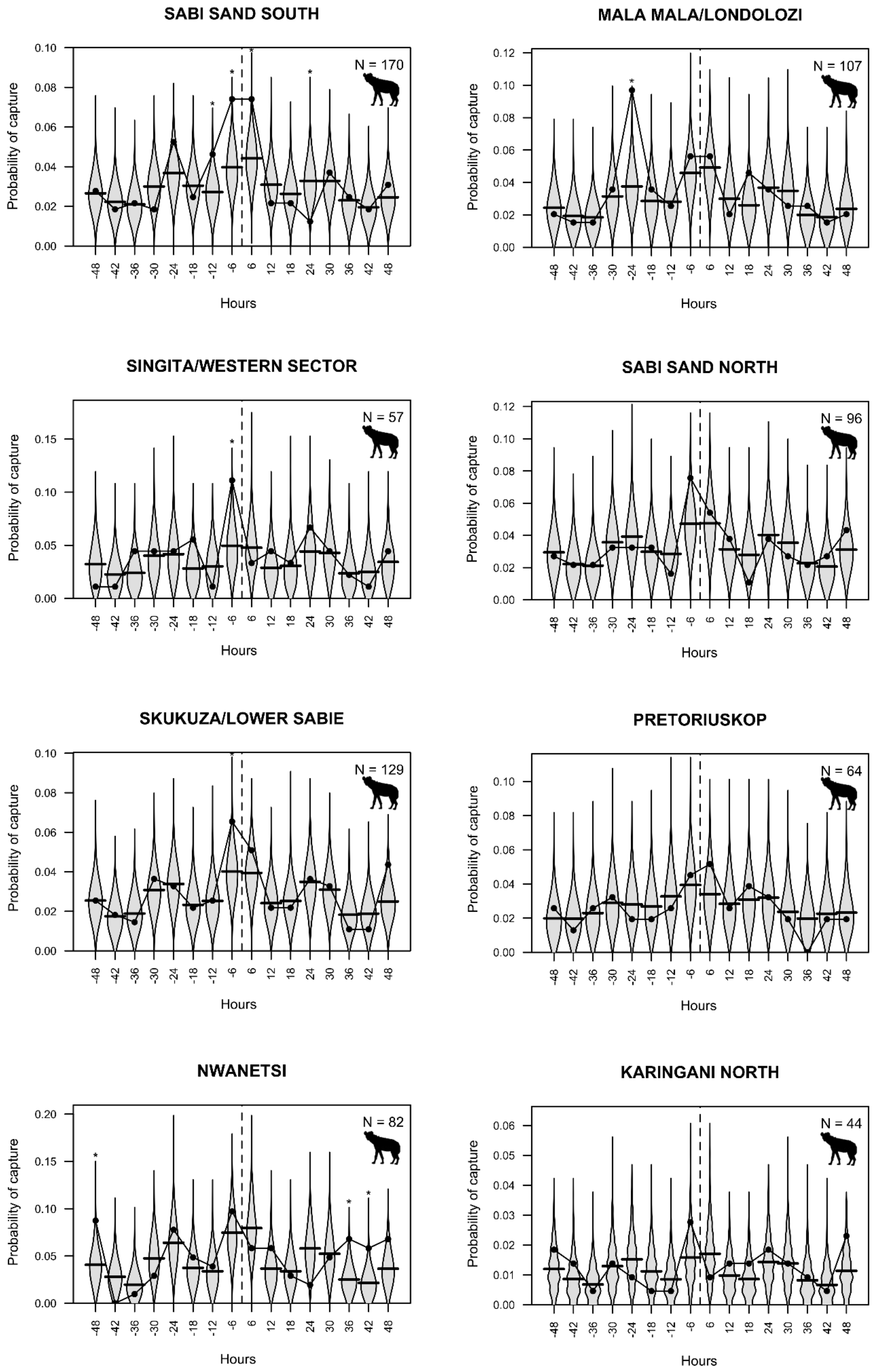

Figure 4.7: Observed probability of capture (black dots) of leopards in six hour intervals for two days before and after the detection of a potential prey species in comparison to the expected distribution of

leopard sightings at those same intervals (grey bean plots). The expected distribution of leopard sightings in each time bin was derived from 1000 randomly simulated iterations of leopard sightings, which account for the activity pattern of the species. The mean expected probability of capture for each six hour interval is shown on the bean plot with a black line. Asterisks indicate cases where the observed and expected probability of capture are significantly different ($p<0.05$). Two sites have either too few data points or data points that are too sparsely distributed to run time to event analyses (Houtboschrand and Karingani South).

Moonlight had a significant effect on leopard activity levels. Increased moon illumination positively correlated with higher leopard RAI scores per night (Estimate = 0.012, Standard Error = 0.005, t-value = 2.371, $P < 0.05$) (Figure 4.8). There was however no interaction between fraction of the moon illuminated and reserve (SSGR, KNP or KGR), or between fraction of the moon illuminated and site (Table 4.6). Leopard kill success also appears to be affected by moonlight, with fraction of the moon illuminated having negative effect on whether leopard observations involved a kill (Estimate = -0.105, Standard Error = 0.037, z-value = -2.823, $p<0.005$).

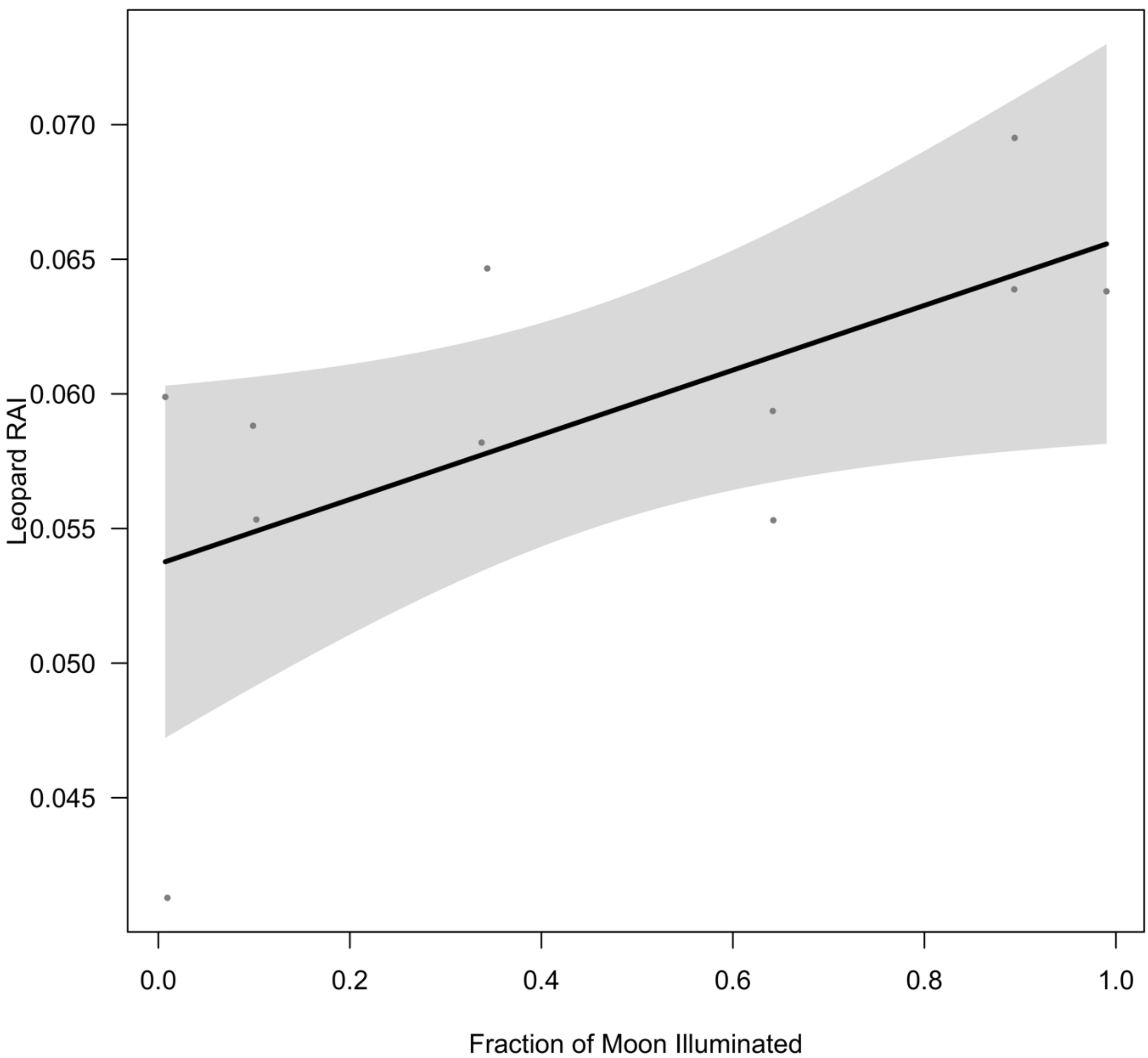

Figure 4.8: Relationship between moon illumination and leopard RAI (Estimate = 0.012, Standard Error = 0.005, t-value = 2.371, $P < 0.05$).

Table 4.5: Model outputs from regression models looking at the relationship between the fraction of the moon illuminated and leopard RAI per night. Leopard RAI was calculated per night for all stations from all sites combined. Models 2 and 3 investigate whether there is an interaction between the fraction of the moon illuminated and the reserve (SSGR, KNP or KGR, with KGR as the baseline), or the site (with Houtboschrand as the baseline).

Coefficient	Estimate	Standard Error	t	p-value	Significance
Model 1: RAI ~ Illumination					
(Intercept)	0.054	0.003	18.386	0	***
Illumination	0.012	0.005	2.371	0.042	*
Model 2: RAI ~ Illumination * Reserve					
(Intercept)	0.04	0.006	7.219	0	***
Illumination	0.029	0.01	3	0.006	**
ReserveKNP	0.003	0.008	0.397	0.694	
ReserveSSGR	0.031	0.008	3.897	0.001	***
Illumination:ReserveKNP	-0.02	0.014	-1.461	0.156	
Illumination:ReserveSSGR	-0.022	0.014	-1.631	0.115	
Model 3: RAI ~ Illumination * Site					
(Intercept)	0.008	0.009	0.833	0.407	
Illumination	0.010	0.016	0.631	0.529	
SiteKaringani_North	0.057	0.013	4.285	0	***
SiteKaringani_South	0.013	0.013	0.998	0.321	
SiteMala_Mala/Londolozi	0.063	0.013	4.761	0	***
SiteNwanetsi	0.033	0.013	2.495	0.014	*
SitePretoriuskop	0.047	0.013	3.536	0.001	***
SiteSabi_Sand_South	0.098	0.013	7.323	0	***
SiteSabi_Sand_North	0.069	0.013	5.191	0	***
SiteSingita/Western_Sector	0.016	0.013	1.217	0.227	
SiteSkukuza/Lower_Sabie	0.059	0.013	4.4	0	***
Illumination:SiteKaringani_North	0.028	0.023	1.231	0.221	
Illumination:SiteKaringani_South	-0.001	0.023	-0.035	0.972	
Illumination:SiteMala_Mala/Londolozi	-0.008	0.023	-0.362	0.718	
Illumination:SiteNwanetsi	-0.002	0.023	-0.103	0.918	
Illumination:SitePretoriuskop	0.005	0.023	0.232	0.817	
Illumination:SiteSabi_Sand_South	0.000	0.023	-0.015	0.988	
Illumination:SiteSabi_Sand_North	-0.009	0.023	-0.371	0.711	

Illumination:SiteSingita/Western_Sector	0.008	0.023	0.352	0.725
Illumination:SiteSkukuza/Lower_Sabie	-0.018	0.023	-0.764	0.447

4.5 Discussion

The predominantly nocturnal behaviour of leopards in all sites surveyed throughout this project is to be expected given that leopard hunting success is generally higher at night than during the day (Martins and Harris, 2013). Leopards are camouflaged ambush hunters, relying on stealth and crypsis for hunting success (Stander et al., 1997; Hayward et al., 2006). Most small and medium ungulate species (a major source of leopard prey) rely predominantly on vision for predator detection, and their vision is substantially less effective at night, meaning that they show diurnal activity patterns (Prugh and Golden, 2013). Leopards however have excellent night vision, allowing them to see prey at low levels of illumination, leading to more successful hunts at night (Balme et al., 2007; Martins and Harris, 2013). The evolutionary development of a range of activity patterns, including both nocturnal and diurnal circadian rhythms has allowed for increased temporal partitioning, helping species to better coexist within landscapes and creating a complex matrix of predator prey relationships, where both are able to persist with neither outcompeting the other (Kronfeld-Schor and Dayan, 2003; Hayward and Slotow, 2009; Prugh and Golden, 2013). Crepuscular peaks in leopard activity may be linked to increased prey encounters at these times, with prey more active around sunrise and sunset (Prugh and Golden, 2013). While camera trap data provides little indication of the behaviour associated with each capture, consistent levels of overall activity between sites indicate that leopards in these areas are likely exposed to similar levels of stress, at least as far as activities requiring movement through space are concerned.

Unlike leopards humans are predominantly diurnal across the world, and this is reflected in a shift towards greater nocturnality in many wild animal species living in human dominated environments (Ohashi et al., 2013; Clinchy et al., 2016; Ordiz et al., 2017; Smith et al., 2017; Gaynor et al., 2018; Havmøller et al., 2020). While the temporal partitioning between humans and leopards observed in this study is simply correlative, and corresponds to the biology of both species, a global meta-analysis has shown increased nocturnality across a wide range of species existing in human-dominated landscapes, regardless of the inherent activity patterns of the animal species in question (diurnal or nocturnal), and regardless of the type of human activity conducted (consumptive, non-consumptive or simply the presence of infrastructure) (Gaynor et al., 2018). The degree to which human activity is restricted to daylight hours is inflated in this study because KNP prohibits tourist activity before dawn and after dusk. The SSGR does not have such strict gate time regulations, but generally game drives start 30 minutes before sunrise and finish 30 minutes after sunset. There are no rules regarding timing of human activity in KGR, but a lack of tourists reduces the chances of human nighttime activity. Human activity at night in all reserves is therefore uncommon.

While overall leopard activity levels were not different between sites, there were differences in activity patterns over a 24 hour period, which are likely driven by a multitude of factors. If human RAI is used as a proxy for level of human disturbance, then the data collected from these camera trap surveys indicate that the four sites within the SSGR had the highest levels of human disturbance. If human presence increases degree of nocturnality, as it has been found to do previously, then leopards in the SSGR should be most nocturnal. This however was not the case, as the highest degree of nocturnality was seen at Nwanetsi in KNP, where human RAI was relatively low. Consequently, this site, despite having one on the lowest human RAIs, also showed the least overlap between human and leopard activity. The sites with the highest proportion of diurnal leopard activity (Pretoriuskop) and the most overlap between human and leopard activity (Houtboschrand) were also located within KNP.

Given that most human activity in these reserves in non-consumptive and therefore not directly harmful to the leopards themselves leopards do become accustomed to the presence of humans in vehicles. This has been recorded most notably in the SSGR, where leopards appear unbothered by the presence of vehicles, allowing particularly good game viewing opportunities for passengers (Balme et al., 2013), although leopards in KNP are also accustomed to the presence of game-viewing vehicles, albeit to a lesser extent than in the SSGR given lower road densities. Conversely, KGR has had virtually no game-viewing activity given its recent establishment, and leopards in the area remain unaccustomed to the presence of non-consumptive human activity. The trend of overall activity within these reserves is opposite to levels of human habituation, with the SSGR having the highest human presence and the most habituated, though still wild, leopards, and the opposite situation in KGR. It is therefore possible that this negates the shift towards greater nocturnality generally observed for wildlife in human dominated landscapes, and that high levels of non-consumptive human activity in the SSGR have allowed leopards to remain active during the daytime after becoming habituated to the presence of humans. Had I placed camera traps in the land surrounding these reserves, where leopards are more commonly persecuted by humans, the effect of humans on leopard activity may have been more prominent.

In the absence of human disturbances, animal activity is most commonly influenced by the need to find food while simultaneously avoiding predators and competitors, all within the constraints of environmental variables such as temperature (Hayward and Slotow, 2009; de Matos Dias et al., 2018; Caravaggi et al., 2018; Havmøller et al., 2020). Mean minimum and maximum temperatures across the study sites vary substantially between seasons, with minimum daily temperatures ranging from 9.5°C in winter to 20.4°C in summer, and maximum daily temperatures ranging from 26.1°C in winter to 32.2°C in summer. The more extreme winter and summer temperatures would be closer to the limits of the thermal tolerance of leopards in the area, which may explain why leopards showed the most diurnal activity at a site sampled during the winter months (Pretoriuskop) and restricted daytime activity at sites sampled during the hotter months. The influence of temperature is further reflected in the variable 'season' being present in the second-best model for predicting the timing of leopard activity. The apparent influence of temperature on leopard activity patterns raises questions about potential climate change driven modifications to activity patterns as well. The decreased diurnal activity exhibited by leopards during hotter months may become even more pronounced as global temperatures rise. In places where human activity also pushes animals towards increased nocturnality, as appears to be the global norm (Gaynor et al., 2018), these influences will likely have additive effects.

Interestingly, neither potential prey nor potential competitor RAIs appear to impact relative timing of leopard activity. Leopards are known to feed primarily on small to medium sized ungulates, most of which are diurnal given their reliance on vision for vigilance (Hayward et al., 2006; Pitman et al., 2012; Pitman et al., 2014; Schwarz and Fischer, 2017). Despite being less active at night these prey species are nevertheless still vulnerable to leopards who benefit from improved crypsis in low light conditions (Martins and Harris, 2013). Temporal partitioning between competitive predatory species has been widely observed, with subordinate predators such as cheetahs and wild dogs generally showing a shift towards more diurnal behaviour to avoid overlapping with more dominant nocturnal predators such as lions and spotted hyaenas (Cozzi et al., 2012; Ramesh et al., 2017a; Pretorius et al., 2021). Leopards generally fall somewhere in the middle of this spectrum, being dominant over wild dogs and cheetahs but subordinate to spotted hyaenas who kleptoparasitise kills and lions who account for a significant proportion of leopard mortality in some areas (Cozzi et al., 2012; Balme et al., 2017a; Balme et al., 2017b; Ramesh et al., 2017a), although anecdotal reports of wild dogs chasing leopards up trees do exist, leaving some uncertainty regarding dominance between these two species. In general leopards are assumed to shift towards more nocturnal behaviour in response to human disturbance, and more diurnal behaviour in response to competition with other predators (Grimbeek, 1992; Azlan and Sharma, 2006; Martins and Harris, 2013). A lack of effect of competitor abundance on broad scale leopard activity, as was the case at these sites, however, has been observed before. Lion distribution does not affect the spatial distribution of leopard activity, as the spatial avoidance of lions by leopards appears to happen at a much smaller scale, with leopards retreating to elevated, less accessible locations such as tree branches to avoid conflict with lions when in close proximity (<50m) (Balme et al., 2017b). It has also been observed that leopards avoid hyena kleptoparasitism by caching prey in trees which are inaccessible to hyaenas (Balme et al., 2017a). It is therefore likely that their arboreal habits allow leopards to avoid both spatial and temporal niche partitioning with competitors. However, time to event analyses did show some evidence of potential competitors following leopards, as a leopard was more likely to be detected at a station in the six hours before a competitor's detection. This has been observed before, and may be attributed to hyenas trailing leopards in an effort to kleptoparasitise their kills (Balme et al., 2019).

The lack of importance of vehicle and pedestrian RAI or pedestrian only RAI as a predictor of leopard activity was unexpected given the ubiquity of human disturbance as a driver of altered wildlife activity patterning globally (Gaynor et al., 2018). The definition of human disturbance in studies looking at impacts of anthropogenic activity however is not straightforward. While human RAI estimated from camera traps has been widely used as an index of human disturbance, it does not differentiate between types of human activity, which can impact the degree to which human activity affects animal populations (Ohashi et al., 2013; Carter et al., 2015; Oberosler et al., 2017). Human RAI is not a suitable metric for consumptive human activities in this study. Given that hunting is illegal in these reserves, any form of illegal offtake occurs by poachers who avoid travelling on roads, drainage lines and game trails to minimise their chances of being caught by rangers. Poachers therefore remain largely undetected by these survey methods and cannot be reliably quantified in this dataset. Anecdotal knowledge of the study area points towards KGR as having the most potential for illegal offtake given its proximity to impoverished communities, and its status as a recently developed protected area with fences that were still incomplete at the time of camera trapping. The SSGR on the other hand, despite having high levels of human activity, has a substantial security budget that allows for well maintained and monitored fence lines and a high density of anti-poaching units, making illegal human offtake highly unlikely (Balme et al., 2019). KNP lies somewhere in between these two reserves with regards to the potential for consumptive human activities. Trends in total human activity and consumptive human activity between reserves are therefore substantially different and could be masking the effects of one another. Additionally, human activity is intricately linked to a number of other forms of disturbance, such as sensory pollution in the form of light and noise (Halfwerk and Slabbekoorn, 2015). The individual effects of each of these can be difficult to disentangle.

The timing of leopard activity, while variable on a daily scale, is also variable on a lunar scale, seen through the positive correlation between increased lunar illumination and leopard activity. The increased likelihood of observing leopards on a kill at times of lower lunar illumination provides a potential explanation for this trend. Increased leopard activity during periods of brighter moonlight could indicate that it takes more activity, and consequently energy, for leopards to meet their feeding requirements because hunting success is lower at higher light levels. This theory is supported by evidence of leopards making more kills during times of lower lunar illumination in the Cedarberg mountains of the Western Cape of South Africa, and by data indicating that prey vulnerability increases with darkness (Prugh and Golden, 2013; Martins and Harris, 2013). However, camera trap data does not allow one to differentiate between different types of activity, and if would be useful to further investigate this relationship using collar data, and determine whether increased activity levels at times of greater lunar illumination are indeed reflective of more time spent hunting. If moonlight affects leopard activity and kill success over a 28 day period, as these results show, and artificial light at night is increasing globally by 6% annually, then it is unlikely that this rise in artificial light at night has not already impacted leopard activity levels to some extent (Hölker et al., 2010a).

Overall, in the greater Kruger ecosystem, it appears that temperature is the most important variable influencing leopard activity patterns with reduced nighttime activity at lower temperatures, and increased nighttime activity at higher temperatures. While overall leopard activity levels did not differ between sites within KNP, SSGR and KGR, activity patterns did. These differences were not however significantly influenced by human, potential prey or potential competitor activity despite the marked differences in these variables between the sites. Given the overwhelming global evidence that human disturbance influences animal activity, it is possible that the sites within this study lacked sufficient variation in this variable to detect its influence on the temporal characteristics of leopard activity patterns, or that the habituation of leopards to game-viewing activities negated this trend. This study may thus serve as an important baseline for leopard activity in the absence of significant anthropogenic impacts. Expanding camera trap surveys into mixed land uses outside of protected areas may offer more insights into the relative importance of environmental variables such as moonlight and temperature, that were important in this study, relative to anthropogenic factors that are greater outside of protected areas.

CHAPTER 5

HOW THE LEOPARD GOT ITS SPOTS: QUANTIFYING THE HERITABILITY OF LEOPARD ROSETTE PATTERNS

Figure 5.1: A camera trap photograph of two leopard cubs playing with each other.

5.1 Abstract

Leopards (*Panthera pardus*) are widely distributed throughout Africa, Asia and the middle east, however populations are declining across much of their range. Declining populations with reduced connectivity have a higher probability of reduced genetic diversity which may ultimately reduce resilience to novel threats including anthropogenic changes. Monitoring genetic diversity is thus clearly an important component of leopard conservation, but it is both expensive and time consuming when done using traditional methods. More recently genetic similarity has been shown to correlate with phenotypic resemblance raising the question as to whether photographs of individuals can be used to infer relatedness. When it comes to pelage patterning however, it is still unclear whether more closely related individuals have more similar markings. In this study I make use of a long-term leopard monitoring program in the Sabi Sand, Mala Mala and Sabie Game Reserves (SSGR) that has collected photographs and life history records of individual leopards over the last 20 years, resulting in a population of individuals with known identities and maternal relationships. I use these photographic data to generate phenotypic similarity scores, using ImageJ and Hotspotter software recognition programs, between all combinations of leopard individuals based on 10 flank rosette measurements (ImageJ) and one overall similarity metric (Hotspotter) for each of the 120 leopard individuals. I also manually scored the number and positioning of leopard whisker spots and assessed the reliability of all metrics using a repeatability analysis. I then ran parent-offspring regressions using observed mother-offspring dyads from the population for each of the 15 phenotypic traits quantified to calculate heritability scores. Of the 15 measured traits six show significant parent-offspring regressions. However, ANOVAs and post-hoc Tukey tests indicate that the relationship between phenotype and relatedness is not present across individuals with varying levels of relatedness. There is also no difference in the similarity scores of parent-offspring and sibling dyads. Therefore, while select pelage patterning traits appear to be heritable, this relationship is not strong enough to allow for phenotypic similarities in pelage patterning obtained from photographs to inform our knowledge on genetic relatedness and ultimately genetic diversity within populations.

5.2 Introduction

Genetic diversity is crucial to the survival and persistence of a species (Frankham, 2005). Numerous species have suffered from physiological, developmental and reproductive abnormalities caused by low levels of genetic diversity, and some have even been brought to extinction (Bonnell and Selander, 1974; Packer et al., 1991; Roelke et al., 1993; Johnson and Dunn, 2006). Given that genetic diversity is a result of thousands of years of natural selection, reductions in genetic diversity, whether through drift or bottlenecking events, cannot be reversed. Genetic diversity is often measured through the heterozygosity present within a population, otherwise known as the proportion of individuals with multiple different alleles coding for the same gene. Higher rates of genetic diversity result in higher rates of heterozygosity, thereby reducing the chances of individuals inheriting two deleterious alleles for the same gene, which can have detrimental and even fatal consequences (Hansson and Westerberg, 2002). Populations with higher genetic diversity are more likely to successfully adapt to a changing environment over time and are less likely to show the consequences of deleterious alleles.

A reduction in the number of individuals present also results in reduced genetic diversity (Lande, 1988). Inbreeding occurs when population size is reduced dramatically, causing related individuals to breed with each other (Packer et al., 1991; Fitzpatrick and Evans, 2009). While dominant deleterious alleles are weeded out of a population relatively effectively through natural selection, recessive deleterious alleles are better able to persist in the gene pools of populations as they are only expressed in homozygous individuals (Allendorf and Leary, 1986). In the context of inbreeding however, recessive deleterious alleles are more likely to be expressed (Westaway et al., 1994). This results in reduced viability, fertility, function and survival, and is known as an inbreeding depression (Frankham, 2005; Ross-Gillespie et al., 2007). For example, the endangered Florida panther population suffered from range and demographic contractions, which resulted in severely reduced levels of genetic diversity, which in turn caused in a number of fitness costs, including cardiac problems and abnormalities in sperm production and quality as well as a visibly kinked tail (Roelke et al., 1993). Population density is often able to increase relatively quickly after the cause of population decline is removed, however genetic diversity does not recover at the same rate (Packer et al., 1991).

Given that inbreeding is detrimental to the persistence of a species, most species have evolved ways of avoiding it: in leopards this is seen in the dispersal behaviour of young males who establish territories far away from those of their mothers and female siblings (Fattebert et al., 2013). However, human modifications to landscapes can have severe consequences on inbreeding avoidance strategies by limiting the size of populations and the movement of individuals (Fattebert et al., 2015; Naude et al., 2020a). Habitat fragmentation, barriers to dispersal and declines in population density are particularly problematic (Naude et al., 2020a). Under these conditions the monitoring of genetic diversity becomes particularly important.

Despite their agility and elusive nature, leopard populations across South Africa have shown a marked decrease in density in recent years (Stein et al., 2016; Rogan, 2021). While these declines are of concern, recent research on the genetic structure of southern African leopard populations through the amplification of two mitochondrial genes (NADH and Cyt-B) has shown that there do not appear to be any significant genetic discontinuities in the southern African leopard population (Ropiquet et al., 2015). Currently, inbreeding is not known to be a major concern to leopard populations. While it has been documented in a protected area with a history of high levels of human offtake (Naude et al., 2020a), the most recent wide ranging study on leopard genetics found relatively high levels of heterozygosity, and consequently low levels of inbreeding, across South African leopard populations

(Ropiquet et al., 2015). However, leopards have been listed as Vulnerable by the IUCN Red List due to a combination of population decline and range loss (Stein et al., 2016). Both of these factors are key drivers behind reductions in genetic diversity (Frankham, 2005; Pitman et al., 2017), as are the effects on dispersal caused by high levels of human offtake (Naude et al., 2020a). Therefore, despite not currently being an immediate threat to leopard populations, genetic diversity and inbreeding in leopards are nonetheless metrics worthy of immediate attention as populations not only continue to decline but become increasingly isolated by the transformation of natural land outside of protected areas.

Devising cost effective, non-invasive methods for such monitoring is thus an important priority for the successful management of leopard populations in South Africa and globally. While genetic diversity is crucial to population health and persistence (Lande, 1988; Frankham, 2005), it can also be a relatively invasive, expensive and time-consuming metric to investigate as it requires animal genetic material, obtained from blood, tissue, hair or scat samples and a series of laboratory procedures involving Deocyribonucleic Acid (DNA) extraction, polymerase chain reactions (PCR) and gene sequencing, all of which are costly and require highly specialised equipment. Cameras used to acquire photographic data are expensive upfront, however have a relatively long lifespan meaning that the same equipment can be used to repeatedly collect data over time with few additional costs, due mainly to batteries. A study comparing costs between camera trap spatial count models and genetic spatial capture recapture models found that the initial genetic survey cost two thirds as much as the camera trap survey, however by the third survey the cumulative cost became lower for camera traps than genetic methods (Burgar et al., 2018). While the non-invasive collection of genetic material has become more common in recent years with improvements in our ability to extract DNA from hair and scat samples (Pilgrim et al., 2005; Sun et al., 2017; Naude et al., 2020a), utilizing data from pre-existing data sets, such as camera-trap images, would further reduce the costs and effort required to monitor genetic health. Given their individual-specific markings (Miththapala et al., 1989), leopards are an ideal candidate species for investigating whether phenotypic similarity, which is readily surveyed from photographic data, can be used a proxy for genetic similarity.

Over a wide range of species, and particularly in humans, symmetry has been found to be an evolutionary favourable characteristic, that often results in greater mating success and consequently increased overall fitness (Grammer and Thornhill, 1994; Møller et al., 1996; Møller and Thornhill, 1998). Deviations from bilateral symmetry, termed fluctuating asymmetries, are understood to provide an indication of environmental stresses, developmental instability, or genetic problems during development, signaling lower fitness (Leary and Allendorf, 1989; Parsons, 1990). Fluctuating asymmetries therefore represent either poor genes or a poor environment, such that despite the presence of potentially good genes environmental stresses disrupt symmetrical growth, warning potential mates of lower fitness levels and consequently decreased mating success. These fluctuating asymmetries can be present in many phenotypic characteristics, including pelage patterns.

The phenotype of an individual is influenced by two factors: the genetic composition of the individual as well as environmental conditions (Cheverud, 1988; Wong et al., 2005). A suite of complex interactions between these factors causes all individuals to appear unique. While genetic sequences code for certain aspects of an individual's phenotype, the expression of these genetic sequences is equally important in the resulting phenotypes, and gene expression is controlled by both pre and post-birth environmental conditions (Wong et al., 2005). These are known as epigenetic effects. The relative importance of genetic and environmental factors varies for all phenotypic characteristics, and those with a stronger reliance on genes versus the environment are considered more heritable traits (Cheverud, 1988).

Despite the effects of environmentally induced variability, the heritability of many phenotypic characteristics causes more closely related individuals to appear more similar (Cheverud, 1988). It is therefore unsurprising that in a broad study of a range of species, a correlation was found between the phenotypic similarity of individuals and their percentage of shared genetic information (Cheverud, 1988). Within species, more closely related individuals have been found to show stronger levels of phenotypic resemblance (Alvergne et al., 2007; Lee et al., 2018). Similarities in facial features perceived by the human eye are able to provide an indication of relatedness in chimpanzees, gorillas and mandrills (Alvergne et al., 2009). Species themselves are also thought to rely on the influence of genetics on phenotypic traits in helping to inform behaviour between individuals: female Java monkeys, vervet monkeys, macaques, chimpanzees and baboons are all able to categorise other individuals on the basis of their matriline and adjust their interactions accordingly (Cheney and Seyfarth, 1982; Dasser, 1988; Rendall et al., 1996; Bergman et al., 2003; Vokey et al., 2004). Whether this is a direct reflection of levels of relatedness or through familiarity alone however has not been confirmed.

Similarities in the phenotypes and genotypes of individuals have also been observed with regards to coat pattern markings in both cheetahs and giraffes, where pairs of related individuals have been found to show a greater degree of similarity than pairs of unrelated individuals (Balme and Hunter, 2013b; Lee et al., 2018). The formation of coat patterns in mammals has a complex genetic basis. The coat patterns of domestic cats are known to be controlled by at least three loci which interact through epistatic effects to produce the wide variety of coat patterns observed today (Eizirik et al., 2010). More generally speaking, coat patterning in felids appears to arise from two distinct processes (Eizirik et al., 2010). The first of these lays down the spatial pattern for skin cell differentiation, and the second regulates melanin profiles in accordance with the already established pattern (Eizirik et al., 2010). In the case of leopard rosette patterns, a two-step reaction-diffusion process involving an interaction between eumelanin (darker in colour), and phaeomelanin (lighter in colour) is likely involved as well

(Turing, 1952; Silvers, 1979). The two-step nature of this process is supported by the role of both genetic and environmental processes in rosette-pattern formation, although how these two steps fit into the framework of the spatial and colour determination of rosettes remains to be investigated (Liu et al., 2006).

Very little is known about the genetic origin of leopard rosette patterns, their level of heritability, symmetry, and how strongly they are influenced by gene-environment interactions. It is possible that a relationship between genetic similarity and pelage pattern may be able to provide an indication of the level of genetic relatedness between individual leopards, allowing for inferences on the genetic health of a population or the broad geographic origin of an individual to be made. In light of the evolutionary advantages of symmetry and the established relationship between genotype and phenotype (Cheverud, 1988; Balme and Hunter, 2013b; Lee et al., 2018) I predict that leopard markings will be symmetrical, and that more closely related leopards will have more similar flank rosette and whisker spot patterns. Given the potential importance of epigenetic effects as well, I also predict that siblings from the same litter will be more phenotypically similar to each other than to their mother, despite both dyads sharing the same degree of relatedness. If pelage patterns are heritable, as predicted, an analysis of the overall degree of similarity between leopard rosette patterns from a population could provide an indication of the genetic diversity present within the population.

5.3 Methods

I have used photographs and life history records of individual free ranging leopards in the SSGR, which includes the Sabi Sand, Mala Mala and Sabie Game Reserves in Mpumalanga, South Africa. The SSGR lies along the south-western boundary of Kruger National Park (KNP) and covers an area of 625km^2 (Figure 5.2). The fence between the SSRG and KNP was removed in in 1993, allowing animals to move freely between the two protected areas. The region consists of a combination of open and semi-wooded savanna and is characterised by hot, rainy summers and cool dry winters (du Toit et al., 2003).

The SSGR is managed as a single conservancy consisting of many privately-owned properties with no internal boundary fences. The reserve is home to multiple ecotourism lodges and is a high-end photo-tourism destination, where qualified guides take guests on two game drives daily. Wildlife within the reserve has become accustomed to the presence of vehicles and consequently it is possible to obtain close-up photographs of leopards (Balme et al., 2013; Balme and Hunter, 2013a; Balme et al., 2017a). Guides have recorded daily game sightings since the 1970s, and this information has been used to document the life histories of more than 400 leopard individuals, including records of mothers with their cubs, which have been used to create a pedigree along matrilines. However, female leopards typically mate with multiple males within a breeding cycle, making paternity assignments unreliable and meaning that cubs from the same litter do not necessarily all share the same father (Balme and Hunter, 2013a; Rouse et al., 2021). I have therefore not used paternity data in analyses, and instead look only at mother-offspring relationships. Guides regularly photograph animals and almost all leopard individuals currently residing within the SSGR are thus known, and are identified by guides based on a combination of their whisker spots and flank rosette patterns (Naude et al., 2020a). I have used these high quality photographs during analyses to determine whether a relationship between relatedness and phenotype exists, which would warrant similar analyses on camera trap images. Coefficients of relatedness between individuals along matrilines were calculated according to the number of generations separating individuals (Koyama, 2016).

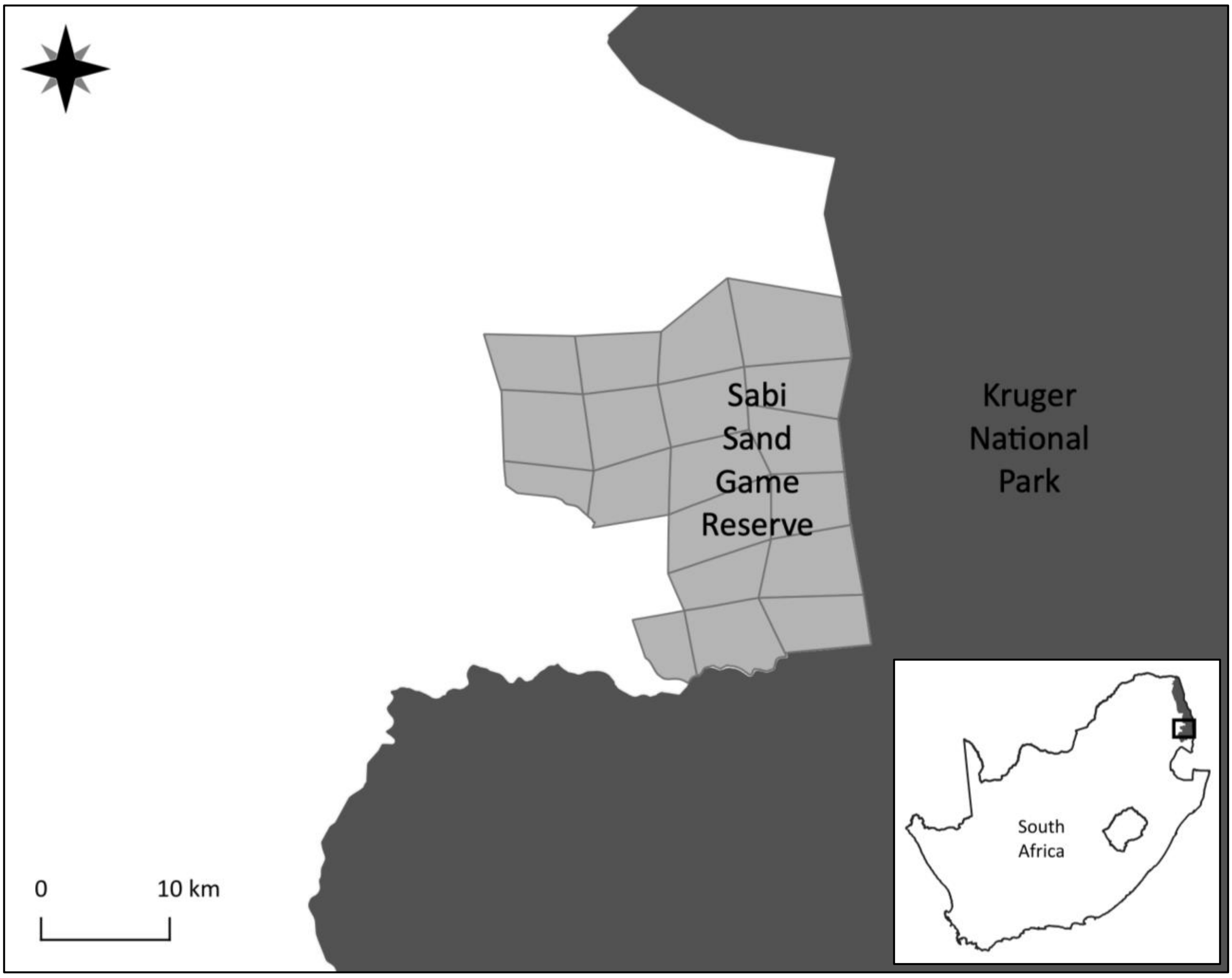

Figure 5.2: Map of the Sabi Sand Game Reserve on the western border of Kruger National Park in South Africa. Grey lines within the Sabi Sand Game Reserve show unfenced internal property boundaries.

Flank rosette patterns of leopard individuals were quantified in two ways: using HotSpotter (Crall et al., 2013b) software to provide a single metric of similarity between all combinations of images, and using ImageJ (Schneider et al., 2012) software to provide 10 measurements of spot characteristics. Leopard whisker spot patterns were also quantified manually. When looking at flank spots I used only images providing a lateral view of the leopard. As a preprocessing step I cropped all images to include only the leopard, and then rotated them so that the leopard's back was horizontal (Figure 5.3).

Figure 5.3: Rotating and cropping an image during the preprocessing step.

Preprocessed images were imported into HotSpotter, and the region of interest was defined as the flank of the individual, extending from the anterior portion of the front leg to the base of the tail and including the entire thorax and abdomen of the animal (Figure 5.4). A similarity analysis was then conducted in Hotspotter, using the precompute queries function to compare all images to each other and create a matrix of resemblance scores between all dyads. HotSpotter extracts a suite of variables for each marking and uses these to define key points. Key points are then matched between all image dyads, with a greater number of matches resulting in a higher resemblance score (Figure 5.5). Resemblance scores are therefore only meaningful when assessed relative to one another, and not in isolation. Data were filtered to only include comparisons between the same side of individuals (either left versus left or right versus right).

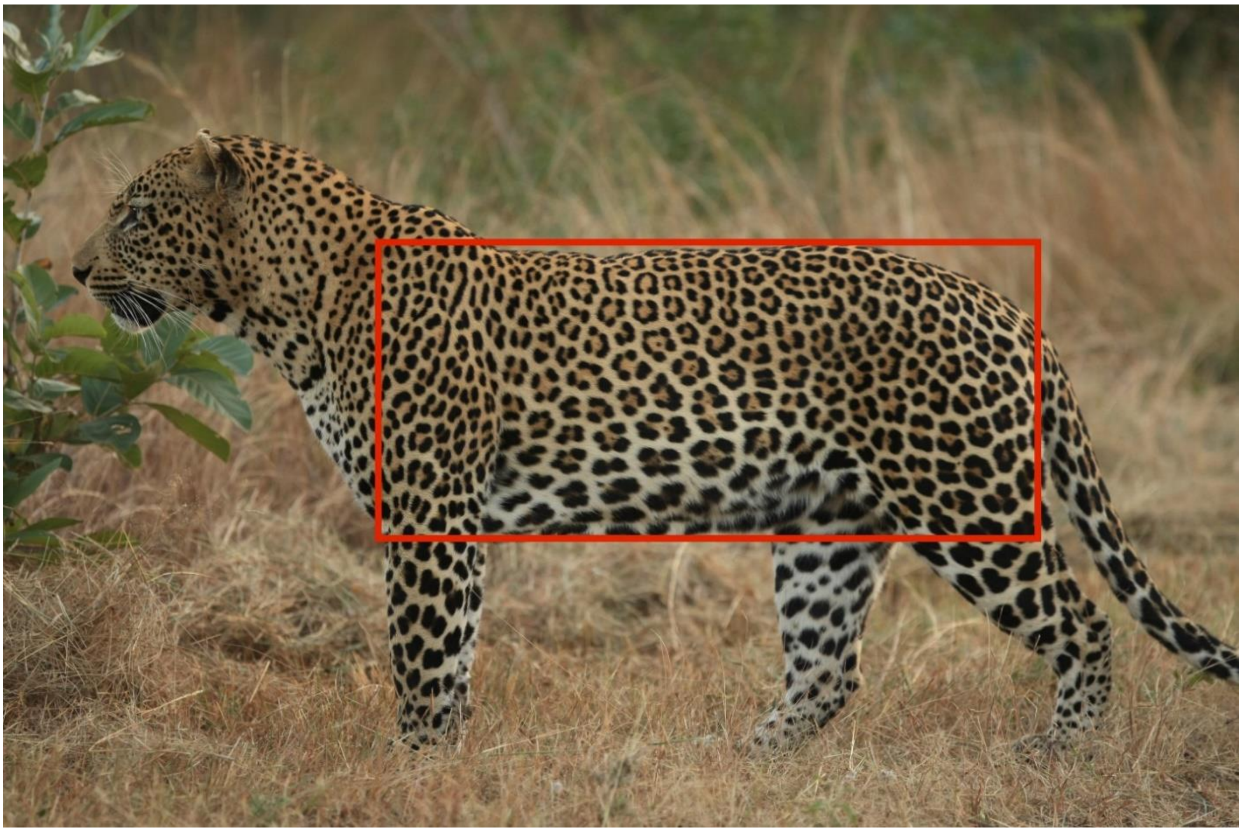

Figure 5.4: Region of Interest (ROI) selection in HotSpotter, shown by the red polygon. The flank is defined as the entire thorax and abdomen of the animal extending from the anterior portion of the front leg to the base of the tail.

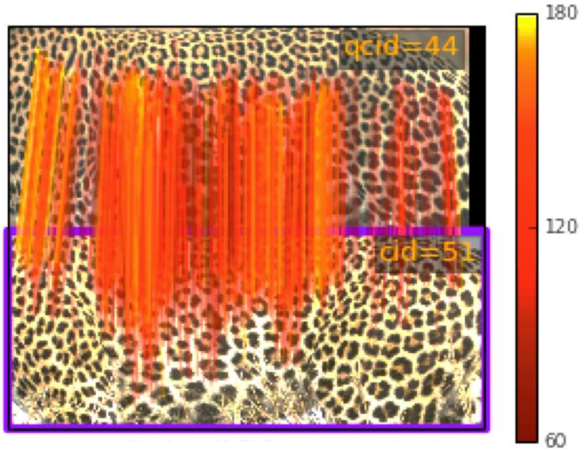

Figure 5.5: Matching of key-points between two images performed by HotSpotter software. Key-points are chosen automatically by the program. Yellow lines represent a higher level of similarity between key-points than red lines. Levels of similarity between key-points are used to generate a total similarity score between images. The two photos shown here are of the same individual hence the high number of matching key-points.

Within ImageJ software, the region of interest was selected as the portion of the leopard's flank running from the back edge of the front shoulder to the front edge of the back leg, and the lowest point along the animal's back to the point at which the stomach meets the hind leg (Figure 5.6). This region of interest is smaller than that used in HotSpotter because when analysing markings individually it is important to remove any background and skin folds, such as those around the shoulders and hips, as these distort marking characteristics. To account for differences in animal size and image resolution, the measurement unit was set to the number of pixels in the height of the region of interest selected on the leopard's flank. All images were therefore measured in leopard units, where one leopard unit is equal to the height of the analysis rectangle. This allowed for markings to be measured relative to the animal's size, and not as absolute measurements. Images were then converted from colour to 8-bit greyscale, and subsequently to bicolour (black and white) images using the default threshold (Figure 5.6) (Lee et al., 2018). In a few instances, where original photographs were under or over exposed, this threshold was changed slightly to ensure that leopard flank rosettes were black, and the surrounding areas of pelage were white. The minimum marking size was set to 0.00001 leopard units to exclude speckles, and the maximum marking size was set to 0.1 leopard units to exclude spots that were merged during marking analysis. All markings cut off by the edge of the rectangle were excluded from analysis. Ten measurements of marking characteristics were then recorded: number of markings, mean marking area, mean marking perimeter, mean angle between the primary axis of an ellipse overlaying the marking and the x-axis of the image (angle), mean marking circularity, mean longest distance between two points along the perimeter of the marking (Feret diameter), mean angle of the Feret diameter (Feret angle), mean aspect ratio of the ellipse fitted to the marking (aspect ratio), mean marking roundness and mean marking solidity.

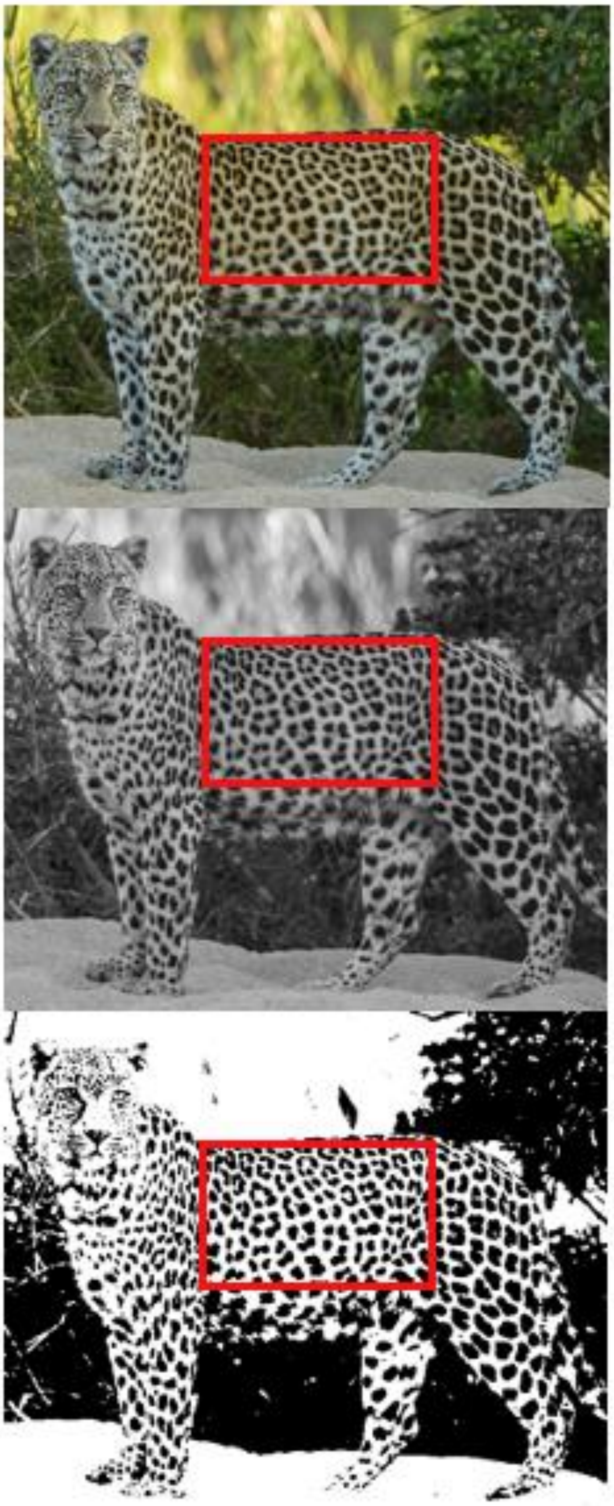

Figure 5.6: Region of interest selection and image manipulation in ImageJ. The region of interest is defined as the portion of the leopard's flank running from the back edge of the front shoulder to the front edge of the back leg, and the lowest point along the back to the point at which the stomach meets the hind leg. Images were converted from colour to 8-bit greyscale and then to bicolour using the default threshold.

Angle and Feret angle were corrected to account for the direction each individual was facing. This is because when looking at a side on view of a leopard flank, the head of the leopard points in opposite directions for left and right flanks. ImageJ however measures angle starting from the same point, and moving in the same direction, for all images. Therefore, if flank rosette markings on both sides are angled in the same direction relative to the head of the individual, the angles of the markings on the right side of the individual, as measured by ImageJ, would be equal to 180 minus the angles of the markings on the left side, as measured by ImageJ. A dissimilarity matrix for each measurement was then created by taking the absolute value of the measurement from one image subtracted from the measurement from the other image for all pairwise combinations of images.

In addition to flank rosettes, leopards have parallel rows of black spots on either side of the muzzle from which whiskers emerge, known as whisker spots. The number and positioning of whisker spots differs between individuals, and between sides of the same individual, making them useful for individual identification. Whisker spots were scored manually with regards to number of spots and spot positioning using an established method (Packer and Pusey, 1993). Spots in the uppermost continuous row of whisker spots, referred to as the reference row, were numbered sequentially starting with the most anterior spot, closest to the leopard's nose. This provided a reference row to which other spots could be compared. All spots located above the reference row were then counted and assigned a position score, based on their position relative to reference row spots (Figure 5.7). If a whisker spot was directly above a spot on the reference row it was given the number of the reference row spot as its position, and if it was located in between two reference row spots it was given the mean on those two numbers as its position. For instance, if a whisker spot was located directly above the second reference row spot its position score would have been 2, and if it was located in between the second and third spots on the reference row it would have been given a position score of 2.5. Each whisker spot was scored using this technique, starting with those in the row directly above the reference row and moving upwards. The total position (referred to as position) was calculated as the sum of the position scores of all whisker spots. The total position score was then divided by the total number of whisker spots to provide an overall whisker spot score (referred to as score):

$$\textit{Whisker Spot Score} = \frac{\sum \textit{position score of each spot above reference row}}{\textit{total number of spots above reference row}}$$

This therefore provided three whisker spot metrics: number, position and score. Left and right sides were analysed separately and then combined to produce an overall value for each individual. A dissimilarity matrix for each metric was created by taking the absolute value of the metric from one image subtracted from the metric from the other image for all pairwise combinations of images.

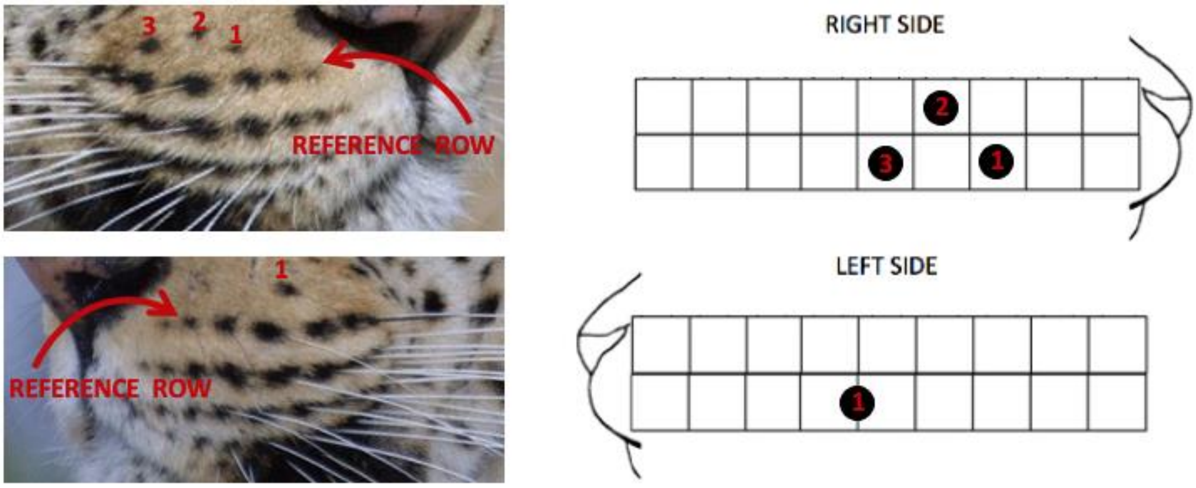

Figure 5.7: The scoring of whisker spots relative to reference row spots.

The number of flank images available for each individual varied between 1 and 24. To account for this I calculated the mean score for each ImageJ measurement for all images of the left and right flank of each individual, therefore producing one result for the left flank and one for the right. When summarising measurements, I averaged measurements between the left and right flanks for individuals where images of both sides were available, and otherwise used only the side that was available (this should not impact results because there is no significant difference in any metrics between the left and right sides of individuals). Where HotSpotter was concerned, I only included comparisons between the same sides of individuals (left versus left or right versus right), and then took the mean score per dyad. I used the same approach of excluding comparisons between left and right sides when calculating dissimilarity scores for ImageJ measurements. In the case of whisker spot scores, I had access to sufficient images to manually score whisker spots for all individuals included in ImageJ and HotSpotter analyses. Given that this was done manually and with sufficient photographic resources to rule out uncertainties, I was able to obtain the number, position and score of whisker spots on both sides of the faces of all individuals, and the values used in analyses are the total of left and right sides combined.

I used paired t-tests to determine whether any metrics differed between the left and right side of individuals. I quantified the phenotypic variation present in flank rosette markings as measured by ImageJ and whisker spot traits by reporting the mean, standard deviation and coefficient of variance of each trait. I also investigated the repeatability of ImageJ measurements using the subset of 81 individuals for which I had access to multiple photos, using a mixed model approach to investigate the within individual correlation among measurements within the package 'rptR' (Stoffel et al., 2017). Only suitably repeatable metrics were used in subsequent analyses. I computed summary dimensions of rosette measurements on the standardised and scaled measurements of the 10 variables using a principal component analysis (PCA).

Trait heritability is defined as the proportion of phenotypic variation which can be attributed to additive genetic effects (Falconer and Mackay, 1996; Lynch and Walsh, 1998; Lee et al., 2018). The heritability of a trait can be tested for using parent-offspring (PO) regression, where a positive relationship between the traits of parents and their offspring is indicative of a heritable trait (Falconer and Mackay, 1996; Lynch and Walsh, 1998). In the case of PO regression, the heritability of a trait is calculated as two times the slope of the linear regression line (Lee et al., 2018). I used PO regression on mother-offspring dyads to assess the heritability of 10 rosette traits measured by ImageJ, the first and second principal components of the combination of these 10 traits and three whisker spot traits.

Additionally, after checking for normality and constant variance, I used ANOVAs and post-hoc Tukey tests to look at differences in phenotypic resemblance per known relatedness class, calculated according to the pedigree. When using relatedness data, dyads with a relatedness score of 0 were excluded from analyses because the lack of paternity data confounds cases where individuals were truly not related and cases where individuals were related through paternal lines. Within the relatedness class of 0.5, which includes parent-offspring and sibling dyads, I looked for differences between the two groups which could be indicative of epigenetic effects brought on by the in-utero environment, again using ANOVAs and post-hoc Tukey tests.

5.4 Results

Flank rosette patterns were quantified for 400 images of 119 leopard individuals (left side of 93 individuals and right side of 99 individuals) and whisker spot patterns were quantified for both sides of 120 individuals (Table A3.1). HotSpotter similarity scores were calculated per dyad and not per individual and were calculated for a total of 10 027 dyads (4649 left and 5378 right), derived from 120 individuals (left side of 94 individuals and right side of 99 individuals). Paired t-tests showed no significant difference between flank rosette marking number, area, perimeter, circularity, Feret, aspect ratio, roundness or solidity, nor whisker spot number, position or score between the left and right sides of individuals (Table 5.1). There was a significant difference between flank rosette marking angle and Feret angle between left and right sides (t-value = 15.76, df = 72, $p < 0.001$ and t-value = 19.27, df = 72, $p < 0.001$ respectively), however this difference disappeared when angles were measured relative to the direction of the leopard's head in the photograph (t-value = 1.24, df = 72, $p = 0.22$ and t-value = 0.96, df = 72, $p = 0.34$ respectively). I have thus used angle and Feret angle measurements relative to the leopard's head in all further analyses.

Table 5.1: Paired t-tests looking at differences between flank rosette marking and whisker spot metrics measured on the left and right sides of leopard individuals. This difference disappeared when angles were measured relative to the direction that the leopard's head was facing (t-value = 1.24, df = 72, p = 0.22 and t-value = 0.96, df = 72, p < 0.34 respectively).

Variable	t	df	p-value
Number	-0.93	72	0.35
Area	1.12	72	0.27
Perimeter	0.88	72	0.38
Angle	**15.76**	**72**	**< 0.001**
Angle relative to head	1.24	72	0.22
Circularity	0.49	72	0.63
Feret	0.94	72	0.35
Feret Angle	**19.27**	**72**	**< 0.001**
Feret Angle relative to head	0.96	72	0.34
Aspect Ratio	0.08	72	0.93
Roundness	0.05	72	0.96
Solidity	-0.09	72	0.93
Whisker Spot Number	-1.18	119	0.24
Whisker Spot Position	-0.06	119	0.95
Whisker Spot Score	1.60	119	0.11

A principal component analysis (PCA) run on the 10 flank rosette marking metrics measured by ImageJ shows that the first principal component consists mainly of traits linked to rosette marking size (number, area, Feret diameter and perimeter), and explained 39.5% of the variance in the data (Figure 5.8). The second principal component, explaining 20.2% of the variance in the data, consists mainly of the aspect ratio, roundness and circularity measurements, therefore describing rosette marking shape. Traits relating to marking solidity, angle and Feret angle contributed the least to the PCA.

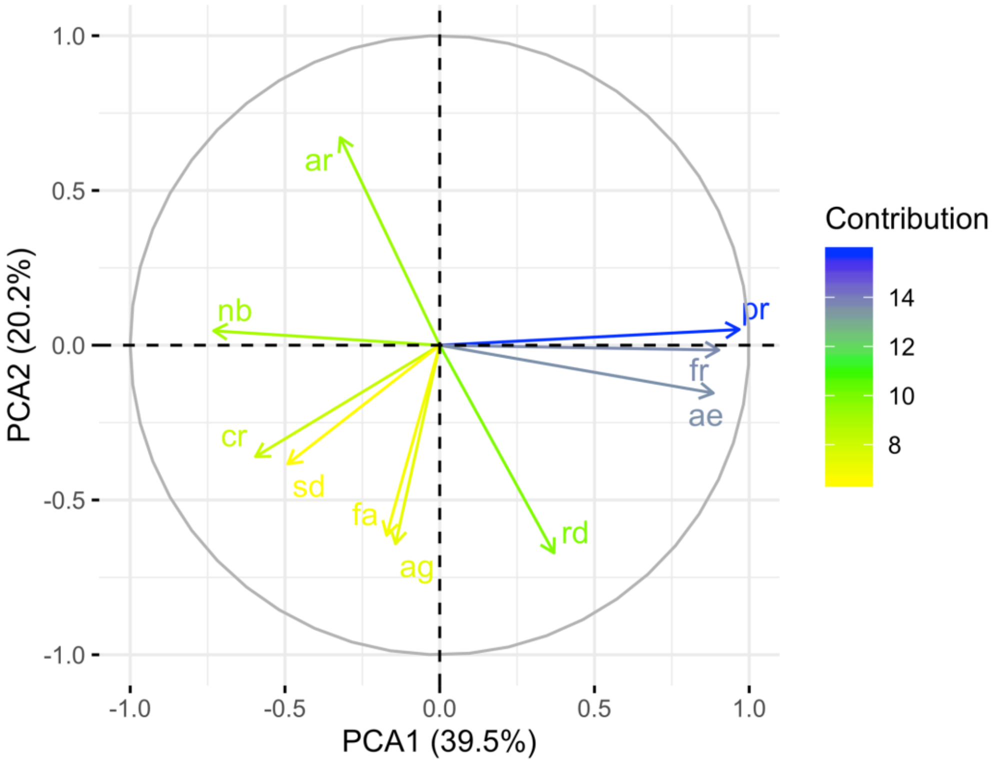

Figure 5.8: Rosette trait measurement contributions to the first and second principal components of a PCA. The 10 rosette trait measurements include number (nb), area (ae), perimeter (pr), angle (ag), circularity (cr), Feret (fr), Feret angle (fa), aspect ratio (ar), roundness (rd) and solidity (sd). The first principal component consisted mainly of traits relating to the size of rosettes (number, area, Feret diameter and perimeter) while the second principal component consisted mainly of the angle and Feret angle measurements.

Leopards had an average of 68.10 rosette markings per flank (SD = 22.40) (Table 5.2). Rosette markings had an average area of 0.0068 leopard units^2 (SD = 0.0030), and an average perimeter of 0.43 leopard units (SD = 0.11). The mean angle of flank rosette markings relative to the head of the leopard was 76.56 degrees, (SD = 10.38), which was similar to the mean Feret angle of 72.03 degrees (SD = 11.67). The mean HotSpotter score between dyads was 302.96 (SD = 484.91), although this ranged from 0 to 38 550. A total of 430 dyads had HotSpotter similarity scores of 0, meaning that HotSpotter was unable to find a single matching key-point between these images. Leopards had on average 6.17 whisker spots (SD = 1.46), with an average position of 22.69 (SD = 6.32) and an average total score, encompassing both number and position of spots, of 7.35 (SD = 0.93).

Coefficients of variability for flank rosette metrics measured by ImageJ and whisker spot metrics ranged from 3.80% to 34.91%, with rosette solidity having the lowest coefficient of variability and rosette area having the highest (Table 5.2). However, the coefficient of variability for HotSpotter scores was much higher, at 160.06%. Repeatability scores varied substantially between metrics, being highest for flank rosette marking Feret diameter (R = 0.55) (Table 5.2). Repeatability scores were high for all ImageJ metrics and whisker spot scores, however the repeatability of HotSpotter scores was low, at only 0.03.

This low level of repeatability precluded further analysis of the relationship between *Hotspotter* similarity scores and genetic relatedness. R^2

Table 5.2: Summary statistics for flank rosette and whisker spot traits and parent-offspring regressions for the 10 rosette measurement variables and their first two associated principal components, as well as the three whisker spot traits, including mean trait measurements (for the entire sample, not only parent-offspring dyads) and their associated standard deviation (SD) and coefficient of variance (CV), repeatability of ImageJ measurements (correlation among measurements from multiple images of the same individual) and parent-offspring (PO) slope coefficients and associated SE, f-statistics p-values and multiple R^2 values, as well as the estimated heritability of the trait. Traits showing significant parent-offspring regression lines are shown in bold.

Model	Number	Area	Perimeter	Angle	Circularity	Feret	Feret Angle	Aspect Ratio	Roundness	Solidity	PC1	PC2	HotSpotter	Whisker Spot Number	Whisker Spot Position	Whisker Spot Score
Mean	68.10	0.0068	0.43	76.65	0.52	0.13	72.03	1.87	0.59	0.81	-	-	302.96	6.17	22.69	7.35
SD	22.40	0.0030	0.11	10.38	0.11	0.03	11.67	0.15	0.04	0.03	-	-	484.91	1.46	6.32	0.93
CV (%)	32.91	34.91	26.83	13.54	21.13	20.01	16.20	7.88	6.12	3.80	-	-	160.06	23.63	27.83	12.71
Repeatability (R)	0.50	0.50	0.40	0.21	0.31	0.55	0.22	0.27	0.29	0.50	-	-	0.03	-	-	-
SE of R	0.06	0.06	0.07	0.07	0.07	0.06	0.07	0.07	0.07	0.06	-	-	0.003	-	-	-
P value (R)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	-	-	< 0.001	-	-	-
PO Slope Coefficient	-0.06	0.20	**0.23**	0.20	**0.32**	0.19	**0.22**	0.14	0.22	**0.36**	0.21	0.27	-	0.22	**0.35**	**0.32**
Coefficient SE	0.14	0.11	**0.11**	0.11	**0.10**	0.11	**0.11**	0.17	0.16	**0.11**	0.11	0.14	-	0.14	**0.14**	**0.11**
$F_{1, 57/65}$	0.19	3.54	**4.51**	7.17	**9.85**	3.24	**4.34**	0.68	1.94	**11.12**	3.70	3.47	-	2.30	**6.70**	**8.02**
P value	0.66	0.06	**0.04**	0.08	**0.003**	0.08	**0.04**	0.41	0.17	**0.002**	0.06	0.07	-	0.13	**0.01**	**0.006**
Multiple R^2	0.00	0.06	**0.07**	0.05	**0.15**	0.05	**0.07**	0.01	0.03	**0.16**	0.06	0.06	-	0.03	**0.09**	**0.11**
Heritability	-0.12	0.41	**0.45**	0.40	**0.64**	0.39	**0.45**	0.28	0.44	**0.72**	0.41	0.54	-	0.44	**0.70**	**0.64**

Flank rosette data included 59 parent-offspring dyads, and whisker spot data included 67 parent-offspring dyads. Parent-offspring (PO) regression indicated that six out of the 15 flank rosette and whisker spot traits measured show significant slope coefficients between mother and offspring: perimeter, circularity, Feret angle, solidity, whisker spot position and whisker spot score (Table 5.2, Figure 5.9). Flank rosette marking solidity had the highest heritability score (heritability = 0.72, $F_{1, 57} = 11.12$, $p < 0.01$), followed by whisker spot position (heritability = 0.70, $F_{1, 65} = 6.70$, $p < 0.05$).

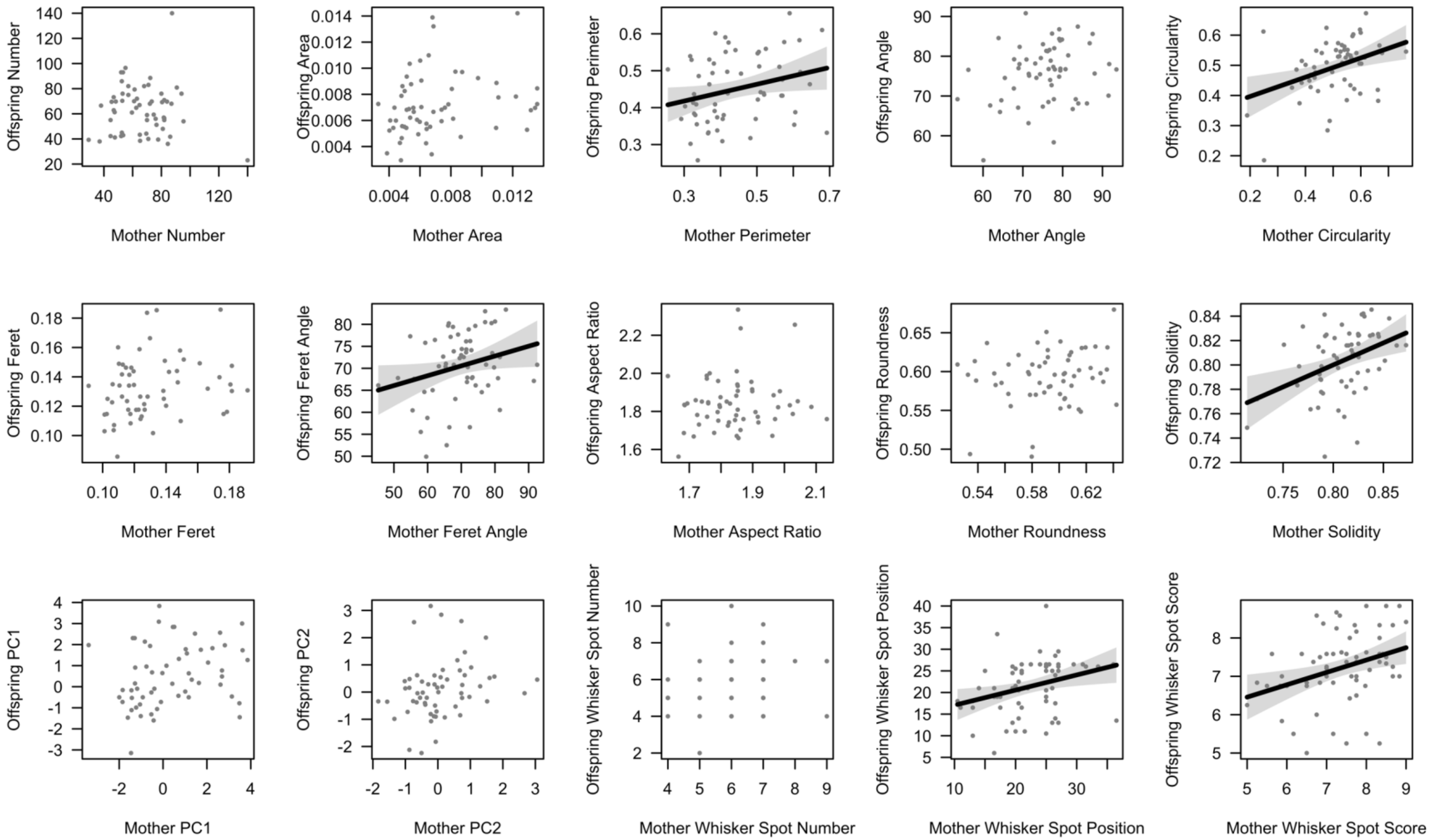

Figure 5.9: Parent-offspring regressions for 10 measurements from image analysis in ImageJ (number of markings, mean marking area, mean marking perimeter, mean angle between the primary axis of an ellipse fit over the marking and the x-axis of the image, mean marking circularity, mean Feret diameter, mean Feret angle, mean aspect ratio of the ellipse fitted to the marking, mean marking roundness and mean marking solidity), the first two principal components of these measurements, and three whisker spot traits (number, position and score). N = 59 parent-offspring dyads for ImageJ and 67 parent-offspring dyads for whisker spots. Regression lines are shown for traits that were significantly correlated.

Two variables, circularity and Feret angle, show a statistically significant decrease in dissimilarity scores with increasing relatedness scores (Figure 5.10). All other metrics measured show an overall trend that is not statistically significant of greater phenotypic similarity, seen through lower dissimilarity scores for Image J and whisker spot metrics, in classes with dyads of a higher level of know relatedness.

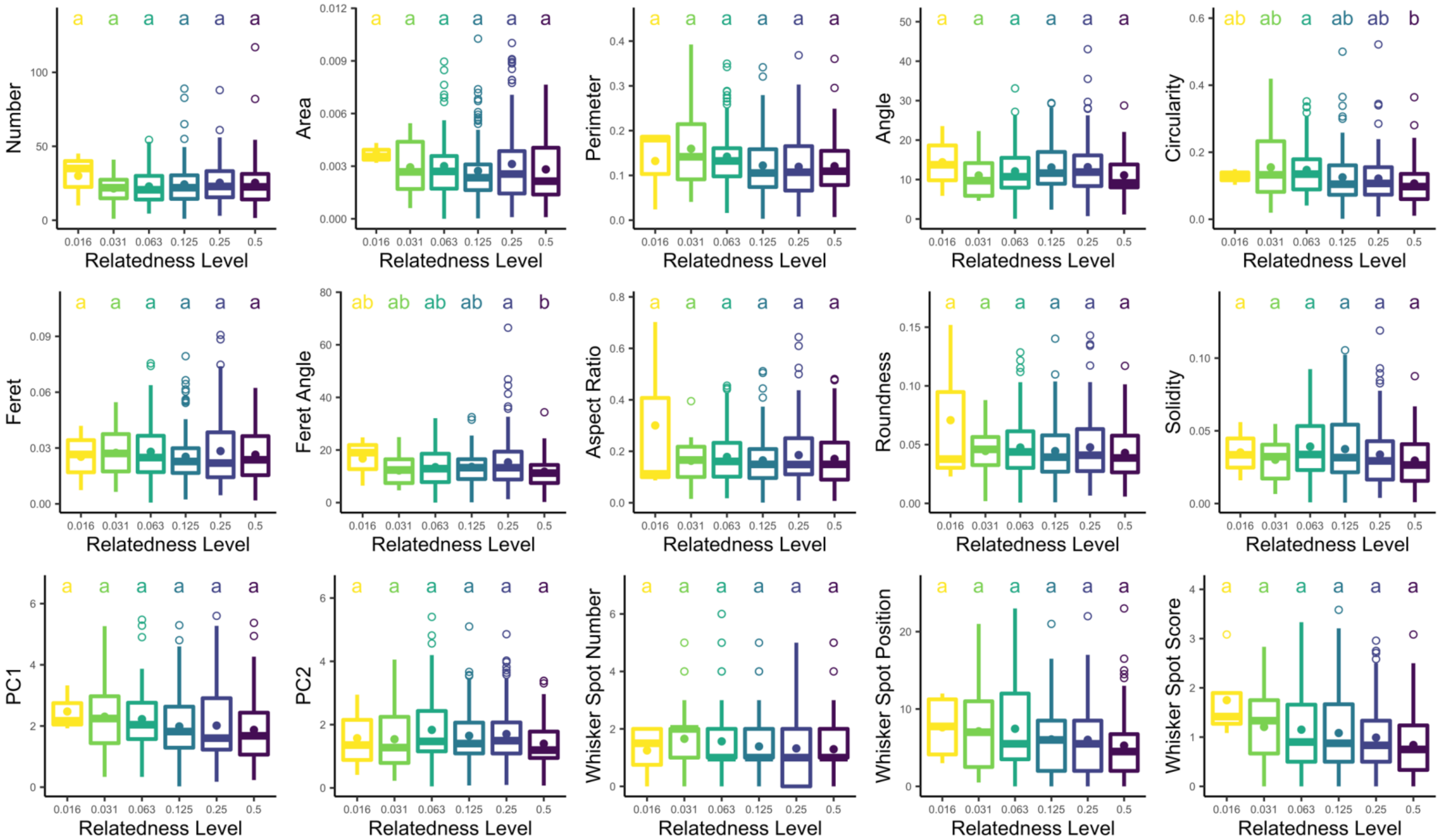

Figure 5.10: Variation in phenotypic resemblance per level of relatedness for dyads with known relationships, excluding dyads with no relatedness. These are dissimilarity scores of 10 metrics from ImageJ (number of markings, mean marking area, mean marking perimeter, mean angle between the primary axis of an ellipse fit over the marking and the x-axis of the image, mean marking circularity, mean Feret diameter, mean Feret angle, mean aspect ratio, mean marking roundness and mean marking solidity), the corresponding first two principal components and three whisker spot traits (number, position and score). N = 94 individuals and 381 dyads for ImageJ and 96 individuals and 410 dyads for whisker spots. Letters represent Tukey test results at significance level of 0.05.

There is very little difference in the amount of phenotypic resemblance between parent-offspring and sibling dyads. Only Feret angle was significantly different between parent-offspring (N = 59 for ImageJ and HotSpotter and 67 for whisker spots) and sibling (N = 8) dyads is, with a lower dissimilarity score among parent-offspring dyads than among sibling dyads (Figure 5.11). No phenotypic metrics were more similar among sibling dyads than parent-offspring dyads.

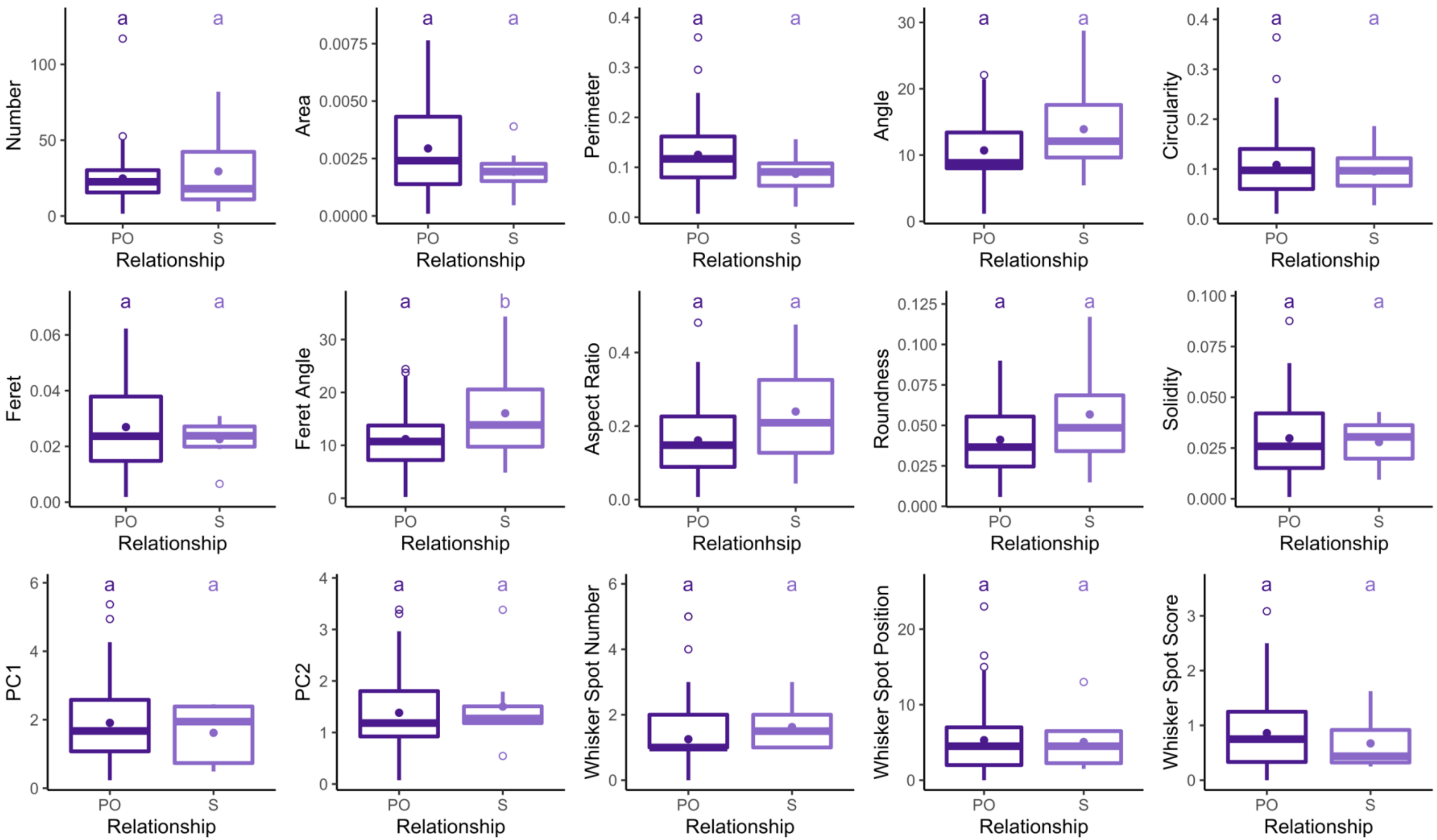

Figure 5.11: Variation in phenotypic resemblance scores between parent-offspring (PO) dyads and sibling (S) dyads. These are dissimilarity scores of 10 metrics from ImageJ (number of markings, mean marking area, mean marking perimeter, mean angle between the primary axis of an ellipse fit over the marking and the x-axis of the image, mean marking circularity, mean Feret diameter, mean Feret angle, mean aspect ratio, mean marking roundness and mean marking solidity), the corresponding first two principal components and three whisker spot traits (number, position and score). N = 59 parent-offspring dyads and 8 sibling dyads for ImageJ and 66 parent-offspring dyads and 8 sibling dyads for whisker spots. Letters represent Tukey test results at significance level of 0.05.

5.5 Discussion

In this study I successfully quantified leopard flank rosette markings according to 10 metrics, and whisker spot patterns according to three metrics. The lack of significant difference in flank rosette marking and whisker spot traits between left and right sides is consistent with current theories on the evolutionary benefits of symmetry (Enquist and Arak, 1994; Møller and Thornhill, 1998). Contrary to our findings regarding leopard symmetry, similar work done on the pelage patterns of cheetahs found differences in the width of tail bands between left and right sides (Balme and Hunter, 2013b). This is an unusual finding which could be due to the relatively low levels of genetic variation present in cheetah populations (O'Brien et al., 1983).

The finding that angle and Feret angle of flank rosette markings differ significantly when the direction an individual is facing is not accounted for provides evidence that rosettes are not randomly placed over a leopard's body, but rather that pattern development happens relative to a certain point on the animal's body. While the mechanisms responsible for mammalian coat patterning remain poorly understood, coat patterning in felids is hypothesised to arise from two separate processes which are triggered by genes at a minimum of three loci interacting through epistatic effects (Liu et al., 2006; Eizirik et al., 2010). One of these processes is thought to be spatially oriented, laying down a pattern for skin cell differentiation, and another responsible for regulating melanin profiles through a reaction-diffusion process involving an interaction between two types of morphogen: eumelanin, which is dark in colour, and phaeomelanin, which is lighter in colour (Turing, 1952; Silvers, 1979; Eizirik et al., 2010). My findings here confirm that directionality is important in the spatial process.

Certain flank rosette markings show a greater degree of variance between individuals than others. Principal component analysis suggests that the combination of variables that is best able to characterise the differences in flank rosette markings between individuals are predominantly size related. These variables, such as number, area and perimeter, consequently, have some of the highest coefficients of variability in comparison to the rest of the variables measured by ImageJ, indicating that they are the variables that differ most between individuals. Whisker spot variables have coefficients of variability that are lower than those associated with the first principal component of flank rosette traits, meaning that they show a lower degree of between individual variation, and consequently may not be as useful for telling individuals apart. Visually this makes sense, as to the naked eye there appears to be a greater level of variation in flank rosette patterns as opposed to whisker spot patterns.

Given that HotSpotter only assigns similarity scores to dyads, and not to individuals themselves, the HotSpotter coefficient of variance is indicative of the variation between dyad similarity scores. The HotSpotter coefficient of variance is over 100%, indicating that the standard deviation is greater than the mean and therefore there is a wide range in HotSpotter scores between dyads. Additionally, however, HotSpotter repeatability scores are an order of magnitude lower than even the lowest ImageJ flank rosette marking or whisker spot trait, indicating that HotSpotter scores do not show high levels of repeatability for different images of the same dyad of individuals. HotSpotter scores are therefore not a reliable method of quantifying phenotypic similarity between individual leopards and should not be used to assess the relationship between phenotype and genotype in leopards. Repeatability scores, which explore the comparison of within individual or dyad variance to between individual or dyad variance in a mixed model framework to provide a measure of the reliability of measurements, confirm that ImageJ and whisker spot measurements are a more reliable method of quantifying flank rosette markings and whisker spots (Stoffel et al., 2017; Lee et al., 2018).

Leopard flank rosette markings and whisker spot patterns both appear to be affected by genetics with a significant correlation in rosette markings and whisker spots between mothers and their offspring for six out of the 15 traits measured. These findings are similar to those for giraffes (Lee et al., 2018) where marking circularity and solidity showed a significant correlation between mothers and their offspring. Circularity and solidity are also correlated in parent-offspring leopard dyads, although heritability scores are slightly higher for giraffes (1.04 and 1.06 respectively) than for leopards (0.64 and 0.72 respectively) (Lee et al., 2018). These heritability scores are relatively high for the heritability of quantitative pelage traits, with zebra stripes in two different regions of the body showing heritabilities of 0.43 and 0.54 respectively (Parsons et al., 2007). Leopards however have additional heritable marking characteristics, namely, perimeter and Feret angle. Also, while the number of whisker spots does not appear to be heritable, their positioning and overall score does. Interestingly, only one heritable trait was an important constituent of the first principal component of a PCA of all ImageJ variables and none have particularly high coefficients of variability, indicating that while certain metrics vary more between individuals these metrics are not necessarily more likely to be heritable. The high levels of variability seen in these metrics cannot therefore be attributed to genetic divergence between individuals.

While parent-offspring dyads show phenotypic similarities with regards to both flank rosette markings and whisker spots, this association between phenotypic resemblance and genetic relatedness isn't as clear across all samples from the population. This is seen through an overarching lack of variation in levels of phenotypic resemblance between known relatedness classes. Only two variables, Feret angle and circularity, show significant differences in the level of flank rosette marking similarity between known relatedness classes, with lower dissimilarity, and therefore a higher level of similarity, in classes of higher relatedness. These differences are therefore not strong enough to allow for the use phenotypic similarity scores regarding leopard flank rosettes or whisker spots to reliably inform our knowledge of how closely related two leopard individuals are, meaning that at a population level this relationship is not of use to biological monitoring.

A lack of difference in similarity between different relatedness classes corroborates similar findings concerning cheetahs (Kelly, 2001). When sections of cheetah flanks were analysed using a computer-aided matching system initially developed for grey seals, related individuals did not show more similar spot patterns. The quality of the photographs however was found to significantly affect similarity coefficients generated by the computer program. Although all images I used went through rigorous quality screening, differences in image quality are likely responsible for the lack of repeatability in HotSpotter scores. However, in contrast to this, Caro and Durant (1991) manually scored cheetah tail bands and did find increased resemblance among related individuals. While computer programs are widely used to assist with individual identification in cases when animals are characterised by markings that cannot be easily quantified by the naked eye, they may nevertheless struggle to quantify the level of similarity between different individuals (Miththapala et al., 1989; Kelly, 2001; Anderson et al., 2010; Crall et al., 2013b). This weakness could be masking the existence of a relationship between genotype and phenotype which has been observed using manual scoring techniques on cheetah tails, and which we observed in this study regarding the positioning of whisker spots as well as the Feret angle of flank rosette markings (Kelly, 2001). Regardless of whether this relationship exists, we do not at this stage have a method that can reliably use phenotypic traits recorded in photographs to provide useful information on levels of genetic relatedness or diversity in populations of leopards.

The highest possible relatedness class includes parent-offspring and sibling dyads, both of which share approximately 50% of their genetic material. Sibling dyads however share the same in-utero environment, which can lead to more similar epigenetic effects (Barros and Offenbacher, 2009; Balme and Hunter, 2013b; Duncan et al., 2014). The overwhelming lack of difference between phenotypic similarity scores for parent-offspring and sibling dyads provides an indication that the in-utero environment shared by siblings is not instrumental to their spot pattern development. This contradicts previous work done on phenotypic similarity in cheetahs, where siblings were found to have more similar tail banding patterns than mother-offspring dyads (Balme and Hunter, 2013b).

Inheritance is a complex process, further complicated where multigenic traits, such as coat patterning, are concerned. Heritability is representative of the proportion of variability in a trait that is accounted for by genetic as opposed to environmental factors (Feldman and Lewontin, 1975; Jacquard, 1983; de los Campos et al., 2015; Lee et al., 2018). The genetic part of this equation involves genes acquired from both parents of an individual (Jacquard, 1983). Additionally, in the case of multigenic traits, the effects of different genes are not necessarily additive, but can include dominant-recessive relationships as well as gene-gene interactions (Feldman and Lewontin, 1975; Jacquard, 1983; de los Campos et al., 2015). The latter is known as broad sense heritability or H^2 (Feldman and Lewontin, 1975; Jacquard, 1983). Heritability that is due only to the additive genetic factors, known as narrow sense heritability or h^2 (de los Campos et al., 2015), involves comparing the midpoint of the parents' phenotype with the offspring phenotype to account for genetic differences between the parents (Jacquard, 1983). I used a similar approach in this study however my pedigree data was limited to matrilines. Therefore, the relationship between phenotype and genotype, which is already complicated by environmental effects, has been further weakened in this study by the lack of paternity data. Including paternity data and regressing the mean of parent phenotypic traits against the offspring trait measurement would therefore likely strengthen the relationship between phenotype and genotype. Additionally, relatedness classes obtained from observed pedigree data are a relatively coarse metric of relatedness, which do not represent the actual amount of shared genetic material, but rather the number of generations separating individuals. Therefore, including genetic relatedness scores, as opposed to observed relatedness scores, also has the potential to strengthen this relationship.

This study, carried out on a single leopard population in a relatively small geographic area, provides an indication that genetic factors do have some influence on leopard flank rosette markings and whisker spots. The discovery of significant mother-offspring correlations in the case of four flank rosette and two whisker spot metrics provides an exciting indication of the relationship between genotype and phenotype in leopard pelage patterns. This is particularly significant given the relative homogeneity of leopard rosette patterns relative to the markings of some other species such as giraffes, where a similar relationship has been observed. The heritability of the traits measured however was not strong enough to provide an alternative to genetic measures in the context of the biological monitoring of genetic diversity in declining and isolated leopard populations. It is possible that if paternity data were included the relationship may be significantly stronger and potentially more useful as a population health monitoring tool. However, the relatively weak parent-offspring correlation coefficients indicate that there is considerable noise in the phenotypic data, likely due to environmental effects, and therefore phenotypic resemblance is unlikely to be of use in determining level of relatedness amongst leopards in a free ranging population. Non-invasive genetic analysis therefore remains our most useful tool in answering questions about genetic diversity and inbreeding. However, it would be interesting to investigate whether the phenotypic variance that has led to the relationships identified in this study could serve as a proxy indicating likely degradation of genetic variance in populations. Also, at a broader geographic scale, the relationship between genetics and phenotype could provide an indication of the origin of leopard individuals. Although there has been no work done on this to date, it would be of a particular use for monitoring source populations in the illegal skin trade, where it could be used to identify the broad geographic region that illegally obtained skins originate from (Naude et al., 2020b). If this relationship holds at a regional level, then there is an opportunity to use the extensive photographic data of leopards captured on camera traps throughout Africa and Asia to produce a source reference library for comparison with photographs of illegally obtained or traded leopard skins.

CHAPTER 6
SYNTHESIS

Figure 6.1: A camera trap photograph of a leopard investigating a camera trap set up in Kruger National Park.

6.1 The value of monitoring populations

The Anthropocene has been characterised by several environmental changes and challenges, many of which are endangering the future of ecosystem functioning. One of the most pervasive of these changes has been habitat loss, leading to reduced ranges, smaller population sizes and an increase in extinction rates across species (Pimm and Raven, 2000; McKee et al., 2004; Crooks et al., 2017; Kotiaho and Halme, 2018; Otto, 2018; Di Marco et al., 2018). All too often, we remain unaware of the status of a species until it is too late, and population decline leading to extinction becomes inevitable (Fagan and Holmes, 2006; Martin et al., 2012). However, while extinction remains the worst outcome for a species, decreased population size and density pose risks for the species itself as well as for the entire ecosystem through ecological cascades (Dirzo et al., 2014; Crooks et al., 2017).

Monitoring populations is a critical component of conservation biology as it provides information on the status and trajectories of species, communities and entire ecosystems (Witmer, 2005; Marsh and Trenham, 2008). Recent technological advances have increased our capacity to both monitor populations effectively and unobtrusively, and to successfully analyse and interpret the datasets emerging from these monitoring efforts (Marsh and Trenham, 2008; Iknayan et al., 2014; Stephenson, 2020; McClure et al., 2020; Li, 2020). Improvements in camera trap technology and the constant refining of statistical methods for analysing the data have greatly improved population monitoring, particularly of rare and elusive individually identifiable species (Royle et al., 2009; Efford et al., 2009; O'Connell et al., 2010; Sollmann et al., 2011; McCallum, 2013; Rich et al., 2014; Rowcliffe et al., 2014; Rich et al., 2019; Kays et al., 2020; Blount et al., 2021).

Monitoring efforts aim to asses spatial and temporal trends in species presence and abundance, and to do this they need to accurately and precisely measure parameters related to these variables (Yoccoz et al., 2001). However, despite advances in the field of biological monitoring, particularly with regards data collection and analysis, many monitoring programs still fail to have the desired impact on management practices, often due either to a lack of ability to detect trends in the data or a missing link with management authorities (Yoccoz et al., 2001; Nichols and Williams, 2006). This brings into question the large sums of money poured into monitoring programs by governments and other organizations alike. Ideally, monitoring programs need to be used in the context of an adaptive management feedback loop, allowing monitoring efforts first to collect baseline data, with specific objectives and hypotheses in mind, and then to evaluate the outcomes of management practices and inform changes that need to be implemented (Lyons et al., 2008, Lindenmayer and Likens, 2010). Once changes are implemented, monitoring needs to occur again, to assess the effects of the changes and inform new ones (Lyons et al., 2008). When monitoring, decision making and the implementation of management strategies occur in an iterative manner and like this monitoring programs are able to reach their full potential, and make the best use of the funds and effort which they consume.

6.2 A more holistic view on population status

To date a substantial focus of monitoring efforts has been on estimating population density (Buckland et al., 2000; Karanth et al., 2004; Sollmann et al., 2011; McCallum, 2013; Athreya et al., 2013; Tobler and Powell, 2013; Elliot and Gopalaswamy, 2017; Noack et al., 2019). While variations in population density undeniably provide important information on the status of populations, density is reliant on a multitude of variables within the population itself, and depending on the species in question, can show a substantial lag in reflecting stressors to which a population is exposed (Clark and Bjørnstad, 2004). For this reason it is helpful to rely on more than just density when assessing populations, and rather move towards a more holistic view of population status (Figure 6.2) (Witmer, 2005; Schmeller et al., 2017). There are two ways of doing this: either by combining different monitoring techniques, or by using a single monitoring tool that provides multiple kinds of data. Camera traps provide an ideal means to acquire multiple kinds of data through a single monitoring intervention, with little disturbance to the species of interest and its habitat (Kelly, 2008; Rowcliffe and Carbone, 2008; Efford et al., 2009; Rowcliffe et al., 2014; Caravaggi et al., 2017). This is particularly important given that there has been a strong movement towards non-invasive methods within the realm of biological monitoring (Caravaggi et al., 2017; Rogan et al., 2019).

There has recently been an explosion of studies investigating the temporal effects of anthropogenic disturbance on wildlife, which has been added to the already enormous bank of literature on the spatial impact of humans on wildlife communities (Cozzi et al., 2012; Swanson et al., 2016; Palmer et al., 2017; Ramesh et al., 2017a; Cusack et al., 2017; Caravaggi et al., 2018; Vilella et al., 2020). Camera traps provide a useful means for recording both spatial and temporal responses of wildlife to human disturbance (Efford et al., 2009; Rowcliffe et al., 2014; Rogan et al., 2019). However, there are trade-offs between the broader scale information gleaned from monitoring entire populations through the use of camera traps and the fine scale data that results from monitoring individual animals with tracking devices (Martins and Harris, 2013; Odden et al., 2014; Van Cleave et al., 2018; Lashley et al., 2018; Edwards et al., 2021). While this trade-off means that developments in the collection and analysis of camera trap data have not negated the use of other forms of monitoring, their potential for monitoring multiple aspects of population status simultaneously are valuable. Thus, in this study, I show how densities vary markedly within a contiguous protected area while activity patterns remain relatively similar. This is not to say that one of these metrics is wrong, but rather that these metrics inform us of different aspects of a population’s status and should be looked at together to gain a broader understanding of the likely stressors affecting the population at hand.

Unfortunately, photographic data is currently unable to inform our knowledge on the level of relatedness between individuals, meaning that it cannot be used in monitoring the genetic health of leopard (*Panthera pardus*) populations. Whether this is due to the noisy nature of phenotypic data given the multigenic nature of the traits and the role of environmental effects, or to an inability of the available image analysis programs to quantify phenotypic resemblance in leopards remains unknown. Currently inbreeding is not a metric which is routinely monitored in leopards. However the genetic health of populations becomes increasingly important in small populations with reduced capacity for dispersal due to habitat fragmentation and artificial barriers (Noack et al., 2019; Naude et al., 2020a). Given their agility, leopards routinely cross both natural and artificial boundaries with relative ease, allowing for dispersal and reducing the chance of inbreeding (Fattebert et al., 2013). However, a recent study has highlighted the potential for opportunistic philopatry in males born into areas with low density populations linked to excessive anthropogenic impacts (Naude et al., 2020a). The escalated probability of inbreeding within isolated protected areas increases the importance of deriving non-invasive methods for monitoring genetic health in conjunction with density in protected areas with limited potential for immigration and emigration, or declining densities.

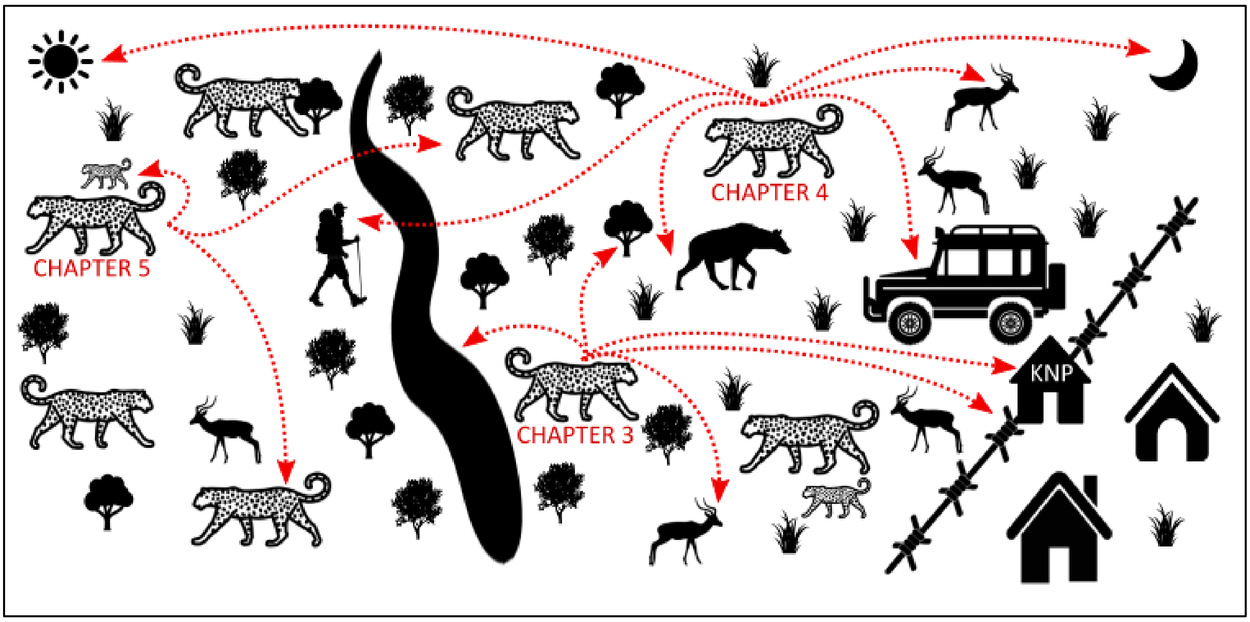

Figure 6.2: A summary schematic of the different aspects of leopard population status investigated in this thesis. These included drivers of density in chapter 3, temporal activity in relation to environmental and anthropogenic impacts in chapter 4 and genetic relatedness measured through phenotypic similarity in chapter 5.

6.3 Monitoring populations at different scales

While it has been feasible to set up and maintain intensive camera trap arrays throughout many small protected areas in South Africa, as has been done by Panthera's long term monitoring program (Rogan, 2021), monitoring programs relying on this methodology become more challenging in areas dominated by large reserves and with access to fewer resources. Running such intensive camera trap arrays over much larger areas becomes near impossible, given limitations on financial and human resources. However, while Kruger National Park (KNP) is the only reserve of its size in South Africa, fewer larger reserves are more common throughout the rest of Africa than the multitude of tiny protected areas that characterizes South Africa (Cantú-Salazar and Gaston, 2010). Therefore, it is worth considering how best to approach such areas. In the case of KNP, we chose specific sections of the park to survey intensively, based on prior knowledge of environmental variables and leopard population densities. In the absence of such knowledge or where there are insufficient resources to run camera trap arrays that meet the demands of spatial capture-recapture (SCR) models, then fewer camera traps could be used to explore activity patterns as a proxy for potential human disturbance (Rowcliffe et al., 2014; Gaynor et al., 2018). In this study leopard activity patterns were similar across a range of protection levels and more influenced by environmental variables such as temperature and lunar illumination than by human disturbance. This suggests that anthropogenic impacts, although clearly present across all study sites, were not of a nature that caused leopards to adjust their activity to avoid them. Given the wide array of studies confirming the ubiquitous effects of human disturbance on animal activity patterns, seen in the increasing nocturnality of populations exposed to greater human disturbance, the relative timing of activity displayed by populations should provide insight into levels of human disturbance (Odden et al., 2014; Clinchy et al., 2016; Smith et al., 2017; Gaynor et al., 2018; Suraci et al., 2019). In this regard KNP may provide an important baseline for leopard activity in a protected area with low levels of adverse human impacts despite high levels of human presence for tourism, negating the need for leopards to adjust their activity patterns.

Camera traps are also useful for providing data on leopard phenotypes within protected areas. As shown in this study, flank rosette markings and whisker spot patterns show a certain level of inheritance, and while insufficient to estimate relatedness or inbreeding coefficients, they could potentially be used to assign leopards to broad geographic regions. Given that offspring have rosette patterns that are significantly more similar to those of their mother, and that leopard populations throughout southern Africa have diverged via isolation by distance (Ropiquet et al., 2015), it is possible that populations in different regions will show different rosette marking characteristics. These broad scale differences in flank rosette markings may therefore allow for source region identification of confiscated leopard skins, providing a less resource intensive and faster way of identifying poaching hotspots and adapting management regimes, than the current reliance on genetic sequencing.

6.4 Diving deeper into density estimates

Density estimation through spatial capture-recapture (SCR) is one of the most widely used techniques for monitoring population status of individually identifiable species (Tobler and Powell, 2013; Balme et al., 2019; Havmøller et al., 2019; Noack et al., 2019; Rogan, 2021; Durbach et al., 2021; Searle et al., 2021b). Density however is not of much use when considered in isolation. The absolute density of animals in an area is not only dependant on population specific variables, but also on environmental variables, making it difficult to determine the baseline density of a population, and hence whether the current density is a cause for concern (Buckland et al., 2000; Hayward et al., 2007; Marsh and Trenham, 2008). For this reason, relative population densities are of far greater use: relative to the environmental carrying capacity for the species in question, or relative to other sites in space or the same site in time (Hayward et al., 2007). While ideally all comparisons should be made with respect to the environmental carrying capacity of the species in question, this is difficult to determine, environment-specific and can change over time (Balme et al., 2019). Because ecological and environmental differences between sites affect spatial as well as temporal comparisons of density, the status of a population requires multiple years and sampling iterations to be confirmed (Witmer, 2005). However, by that point the population may already be in steady decline, and the resulting changes in management incorporated might show less success than they could have had they been implemented earlier (Soulé, 1985).

There are a number of population specific variables that are critical to the overall density of a population as well as its resilience, and which can be informative in determining a population's trajectory (Sibly and Hone, 2002; Sibly et al., 2003; Prange et al., 2003; Gamelon et al., 2017). Population demographics, most importantly age structure and sex ratio, have a strong influence on processes affecting density, and in turn affect other density related variables such as reproductive and survival rates (Mech, 1975; Kruuk et al., 1999; Langvatn and Loison, 1999; Prange et al., 2003). These variables are not only important for ensuring sufficient mate choice, but also important because of age and sex specific behaviours (Balme et al., 2010b; Fattebert et al., 2013; Braczkowski et al., 2015). Differences in the relative proportions of males and females as well as subadults and adults can be used to indicate disturbance sooner than population trends as determined through changes in density alone (Bender, 2006). Thus, for example, populations experiencing high levels of illegal hunting have lower ratios of adult males to subadult males resulting in reduced dispersal of subadults and an increased risk of inbreeding. However, while age and sex ratios influence demographic processes, they are also themselves influenced by demographic processes such as fecundity and survival, and different demographic processes can cause similar skews in age and sex ratios. It is therefore important that investigations into age and sex ratios include a further step looking at the demographic processes causing skewed ratios, to allow for adaptive management to consider both causes and effects, and how they interact with one another.

Areas that are dominated by young males can provide an indication of an ecological trap: an area appearing to be appropriate habitat, but characterised by the presence of threats to population persistence, preventing subadults from surviving to adulthood (Kristan, 2003). Similarly in cougars, areas which are more disturbed and where survival is lower are dominated by young dispersing males (Robinson et al., 2008). This is because as individuals are removed from the population by a threat the newly open territories are most likely to be claimed by a dispersing young male in search of a territory of his own (Robinson et al., 2008). This phenomenon is known as compensatory immigration, and results in very little change in density, but a substantial change in age and sex ratios (Robinson et al., 2008; Lieury et al., 2015). Areas like these are often on the brink of population decline and have a density that is maintained only by emigration from a source population, and are hence vulnerable to extirpation should the source population decline (Herrando-Pérez et al., 2012; Lieury et al., 2015; Gervasi et al., 2015).

Age and sex ratios can also be skewed by disturbance in other ways. In contrast to compensatory immigration, population senescence occurs when repeated disturbances within a population disrupt its stability, preventing young individuals from reaching maturity and resulting in an ageing population (Rosenblatt et al., 2014). Most large carnivores are characterised by strong territoriality, and therefore require a certain degree of population stability in order to persist (Balme et al., 2009; Packer et al., 2009; Balme and Hunter, 2013a). This is because territorial males are known to commit infanticide when moving or increasing the size of their territories, in order to allow for more breeding opportunities with females in the area (Packer and Pusey, 1983; Balme and Hunter, 2013a). When territorial males are lost from a population, the population suffers from lower rates of successful breeding and cub recruitment (Balme et al., 2013; Rosenblatt et al., 2014). Population senescence has been documented in lions, a species which, similar to leopards, requires a certain degree of population stability for successful breeding and cub recruitment due to high levels of infanticide in turbulent populations (Balme et al., 2013; Rosenblatt et al., 2014).

Leopards are a sexually dimorphic species, where males are substantially larger than females and characterised by the presence of a large dewlap underneath the neck (Hunter et al., 2013). Their larger size makes them a more attractive target to hunters (Balme et al., 2012). Therefore, populations dominated by females tend to be indicative of populations subject to targeted hunting, where males, which produce more attractive trophies, are removed in greater proportions in comparison to their smaller, and consequently less attractive, female counterparts (Braczkowski et al., 2015). Additionally, the behaviour of adult male and female leopards differs, which can reinforce the occurrence of female dominated populations in areas of high hunting activity. Male leopard territories tend to be larger than those of females, and males also tend to patrol boundaries more rigorously (Bailey, 1993). This increased movement increases their chances of making contact with hunters, or of being located by hunters through tracks or even their sawing vocalisations, associated with territorial patrols (Balme et al., 2012; Braczkowski et al., 2015).

In recovering leopard populations, the opposite sex bias is more likely, again because of behavioural differences between males and females. Males who disperse further and have larger territories than females are most likely to colonise the once disturbed landscape, with very few females moving far enough to occupy space in such an area (Fattebert et al., 2016). It can therefore take a long time for a disturbed landscape to be recolonised by a self-sustaining leopard population, as females will slowly move in from the edges but will likely require many generations to reach the core of the previously disturbed site, and provide mating opportunities to males in the area in order to sustain a reasonable density in the region (Logan and Sweanor, 2001; Fattebert et al., 2016).

In areas where leopard populations remain unaffected by anthropogenic mortality, populations have been found to consist of a ratio of approximately 40% males to 60% females, and similarly 40% subadult to 60% adult (Balme et al., 2019). This is because of the larger territory size characteristic of males, and low rates of cub survival (Balme et al., 2013; Braczkowski et al., 2015). Throughout this study I have looked mainly at population density, and not the demographic composition of populations at different sites because of the urgent need for this baseline density data. SCR models do however provide a reliable means of investigating the demographic composition of populations given that they allow for differences in detection between groups (males and females or subadults and adults) to be accounted for through the use of hybrid mixture models (Sollmann et al., 2011; Havmøller et al., 2019; Rogan, 2021). To better understand population status and identify at-risk populations before densities plummet, looking beyond density and into the demographic composition of populations from which density estimates are derived is important. Completing this step, however, was beyond the scope of this thesis as accurately ageing thousands of leopard photographs requires multiple independent observers for verification, which I did not have access to within the required timeframe. Including demographic information in population assessments builds on the idea of moving towards a more holistic view of a population status rather than looking at metrics separately. This may assist in providing early warning signs of decline, allowing for management regimes to be modified and improved as early as possible. However, metrics of population demography are most useful when looked at in conjunction with baseline density information. This study therefore provides the basis upon which further demographic studies can, and should, be carried out.

6.5 The future for leopards in Africa

Globally, large carnivores are in decline. Faced with the combined effects of land use change, loss of access to prey and persecution by humans, both targeted and incidental, populations are shrinking and ranges are contracting (Becker et al., 2013; Ripple et al., 2014; Jacobson et al., 2016; Bleyhl et al., 2021). Despite being one of the most tolerant and adaptable of the planet's large carnivore species, leopards are no exception to this trend (Balme et al., 2010b; Henschel et al., 2011; Swanepoel et al., 2014; Stein et al., 2016; Rogan, 2021). Their solitary, elusive nature makes them difficult to monitor, and thus they have been understudied relative to the rest of their guild (Balme et al., 2014; Jacobson et al., 2016). However, their extreme agility and wide habitat tolerance allows them to both access and persist in areas that remain unavailable to most other large carnivore species, putting them at even greater risk of anthropogenic mortality (Balme et al., 2010b; Athreya et al., 2013; Fattebert et al., 2013; Jacobson et al., 2016; Bleyhl et al., 2021). Additionally, there is an increasing and unsustainable demand for their skins for use in traditional ceremonies by the Shembe Church in southern Africa, which further threatens populations (Naude et al., 2020b). Population level monitoring within protected areas is thus crucially important for this species as early signs indicate that densities are declining in a number of government run reserves across the country (Rogan et al., in press).

Leopard population monitoring efforts have greatly increased over the last 10 years, since the initiation of Panthera's leopard monitoring program (Rogan, 2021). Initially conceived in South Africa, the program now reaches a number of other southern African countries including Angola, Mozambique, Namibia, Zambia and Zimbabwe and provides valuable information on the status of leopard populations in these areas. Increased monitoring has been invaluable for leopard conservation across the continent. The data collected over these years has been used to guide important management decisions, help reduce human-wildlife conflict and retaliatory killings and improve the future for leopards (Balme et al., 2009; Balme et al., 2010a; Balme et al., 2012; Pitman et al., 2015; Stein et al., 2016; Jacobson et al., 2016). Unfortunately however, leopard populations across many reserves in South Africa are still declining (Stein et al., 2016; Jacobson et al., 2016; Rogan, 2021). This concerning reality has often been mitigated at a national level by an underlying but untested assumption that KNP is a stronghold for leopards in the country, despite only a single assessment having been conducted in the area (Maputla, 2014). This is in stark contrast to most other large mammal species in the park which have been routinely monitored with annual aerial game counts and call-up surveys (Redfern et al., 2002; Ferreira et al., 2010; Chirima et al., 2012; Ferreira and Funston, 2020).

While the previous study (Maputla, 2014) suggested healthy leopard populations in the southern regions of KNP, the study suffered from a lack of resources causing inter-trap distances to become too high, particularly in the south of the park. This has limited confidence in the density estimates provided, meaning that they cannot be used as a reliable baseline for future comparisons. The outcomes of this study are thus important not only as a follow up survey, but to provide the first density estimates with robust confidence levels for sites both within and bordering KNP. High densities in the well resourced and long established Sabi Sand Game Reserve (SSGR) relative to the recently established Karangani Game Reserve (KGR) which has much lower leopard densities suggest that leopard population density is closely tied to the level of protection afforded to protected areas (Balme et al., 2019). Future surveys can build on the data presented here to assess the rate of recovery of KGR relative to the SSGR and to continue assessing key sites within KNP to monitor threats linked to the illegal harvesting of wildlife in general and leopards in particular.

This study indicates that despite the controversial nature of fences, and the concept of fortress conservation more generally (Berkes, 2007; Newmark, 2008; Creel et al., 2013; Büscher, 2015), leopard populations do better in certain reserves than others. While I did not have sufficient data on illegal human offtake within the reserves studied to directly link variations in leopard density with poaching pressure, leopard population density was substantially higher in the reserve considered least accessible to poachers, and considerably lower in the reserve where I expect anthropogenically driven leopard mortalities have been most common in recent years. Large carnivores are known to be most abundant when they are separated from densely populated human areas (Balme et al., 2010b; Packer et al., 2013a; Havmøller et al., 2019; Searle et al., 2021b), which introduce a diverse array of direct and indirect threats (Balme et al., 2009; Thorn et al., 2012; Broekhuis et al., 2020; Jordan et al., 2020). However, only a small percentage of land, both in South Africa and globally, is currently protected in any way, and an even smaller percentage is protected against any form of consumptive use, with some reserves allowing subsistence hunting and gathering, and others subsisting off the revenue generated by trophy hunting (Government of South Africa, 2008; South African National Parks., 2016; Clements et al., 2019). In terms of the persistence of large carnivore populations, as well as general ecological function, these reserves and community-based conservation efforts are undoubtedly better than an urban jungle, despite not hosting populations that necessarily reach their natural carrying capacities (Creel et al., 2013; Clements et al., 2019). In addition to providing more space in which wild animals can exist, they help to maintain connectivity between more strictly protected areas (Di Minin et al., 2013; Pitman et al., 2017; Ashrafzadeh et al., 2020). While strictly protected, fenced reserves allow the greatest potential for populations of apex predators to reach ecological carrying capacity (Packer et al., 2013a; Packer et al., 2013b), they are not without their costs which include habitat fragmentation, the interruption of migration routes, genetic isolation and economic drawbacks to surrounding communities (Creel et al., 2013). Therefore, I would argue that maintaining strictly protected, fenced reserves is only worthwhile if they are actually succeeding at maintaining ecosystems that are effectively protected from detrimental anthropogenic activities. If not, then unless adaptive management is being used to improve conservation outcomes it becomes more difficult to justify the use of the fortress conservation approach as the benefits may no longer be outweighing the costs. It is clear that fortress conservation currently plays an important role in large carnivore conservation by reducing the anthropogenically driven threats to which populations are exposed, however alone it remains insufficient, and community-based conservation initiatives, reserves allowing carefully-managed anthropogenic offtake and human-wildlife coexistence programs are equally important in the bigger picture (Balme et al., 2010a; Boudreaux and Nelson, 2011; Creel et al., 2013; Dolrenry et al., 2016).

While leopards have been understudied relative to most other large carnivores, and to many wild felids as well, they nevertheless benefit from being a charismatic ‘big and furry’, and we thus have a better idea about their ecology and conservation status than many other less well known and studied taxa (Colléony et al., 2017; Albert et al., 2018). However, as apex predators, leopards play a crucial role in the environment, and the local extirpation of populations, or the existence of populations at levels far below their carrying capacity, can cause a slew of detrimental ecological cascades (Dalerum et al., 2008;

Ripple et al., 2014). Changes to the timing of their activity which affect interspecific relationships can also have far reaching consequences (Sévêque et al., 2020). They can therefore be considered an umbrella species, whose conservation will have benefits far beyond the species itself (Roberge and Angelstam, 2004; Dalerum et al., 2008).

Unlike most forms of science where experimentation and replication are used to verify results, conservation biology is a crisis discipline with decisions typically made under pressure, often with limited datasets and little room for experimentation or investigation (Soulé, 1985; Robinson, 2006). All too often, this results in a heavy bias towards reactive measures, and a limited focus on proactive ones (Cook et al., 2014). Clearly there is a need for proactive, quick decisions to be made on essential processes such as curbing human intrusions into protected areas. However, there is also a need for carefully planned long term monitoring and the use of before and after studies to determine how best to stabilise populations or ecosystems that have been shown using robust data to be on a downward trajectory (Martin et al., 2012; Cook et al., 2014). The use of a multitude of metrics of population status, resulting in a holistic view on population health, is helpful in detecting small changes in populations, and can allow for management interventions to be adapted before a situation crosses a point of no return (Witmer, 2005). It is my hope that this thesis has shown how metrics readily obtained through camera trapping can be applied to monitoring leopard populations. While the phenotypic similarity of photographed leopards does provide information on levels of genetic similarity, the resolution of these data proved too coarse to reliably inform management on the potential threats of inbreeding through anthropogenic disruptions. However, there is the potential for phenotypic data to be used for the geographic assignment of leopard skins to different regions of Africa and this remains an exciting challenge for future research. Furthermore, while leopard activity derived from time stamps of leopard photographs did not reveal an impact of anthropogenic factors, the methods used here may well provide a useful approach for assessing levels of human disturbance linked to negative actions such as hunting. Additionally, the activity data presented here may serve as a useful baseline for leopards that are currently experiencing only limited negative human interactions. This baseline will be useful for subsequent studies at these sites and in other protected areas in the region. Lastly, the main contribution of this study is the production of a robust series of density estimates across a range of sites that will serve as a critical baseline for future comparisons both within KNP and in other smaller protected areas which have lower ecological integrity and greater human impacts.

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LIST OF ABBREVIATIONS

AIC	Akaike's Information Criterion
AICc	Akaike's Information Criterion corrected for small sample sizes
ANOVA	Analysis of variance
AU	Area of use
CCF	Cross correlation function
CI	Confidence interval
CTFM	Camera Trap File Manager
CV	Coefficient of variance
dAIC	Delta AIC
df	Degrees of freedom
DNA	Deoxyribonucleic Acid
DNB	Day/Night Band
FAO	Food and Agriculture Organisation of the United Nations
GB	Gigabyte
GDP	Gross domestic product
GPS	Global Positioning System
ID	Identity
IUCN	International Union for Conservation of Nature
kg	Kilogram
KGR	Karingani Game Reserve
km	Kilometer
KNP	Kruger National Park
m	Meter
mm	Milimeter
MODIS	Moderate Resolution Imaging Spectroradiometer
N	Number
NDVI	Normalised Difference Vegetation Index
NGO	Non-Governmental Organisation
PCA	Principal component analysis
PCR	Polymerase Chain Reaction
PO	Parent-offspring

R	Repeatability
RAI	Relative abundance Index
ROI	Region of Interest
SANParks	South African National Parks
SCR	Spatial capture-recapture
SE	Standard Error
SSGR	Sabi Sand Game Reserve (Sabi Sand, Mala Mala and Sabie Game Reserves)
Veg	Vegetation
VIIRS	Visible Infrared Imaging Radiometer Suite

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APPENDICES

Table A3.1: Moths during which camera traps were deployed at each site. The dry season, coloured in grey, spans from April to September and the wet season spans from October to March.

Site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Season
Sabi Sand South				X	X	X							Dry
Mala Mala/Londolozi							X	X	X				Dry
Singita/Western Sector										X	X	X	Wet
Sabi Sand North					X	X	X						Dry
Skukuza/Lower Sabie			X	X	X	X							Dry
Houtboschrand										X	X	X	Wet
Pretoriuskop						X	X	X					Dry
Nwanetsi								X	X	X			Dry
Karingani North			X	X	X								Dry
Karingani South			X	X	X								Dry

Table A3.2: Correlation coefficients for covariates included in spatially explicit capture-recapture (SECR) models.

	NDVI	Rivers	Edge	Prey	Reserve
NDVI	1.000	0.113	-0.293	-0.140	-0.217
Rivers	0.113	1.000	0.028	-0.262	-0.253
Edge	-0.293	0.028	1.000	-0.096	0.010
Prey	-0.140	-0.262	-0.096	1.000	0.821
Reserve	-0.217	-0.253	0.010	0.821	1.000

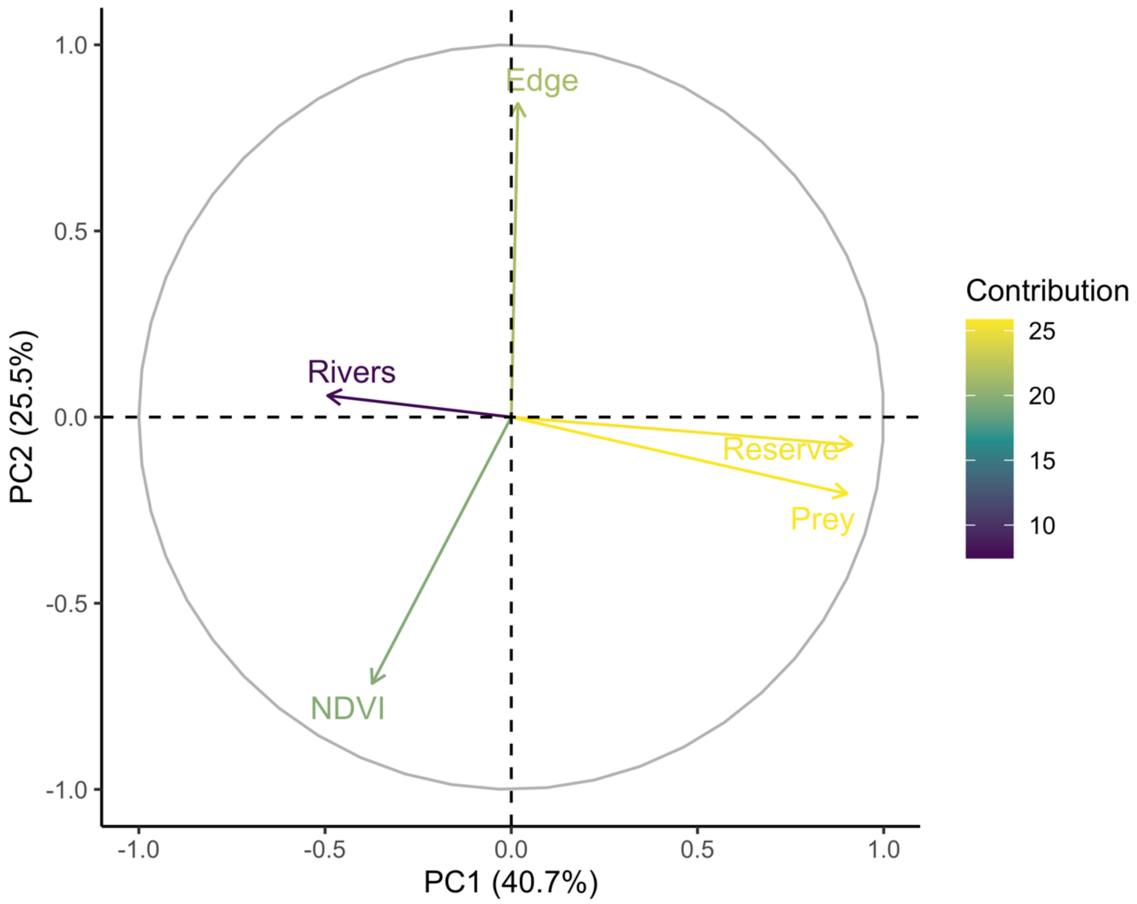

Figure A3.1: Principal component analysis for covariates included in spatially explicit capture-recapture (SECR) models.

Table A3.3: Detection parameter standard errors.

ID	Southern λ_0		Central λ_o		Southern σ		Central σ		P_{male}
	Female	Male	Female	Male	Female	Male	Female	Male	
M18	0.0015	0.0017	0.0077	0.0034	69	76	91	170	0.029
M16	0.0015	0.0017	0.0083	0.0032	69	76	81	162	0.029
M15	0.0015	0.0017	0.0082	0.0032	69	78	80	160	0.029
M6	0.0015	0.0017	0.0082	0.0031	69	78	78	160	0.029
M9	0.0015	0.0017	0.0083	0.0032	70	78	78	157	0.029
M14	0.0015	0.0017	0.0082	0.0031	69	79	79	157	0.029
M17	0.0015	0.0017	0.0082	0.0031	69	78	78	160	0.029
M8	0.0015	0.0017	0.0082	0.0032	70	79	77	152	0.029
M12	0.0015	0.0017	0.0082	0.0031	70	79	77	151	0.029
M13	0.0016	0.0017	0.0086	0.0031	67	80	74	150	0.029
M7	0.0015	0.0017	0.0084	0.0032	72	79	76	149	0.029
M2	0.0015	0.0017	0.0083	0.0031	70	78	76	155	0.029
M10	0.0015	0.0017	0.0082	0.0031	70	79	78	156	0.029
M3	0.0015	0.0017	0.0082	0.0031	70	79	78	156	0.029
M0	0.0015	0.0017	0.0082	0.0032	71	80	74	144	0.029
M4	0.0015	0.0017	0.0082	0.0032	72	80	74	145	0.029
M5	0.0015	0.0017	0.0082	0.0031	72	80	74	145	0.029
M11	0.0015	0.0017	0.0082	0.0031	72	81	74	144	0.029
M1	0.0015	0.0017	0.0083	0.0031	72	80	74	145	0.029

Figure A4.1: Proportion of camera trap photos of leopards captured during the night (dark grey) versus day (light grey) at all sites, with sunrise and sunset times set as the cut-off between night and day. Proportions differ significantly between sites (Pearson's Chi-squared test = 22.474, df = 9, $p < 0.05$).

Table A4.1: Comparisons between activity estimates for all sessions derived from kernel density estimates and associated Wald statistics and p values.

Sessions	Difference in Activity	Standard Error	Wald Statistic	p-value
Sabi Sand South: Mala Mala/Londolozi	-0.039	0.084	0.220	0.639
Sabi Sand South: Singita/Western Sector	0.055	0.083	0.449	0.503
Sabi Sand South: Sabi Sand North	-0.075	0.080	0.887	0.346
Sabi Sand South: Skukuza/Lower Sabie	-0.100	0.070	2.081	0.149
Sabi Sand South: Houtboschrand	0.091	0.108	0.717	0.397
Sabi Sand South: Pretoriuskop	-0.015	0.086	0.030	0.863
Sabi Sand South: Nwanetsi	-0.005	0.071	0.004	0.949
Sabi Sand South: Karingani North	0.036	0.073	0.248	0.619
Sabi Sand South: Karingani South	-0.059	0.091	0.424	0.515
Mala Mala/Londolozi: Singita/Western Sector	0.095	0.094	1.013	0.314
Mala Mala/Londolozi: Sabi Sand North	-0.036	0.092	0.152	0.697
Mala Mala/Londolozi: Skukuza/Lower Sabie	-0.061	0.083	0.540	0.462
Mala Mala/Londolozi: Houtboschrand	0.131	0.117	1.250	0.264
Mala Mala/Londolozi: Pretoriuskop	0.025	0.097	0.064	0.800
Mala Mala/Londolozi: Nwanetsi	0.035	0.084	0.171	0.679
Mala Mala/Londolozi: Karingani North	0.076	0.086	0.780	0.377
Mala Mala/Londolozi: Karingani South	-0.020	0.101	0.038	0.846
Singita/Western Sector: Sabi Sand North	-0.131	0.090	2.081	0.149
Singita/Western Sector: Skukuza/Lower Sabie	-0.156	0.082	3.643	0.056
Singita/Western Sector: Houtboschrand	0.036	0.116	0.096	0.757
Singita/Western Sector: Pretoriuskop	-0.070	0.096	0.537	0.464
Singita/Western Sector: Nwanetsi	-0.060	0.083	0.523	0.469
Singita/Western Sector: Karingani North	-0.019	0.084	0.052	0.819
Singita/Western Sector: Karingani South	-0.114	0.100	1.305	0.253
Sabi Sand North: Skukuza/Lower Sabie	-0.025	0.079	0.103	0.748
Sabi Sand North: Houtboschrand	0.166	0.114	2.134	0.144
Sabi Sand North: Pretoriuskop	0.060	0.093	0.418	0.518
Sabi Sand North: Nwanetsi	0.071	0.080	0.778	0.378
Sabi Sand North: Karingani North	0.111	0.081	1.869	0.172
Sabi Sand North: Karingani South	0.016	0.098	0.027	0.870
Skukuza/Lower Sabie: Houtboschrand	0.192	0.107	3.207	0.073

Skukuza/Lower Sabie: Pretoriuskop	0.086	0.085	1.019	0.313
Skukuza/Lower Sabie: Nwanetsi	0.096	0.070	1.882	0.170
Skukuza/Lower Sabie: Karingani North	0.137	0.071	3.652	0.056
Skukuza/Lower Sabie: Karingani South	0.041	0.090	0.212	0.645
Houtboschrand: Pretoriuskop	-0.106	0.118	0.806	0.369
Houtboschrand: Nwanetsi	-0.096	0.108	0.788	0.375
Houtboschrand: Karingani North	-0.055	0.109	0.256	0.613
Houtboschrand: Karingani South	-0.150	0.122	1.524	0.217
Pretoriuskop: Nwanetsi	0.010	0.086	0.014	0.905
Pretoriuskop: Karingani North	0.051	0.087	0.341	0.559
Pretoriuskop: Karingani South	-0.044	0.103	0.185	0.667
Nwanetsi: Karingani North	0.041	0.073	0.312	0.576
Nwanetsi: Karingani South	-0.055	0.091	0.360	0.549
Karingani North: Karingani South	-0.095	0.092	1.069	0.301

Table A4.2: Estimates of activity pattern overlap between leopards and humans, prey (bushbuck, grey duiker, grysbok, impala, klipspringer, nyala, reedbuck, steenbok and suni) and competitors (lions and hyaenas) based on times of observation. Confidence intervals (CI) are calculated from 1000 bootstrap samples and have been bias corrected.

Site	Human Overlap Estimate (Dhat 4)	Human Bootstrap 95% CI	Prey Overlap Estimate (Dhat 4)	Prey Bootstrap 95% CI	Competitor Overlap Estimate (Dhat 4)	Competitor Bootstrap 95% CI
Sabi Sand South	0.36	0.27 – 0.37	0.55	0.47 – 0.58	0.83	0.78 – 0.89
Mala Mala/Londolozi	0.38	0.30 – 0.42	0.60	0.52 – 0.65	0.83	0.78 – 0.89
Singita/Western Sector	0.36	0.25 – 0.41	0.48	0.36 – 0.54	0.86	0.81 – 0.96
Sabi Sand North	0.38	0.29 – 0.42	0.52	0.44 – 0.56	0.84	0.80 – 0.92
Skukuza/Lower Sabie	0.32	0.24 – 0.35	0.53	0.46 – 0.57	0.87	0.85 – 0.94
Houtboschrand	0.49	0.35 – 0.64	0.61	0.43 – 0.73	0.71	0.58 – 0.87
Pretoriuskop	0.41	0.31 – 0.45	0.70	0.62 – 0.75	0.69	0.62 – 0.76
Nwanetsi	0.20	0.09 – 0.22	0.41	0.30 – 0.45	0.85	0.80 – 0.93
Karingani North	0.33	0.25 – 0.35	0.47	0.38 – 0.50	0.76	0.70 – 0.84
Karingani South	0.26	0.13 – 0.32	0.46	0.33 – 0.54	0.79	0.71 – 0.93

Table A5.1: Number of images associated with each leopard individual within ImageJ and Hotspotter. Whisker Spots were manually counted for all individuals included in ImageJ and Hotspotter analyses, providing a single score for each individual which is equal to the sum from both the left and right side.

Leopard	ImageJ Total	ImageJ Left	ImageJ Right	Hotspotter Total	Hotspotter Left	Hotspotter Right	Whisker Spots
34F	3	3	0	3	3	0	1
AirstripM	4	3	1	4	3	1	1
AndersonM	2	1	1	2	1	1	1
BahutiM	1	0	1	1	0	1	1
BasileF	4	3	1	4	3	1	1
BeaumontsM	0	0	0	1	1	0	1
BicycleCrossingM	7	4	3	7	4	3	1
BulalaM	4	1	3	4	1	3	1
CampbellKoppiesF	4	1	3	4	1	3	1
CampPanM	3	2	1	3	2	1	1
Dam3F	2	1	1	2	1	1	1
DewaneM	15	8	7	15	8	7	1
DudleyRiverbankF	2	1	1	2	1	1	1
EmsagwenM	7	3	4	7	3	4	1
HlabankunziF	7	2	5	7	2	5	1
HlaruliniF	2	1	1	2	1	1	1
HlaruliniM	2	2	0	2	2	0	1
HomeliteM	1	1	0	1	1	0	1
Hosa0M	2	1	1	2	1	1	1
Hukumuri3YM	2	0	2	2	0	2	1
HukumuriF	1	0	1	1	0	1	1
Indu0M	1	0	1	1	0	1	1
IngridDamYF	1	0	1	1	0	1	1
InyathiniM	2	0	2	2	0	2	1
IslandF	1	0	1	1	0	1	1
JakkalsdraaiF	4	3	1	4	3	1	1
KapenF	5	3	2	5	3	2	1
KarulaF	1	1	0	1	1	0	1
KashaneM	24	11	13	24	11	13	1
KellyDamF	1	1	0	1	1	0	1

Leopard	ImageJ Total	ImageJ Left	ImageJ Right	Hotspotter Total	Hotspotter Left	Hotspotter Right	Whisker Spots
KhokovelaF	2	1	1	2	1	1	1
KigeliaF	4	3	1	4	3	1	1
Kikilezi2016M	1	0	1	1	0	1	1
KikileziF	12	2	10	12	2	10	1
KunyumaM	1	0	1	1	0	1	1
KwatileF	4	2	2	4	2	2	1
KwelaKwelaF	1	1	0	1	1	0	1
LamulaM	5	2	3	5	2	3	1
Lisbon7YM	1	0	1	1	0	1	1
LisbonF	3	2	1	3	2	1	1
LittleBush6YF	2	1	1	2	1	1	1
LittleBushF	2	1	1	2	1	1	1
MafufunyaneM	5	4	1	5	4	1	1
MahlathiniM	1	0	1	1	0	1	1
MakubelaF	3	1	2	3	1	2	1
MakwelaF	4	3	1	4	3	1	1
MambiriM	2	1	1	2	1	1	1
MandleveM	1	1	0	1	1	0	1
ManyelethiM	1	0	1	1	0	1	1
MarthlyM	3	1	2	3	1	2	1
MashabaF	5	2	3	5	2	3	1
MashiabonjM	2	1	1	2	1	1	1
MatshapiriF	2	2	0	2	2	0	1
MawelawelaM	1	0	1	1	0	1	1
MbavalaM	1	0	1	1	0	1	1
MetsiF	2	1	1	2	1	1	1
MobeniF	1	1	0	1	1	0	1
MsuthuF	1	0	1	1	0	1	1
MvulaM	4	1	3	4	1	3	1
MxabeneF	2	1	1	2	1	1	1
MxabeneM	6	3	3	6	3	3	1
0nga1a2013M	3	1	2	3	1	2	1

Leopard	ImageJ Total	ImageJ Left	ImageJ Right	Hotspotter Total	Hotspotter Left	Hotspotter Right	Whisker Spots
0ngaF	3	2	1	3	2	1	1
NdzanzeniF	1	1	0	1	1	0	1
NdziloF	1	0	1	1	0	1	1
Newington32M	3	2	1	3	2	1	1
NewingtonM	3	2	1	3	2	1	1
NgoboswanF	9	4	5	9	4	5	1
NhlanguleniF	3	1	2	3	1	2	1
NkoveniF	3	3	0	3	3	0	1
NottensF	1	0	1	1	0	1	1
NseleF	1	1	0	1	1	0	1
NwetiM	13	10	3	13	10	3	1
NyeletiF	1	0	1	1	0	1	1
NyeletiM	6	3	3	6	3	3	1
OstrichKoppiesF	4	3	1	4	3	1	1
OthawaM	8	5	3	8	5	3	1
QuarantineM	2	1	1	2	1	1	1
RavenscourtF	3	1	2	3	1	2	1
RavenscourtM	10	4	6	10	4	6	1
RidgeRockM	2	0	2	2	0	2	1
RiverRocksM	1	1	0	1	1	0	1
RobsonsM	4	2	2	4	2	2	1
RockDriftM	4	3	1	4	3	1	1
SalayexeF	2	1	1	2	1	1	1
SandRiverM	4	2	2	4	2	2	1
SchotiaF	3	2	1	3	2	1	1
ScotiaF	1	1	0	1	1	0	1
SelatiM	7	3	4	7	3	4	1
ShadowF	2	1	1	2	1	1	1
ShangwaF	4	3	1	4	3	1	1
TambotiF	7	3	4	7	3	4	1
TasselberryF	3	2	1	3	2	1	1
TatowaF	1	1	0	1	1	0	1

Leopard	ImageJ Total	ImageJ Left	ImageJ Right	Hotspotter Total	Hotspotter Left	Hotspotter Right	Whisker Spots
Tavangumi7YM	1	1	0	1	1	0	1
TeardropF	1	0	1	1	0	1	1
TegwaanM	1	0	1	1	0	1	1
ThlangisaF	8	5	3	8	5	3	1
Tinga0M	6	1	5	6	1	5	1
TiyaniF	1	0	1	1	0	1	1
TjellahangaM	3	1	2	3	1	2	1
TorchwoodM	4	1	3	4	1	3	1
TsakaniF	1	0	1	1	0	1	1
TulamanziM	3	1	2	3	1	2	1
TutlwaF	4	3	1	4	3	1	1
Vomba112012M	2	0	2	2	0	2	1
VombaF	5	3	2	5	3	2	1
WallingfordM	7	3	4	7	3	4	1
WarthogWallowF	1	1	0	1	1	0	1
WestStreetM	2	1	1	2	1	1	1
WhiteDam4YM	1	1	0	1	1	0	1
WhiteDamF	3	2	1	3	2	1	1
Xikavi82015M	1	0	1	1	0	1	1
XikaviF	6	1	5	6	1	5	1
XiluvaF	1	1	0	1	1	0	1
XinzeleM	7	4	3	7	4	3	1
XongileF	1	1	0	1	1	0	1
XovonikelaM	3	1	2	3	1	2	1
XuvatiM	1	0	1	1	0	1	1
YoungNottensF	3	1	2	3	1	2	1