

THE SUSCEPTIBILITY OF LEOPARDS (*PANTHERA PARDUS*) TO TROPHY HUNTING



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**Thesis submitted for the degree of Master of Science in Zoology (by Research)
University of Oxford**

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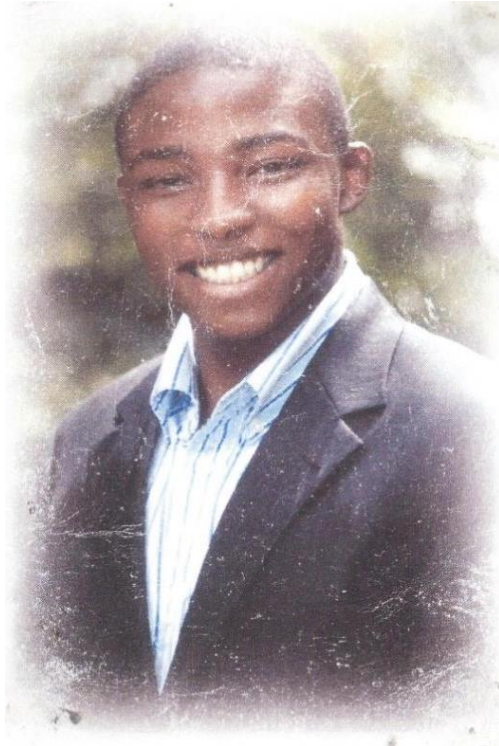
ABSTRACT

The trophy hunting of African leopards *Panthera pardus pardus* may generate revenue to help foster their conservation. However, leopards are sensitive to hunting and populations decline if overharvested. The practice therefore requires careful management grounded in robust estimates of population density/status. Camera-trap surveys are commonly used to establish leopard numbers, and may guide harvest quotas. However, such surveys are limited over wide spatial scales and many African governments lack resources to implement them.

In this thesis I explore the potential use of a harvest composition scheme applied to puma *Puma concolor* in North America, to monitor leopards. The method hinges on the susceptibility of different leopard cohorts to hunting and if this varies, then predictions can be made about harvest composition. Susceptibility is likely to be governed by space use, encounter rates with bait lures (a common method used to attract leopards to hunting hides) and hunter selectivity. Thus in this thesis I explore leopard susceptibility to these factors using a protected leopard population in northern Zululand, South Africa. In my first chapter I examine using scent lures in camera-trapping. Against a backdrop of a passive survey I show adult males, females and sub-adults are captured at similar rates compared to a passive survey using lures. The use of lures does not appear to violate closure assumptions or affect spatio-temporal patterning, but their use appears limited as density estimate precision is not improved.

My second chapter examines ecological (likelihood of encountering a hunter) and anthropogenic (attractiveness to hunters) susceptibility of leopards to trophy hunting. I show that adult males are the most susceptible cohort to hunting (sub-adults least susceptible). I then take the incident rates from ecological and anthropogenic models and create a theoretical harvest composition using population parameters of protected leopards.

My third data chapter departs from hunting susceptibility and examines determinants of leopard trophy package price across Africa. I show that factors such as trophy quality, outfitter leopard hunting reputation and hunt success have little impact on price determination. Instead, overall outfitter reputation and the number of charismatic species in a package are positively correlated with price. These results have important consequences on several sustainable leopard hunting schemes proposed in the literature.



***Dedicated to the memory of Silumko “Slinky” Njenje
my close friend from St Stithians Boys College and an ethical game hunter
who tragically passed away in a car accident on the 13th of July 2008.
The memory of him lives on.***

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CHAPTER ONE:

INTRODUCTION

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CHAPTER 1

INTRODUCTION

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1. Introduction

1.1 The Ecology and Conservation of the Leopard

The leopard *Panthera pardus* is the most widespread large felid on earth (Nowell & Jackson, 1996) and it is found in at least 75 countries over 150 degrees of latitude (Henschel et al., 2008). It has the widest habitat tolerance of any old-world felid, and may be found in tropical forests, savannas, alpine mountains and even true deserts (Busby et al., 2011; Henschel et al., 2011; Hunter & Barrett, 2011). This wide habitat tolerance is owed largely to the leopard's diverse diet. Indeed, as the smallest member of the *Panthera* genus, the leopard has evolved a body size allowing it to exploit the widest variety of prey of any large carnivore, with over 100 prey species recorded in its diet worldwide (Hayward et al., 2006). It prefers bovids in the 10-40 kg weight range (Hayward et al., 2006) but has the ability to subsist on rodents and small ungulates for short periods, and when preferred prey is limited (eg. Henschel et al., 2011; Brackowski et al., 2012). In well-protected prey rich savannas for example, the impala *Aepyceros melampus* often constitutes >60% of its diet (Balme et al., 2007; Owen-Smith & Mills, 2008; Bailey, 1993), while in the rainforests of the Congo basin where bushmeat hunters compete with leopards for medium and large-sized bovids, it subsists primarily off small duikers *Cephalophus* spp. and the brush-tailed porcupine *Atherurus africanus* (Henschel et al., 2011). The leopard may also persist in or near human-dominated landscapes, including those largely devoid of wild ungulate prey (eg. Athreya et al., 2013). In these areas it scavenges upon and hunts livestock and domestic dogs *Canis familiaris* (eg. Butler et al., 2004; Edgaonkar & Chellam, 2002).

This dietary flexibility, coupled with its tolerance for human activity, means it is often the last remaining large felid to disappear from an area (eg. Henschel et al., 2010). Indeed, in many parts of its present day range the leopard is a remnant of a far larger carnivore guild (formerly characterized by species such as lion *Panthera leo*, tiger *Panthera tigris* and spotted hyena *Crocuta crocuta*), and in many of these systems, it now fulfills the role of apex predator (eg. Martins & Harris, 2013; Braczkowski et al., 2012).

The leopard warrants conservation attention for ecological, cultural, existential and economic reasons (Macdonald et al., 2010). Firstly, within its role as an intermediate or apex predator it exudes top-down pressures on lower trophic levels, chiefly through herbivore predation and as a mesopredator suppressor. For example in Malaysia's Pasoh forest, the extirpation of leopards and tigers has led to 10-100 fold increases in wild pig *Sus scrofa* densities compared to populations where these felids are present (Ickes et al., 2001; Ickes & Williamson, 2000). This is significant as a population increase of medium and large-sized herbivores may lead to an increase in browsing pressure and the reduced recruitment of some plant species (Ripple & Beschta, 2008; Ripple & Beschta, 2006). The leopard also serves as a mesopredator suppressor, and probably exudes similar pressures on smaller carnivores, as the jaguar *Panthera onca* does on ocelots *Leopardus pardalis* and puma *Puma concolor* where the three occur in sympatry (Moreno et al., 2006). Additionally one study implemented in Ghana suggests that a local release of olive baboons *Papio hamadrayas* was attributed to the extirpation of leopards and lions (Brashares et al., 2010).

Apart from its ecological and existential values, the leopard is an important economic commodity due to the revenue that it can generate from eco-tourists and trophy hunters (Balme et al., 2010). For example, the leopard is the second most sought after large mammal and also the second most watched species by tourists on safari in South Africa's Shamwari Private Game Reserve (Maciejewski, 2012); similarly it is an important viewing species in South Africa's Kruger National Park (Di Minin et al., 2012). The leopard is also a highly valued hunting trophy in Africa (Johnson et al., 2010) and an individual can fetch in excess of \$24 000 (Jorge et al., 2013). This value is emphasized in countries like Mozambique where it forms the mainstay of the trophy hunting industry (Jorge et al., 2013). Leopard skins and body parts are traded widely in Central, West and southern Africa (Henschel et al., 2011; Ray et al., 2005), and in South Africa skins can fetch between \$430-900 (Brackowski, pers. observation). It may be argued that the leopard has further value as a potential flagship species as it is a valuable 'umbrella' for smaller and less charismatic species (Dickman et al., submitted), and indeed it is used in the marketing schemes of several lodge and tour operators in South Africa's Cederberg and Baviaanskloof mountain ranges (Martins & Martins, 2006).

The leopard is at present listed as Near Threatened on the IUCN's red list (Henschel et al., 2008). The Convention on International Trade in Endangered Species (CITES) has afforded it its highest level of protection through its Appendix 1 conservation listing since 1975 which mandates governments to place a strict control on the international trade of skins and body parts (www.cites.org; accessed 12 June 2013). Although significant populations of leopards still exist in localized parts of sub-Saharan Africa and Asia, it has already disappeared from at least 37% of its

historical range (Ray et al., 2005) and leopards have become extinct in seven countries including Kuwait, Singapore and the island of Zanzibar, and in North Africa and Russia's Primorski Krai, they are on the verge of extinction (Hebblewhite et al., 2011; Henschel et al., 2008).

Similarly to other large felids, leopards are threatened by a variety of anthropogenic activities. Direct threats include retaliatory killings by pastoralists (eg. Balme et al., 2009b; McManus, 2009), poorly-regulated trophy hunting (Balme et al., 2010, Macdonald et al., 2010), snaring and harvest for the skin and body-part trade (Fattebert et al., 2013; Ray et al., 2005). Secondary threats likely to affect leopards spatially include habitat modification (Swanepoel et al., 2012) and snaring of preferred prey (eg. Lindsey et al., 2013). Where people raise livestock, leopard-pastoralist conflict is the most common source of anthropogenic induced leopard mortality, owed both to their actual and perceived predation on livestock (Wang & Macdonald, 2010; Mizutani & Jewell, 1998). Snaring of leopards and their prey is another pervasive activity across much of Africa, and is likely to increase due to the protein demands of rural communities at reserve edges (Lindsey et al., 2013). The illegal trade in leopard skins is also likely to be a major threat to populations in South Africa where the adult male demographic of 5-11 million Shembe Zulu Baptists is required to wear a leopard skin in religious ceremonies (Tristan Dickerson, pers.comm).

For the above reasons, it may be argued that leopard conservation is likely to be a challenge. On the one hand, it is clear that the species deserves management and conservation attention which will ensure its persistence within protected areas and

beyond (Swanepoel et al., 2012). However on the other, the economic requirements of people who occur in sympatry with the species need to be met. There is thus an increased need for the development of species management techniques which will enhance the environmental conditions for such a sympatry to occur (Balme et al., 2013). For example, Funston et al (2013) showed that if Zimbabwean wildlife ranchers hunted a limited number of leopards on the Save Valley conservancy, this would significantly outweigh the costs of any predation by leopards on valuable game species. Similarly, land leased by the “& Beyond” corporation from rural communities in northern Zululand is used as a large wildlife preserve (Phinda) where luxury wildlife viewing safaris are used to generate profit (Hunter, 1998). Leopard sightings on this reserve occur at higher frequencies than surrounding reserves (Shannon Chapman, pers.comm) and contribute to the profits of “& Beyond” (Hunter et al., 2003). However, both of these examples are dependent on rigorous management, and in Save Valley, if trophy hunting is poorly regulated and abused, it's leopard population may decline which will curtail landowner profits. Similarly, Phinda reserve's increased leopard sightings are in large part owed to a series of legislative reforms (Balme et al., 2010; Balme et al., 2009b) which led to a population recovery after 2006. If these had not been made, this may have impacted on the reputation of Phinda as a renowned destination for leopard sightings.

Despite these examples, some may argue that the leopard is less of a conservation priority than the vulnerable lion and endangered tiger (eg. Hunter & Balme, 2004) and indeed, it has lost less of its range, still has several population strongholds in Africa and Asia (Spong et al., 2000) and continues to persist in many regions where tigers and lions have been extirpated (eg. Henschel et al., 2010; Ramakrishnan et

al., 1999). However a pro-active approach to the management of the leopard through corridor establishment, bettered livestock husbandry methods (eg. Balme et al., 2009b; McManus, 2009) and rigorous population monitoring for the establishment of sustainable hunting quotas (eg. Packer et al., 2011; Balme et al., 2010) is likely to prevent the leopard from declining to a position in which tiger and lion populations are currently (see Riggio et al., 2013).

1.2 Problem Context and Thesis Overview

At present there are increased calls by members of the scientific community for leopard research to be targeted at the threats facing leopards across their range of occurrence. Indeed, Balme et al (2013) showed that the majority of leopard studies to date ($n = 232$ peer reviewed articles from 42 countries) have focused on topics such as feeding ecology, space use and inter/intra-specific interactions, with far fewer being dedicated to applied topics. Similarly Pitman's (2012) review of 217 publications with leopards as the focal species, suggested <20% of these pertained to conservation and management of the species. One topic cited by Balme et al (2013) in need of particular research attention is leopard trophy hunting, a poorly understood but widespread practice, presently implemented in 12 African countries (Balme et al., 2010).

Trophy hunting has been listed as one of the most pressing threats to the persistence of leopards in Africa, particularly over a prolonged temporal scale (Balme et al., 2009b; Packer et al., 2009). Although the practice can be managed successfully through limiting offtake and targeting old male leopards (Balme et al.,

2010; Packer et al., 2009), leopards are generally sensitive to hunting. Solitary felids like leopards practice non-parental infanticide and unlike pride living lions, leopard females lack the “safety net” of co-operative defense against infanticidal males (Balme & Hunter, 2013; Packer et al., 2009). Levels of infanticide in populations buffered against anthropogenic mortality are naturally high (>40% of cub mortality; Balme et al., 2012) but the added mortality of adult males shot by hunters, and the resultant turnover in new, incoming infanticidal males has the potential to elevate infanticidal events to levels where females struggle to raise a litter of cub to independence (Balme & Hunter, 2013).

In light of these factors, leopard trophy hunting requires careful management by authorities, particularly in delineating offtake levels. This is lacking in many African countries, and leopards continue to be hunted in the absence of robust information on their population status (Balme et al., 2010). Quotas are usually based upon expert guesstimates and a primitive rainfall-prey biomass model developed for sub-Saharan Africa by Martin & De Meulenaer (1988). Worryingly, leopard hunting has also followed an exponential trend over the previous three decades, from just a few hundred individuals being hunted annually in the early eighties to > 2000 shot in 2005 alone (Palazy et al., 2011).

Camera-trap surveys coupled with capture-recapture statistics may aid researchers and authorities in establishing leopard densities and in turn, these may be used in guiding hunting quotas. However many African environmental ministries are underfunded and incapacitated to implement camera-trap surveys at the scale required to estimate leopard density for robust quota setting (Balme et al., 2010).

Although the quota system is likely to continue to be the *modus operandi* for environmental ministries across Africa, population persistence is a management objective that they recognize as a priority for both trophy hunting and photographic safaris, and achieving that requires reliable data and population management.

For the above reasons it may be argued that there is a need to focus attention away from establishing population density and to monitoring the trends of leopard populations over time. African governments could benefit from the development of practical and cost-effective means which they may use to monitor the sustainability of leopard hunting, and manage their hunting quotas adaptively when necessary. One potential solution may lie in monitoring the sex-age ratios of harvested leopards, a technique used by Anderson & Lindzey (2005) for North American pumas. In essence the technique uses differential vulnerability of cohorts to hunting (Barnhurst, 1986) combined with an examination of harvest composition under varying scenarios of hunting pressure. Resultantly, the varying degrees of deviation from a harvest composition under light or null pressure may reflect changes in demographic composition and population trend. The technique has significant potential in Africa as the majority of ministries that allow leopard hunting collect mandatory post mortem hunt information from hunters (usually photographs and morphometric measurements). However the method requires testing before implementation, particularly in understanding if differential vulnerability to hunting exists within leopards.

In this thesis I first examine whether differential vulnerability to hunting exists in African leopards. Leopards are typically hunted using a carcass bait which is

dragged along a road. This leaves a scent lure on the road, which they may follow to a hunting hide where the carcass bait is hung. Thus, vulnerability may be affected by how leopards respond to encountered scent trails, and in my first data chapter (chapter three) I examine how different leopard cohorts respond to the presence of a scent lure. I perform two camera-trap surveys (a non-lure and treatment survey using lures) on South Africa's Phinda Private Game Reserve and examine if any of three leopard cohorts (adult male, adult female and sub-adult) show an increase in capture rates between the non-lure survey and a survey employing the use of "glob bucket" scent lures (a bucket filled with the matured entrails of leopard prey species). In this chapter I also examine how lures affect the spatio-temporal patterning of leopards and if they contribute to the violation of geographic closure, a process where animals immi/emigrate from the study area (Otis et al., 1978). Finally I examine if the use of lures increases photographic leopard captures and increases the precision of non-spatial and spatial density estimators.

The vulnerability of leopards to hunting is also likely to be affected by (i) the spatial movement of leopards and their likelihood of encountering a hunter (which I term ecological susceptibility) and (ii) the preference of hunters for a particular cohort (eg. adult males) (which I term anthropogenic susceptibility). Thus in chapter four I use four years of historical camera-trap and spatial data of a radio-collared leopard population on Phinda Private Game Reserve. Specifically, I examine the ecological susceptibility of leopards to encountering a hunter, using camera-traps as surrogates for hunters. I then examine anthropogenic susceptibility to hunters through structured questionnaire surveys, which examine the preference of hunters for different age and sex cohorts of leopards. I then combine ecological susceptibility with the

anthropogenic susceptibility for different leopard cohorts and construct a theoretical harvest composition from incident rates derived from general linear models (GLM).

For my fifth chapter I depart from the topic of leopard vulnerability to hunting and conclude my thesis with an investigation of the potential drivers of leopard trophy-hunting package price across the African continent. The economics of the trophy hunting industry has been a topic that has received increasing attention over the previous decade (eg. Lindsey et al., 2013; Lindsey et al., 2012; Lindsey et al., 2007; Samuelsson et al., 2007). However the majority of research has been targeted at the economic significance of the practice (eg. Lindsey et al., 2007; Samuelsson et al., 2007), the drivers of inter-family variation in price (eg. Johnson et al., 2010) and investigations of price-rarity correlations (eg. Prescott et al., 2012; Palazy et al., 2011). There has been considerably less effort dedicated to understanding the potential determinants of trophy package price at the species level and why this varies at regional scales. In chapter five I use the leopard as a model species for investigating the variability in trophy package price at the species level. I create a suite of *a priori* hypotheses, which aim to test potential variability in package price, and I do this based upon available trophy hunting market knowledge (eg. Lindsey et al., 2007). I then identify a suite of potential determinants of trophy package price, and these include quota size, SCI trophy quality, hunter reputability, hunt duration and package species composition. I use these as potential predictors in a set of GLM's to examine the variations in package price. This paper chapter is one of the first in the literature to attempt to examine the potential drivers of hunt package price at the species level and lends important insights into the potential applicability of age-based hunting regulations for leopards, and what product information may be

used by outfitters in order to maximize the profit generated from hunts (in order to better serve conservation activities of the species).

I conclude the thesis with the inclusion of a preliminary draft of a short, technical manual I compiled for young biologists to assist them in the analysis of felid capture re-capture data. The manual is written as a “walkthrough” tutorial and uses the most up to date spatially explicit capture re-capture programmes to analyse a historic camera-trap dataset on leopards from Phinda Private Game Reserve (kindly provided by the Panthera Foundation’s Munyawana leopard programme). From the exploration of raw data to formatting and analysis, it uses proven “R” code which may be easily customized to the personal projects of its users.

The three data chapters featured in this thesis are presented as publication submissions. Although they have the input and commentary of several co-authors, the greater part of their contents is directly attributed to the candidate. This is in accordance with Oxford University’s Examination Schools Rules and Regulations (as stipulated in the December 2013 edition of the GSO-20a form – accessed online on the 29th of December 2013).

CHAPTER TWO:

STUDY AREA

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CHAPTER 2

STUDY AREA

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2. Study Area

2.1 Location and history

The data used in chapters three and four were collected on Phinda Private Game Reserve (27° 51' 30" S , 32° 19' 00" E), a protected wildlife preserve located in the north of South Africa's Kwazulu-Natal province, approximately 80 km from the Mozambique border (Figure 1.1). Phinda was established in 1991 from an aggregation of livestock, wildlife and crop farms and is presently 180 km² in size (Legendijk et al., 2011). It is owned by the Nqobogazi and Mduku rural Zulu communities and is under the custodianship of the "& Beyond" corporation who manage it primarily for wildlife conservation and ecotourism (Trollope et al., 2011). It forms part of the larger unfenced Munyawana conservancy (270km²), an aggregation with the Zuka, Bumbeni, Pumalanga and Mziki landowners (Morgan, 2010). For the purposes of the study site description, I provide information for the entire Munyawana, as Phinda is unfenced and leopards range over the entire conservancy.

The Munyawana is located in the Maputaland-Pondoland-Albany hotspot of biodiversity, an area noted for high levels of biological diversity and endemism (Gaugris & Van Rooyen, 2008). It runs in a North-South direction and is predominantly flat. Altitude rarely extends beyond a few metres above sea level for most of the reserve, except for a few intermittent hills and in the south-west where it reaches 201m a.s.l, at the southern tip of the Ubombo mountain range (Hunter, 1998). The Munyawana has an aggregation of small non-perennial streams as well

as artificial waterholes, which are provisioned in winter by pumped borehole water. Perennial water is limited to the Mzinene and Munyawana rivers, the prior demarcating the reserves southern boundary, while the latter bisects the reserve at its midpoint. On its eastern and south-western border, the Munyawana is surrounded by human settlements as well as an aggregation of varying sized private land holdings, engaged primarily in wildlife ranching and livestock or pineapple farming (Hunter, 1998). The Munyawana's western border is surrounded by the large 40 000 hectare, state owned Mkhuze game reserve, which connects to the iSimangaliso wetland park in the east.

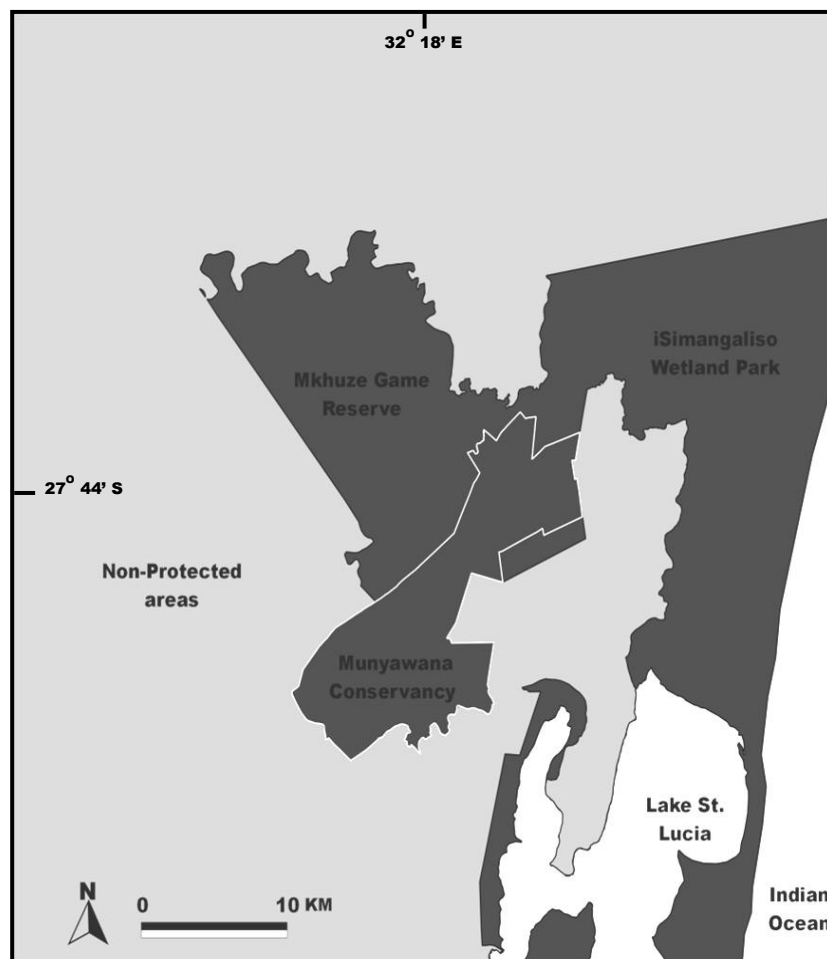


Figure 1.1: Location of the study area demarcating the Munyawana conservancy (white border) and other gazetted reserves as well as non-protected areas in the broader Hluhluwe region.

2.2 Climate

The Munnyawana has a sub-tropical climate characterized by hot, humid summers (November-April) and warm, dry winters with no frost formation (May-October; Lagendijk et al., 2011). Summer temperatures in the region average 33°C, but on some afternoons may reach into the mid-forties. Winter temperatures are mild and average 25.5°C but may drop to a few degrees on some mornings (Hunter, 1998). The Izwelethle weather station, located in the south of the reserve, recorded a yearly rainfall average of 779±47.89 mm between 1995 and 2012, and the majority of this fell within the summer months (Figure 2.2; Naylor, unpublished.data).

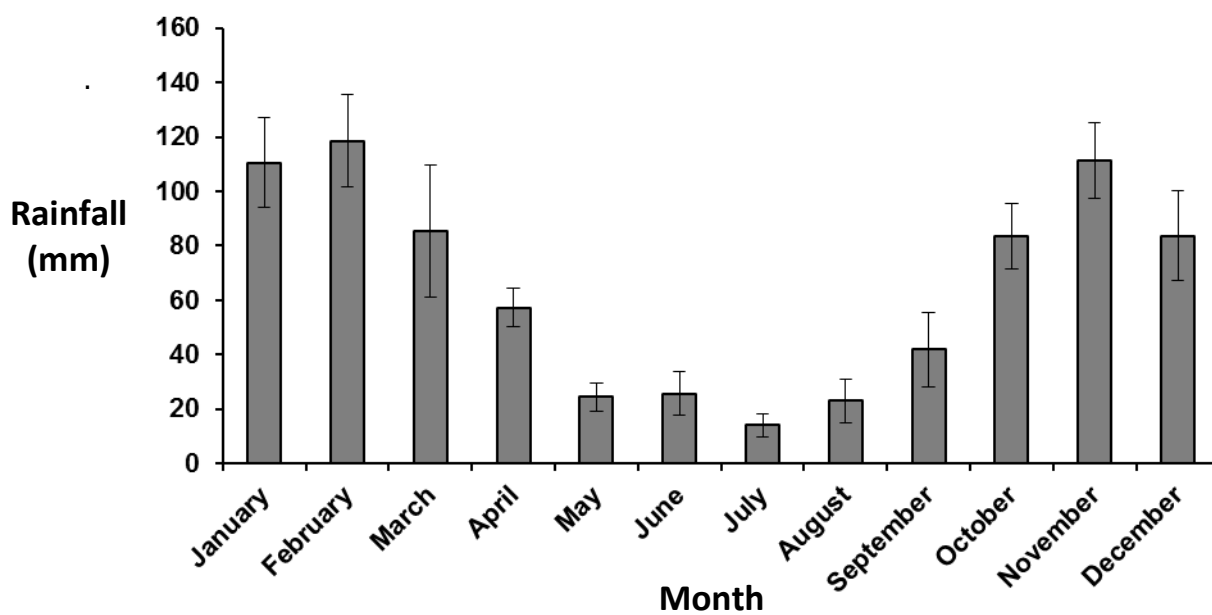


Figure 2.2: Monthly rainfall averages (with standard error) derived from the 1995-2012 rain gauge dataset collected at Izwelethle weather station located in the south of Phinda Private Game Reserve.

2.3 Habitat types

The Muniyawana's landscape is characterized by a mosaic of savanna woodland varieties, as well as a few small patches of endemic and highly threatened sand forest (Druce et al., 2008). Its soils include black-clay and duplex soils which arise from Dwyka, Eccra, Beaufort sedimentary formations as well as Lembombo igneous rock sediments (Trollope et al., 2011). Sandy, acidic soils from ancient dune formations which arose in the Pliocene (Botha & Porat, 2007) may also be found near the centre of the reserve. Many descriptions of the Muniyawana's vegetation exist (eg. Mucina & Rutherford, 2006; Hunter, 1998; Acocks, 1988), however a recent and comprehensive description may be found in Van Rooyen & Morgan (2007) who performed a spatial inventory of the regions flora, human settlements and water bodies. These authors described 23 main vegetation types on the reserve.

Six of the most extensive vegetation communities include the *Acacia nilotica*-*Dichrostachys cinerea* open shrub savanna, *Acacia tortilis* savanna, *Combretum apiculatum* mountain bushveld, *Pteleopsis myrtifolia* open to dense bushveld, *Terminalia sericea* bushveld and woodlands, as well as the highly threatened and fragmented *Drypetes arguta* sand forest (Van Rooyen & Morgan, 2007; Figure 2.3). The *Acacia nilotica*-*Dichrostachys cinerea* and *Acacia tortilis* savannas are classical forms of open shrub savannah. They occur mainly on flat terrain, along drainage lines and fields in the centre and south of the reserve (Van Rooyen & Morgan, 2007). These savannah varieties are dominated by acacia thorn tree species, namely the Nile thorn *Acacia nilotica*, and umbrella thorn *Acacia tortilis*. These are also interspersed with smaller species such as the sickle bush *Dichrostachys cinerea*, magic guarri *Euclea divinorum* and buffalo thorn *Ziziphus mucronata*. The grass

sward in these vegetation communities is comprised of patches of increaser species such as curly leaved love grass *Eragrostis rigidior*, sweet smother grass *Dactyloctenium austral* and numerous *Aristida* species. It also has swathes of more productive grass species such as broadleaf panicum *Panicum deustum* and red grass *Themeda triandra*. The *Combretum apicatum* mountain bushveld is a woodland community found on the foothills of the Lebombo mountains. It is characterized by the red bushwillow *Combretum apicatum*, a semi-deciduous, hard wood species (Hunter, 1998) as well as the buffalo thorn and a dense cover of sickle bush. Herbaceous stems in this savannah variety include red grass and black spear grass *Heteropogon contortus*. The *Terminalia sericea* bushveld is comprised of a medium cover of woodland and is characterized by the occurrence of the silver cluster-leaf *Terminalia sericea*, interspersed with marula *Sclerocarya birrea* and monkey orange *Strychnos spinosa* (Van Rooyen & Morgan, 2007). *Pteleopsis myrtifolia* open to dense bushveld is a dense woodland which occurs in the Central-Northern reserve section. It often borders stands of sand forest and is dominated by a high occurrence of stink bushwillow *Pteleopsis myrtifolia* as well as diagnostic scrubs such as the small red-heart *Hymenocardia ulmoides*, and the Rock jackal-coffee tree *Tricalysia capensis* (Van Rooyen & Morgan, 2007; Hunter, 1998). The *Drypetes arguta* sand forest has a much more limited occurrence on the Munyawana and its physiognomic composition also contrasts with these other communities, resembling a coastal forest rather than a savannah formation. It occurs on sandy, acidic soils and is characterized by large woody stems such as the Lebombo wattle *Newtonia hildebrandtii*, stink bushwillow and false tambotie *Cleisanthus schlechteri* while smaller species include the small red-heart and the small lavender croton

Croton pseudopulchellus (Matthews, 2007; Hunter, 1998). The sand forests understorey is poorly developed with a lack of grass species.

Leopards on the Muniyawana appear to record similar hunting success in its varying habitats, except in grassland where kill rates are significantly lower (Balme et al., 2007). Leopards on the Muniyawana instead prefer to hunt in habitats where it is easier to catch prey (not necessarily where prey is common), and intermediate vegetation cover appears to be the most important variable contributing to hunt success (Balme et al., 2007). The *Terminalia sericea* bushveld and woodlands is one of these optimum habitats, as is the more open palmveld located to the Northeast of the reserve.

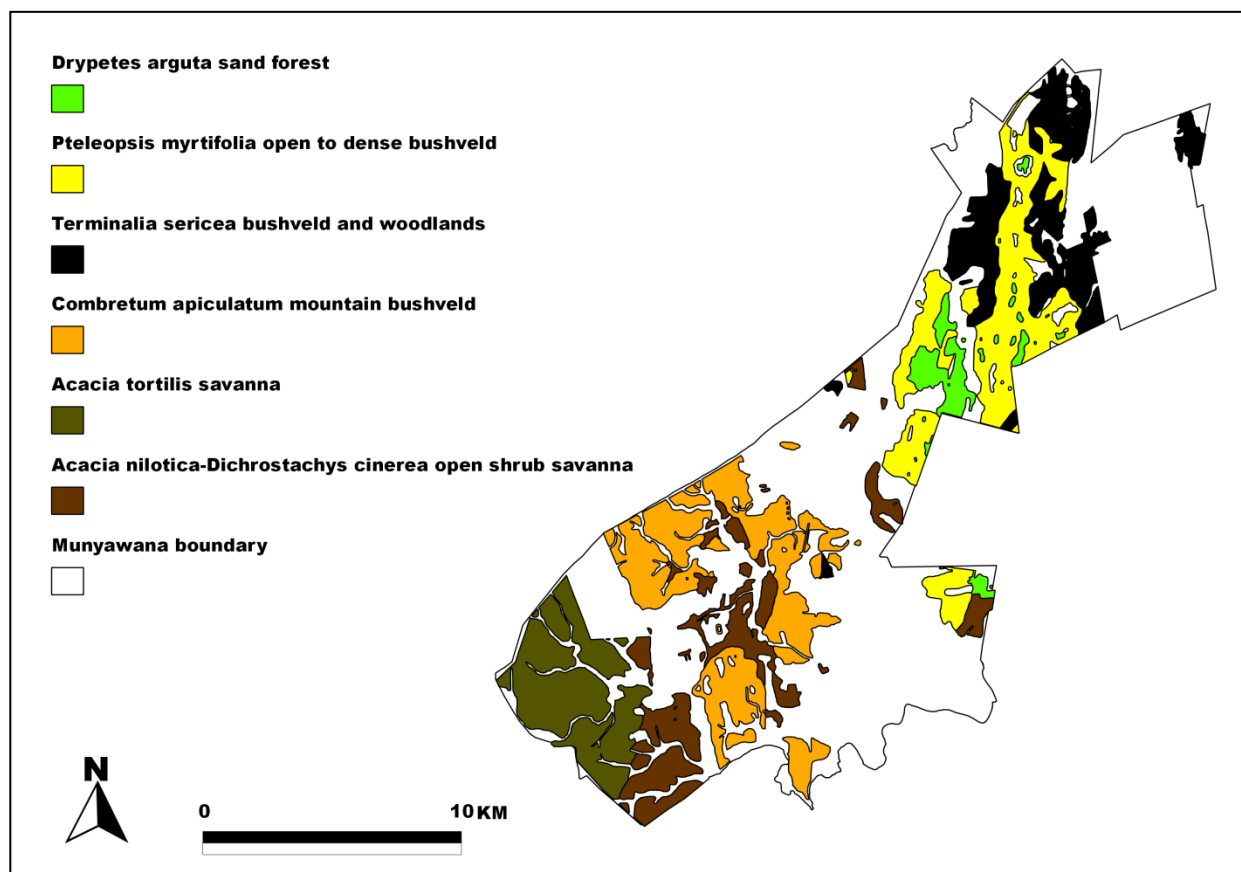


Figure 2.3: The six largest vegetation varieties described by Van Rooyen & Morgan (2007) on the Muniyawana, along with the location of threatened sand forest patches. Mixed bushveld and savanna aggregations comprise the remaining 17 vegetation types, and on this map they are represented by white shading.

2.4 Mammalian assemblage

The Muniyawana has a rich mammalian assemblage characterized by largely complete herbivore and carnivore guilds which were reconstructed over the years since its inception in 1991 (Hunter, 1998). This is notable as prior to Phinda's establishment; much of the regions historically indigenous fauna had been severely depleted or completely extirpated. Notable large mammals (with accompanying population estimates) present on the Muniyawana today include the African elephant *Loxodonta africana* (~100), hippopotamus *Hippopotamus amphibious* (50) and the black and white rhinoceros, *Diceros bicornis* and *Ceratotherium simum* respectively (27 & 137). The larger members of the ungulate community include buffalo *Syncerus caffer* (350), blue wildebeest *Connochaetes taurinus* (500) and plains zebra *Equus quagga* (400). Medium-sized species which comprise important leopard prey include the nyala *Tragelaphus angasii* (4000), impala (2000) and warthog *Phacochoerus africanus* (1000) are also abundant and widespread through the conservancy (Trollope et al., 2011).

The large carnivore guild on the Muniyawana is mostly complete and the extant population of leopards and spotted hyaena present in the early nineties were augmented with the introductions of African lions and cheetah *Acinonyx jubatus* between 1992-1994 (Hunter et al., 2007; Hunter, 1998). The reserve also receives occasional nomads/packs of African wild dogs *Lycaon pictus* from the neighbouring Mkhuze game reserve and the Hluhluwe-Imfolozi Park to the south-west. Several notable smaller mammals on the reserve include the red duiker *Cephalophus natalensis*, suni *Neotragus moschatus* and two primates, the Chacma baboon *Papio ursinus* and vervet monkey *Chlorocebus pygerythrus*. The populations of lion, nyala

and rhinoceros are managed within a limited capacity on the conservancy, primarily through live sales and culling by “& Beyond” management. A selection of camera-trap images of some of these species is provided in Figure 2.4.



Figure 2.4: A selection of small, medium and large-sized mammals caught with Panthera IV camera-traps on Phinda Private Game Reserve in the 2012 survey season. Clockwise from top right, cheetah, African elephant, porcupine *Hystrix africaeaustralis*, spotted hyena, plains zebra, leopard, white-tailed mongoose *Ichneumia albicauda*, white rhinoceros and warthog (All photographs © Alex Brackowski/Panthera).

CHAPTER THREE:

EFFECT OF LURES ON THE RIGOUR AND PRECISION OF DENSITY ESTIMATES FROM A CAMERA-TRAP SURVEY OF A PROTECTED LEOPARD POPULATION

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CHAPTER 3	EFFECT OF LURES ON THE RIGOUR AND PRECISION OF DENSITY ESTIMATES FROM A CAMERA-TRAP SURVEY OF A PROTECTED LEOPARD POPULATION
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3. Effect of lures on the rigour and precision of density estimates from a camera-trap survey of a protected leopard population

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3.1 Introduction

Camera-traps are widely used as a research tool to study cryptic species (O'Connell et al. 2011). In particular, camera-trap data are often coupled with closed capture-recapture (CR) models to estimate the population abundance and density of large carnivores (Tobler & Powell, 2013). This method has recently been strengthened by the incorporation into the CR framework of spatial information on captured individuals, removing the edge effect typically associated with traditional non-spatial estimators (Royle et al., 2009; Efford, 2004). Importantly, the effective survey area is

no longer defined by the inclusion of an ad hoc buffer extending beyond the camera-trap grid (Balme et al. 2009a), but by a homogenous distribution of potential home-range centres, from which density is calculated (Gopalaswamy et al., 2012b).

Despite these recent advances, biologists continue to seek ways to improve camera-trap surveys; most notably, their precision given the low detection rates often associated with camera-trap studies (Gerber et al. 2012). Precise population estimates are required to inform appropriate conservation actions and to monitor the outcomes of management decisions (eg. Balme et al., 2009b). Increasing the number of recaptures can reduce error but it may also violate the fundamental principles of CR; insofar as sampling periods must be short enough to ensure demographic closure (Williams et al., 2002; Karanth & Nichols, 1998); hence, increasing the length of surveys is not necessarily a legitimate option. Similarly, increasing sampling effort by increasing the number of camera-traps deployed is not always logistically feasible (eg. Marnewick et al., 2008). Increasing the precision of camera-trap studies can be improved by augmenting camera-trap data with ancillary biological information (e.g. from faecal DNA; Sollmann et al., 2013; Gopalaswamy et al., 2012a), but this may be practically challenging, particularly at tropical sites where carnivore scat decomposes rapidly (MacKay et al., 2008).

An alternative option that is increasingly used in camera-trap studies is to entice animals to camera-traps by placing an attractant nearby (Thorn et al., 2009). This may be a scent lure such as a perfume/cologne (eg. Brackowski & Watson, 2013; Thomas et al., 2005) or a food attractant that is inaccessible to the animal (eg. Gerber et al., 2012). Baiting is another strategy and entails the use of a food reward such as a carcass or meat (eg. Ariefiandy et al., 2013; Noyce et al., 2001). However,

the use of attractants can be laborious and expensive, and they are only likely warranted if they increase capture rates significantly (Thorn et al., 2009). Attractants may also influence the movement of individuals onto and off the camera-trap grid, potentially violating the assumption of geographic closure (Gerber et al., 2012). Despite this, attractants have been used in camera-trap studies on species ranging from rodents to large carnivores (Lazenby & Dickman, 2013, Ariefiandy et al., 2013; Grant, 2012). Attaining a better understanding of the effects of attractants in camera-trap surveys is necessary to determine whether they are an appropriate means of improving the precision of population density estimates.

In this paper we examine how the use of a scent lure affects the behaviour of African leopards *Panthera pardus* during a camera-trap survey, and the precision of the resultant density estimates. We use leopards as a model species as, like many large carnivores, their numbers are difficult to monitor and there are few reliable population estimates for the species, even though leopards are sensitive to anthropogenic mortality and have suffered significant range loss in recent decades (Ray et al. 2005). Leopards are also important revenue generators for the trophy hunting (Lindsey et al. 2012) and photo-tourism (Di Minin et al. 2012) industries. Accurate and precise estimates of leopard population density are thus required to inform management practices aimed to ensure their long-term persistence (Balme et al. 2013).

We assess (i) whether the use of lures violates the assumptions of geographic closure by examining the spatio-temporal patterning of leopard captures in a passive (ie. non-lure) and treatment survey where we make use of scent lures, (ii) whether the use of lures increases the number of leopard captures and recaptures, and thus

the precision of density estimates in the treatment survey, and finally (iii) the performance and levels of error associated with a traditional non-spatial CR density estimation method and two recent spatially-explicit CR approaches.

3.2 Methods

3.2.1 Study area

The study was conducted on Phinda Private Game Reserve (27° 51' 30" S , 32° 19' 00" E, hereafter Phinda) located in South Africa's Kwazulu-Natal province, approximately 80 km from the Mozambique border (Figure 3.1). Phinda (140 km²) forms part of the Munyawana conservancy (270km²), which is located adjacent to two large protected reserves, the Mkhuze Game Reserve and the St Lucia Wetland Park. Phinda also borders a number of private game reserves, cattle ranches and local communities, which are typically hostile towards leopards (Balme et al. 2009b). The landscape is dominated by savanna interspersed with broad-leafed woodland, grassland and relict patches of Licuati Sand Forest, a threatened and fragmented tropical dry forest with high levels of plant and animal endemism. Further details on the study area and its faunal assemblage may be found in Balme et al (2007).

3.2.2 Camera-trapping

We implemented two camera-trap surveys - a 'passive survey' where no lures were deployed, which ran from 14 August–22 September 2012, and a 'treatment survey' where lures were deployed, which ran from 06 October–14 November 2012. Both surveys were 40 days in length and the spatial layout of camera-trap stations remained consistent (Figure 3.1). We used Panthera[®] IV digital camera-traps, set out

in a paired format across 30 stations, totalling 60 camera-traps. A minimum of two camera-taps were present per mean female leopard home-range (30 km^2 ; Fattebert et al., submitted) to ensure no animal had a zero probability of capture (Balme et al., 2009a). Camera-traps were mounted to wooden posts, 40 cm from the ground and were monitored every four days to replace memory cards and batteries, and to administer lures.

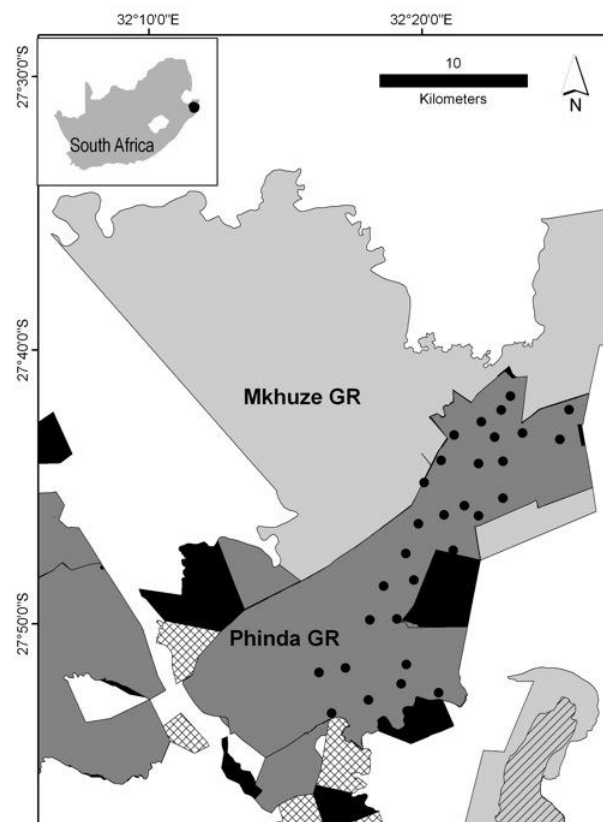


Figure 3.1: The location of the Phinda Private Game Reserve and its 30 station camera-trap array in a wider matrix of varying land use types. Black properties represent small private game farms and hatched properties represent cattle farms. The state owned Mkhuze and St Lucia Wetland Park are shaded in light grey.

Leopards regularly use roads during territorial patrols and are often attracted to decomposing carcasses upon which they scavenge (Bothma & Walker, 1999; Bailey, 1993). Our lure therefore comprised a scent trail of decomposed entrails (from the

three main leopard prey species in Phinda; nyala, impala, and warthog; Balme et al., 2007) that was deposited on the roads along which our camera-traps were placed. The majority of entrails were from nyala that had died during game translocation operations, which Phinda facilitated between June-December 2012. The other species were used if found opportunistically. The scent trail was laid for a distance of 500 metres on either side of camera-traps and refreshed every four days (Figure 3.2). This protocol is similar to that employed by trophy hunters wishing to attract a leopard to a bait near a shooting hide (see Braczkowski et al., submitted). However, as we provided no reward for leopards, we considered our scent trail a lure rather than a bait. We created separate capture histories for leopards photographed in the passive and treatment surveys, in order to compare closure estimates, spatio-temporal patterns and density estimates. The identity of leopards was determined by the unique spot patterns on their pelage (Miththapala et al., 1989), and their sex and age (adult or sub-adult) estimated using distinctive morphological features (Balme et al. 2012). We used a Fisher's exact test (Zar, 1999) to examine differences in capture rates among sex and age classes in the passive and treatment surveys.

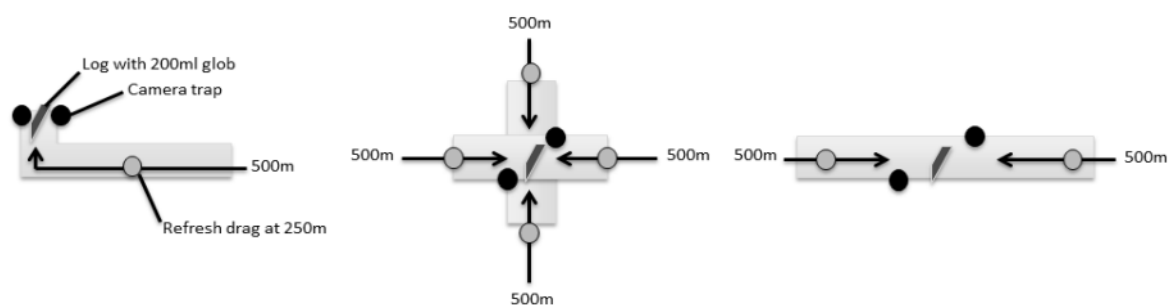


Figure 3.2: Three lure designs tailored to the spatial layout of dirt roads on Phinda. Scent trails were refreshed every 250 metres for each of the three road layouts.

3.2.3 Population closure

Leopards are long lived (up to 19 years in the wild; Balme et al., 2013); hence, our survey period of 40 days seems sufficiently short to assume demographic closure (Karanth & Nichols, 1998). We assessed geographic closure using the closure test of Otis et al. (1978) which assumes heterogeneity in recapture probability. We also used the closure test of Stanley & Burnham (1999) which assumes a variation in time of recapture probability. Both tests were run in the statistical programme *CloseTest* version 3 (Stanley & Burnham, 1999; available online from: <http://www.fort.usgs.gov/products/software/cloctest/>). As a lure has the potential to attract or deter animals from the sampling grid (Gerber et al., 2012; Noyce et al., 2001), a violation in closure will likely be reflected by lower detection rates at camera-traps located at the edge of the sampling grid (Gerber et al., 2012). We therefore tested whether the number of individual leopards and captures recorded on cameras near the edge of our camera-trap grid decreased between the passive and treatment surveys. As the spatial layout of Phinda's camera-trap grid resembles an hourglass (Figure 3.1), we used an MCP to demarcate "edge" camera-traps, and considered those enclosed within the MCP as "core" stations. We considered leopards as core individuals if >50% of their captures were at core camera-traps. The same rationale was used in the identification of edge individuals. We used a chi-square contingency table test with a Yates correction for continuity to examine whether the number of edge individuals and their photographic captures decreased between the passive and treatment surveys.

3.2.4 Spatio-temporal patterning

We followed Gerber et al (2012) in assessing the influence of lures on the spatio-temporal behaviour of leopards during the passive and treatment surveys. We compared the maximum distance moved by individuals detected at more than one camera-trap during both surveys using a Wilcoxon Signed Ranks test (Zar, 1999). We also examined the distribution of times when male and female leopards were captured on camera-traps during the two surveys. We sub-divided the photographic events into five distinct periods (00:00 – 06:00; 06:00 – 12:00; 12:00 – 16:00; 16:00 – 20:00; 20:00 – 00:00) for both males and females and compared their frequencies for both the passive and treatment surveys using a Fishers exact test. We also examined whether a relationship existed between capture rates and the freshness of a scent trail and expected the highest number of captures to be recorded on the day a scent trail was laid, and captures would decline thereafter. Finally due to the variation in road design (Figure 3.2) we examined whether the highest number of events would be recorded in areas with the highest drag effort (eg. 2000 m) through a general linear model. We compared this to the number of events recorded during the control survey on the different road designs.

3.2.5 Density estimation

We used the software CAPTURE (Otis et al., 1978) to estimate leopard population density using traditional, non-spatial CMR analysis. Following Balme et al (2009a), we sub-divided our 40 sampling days into twenty 48-hour sampling occasions, only counting an individual leopard once during an occasion. We used the model selection function in CAPTURE to determine which model best fitted our data. For each survey, we estimated the size of our effectively sampled area by adding a

buffer equal to half the mean maximum distance moved (HMMDM) by individuals photographed on more than one occasion to our camera-trap grid (Balme et al. 2009a). We divided the abundance estimate determined by CAPTURE by the effectively sampled area to estimate leopard density in the passive and treatment surveys.

We also estimated leopard population density at Phinda using two spatially-explicit CR approaches. We used the maximum likelihood based estimator secr (Efford, 2004) and the Bayesian estimator SPACECAP (Gopalaswamy et al., 2012b). These estimators record individual captures as well as spatial information from capture locations in order to estimate density. We followed Athreya et al (2013) and Gopalaswamy et al (2012b) in creating a 15 km buffer around our outermost camera-traps. Within this buffer we placed a homogenously distributed set of potential home-range centres spaced at 0.336 km² intervals (Figure 3.1 SI). We removed non-suitable leopard habitat (> 3 settlements per 0.336 km² grid and the St Lucia lake water body; see Supporting Information for habitat mask creation procedure). Both of these estimators use these home-range centres to model density by relating the probability of capturing a leopard at a particular camera-trap to the distance of the camera-trap from a central point in each leopards home-range (Gopalaswamy et al., 2012b). In secr we modelled leopard density (D) and sigma (σ), which represents a movement parameter of the animal (Gopalaswamy et al., 2012b); as constants (~1), while altering the encounter rate at home-range centres (g0) with five covariates for the passive and treatment surveys (Tables 3.1 SI). We also followed Tobler et al (2013) and Sollmann et al (2011) by including a sex covariate in the model. We maximised models in secr using conditional likelihood as this results in a likelihood

which ignores nuisance parameters within the model. We used Akaike's Information Criterion (AIC) to evaluate our models in secr. We used the corrected AIC (AICc) in the model selection process which penalises models based upon the number of parameters and adjusts for low sample sizes (Boyce et al., 2002). We chose the model with the lowest AICc. If the second ranked model showed a ΔAIC of <2 we used model averaging (except for models using the sex covariate). At present SPACECAP only allows for the creation of a model with trap response present or absent; we present both. For both of these models we ran SPACECAP with 40 000 iterations, discarded 5000 iterations (training the model) and set a data augmentation value of 10x the number of individuals photographed on camera-traps. We assessed model fitness in SPACECAP through the Bayesian *P-value* which is deduced from individual encounter frequencies. A Bayesian *P-value* close to either 0 or 1 is indicative of an inadequate model (Gopalaswamy et al., 2012b). We also assessed whether Markov Chain Monte Carlo (MCMC) chains reached convergence in SPACECAP by examining the Geweke diagnostic statistic (Gopalaswamy et al., 2012b). The Geweke diagnostic statistic provides a measure of chain convergence for the parameters of interest (namely g_0 , sigma and density). If this statistic exceeds a value of 1.6 MCMC chains have not converged. A detailed explanation on CAPTURE, secr and SPACECAP as well as the models used therein is provided in the Supporting Information section.

All statistical analyses were performed in the R statistical environment (R Development Core Team, 2008) and results are provided with means ($\bar{x} \pm S.E$) and standard error as a measure of precision where appropriate.

3.3 Results

Fifteen leopards were captured on 40 occasions during the passive survey, and fourteen leopards on 39 occasions in the treatment survey (Table 3.1). Nine individuals were captured during both surveys. We detected no significant difference in cohort-specific captures between surveys (Fisher's exact test, $p = 0.90$).

Table 3.1: Capture statistics of adult male, adult female and sub-adult leopards during the passive and treatment camera-trap surveys on Phinda Private Game Reserve implemented in 2012.

Survey	Adult male			Adult female			Sub-adult		
	Individuals	Captures	Recaptures	Individuals	Captures	Recaptures	Individuals	Captures	Recaptures
Control	5	20	15	8	17	9	2	3	1
Lure	7	19	12	4	16	12	3	4	1

3.3.1 Population closure

The closure test of Otis et al (1978) suggested no violation of permanent population closure for either the passive ($Z = 1.16$, $p = 0.88$) or treatment ($Z = 1.35$, $p = 0.91$) surveys. Similarly, the test of Stanley and Burnham (1999), which incorporates time variation in recapture probability, suggested population closure for both the passive ($X^2 = 16.94$, d.f = 14, $p = 0.26$) and treatment ($X^2 = 12.20$, d.f = 15, $p = 0.66$) surveys. There was also no difference in the number of edge individuals ($X^2 = 0.02$, d.f = 1, $p = 0.88$) or edge captures ($X^2 = 1.96$, d.f = 1, $p = 0.16$) recorded during the two surveys.

3.3.2 Spatio-temporal patterning

The maximum distance moved by leopards captured on more than one occasion was similar for the passive (mean = 4.95 km, range = 0-11.8 km) and treatment

(mean=5.34 km, range = 0-10.4 km) surveys, and when this was compared for individuals photographed during both surveys we found no significant differences in maximum distances moved ($W = 31$, $p = 0.96$). We found no difference in time-specific captures between the passive and treatment survey for males (Fisher's Exact test, $p = 0.79$) and females (Fisher's Exact test, $p = 0.79$). Our examination of the distribution of leopard captures over the period after a drag, suggested no clear spike, especially on the day or after a drag had been laid (Figure 3.3). Our GLM examining drag effort suggested the highest number of events during the lure survey were encountered on 1500m and 2000 m road drags, contrastingly there was no strong evidence for crossroads (2000m) and t-junctions (1500m) to record the highest events in the control survey (Table 3.3 & 3.4 SI).

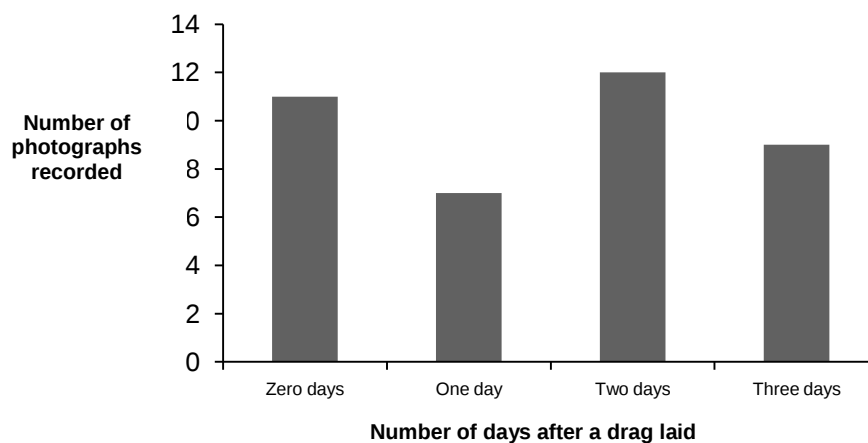


Figure 3.3: Mean number of leopard photographs recorded on the days after a scent trail had been laid on roads.

Most leopards were captured at night (85% of captures in the passive survey and 74% in the treatment survey).

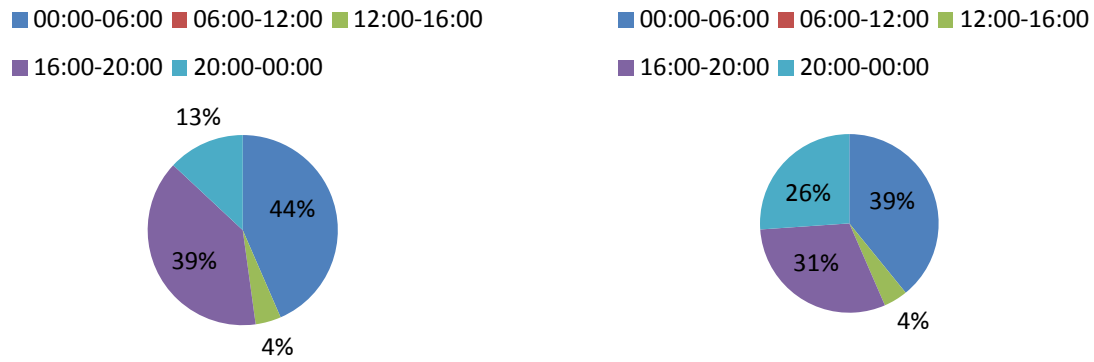


Figure 3.4: Pie chart highlighting the proportions of male leopard photographic event times for a) the passive survey, and b) the treatment survey on Phinda Private Game Reserve.



Figure 3.5: Circular distribution of female leopard photographic event times for a) the passive survey, and b) the treatment survey on Phinda Private Game Reserve.

3.3.3 Photographic captures and density estimates

The heterogeneity model $M(h)$ fit our data best for both the passive and treatment surveys in CAPTURE. Using the jackknife estimator, CAPTURE estimated population abundance at 17 ± 4.3 leopards for the passive survey, yielding a density of 7.28 ± 2 leopards/100 km² when a buffer based on HMMDM (2.48 km) was applied to our survey area (Table 3.2). Population abundance estimated by CAPTURE for the treatment survey was 23 ± 6.6 leopards, resulting in a density of 9.28 ± 2.9 leopards/100 km² with a HMMDM buffer of 2.67 km.

Table 3.2: Critical values including the buffer sized used, density and error of the non-spatial estimator CAPTURE, passive (bk covariate) and treatment (sex covariate) surveys in secr and the null SPACECAP model implemented in 2012 on Phinda Private Game Reserve.

Estimator	Control					Lure				
	Buffer width	Captures	D	SE (SD)	CI	Buffer width	Captures	D	SE (SD) [£]	CI
CAPTURE	2.48	38 ^{\$}	7.28	2	6.00-14.99	2.67	36	9.26	2.9	6.85-18.53
secr	15	40	3.40	1.20	1.73-6.65	15	39	3.47	1.22	1.78-6.79
SPACECAP*	15	40	3.96	1.09	1.91-6.02	15	39	3.42	1.13	1.35-5.59

*The trap absent model is presented for SPACECAP

£ SPACECAP presents a posterior SD while secr makes use of SE

\$ The X matrix in CAPTURE only allows the recording of one event at multiple sites – this is not the case in SPACECAP/secr

The most parsimonious model in secr from our passive survey included the site response parameter and estimated a density of 3.40 ± 1.20 leopards/100 km² (Table 3.3). The most parsimonious model from the treatment survey included the sex variable and estimated a density of 3.47 ± 1.22 leopards/100 km² (Table 3.4). However, the next best ranked model (using the trap response covariate), recorded a ΔAIC of 1.11 and estimated a density of 3.28 ± 1.27 leopards/100 km². The SPACECAP estimator yielded a density of 3.91 ± 1.07 leopards/100 km² for the passive survey in the absence of the trap response variable, and 4.00 ± 1.27 leopards/100 km² using the trap response variable. The SPACECAP density estimate for the treatment survey was 3.51 ± 1.10 leopards/100 km² in the absence of the trap response variable, and 3.58 ± 1.29 leopards/100 km² with the trap response variable.

Table 3.3: Model definitions, AIC scores and density estimates with lower and upper confidence intervals for the 2012 passive survey on Phinda Private Game Reserve created in secr.

Model	No of par	logLik	AIC	AICc	$\Delta AICc$	AICcwt	Density	l.c.I	u.c.I
g0~bk sigma~1	3	-202.97	411.95	414.13	0.00	0.98	3.40	1.73	6.65
g0~1 sigma~1	2	-208.78	421.56	422.56	8.43	0.01	3.39	1.85	6.22
g0~b sigma~1	3	-207.85	421.69	423.87	9.75	0.01	2.79	1.48	5.28
g0~sex sigma~1	3	-208.22	42.45	424.63	10.5	0.00	3.48	1.90	6.41
g0~Bk sigma~1	3	-208.30	422.59	424.77	10.65	0.00	3.40	1.86	6.21
g0~sex sigma~sex	4	-207.10	422.21	426.21	12.08	0.00	3.96	2.10	7.44
g0~h2 sigma~1	4	-208.78	425.56	429.56	15.43	0.00	3.39	1.85	6.22

The Bayes P-values in SPACECAP indicated adequate model performance for all surveys (control survey: trap response absent - $p = 0.53$, trap response present - $p = 0.54$; treatment survey: trap response absent - $p = 0.59$, trap response present - $p = 0.57$) and Geweke diagnostics statistics suggested that MCMC parameters reached convergence in all cases.

Table 3.4: Model definitions, AIC scores and density estimates with lower and upper confidence intervals for the 2012 lure survey on Phinda Private Game Reserve created in secr.

Model	No of par	logLik	AIC	AICc	$\Delta AICc$	AICcwt	Density	l.c.I	u.c.I
g0~sex sigma~sex	4	-191.32	390.63	395.08	0.00	0.49	3.47	1.78	6.79
g0~bk sigma~1	3	-193.89	393.79	396.19	1.11	0.28	3.28	1.58	6.82
g0~1 sigma~1	3	-194.94	395.87	398.27	3.20	0.10	3.40	1.68	6.88
g0~sex sigma~1	2	-196.83	397.67	398.76	3.69	0.08	3.30	1.70	6.43
g0~Bk sigma~1	3	-196.19	398.37	400.77	5.70	0.03	3.31	1.71	6.41
g0~b sigma~1	3	-196.82	399.65	402.05	6.97	0.02	3.23	1.56	6.66
g0~h2 sigma~1	4	-196.00	399.99	404.44	9.36	0.00	3.59	1.78	7.24

3.4 Discussion

An important foundation for estimating population abundance using capture-recapture sampling is geographic closure (Karanth & Nichols, 1998). Lures and other attractants may compromise geographic closure by prompting temporary immigration or emigration of animals into or out of a survey area. However, our results showed that lures had no effect on the distances moved by leopards, the timing of leopard captures or the spatial distribution of captures. Population closure was also confirmed for both our passive and treatment surveys by the Otis et al (1978) and Stanley & Burnham (1999) closure tests. Gerber et al. (2012) similarly found that the presence of a lure did not influence the spatio-temporal behaviour of Malagasy civet

Fossa fossana. They suggested that the Pradel model (Pradel, 1996) was more suitable for evaluating population closure (as it is highly flexible in modelling recapture variation and less susceptible to Type I statistical errors when there is a behavioural effect), but our sample sizes were inadequate to run this analysis. Nonetheless, given our other findings, we are confident that the CR model assumptions were met for both surveys.

The use of lures appeared to have little effect on the behaviour of leopards spatially and temporally. Notably however, although the capture rates for sexes were similar for the two surveys, for the lure survey we recorded only half the number of adult female leopard individuals. It is plausible that certain females are reluctant to approach lure sites. Leopards are an infanticidal species (Balme & Hunter, 2013) and previous studies which reported a marked male bias in the photographic capture rates of leopards on trails in the Kruger Park and Cederberg mountains (eg. Maputla et al., 2013; Martins & Harris, 2013) postulated that this may reflect female avoidance of infanticidal males. Male leopards have also been known to kleptoparasitize carcasses from conspecific females and even kill and consume them (Steyn & Funston, 2006). This may be another reason for the lower number of female leopards photographed during the lure survey.

Importantly, the lure survey did not improve leopard photographic capture or recapture rates, and hence the precision of our abundance estimates using modern spatially explicit methods. This may be due to the limited range over which our lures were effective. Felids do not possess a particularly acute sense of smell (Sunkist & Sunkist, 2002); hence, leopards were only likely to detect scent trails in close proximity. Leopards may also have become habituated to lures over the course of

the study, as no benefit was gained by individuals that followed scent trails. It is also possible that leopards may be more predisposed to scavenging, and thus to respond to lures, in arid areas where prey abundance is lower. Phinda is a productive system and earlier research demonstrated that the leopard population was not constrained by prey availability (Balme et al., 2010). We did however observe a higher number of photographs on camera-traps located on road-crossings and a t-junction during the lure survey (particularly one fourway crossing which recorded eight leopard photographs). This was not observed during the control survey, and may be suggestive that higher lure effort on large road crossings may increase photographic captures. Overall however, luring did not improve the number of photographic captures recorded.

Studies on leopards elsewhere and carnivores more broadly suggest that capture rates may be increased by using baits (i.e. where the target species is rewarded) rather than lures. Grant (2012) placed stillborn cattle fetuses near camera-traps in Mangwe, Zimbabwe, and showed a twenty-fold increase in the number of leopard captures when compared to a failed non-baited survey. Similarly, Du Preez (2014) found that the presence of baits near camera-traps increased leopard captures four-fold in a survey at Zimbabwe's Buby Valley. Although these results appear promising, baits may be more likely to affect the spatial behaviour of carnivores than lures, and may therefore be more likely to compromise geographic closure in CMR studies. Leopards can remain sedentary, feeding on a single carcass for up to a week if it is large enough (Bailey, 1993). Such a change in an individual's daily routine may be significant in the context of a 40-day camera-trap survey. The

detection distance of baits may also be larger than lures, artificially drawing individuals into the sampling area and potentially biasing population estimates.

The density estimates from the two spatially-explicit capture-recapture approaches (maximum likelihood and Bayesian) were comparable, but were significantly lower than estimates derived using traditional, non-spatial methods. This concurs with previous research (Pesenti & Zimmerman., 2013; Noss et al., 2012; Obbard et al., 2010) which shows that non-spatial CR analyses typically overestimate population density by underestimating the distances moved by animals. Furthermore, spatially-explicit CR models are generally more robust to changes in the camera-trap array, the sizes of sampled areas and the movement patterns of individuals (Sollmann et al., 2011). This was reflected in our study by a 27% increase in density estimates between the passive and treatment surveys using the non-spatial estimator, compared to a 2-14% change using spatial estimators. Additionally, our list of density results obtained from our candidate models in secr suggested very similar results (total 80 day range: 2.79-3.96 leopards/100 km²). These results suggest that it was highly unlikely that leopard density varied much over our study given its duration and the short interval between surveys. Our most parsimonious model in our passive survey in secr made use of the site response parameter, and this along with the transient response parameter (Bk) is a model highly recommended by Efford (2013). This result accords with previous studies which found large felids to regularly exhibit a behavioural response to camera-traps (Karanth et al., 2011). Similarly, our two most parsimonious models from our treatment survey made use of the trap response parameter, as well as a sex-specific encounter rate at activity centre and sigma.

The application of scent trails was laborious and difficult to justify for our study given the lack of improvement in the precision of density estimates. However, capture probability in our passive survey was sufficiently high to produce reliable population estimates (Harmsen et al., 2011), even in the absence of attractants. This may not be the case in lower density populations, or for species which are less routine in their movement patterns and thus more difficult to camera-trap. In such cases the use of an attractant may be warranted. For felids, this may require the deployment of baits rather than lures; however, we recommend that this only be done after the effects of baiting on population and spatial parameters have been assessed, preferably using a similar approach as this study (i.e. with a passive and treatment period). Lures may be adequate for species with superior olfactory senses such as hyaenids (Thorn et al., 2009) or viverrids (Gerber et al., 2012), where they are likely preferable to baits.

These results suggested that although using lures did not lead to the violation of CR model assumptions in a savanna environment, it also did not result in increased precision of leopard density estimates, so may be of limited use for researchers. Insights such as these are important in assisting biologists and conservation managers in determining which approaches should be used or avoided for the most cost- and time-efficient method to enumerate leopards. Therefore, this paper may serve as a useful reference to future researchers, in developing an alternative method which may increase leopard recaptures and generate further valuable data for future conservation planning.

3.5 Supporting Information

3.5.1 Explanation of density estimators

CAPTURE is a statistical programme used to implement closed capture-recapture population abundance estimates (Otis et al., 1978). CAPTURE uses seven models to estimate abundance, each varying in their assumptions regarding capture probability. As leopards are territorial, different individuals may have varying numbers of cameras within their ranges (Karanth et al., 2011). They may also exhibit a trap “happy” or “shy” response to cameras. Four models are therefore typically applicable to the analysis of their capture-recapture data (Karanth et al., 2011). These include models M_0 , M_h , M_b and M_t which consider equal capture probabilities, heterogeneity in capture probability, a trap-response behaviour as well as variation from one sampling occasion to another (Otis et al., 1978). We also made use of the more complex mixed-combination models M_{bh} , M_{th} , M_{tb} , M_{tbh} within CAPTURE and a full explanation of these may be found in Otis et al (1978). CAPTURE provides a series of goodness-of-fit and between model statistics as well as a model selection algorithm and suggests the most appropriate model to the user (Karanth & Nichols, 1998; Otis et al., 1978).

The SCR framework estimates animal density from a set of individual animal photographs collected at capture locations nested within a broader network of potential leopard home-range centres (Efford, 2013). It is considered robust to the “edge effects” typical of non-spatial estimators and does not require the user to estimate the effective trapping area around their camera-traps (Efford, 2004). The SCR modelling framework assumes successive animal captures are independent, animal home-ranges are approximately circular and their potential range centres are

distributed in a random poisson point process (Efford, 2013; Noss et al., 2012). Both packages model the distribution of potential leopard home-range centres and distance-dependent detection, with capture probability being a declining function of the distance between home range centres and camera-traps (Efford et al., 2004). The secr package uses maximum likelihood based inference while SPACECAP uses a process known as data augmentation which adds to a dataset of known leopards with an enlarged set of all zero-encounter histories usually in the order of 5-10 times the number of photographed individuals (Gopalaswamy et al., 2012a; Noss et al., 2012). Markov chain Monte Carlo (MCMC), then simulates samples from the joint posterior distribution of the unknown quantities in the given model (Sollmann et al., 2011). SPACECAP currently allows for two model definitions, namely one with trap response present or trap response absent (Gopalaswamy et al., 2012b) and we present both models.

The secr package models the density of animals per hectare (D), the encounter rate at an animal's activity centre (g_0) and the scale parameter (σ) which describes the decline of encounter rate with increased distance from an animal's activity centre (Efford, 2013). We provide a description and explanation of other potential model combinations which we did not run in Table 1 of the Supporting information section.

3.5.2 Habitat suitability mask protocol

Both secr and SPACECAP require the user to create a habitat suitability mask which denotes areas in the landscape which are likely to feature potential leopard home-range centres (Efford et al., 2013; Gopalaswamy et al., 2012b). In order to do this we used the *rgdal* package in R to create a polygon around our outermost camera-traps

and buffered it by 15 km (Gopalaswamy et al., 2012b). This buffer width has been suggested for large carnivores such as tigers *Panthera tigris*, pumas and jaguars (Gopalaswamy et al., 2012b; Noss et al., 2012) and is applied to ensure that animals residing outside it are not detected by camera-traps within the buffered area. We then followed the example of Chapman (2012) and Whittington-Jones (2011) in identifying areas of potential leopard home-range centres. We overlaid human settlement density data (Electricity supply commission, South Africa) over 0.336 km² grids in our 15 km buffer (the recommended range centre spacing; Gopalaswamy et al., 2012b) and removed centres located within a grid with four or more settlements outside of protected reserves (Figure 3.1; SI). Leopards regularly frequent lodges and rest camps in the protected Mkhuze and Phinda reserves and even bear cubs there (Guy Balme unpublished data; Fattebert et al, submitted), we therefore considered these settlement varieties as locations of potential range centres. We believe the approach using human settlements is a prudent one, particularly in the broader landscape outside of Phinda as historic leopard surveys on cattle farms in the region, suggest leopard presence follows a marked decline along the gradient of reserve protection from Mkhuze, Phinda and finally cattle/pineapple farms (Balme et al., 2009b).

For comparative purposes, we used the above criteria in removing settlements from our HMMDM masks created for both the control and lure surveys (Figure 3.1; SI).

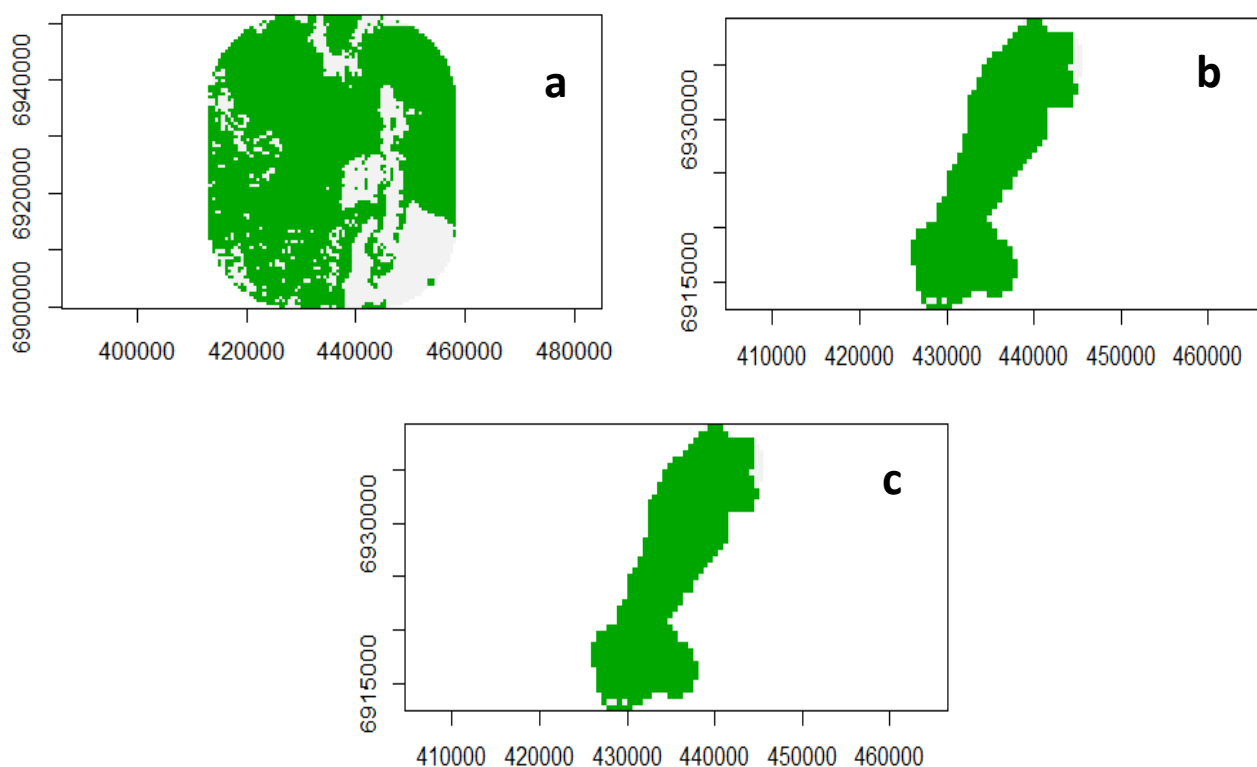


Figure 3.1 SI: Habitat suitability masks generated in R according to human settlement criteria for a) spatially explicit packages *secr* and *SPACECAP* b) CAPTURE using a HMMDM buffer (2.47 km) for the passive survey and c) CAPTURE using a HMMDM buffer (2.67 km) for the treatment survey. Green cells indicate suitable habitat and grey cells denote unsuitable habitat cells containing > 3 human settlements.

Table 3.1.SI: Some default and user generated predictor variables used in the construction of some leopard density models for the Phinda passive and treatment surveys in *secr* (Table adapted from Efford, 2013).

Variable	Description	Variable function
g0~1	Constant	Parameter kept constant across sessions and occasions
g0~b	Learned response	Step change in parameter after initial detection of animal
g0~t	Time factor	One level for each occasion
g0~h2	2-class mixture	Finite mixture model with two latent classes
g0~h2*b	Learned + heterogeneity	Learned response with heterogeneity
g0~T	Time trend	Linear trend over occasions on a link scale
g0~B	Transient response	Parameter dependent on previous occasion detection
g0~bk	Animal x site response	Site-specific step change
g0~Bk	Animal x site response	Site-specific transient response
g0~k	Site learned response	Site effectiveness changes once animal is caught
g0~K	Site transient response	Site effectiveness depends on preceding occasion
g0~Sex*	Sex of animal	Male and female specific detection

*Animal-specific covariate modelled for g0 alone and also as a function of sigma

Table 3.2.SI: Values of encounter rate at animal activity centre (g_0) and scale parameter for the two spatial estimators, secr (bk – passive; sex – treatment) & SPACECAP (null model) derived for the passive and treatment survey on Phinda.

Estimator	Control		Lure	
	$g(0)$	σ	$g(0)$	σ
secr	0.01±0.005	4454.23±916.40	0.02±0.006	4711.64±1260.93
SPACECAP	0.03±0.008	3476.70±566	0.03±0.01	3516±759.70

Table 3.3.SI: Parameter estimates from a GLM evaluating the influence of road structure on the number of photographic events recorded on camera-traps during the control survey.

Coefficients	Estimate	SE	t-value	Pr (> t)
500	0.67	0.82	0.81	0.43
1000	0.79	0.99	0.8	0.43
1500	0.33	2.17	0.15	0.88
2000	2.33	1.64	1.42	0.17

Table 3.4.SI: Parameter estimates from a GLM evaluating the influence of road structure on the number of photographic events recorded on camera-traps during the lure survey.

Coefficients	Estimate	SE	t-value	Pr (> t)
500	0.67	0.61	1.1	0.28
1000	0.49	0.73	0.67	0.51
1500	3.33	1.6	2.08	0.05
2000	3.33	1.21	3.17	0.005

CHAPTER FOUR:

WHO BITES THE BULLET FIRST? EXAMINING THE USE OF HARVEST COMPOSITION AS A METRIC OF LEOPARD PANTHERA PARDUS POPULATION TREND

CONTENTS

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4. Who bites the bullet first? Examining the use of harvest composition as a metric of leopard *Panthera pardus* population trend

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4.1 Introduction

Trophy hunting is a popular form of recreation that can be conducted as a wildlife management tool, and thereby has potential to contribute to species' conservation (Lindsey et al., 2007; Loveridge et al., 2007). It can generate important revenue for landowners, contribute to national GDPs, and hunters may enforce anti-poaching and land management approaches that protect wildlife and natural habitat (Lindsey

et al., 2007). Trophy hunting differs from other forms of harvest (e.g. for bushmeat or the medicinal trade) in that offtake can be regulated and is typically selective, focusing on individuals with attractive secondary sexual attributes such as large horns, tusks or manes (Crosmarty et al., 2013; Whitman et al., 2004; Leader-Williams et al., 2001). However, when poorly managed (e.g. when there is consistent phenotypic selection, young animals are targeted or quotas are too high), trophy hunting can cause social disruption (Milner-Gulland et al., 2003), inheritance of undesirable traits (Coltman et al., 2003) and localized population declines (Packer et al., 2009; Lindsey et al., 2007).

Ideally, trophy hunting quotas should be based on robust population estimates, but wildlife management authorities rarely possess such data because of time, funding and logistical constraints (Clark et al., 2005). Often the only data available are post-mortem reports that include the effort and success of hunts, and the sex and age of harvested animals (Litvaitis & Kane, 1994). Age-sex ratios of harvested individuals can sometimes provide an index of population trend (Bunnefeld et al., 2009; Roseberry & Klimstra, 1974), particularly for wide-ranging, cryptic species such as large carnivores which are difficult to enumerate and are sensitive to the effects of trophy hunting (Anderson & Lindzey, 2005; Lee & Taylor, 1994; Barnhurst, 1986). However, an important caveat of such an approach is that relative susceptibility to hunting varies predictably among age and sex classes. Several factors may influence susceptibility to hunting, most notably the movement patterns of individuals (Barnhurst, 1986; Beecham, 1980) (which we term ecological susceptibility) and their attractiveness to hunters (Mysterud, 2011) (which we term anthropogenic susceptibility), which combine to determine overall susceptibility.

Leopards are one of the most sought-after big game trophies; presently, 12 African countries are permitted by the Convention for the International Trade in Endangered Species (CITES) to export a collective 2648 leopard skins procured through trophy hunting each year (Balme et al., 2010). Due to a widespread paucity of data on leopard numbers (Balme et al., 2013), most range states base leopard hunting quotas on expert guesstimates or an over-simplified model that correlated leopard density to rainfall (Martin & de Meulenaer, 1988) but ignored important factors such as anthropogenic mortality and prey availability (Marker & Dickman, 2005). This is of particular concern as leopards are demographically sensitive to over-harvesting, due to traits such as infanticide by males (Balme & Hunter, 2013; Balme et al., 2009b) which often results in social perturbation (Tuytens & Macdonald, 2000). Moreover, leopards are important revenue generators for hunters (leopards contribute 8-20% of gross national trophy hunting income in East and southern Africa; Lindsey et al., 2007) and photo safari operators alike (Di Minin et al., 2012; Maciejewski, 2012). Many African countries already mandate trophy hunters to provide post-hunt data, which include photographic, morphometric and dental information that can be used to accurately age and sex harvested individuals (Balme et al., 2012). As such, harvest composition has potential as a valuable tool for monitoring leopard populations at scales relevant to management, and so to inform future conservation decisions.

In this paper we use a combination of camera-trapping and radio-tracking in order to determine the ecological susceptibility of leopards to hunting and photographic questionnaire interview data drawn from hunters to assess anthropogenic susceptibility. From these results we assess the relative susceptibility to hunting of

different age and sex classes of African leopards. We then use our results from ecological and anthropogenic susceptibility models and create a theoretical harvest composition using population parameters from a leopard population near an ecological capacity in the Sabi-Sand game reserve.

4.2 Methods

4.2.1 Study Area

We collected data on leopard population dynamics in Phinda Private Game Reserve (27° 51' 30" S, 32° 19' 00" E, hereafter Phinda) between April 2002 and December 2012. Phinda forms part of the Mnyawana Conservancy (270km²) which is located in the Maputaland-Pondoland-Albany Biodiversity Hotspot in northern KwaZulu-Natal South Africa (Figure 4.1). Phinda receives an average of 550 mm of rainfall annually, which falls mainly between October and March. Phinda's vegetation is dominated by several varieties of savanna, but broad-leaved woodland interspersed with grassland is a common physiognomic form found across much of the reserve (Balme et al., 2007). Forty-two large mammal species have been recorded on Phinda, including important leopard prey such as the nyala, impala and warthog (Balme et al., 2007). Phinda also has a functionally complete large carnivore guild, with resident populations of re-introduced lion and cheetah, and native spotted hyena, leopard as well as transient African wild dog *Lycaon pictus* populations (Balme et al., 2007).

4.2.2 Likelihood of encountering a hunter (ecological susceptibility)

Leopards are usually hunted from a stationary hide or blind positioned 50-80 m from a bait (typically the carcass of a locally common prey species) hung in a tree (Grant,

2012). We used camera-trap data to estimate the relative frequency that different age and sex classes of leopards encounter blinds. Hunters typically drag baits along game trails or dirt roads for 500-1000 m to lure an animal to a blind (Grant, 2012). The likelihood of an individual responding to the lure may vary in a population (Ferreira & Funston, 2010), but we demonstrated that response rates (as determined by photographic captures) was similar among leopard age and sex classes at our study site (Brackowski et al., submitted; Chapter 3). We were therefore confident that the absence of a bait at camera-trap stations was unlikely to affect our cohort-specific encounter rates.

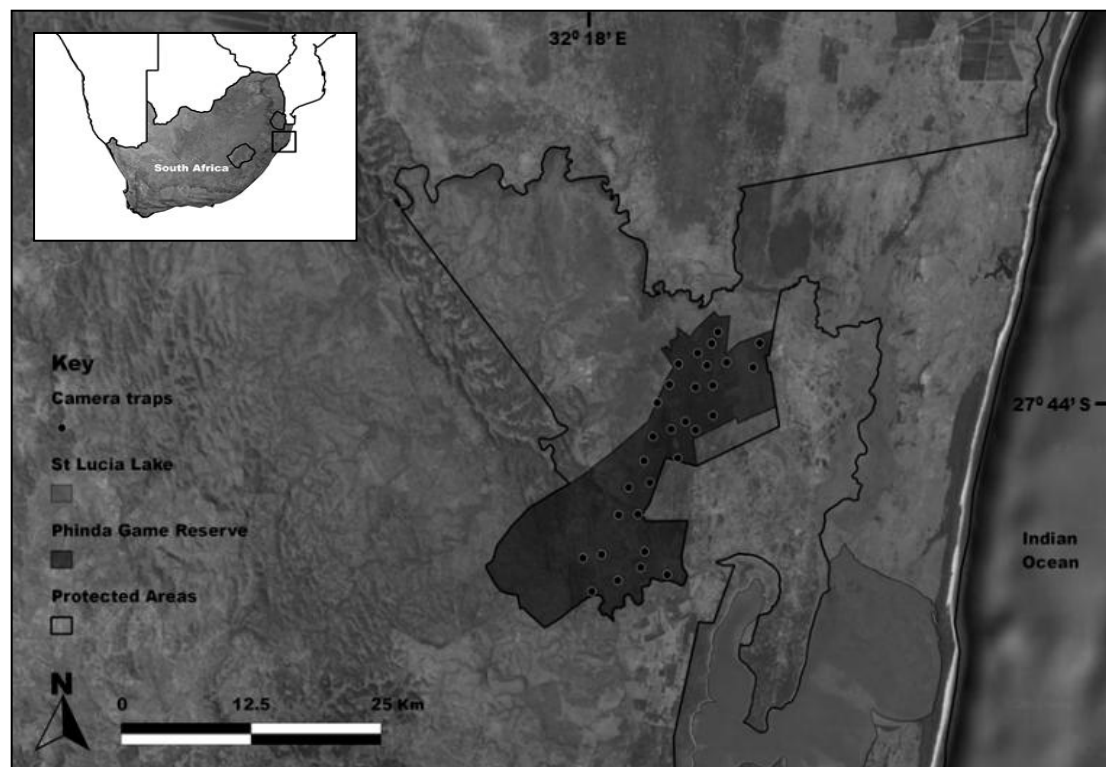


Figure 4.1: Location of the Phinda Private Game Reserve and its 30 camera-trap station array. The protected Mkhuze game reserve and broader unprotected landscape are also provided for

We undertook four 40-day camera-trap surveys in 2005, 2007, 2009 and 2011. All surveys took place during the dry season. We deployed 30 paired stations, comprising 35-mm Deercam[®] Dc300 (Deercam, Park Falls, WI, USA) and Panthera[®]

IV digital camera-traps, across 140 km² (Balme et al., 2009a). Hunters usually only set 3-5 baits during a leopard hunt and the mean size of property on which leopard hunts are conducted in KwaZulu-Natal is 15 km² (G. Balme, unpublished data). Hence, the density of camera-traps in our study area was comparable to the density and spacing of baits deployed during a typical leopard hunt. The distribution of camera-traps also ensured that no leopard had a zero probability of being captured (i.e. ≥ 4 stations were present in the mean female leopard home-range recorded on Phinda; mean = 29.4 ± 1.5 km²; Fattebert et al., submitted). Camera-traps were checked every 2-3 days to replace batteries and film, and download images. Individual leopards were distinguished using their unique pelage patterns (Miththapala et al., 1989) and assigned to one of three demographic cohorts based on their morphological characteristics (Balme et al., 2012): 1) adult males >3 years; 2) adult females >3 years, and 3) sub-adults of 1-3 years. We grouped male and female sub-adults as we found no difference in the mean numbers of photographs recorded between sexes (Two-sample t-test; d.f = 1; t = 0.88; p = 0.54). If a leopard changed cohort from one year to the next (i.e. a sub-adult became an adult), it was re-assigned to the appropriate demographic class (Noyce et al., 2001).

For each of the four camera-trap surveys, we investigated how many times each member of a cohort encountered a camera-trap station, correcting for the proportion of time they spent in the survey area. A sample of leopards was radio-collared throughout the study (see Balme et al (2007) for full details of capture and immobilization); hence, we used radio-telemetry data to estimate the proportion of time leopards spent in the survey area. In order to provide sufficient spatial data, we present three months of radio-telemetry data, with each 40-day camera-trap survey

nested in the middle of the three months. We only used one location per individual per day to ensure data from VHF and GPS collared leopards were comparable (Balme et al., 2010). We added a buffer equal to the mean camera-trap spacing (1.67 km, Figure 4.2) to the outermost camera-traps, and divided the number of telemetry locations recorded for each leopard inside the buffered survey area by the total number of telemetry locations collected over the three-month radio-tracking period.

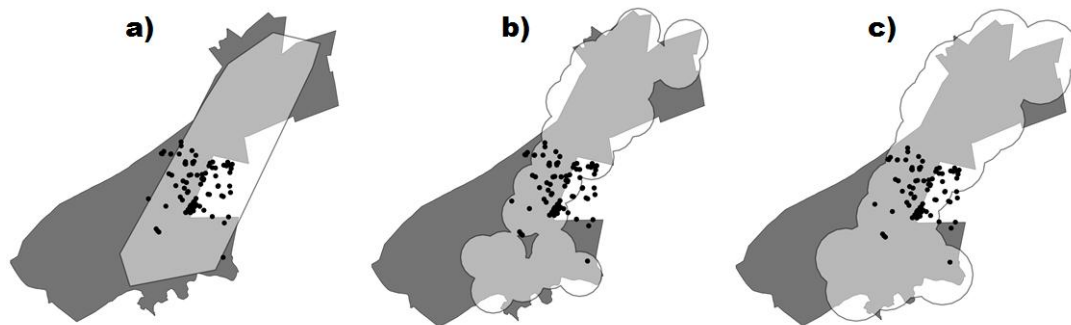


Figure 4.2: Comparisons between a) Minimum convex polygon, b) Mean camera spacing and c) Mean maximum distance moved outside study area buffers with the points of male leopard M62 during the three month radio-tracking period in 2011.

We used a General Linear Model (GLM) to assess cohort-specific encounter rates to camera-traps. We examined the effects that cohort, year and the relative time spent by individual leopards in the survey area had on the total number of captures recorded for each collared leopard. The relative time each leopard spent within the survey area was used as the offset parameter in the model and we censored any animal with <10 telemetry locations for a given 3-month period. To test the robustness of using a minimum threshold of ≥ 10 locations for each leopard, we created a second model using only animals with ≥ 30 locations and compared those parameter estimates to the original model. Models were fitted with a negative binomial distribution using the MASS package in R (Venables & Ripley, 2002) as this

provides a better fit for over-dispersed count data when compared to the traditional Poisson distribution (Venables & Ripley, 2002).

We hypothesized that leopards would exhibit varying susceptibility to trophy hunting due to both the differences in their movement patterns and preference by trophy hunters. We hypothesized that adult leopard males would be recorded on camera-traps with a higher frequency than adult females and sub-adults due to (a) males ranging more widely (Mizutani & Jewell, 1998; Bailey, 1993) and (b) potential avoidance of trails and roads by females, which are frequently patrolled by adult males (Maputla et al., 2013; Martins & Harris, 2013). We also hypothesized that due to their occupancy of temporary home ranges (Sunquist, 1983), sub-adult leopards would be photographed at a lower rate when compared to adults, and due to their smaller size would not be sought after by hunters.

4.2.3 Attractiveness to hunters (anthropogenic susceptibility)

We examined the relative attractiveness of leopard cohorts to trophy hunters using a structured questionnaire survey. Survey participants (Professional hunters - PH) were randomly selected from the membership lists of national professional hunting associations from the seven main leopard hunting countries (Balme et al., 2012). The questionnaire contained 25 side-profile photographs (minimum 300 ppi; Figure 4.3) of different known-age and sex leopards from a long-term study in the Sabi-Sand Game Reserve, South Africa (Balme et al., 2012). Hunters were asked whether they would decide to shoot a leopard, and on which day during a 14-day hunting safari they would make this decision (14 days is the typical duration for leopard hunts in East & southern Africa; Booth, 2009). Responses were placed on a

numeric ordinal scale (a) 3 = willing to shoot on the first day of a 14-day safari; (b) 2 = willing to shoot on the seventh day of a 14-day safari; (c) 1 = willing to shoot on the fourteenth day of a 14-day safari (d) 0 = unwilling to shoot the leopard at any stage of the hunt. Hence, our ordinal scale reflected trophy preference, with scores closer to three more attractive to hunters than those closer to zero. We used the same demographic cohorts used in the camera-trap analysis to build two GLMs: the first examined leopard attributes, i.e. the effects of leopard age and sex on the average score that each photograph achieved, and the second explored the effect of hunter attributes, i.e. the effects of hunter experience, in terms of the number of years that the PH had guided hunts, the number of leopard hunts they had guided, and the number of countries in which they had hunted leopards, on the average score assigned to photographs. Importantly, the hunter preference for different leopards (as determined from the questionnaire survey) serves as a proxy to what is actually hunted.

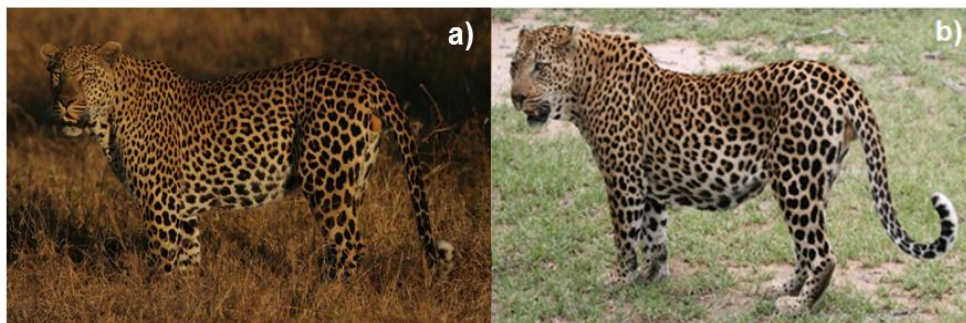


Figure 4.3: Comparisons of photograph presentations used in our hunter selectivity tests. Photograph a) is a six and a half year old male and b) is an 11^{1/2} year old male; all photographs in the test were taken in South Africa's Sabi-Sand. Each hunter had to assign a score (based on their inclination to shoot a leopard during a 14 day hunt) for each leopard shown in the questionnaire. The age and sex of leopards was censored from hunters.

We hypothesized that photographs of adult male leopards would score significantly higher than those of adult female and sub adults due to their larger body size (Balme

et al., 2012). We also hypothesized that more experienced hunters would exercise greater caution in deciding to shoot animals, and therefore record lower scores than less experienced hunters.

4.2.4 Construction of a theoretical harvest composition

We constructed a theoretical harvest of harvest composition (in percent units) using the incident rates from leopard encounters with camera-traps (ecological model) obtained on Phinda, corrected using the incident rates from our hunter selectivity surveys (social model). We used cohort ratios from an intensively studied protected population of leopards in the Sabi-Sand game reserve (Balme et al., 2012). A five year population mean comprised 21.4 ± 1.03 adult males, 34 ± 0.84 adult females and 17.6 ± 1.81 sub-adults. This yielded a 5 year proportion of 29.31% adult males, 46.57% adult females and 24.11% sub-adults. Using these proportions we constructed the following formula:

$$P1 = \frac{n1 * er1 * hr1}{\sum(n * er * hr)} * 100$$

We derive the expected proportion of each cohort (P1) in the harvest whereby $n1$ is the proportion of individuals present in a cohort derived from the Sabi Sand population, $er1$ is the cohort-specific estimate derived from our GLM examining camera-trap encounters (ecological susceptibility) and $hr1$ is the cohort-specific estimate derived from our hunter survey (anthropogenic susceptibility). Because our offset parameter was expressed as a percentage, we multiplied the cohort-specific estimate (expressed as its exponent) from our ecological model by 100.

All statistical analyses were performed in the R statistical environment (R Development Core Team, 2008) and results are provided with means ($\bar{x} \pm \text{S.E}$) and standard error as a measure of precision.

4.3 Results

There were on average 1.8 ± 0.8 adult male, 4.5 ± 0.6 adult female, and 3.5 ± 0.8 sub-adult leopards radio-collared in the study population during the four surveys. We obtained 19.3 ± 3.9 photographs of adult male leopards per survey, 6.0 ± 3.1 of which were collared ($35.21 \pm 17.6\%$ of total captures). We obtained 19.3 ± 0.1 photographs of adult females per survey, 13.8 ± 2.8 of which were collared ($74.6 \pm 37\%$ of total captures). We obtained 7.8 ± 2.6 photographs of sub-adults and 4.3 ± 2.6 of these were collared ($55 \pm 27.5\%$ of total captures). These proportions were significantly different across the cohorts over the four surveys (Pearson chi-square; $X^2 = 11.1$; d.f = 1; $p = <0.0001$). The proportions of collared, collared photographed and total photographed leopards for each cohort can be found in Supporting Information (Figure 4.1 SI).

4.3.1 Likelihood of encountering a hunter and model sensitivity

On average, we used 119 ± 67 telemetry locations (range = 14-217) from 9.75 ± 0.65 individuals (range = 8-11) to construct our GLM (Table 4.1). Although not significant, ($F_{(2,36)} = 2.83$, $p = 0.07$), adult female leopards (mean = $92.39\% \pm 1.44$) typically spent more time inside the survey area than did adult males (mean = $84.71\% \pm 7.74$) and sub-adults (mean = $73.86\% \pm 8.57$).

Table 4.1: GPS points, photographic events and relative time spent in the study area by collared leopards on Phinda Private game reserve, South Africa (2005-2011).

Year	Cohort	Collared individuals	Total number of telemetry locations	Telemetry locations inside study area	Mean relative time inside study area	Number of captures (collared population)	Number of captures (total population)
2005	♂	4	217	157	72.35	14	16
	♀	5	175	166	94.86	18	21
	Subs	2	55	52	94.55	2	2
2007	♂	1	14	14	100.00	2	10
	♀	4	138	120	86.96	11	12
	Subs	6	114	77	67.54	12	16
2009	♂	0	NA	NA	NA	0	27
	♀	6	96	88	91.67	20	21
	Subs	2	21	20	95.24	1	5
2011	♂	2	179	144	80.45	8	24
	♀	3	164	158	96.34	6	23
	Subs	4	139	90	64.75	2	8
Total		39	1312	1086	84.20	96	185

A log-likelihood ratio test comparing a model incorporating cohort, year and offset as predictors versus a model omitting cohort, suggested that cohort was a statistically significant predictor of camera-trap capture rates ($p=0.05$; $d.f=2$; $X^2=5.79$). However, we removed the influence of year from our final model as it was not a significant predictor of captures, and the model discounting year yielded a lower AIC score (AIC=155.63 compared to AIC=160.31) and also featured lower overdispersion (null deviance: 52.09 on 38 d.f vs 52.90 on 38). Exponentiation of our GLM coefficients indicated that adult male (estimate = 4.00) and adult female (estimate = 3.27) leopards were similarly likely to encounter a camera-trap, when accounting for the proportion of time they spent in the survey area (Table 4.2). Sub-adults (estimate = 1.64) were less likely to encounter a camera-trap than were either adult males or adult females (Table 4.2). Our second GLM including only animals with ≥ 30 telemetry locations performed similarly to the original model, except for sub-adult parameter estimates which were near significant (Table 4.1 SI).

Table 4.2: Parameter estimates from our GLM camera-trap encounter GLM using only collared animals with ≥ 10 telemetry points.

Coefficients	Estimate	2.5% CI	97.5% CI	Exponentiated estimate	Std.error	z-value	Pr (> z)
Intercept (Adult females)	-3.42	-3.79	-3.06	3.27	0.19	-18.36	<0.005
Adult males	0.2	-0.48	0.87	4	0.35	0.58	0.56
Sub-adults	-0.69	-1.38	-0.03	1.64	0.34	-2.01	0.04

Residual deviance: 46.24 on 36 d.f

AIC: 155.63

Theta: 3.42

4.3.2 Attractiveness to hunters

The questionnaire survey was completed by 39 professional hunters that had hunted leopards in Botswana, South Africa, Namibia, Tanzania, Zambia and Zimbabwe. Our GLM assessing the relative attractiveness of cohorts to hunters suggested that both the sex ($F_{(1, 22)} = 14.83$, $p = <0.005$) and age ($F_{(1, 22)} = 13.97$, $p = < 0.05$) of leopards were significant predictors of mean photograph score. A Tukey HSD test revealed that adult males (mean = 2.66 ± 0.12) scored significantly higher than adult females (mean = 1.31 ± 0.30) and sub-adults (mean = 0.90 ± 0.17 ; Table 4.3), suggesting they were more desirable as trophies. Our GLM examining hunter experience revealed that hunters that had hunted for longer scored significantly lower than less experienced hunters ($F_{(1,33)} = 9.18$, $p = <0.005$), which suggests more conservatism during hunting. Similarly hunters which guided more hunts scored lower than those with fewer hunts, and this difference approached significance ($F_{(2,33)} = 3.73$, $p = 0.05$), again suggesting more caution. The number of countries hunted in did not affect scores ($F_{(2,33)} = 0.11$; $p = 0.90$). These results suggest more experienced hunters were more likely to shoot the preferred leopard cohort (ie. adult males). The incident rates from our GLM examining the effect of cohort on hunter score, and those used in the construction of our theoretical harvest composition can be found in Table 4.3.

Table 4.3: Parameter estimates from a GLM exploring the effects of cohort on leopard photograph score as derived from 39 completed hunter selectivity tests.

Coefficients	Estimate	2.5% CI	97.5% CI	Exponentiated estimate	Std.error	t-value	Pr (> z)
Intercept (Adult females)	1.31	0.72	1.91	3.71	0.29	4.6	<0.005
Adult males	1.35	0.63	2.06	14.30	0.34	3.91	<0.005
Sub-adults	-0.42	-1.16	0.32	2.44	0.36	-1.17	0.25

Residual std.error: 0.64 on 22 d.f

4.3.3 Construction of a theoretical harvest composition

The theoretical harvest composition derived from our ecological (camera-trap encounter) and anthropogenic (hunter selectivity test) GLM model parameter estimates provided a harvest proportion of 24% adult females: 72% adult males: 4% sub-adults.

4.4 Discussion

Our results support the hypothesis that leopards exhibit varying susceptibility to trophy hunting and suggest that adult male and female leopards share a similar risk of encountering a trophy hunter, but that adult males are more vulnerable to harvesting as they are preferred by hunters as trophies. Sub-adult leopards are the least susceptible demographic class to trophy hunting as they would seldom encounter a hunter and, even if encountered, are less desirable as trophies. We have provided a theoretical harvest composition for a protected leopard population at capacity. Deviations from this could be used to track changes in population status, or at least indicate that a leopard population is over-exploited (particularly if a link is made between cohort ratios and population size via an independent cross validation method). A proportional increase in adult female and particularly sub-adult leopards

in a harvest may be suggestive of a population in decline due to over-exploitation of the population, particularly under increased harvest rates, since the most vulnerable cohort (i.e. adult males) is likely to be depleted first (Anderson & Lindzey, 2005). Anderson & Lindzey (2005) showed this to be the case in their study and the increase of adult female puma coincided with decreased population size. Conversely, we suggest a proportional increase in the number of adult male leopards harvested, all else being equal, may suggest an increasing population.

Our findings differ from susceptibility indices estimated for puma *Puma concolor*, which suggest transient males are most susceptible to harvesting (Barnhurst, 1986). This highlights the need for determining species-specific estimates of vulnerability to hunting, which incorporate the main hunting method used (for puma this is mainly hounds, while for leopards, carcass baits). Interestingly, we did not record a marked male-bias in capture rates as documented by other camera-trap studies on leopard (eg. Maputla et al., 2013; Martins & Harris, 2013) and jaguar *Panthera onca* (eg. Conde et al., 2010, Miller & Miller, 2005). We attribute this to the concentration of camera-traps in our survey area, which appear to have captured the movements of adult females satisfactorily (Balme et al., 2009a).

The lower encounter rates recorded for sub-adults are likely due to their spatial patterns. Dispersing sub-adult carnivores (Fattebert et al., submitted; Sunquist, 1983) often establish small, temporary home ranges in which they settle for a few months before making a considerable foray (Fattebert et al., 2013). Beier (1995) for example found that dispersing Californian pumas occupied home ranges as small as 2% of the size of adult male ranges, sometimes for several months, and indeed this

has been demonstrated in leopards (Fattebert et al., 2013). Such confined movement would strongly reduce the probability of a sub-adult encountering a camera-trap. Exploratory forays by sub-adults outside of these ranges may also lower their detection probability. The low number of sub-adult leopard photographs may also be aligned to the “landscape of fear” model, traditionally used to explain predator-prey interactions (e.g. Berger, 2007; Laundre et al., 2001). Camera-traps in our study were located along game trails and roads frequently used by adult male leopards to patrol their territories (Maputla et al., 2013; Henschel & Ray, 2003). Sub-adults may avoid these areas to reduce the risk of encountering resident conspecifics likely to be hostile. (Female jaguars used a similar strategy to avoid adult males in several South American camera-trapping sites (Palomares et al., 2012). Sub-adult lions in Hwange National Park, Zimbabwe also avoided large trails due to their popularity with older resident conspecifics (Elliot in prep).

The relative attractiveness of leopards as trophies appears to be solely a function of their size. Leopards exhibit striking sexual size dimorphism, with adult males typically 60% larger than females (Hunter & Barrett, 2011) and it was thus unsurprising that males were preferred by hunters. Adult females and sub-adults, in contrast, are similarly sized (Hunter & Barrett, 2011) and hunters showed no preference for either class. Our results support the findings of (Balme et al., 2012) which suggested hunters could distinguish mature males but not females and sub-adults. Worryingly, many hunters (87% of respondents) were still willing to hunt a female at some stage during a hunt, even though this is illegal in most countries (Balme et al., 2010). Using genetic data, Spong et al (2000) similarly showed that females comprised 27% of 77 leopard trophies hunted in Tanzania between 1995 and 1998, even though only

males can be hunted there legally. The hunting of adult females has important ramifications for population viability as they are the key reproductive unit (Daly et al., 2005) and are typically more difficult to replace than adult males, due to male-biased dispersal (Anderson & Lindzey, 2005). Stipulating (and strictly enforcing) that only mature, adult males can legally be hunted will essentially eliminate the possibility of hunters mistakenly harvesting females. Restricting offtakes to males aged ≥ 7 years would further improve the sustainability of trophy hunting, as by this age male leopards have had the opportunity to rear at least one litter to independence which is sufficient to ensure population persistence (Packer et al., 2009). However leopard trophy hunters may require training in aging techniques and the aging test results of Balme et al (2012) suggested hunters were less proficient in aging leopards when compared to guides and scientists.

4.4.1 Caveats and concerns

Importantly, our measures of leopard trophy hunting susceptibility have a number of limitations, and this places a need for ground-truthing of the theoretical harvest composition provided here. Firstly, although our hunter preference test suggests trophy hunters prefer adult male leopards, it is possible that an adult male leopard will not always encounter a bait. This is motivated by the fact that leopard hunts typically last 14 days (contrastingly our parameter estimates are taken from camera surveys which took 40 days – albeit, we only made use of collared individuals). Trophy hunter preferences therefore represent a proxy for what is really hunted. We also appreciate that although the hunters examined in our trophy test were not provided with the age/sex of the animal presented, the preferences reflected in this study may not be an accurate representation of what they will actually shoot in the

field. A field study undertaken in Tanzania showed that adult females constituted nearly 30% of a sample of skins obtained from trophy hunts (despite it is illegal to hunt them there). This pattern is consistent for leopards advertised on outfitter websites which are represented mainly by individuals estimated to be between 2-7 years of age (ie. Prime and young adults; Chapter 5, this thesis).

Our theoretical harvest composition is also based upon population parameters from a protected population near an ecological capacity and does not consider how the susceptibility of different cohorts changes under varying levels of harvest. In a scenario where adult males have been depleted it is possible that there may be a feedback loop and adult female and sub-adult susceptibility increases. We also appreciate that due to the potential changes in hunter competency at being able to age/sex leopards (see Balme et al., 2012) it is plausible that harvest composition may be reflective of poor hunter aging ability rather than a depletion of the most susceptible cohorts

We appreciate that due to the above factors at this stage, the theoretical harvest composition may be considered a coarse index and it requires ground-truthing, and validation with at least one other independent index (eg. Hunt effort, change in occupancy etc.). An examination of varying harvest pressures (typically governed by varying provincial quotas) could be compared to the theoretical harvest provided here, and could be achieved by examining the harvests of several provinces/districts in which leopards are hunted under varying harvest quota scenarios, similar to the method employed by Anderson & Lindzey (2005).

4.4.2 Conclusions

It is doubtful whether African governments have the funds or capacity to estimate leopard densities at the scale required for robust quota setting, and our results provide some promise for the trial of a harvest composition monitoring scheme. Monitoring harvest composition may provide environmental ministries with an adaptive management platform, where quotas may be adjusted in accordance with population trend, and particularly by monitoring the proportion of the sub-adult cohort proposed here. However for the method to be effective, it will require a well policed post-mortem verification scheme of hunted animals, as well as a degree of honesty from hunters. We suggest this could be achieved through the removal of a small piece of skin from each pelt which may be tested genetically for sex (Spong et al., 2000).

4.5 Supporting Information

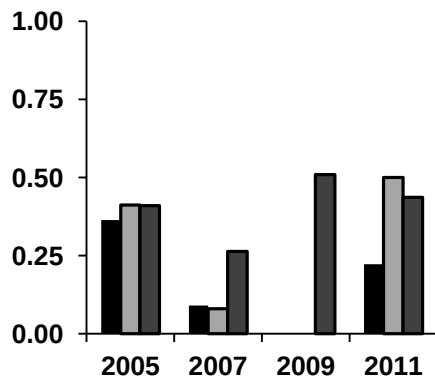


Figure 4.1a SI: Proportions of adult male leopards in collared (black), collared photographed (light grey) and total photographed (dark grey) samples recorded on Phinda.

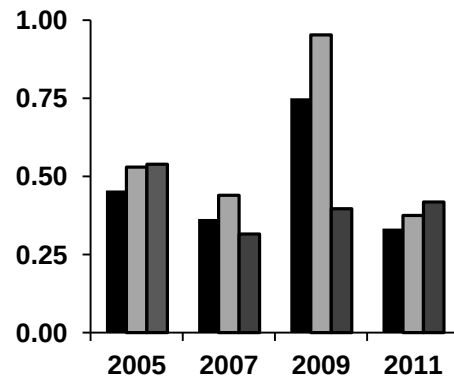


Figure 4.1b SI: Proportions of adult female leopards in collared, collared photographed and total photographed samples recorded on Phinda.

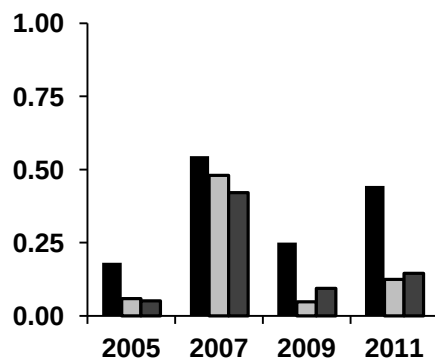


Figure 4.1c SI: Proportions of sub-adult leopards in collared, collared photographed and total photographed samples recorded on Phinda.

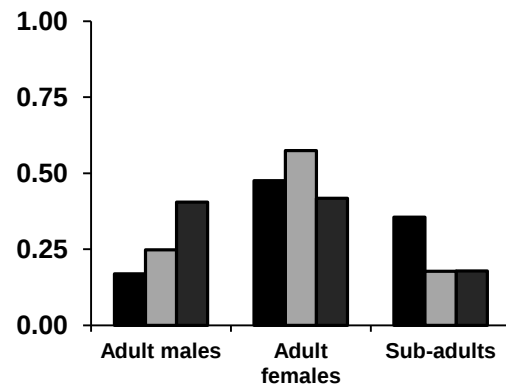


Figure 4.1d SI: Four year means of collared, collared photographed and total photographed populations of adult males, females and sub-adults recorded on Phinda, presented with standard error .

Table 4.1 SI: GLM parameter estimates using only collared animals with ≥ 30 telemetry points. Model input and structure remained constant for comparison to our model using ≥ 10 telemetry points.

Coefficients	Estimate	2.5% CI	97.5% CI	Exponentiated estimate	Std.error	z-value	Pr (> z)
Intercept (Adult females)	-3.41	-3.94	-2.87	3.3	0.27	-12.56	<0.005
Adult males	0.26	-0.7	1.23	4.29	0.49	0.52	0.6
Sub-adults	-1.88	-4.85	-0.06	0.5	1.11	-1.69	0.09

Residual deviance: 17.99 on 13 d.f

AIC: 68.63

Theta: 2.93

CHAPTER FIVE:

ROSETTES, REMINGTONS AND REPUTATION: ESTABLISHING POTENTIAL DETERMINANTS OF LEOPARD PANTHERA PARDUS TROPHY HUNT PACKAGE PRICE ACROSS AFRICA

CONTENTS

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5. Rosettes, Remington's and Reputation: Establishing potential determinants of leopard *Panthera pardus* trophy hunt package price across Africa

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Author contributions: Conceived and designed the experiments: GB, AB, PJ. Performed the experiments: AB. Analysed the data: AB. Contributed reagents/materials/analysis tools: GB. Wrote the paper: AB, GB, AD, DM, PJ, LH.

5.1 Introduction

Trophy hunting is a commonly used tool in the management of many terrestrial mammals worldwide (Packer et al., 2009; Lindsey et al., 2006; Milner et al., 2006; Harris & Pletscher, 2002). However, its use is increasingly debated, particularly when large, charismatic and threatened species are concerned (Hunter et al., 2013). To date, several studies have suggested that the selective harvest of a few individuals may generate revenue for local economies and contribute to the protection of wildlife populations and wilderness areas (Lindsey et al., 2007; Bond et al., 2004; Lewis & Alpert, 1997). However, there can be problems associated with

the use of trophy hunting in this way, such as dubious quota setting (Balme et al., 2010; Lindsey et al., 2006), population declines resulting from the setting of quotas at too high a level (Loveridge et al., 2007; Balme et al., 2009b) and even a decrease in the size and quality of heritable secondary sexual traits in some species (Von Brandis & Reilly, 2007; Coltman et al., 2003).

An understanding of how hunters value wildlife can contribute to its efficient management. The economic framework that underpins trophy hunting has been the focus of considerable recent research. The majority of this research has been into topics such as the significance of the industry to local economies (Saayman et al., 2011; Wenzel, 2011; Lindsey et al., 2007; Samuelsson & Stage, 2007), species-specific contributions to the hunting industry (Jorge et al., 2013; Lindsey et al., 2013; Lindsey et al., 2012) and determinants of trophy price at the inter-family level (eg. Johnson et al., 2010). There have also been numerous studies which have investigated price-rarity correlations of popularly hunted species (eg. Palazy et al., 2012; Palazy et al., 2011; Johnson et al., 2010).

There is considerably less literature which describes the factors that govern the price of wildlife species available in hunt packages, and specifically what influences hunting outfitters in setting the price of hunting packages. Little & Berens (2008) for example used a hedonic price model to evaluate factors which predicted the price of a series of heterogeneous hunt transactions in the south-western United states. Similarly, Livengood (1983) and Wennergren et al (1977) used *inter alia* factors such as hunt success, hunter congestion and property size in predicting the price paid by hunters to hunt at deer hunting concessions. Studies such as these have

implications for both hunting outfitters, and the conservation authorities regulating trophy hunting. If the main role of trophy hunting in conservation is to generate revenue to support conservation, then it is important to know which factors are the most important in determining package price. For instance, if trophy size is the most significant factor affecting package price, then it further reinforces the need for hunting companies to set conservative quotas and, if relevant, implement age-based regulations (Rivrud et al., 2013; Packer et al., 2009), in order to ensure that the offtake does not result in eventual trophy size reduction. Similarly, if hunting packages in relatively wild, unspoiled places generate significantly more revenue than others, then that is important knowledge for developing future packages and provides further economic incentives to maintain those areas.

In this paper we aim to identify potential determinants of trophy package price at the species level for the African leopard *Panthera pardus*, a large solitary felid, thought to be in a state of decline across large tracts of its African range (Ray et al., 2005). We use the leopard as a model species mainly because the majority of leopard hunting takes place in seven African countries (Balme et al., 2010), and there is considerable potential to detect variation in the package prices set by outfitters. Additionally, it is a popularly hunted species and is of conservation concern (Balme et al., 2013; Palazy et al., 2011).

We use a sample of leopard hunt package prices (obtained from the websites of hunting outfitters), to explore the variation in trophy package price on a regional level. We then attempt to explain variation in leopard hunt package price. Our analyses integrate a variety of data ranging from trophy records taken from the SCI

record book and hunter websites to hunt return forms detailing success and failures of attempted leopard hunts.

5.2 Methods

5.2.1 Sources of leopard trophy package price

The United States is the largest market for African trophy hunting safaris and the majority of hunts are sold at hunting conventions there (Lindsey et al., 2012). We obtained leopard hunt package prices from the websites and pamphlets of leopard hunting outfitters advertising their hunts at the Dallas and Houston Safari Clubs and the Atlanta African Hunting Show in 2011. As price is often accepted as a measure of economic value in traditional market economies, we used the price of leopard trophy hunt packages as a proxy of their attractiveness (Lindsey et al., 2007). Leopard hunts are typically sold as part of a hunting package (Leader-Williams et al., 1996) where a standard daily fee (which includes accommodation and logistic costs) is charged regardless of the success of the hunt over a fixed minimum number of days. If the hunt is successful, the client is also charged a trophy fee which is typically set by the local conservation authority (though the outfitter may add a premium to this). We used price information from the seven main leopard hunting countries, omitting the smaller hunting states from analyses as they contribute minimally to leopard trophy exports (see CITES online database; <http://www.unep-wcmc-apps.org/citestrade> & Table 5.1).

Table 5.1: Country size, CITES quota size and mean trophy exports for the 2006-2010 period obtained from the CITES database.

Country	Country size (km ²)	Quota	5 year mean export
Botswana	600 370	130	44 ± 6.69
Central African Republic	622 984	40	23.6 ± 6.67
Ethiopia	1 127 127	500	0 [£]
Kenya	582 650	80	0 ^{\$}
Malawi	118 480	50	0*
Mozambique	801 590	120	37 ± 2.81
Namibia	825 418	250	197.4 ± 32.46
South Africa	1 219 912	150	114.2 ± 11.73
Tanzania	945 203	500	280.4 ± 28.18
Zambia	752 614	300	68.8 ± 6.21
Zimbabwe	390 580	500	251.4 ± 11.72
Uganda	236 040	28	1 ± 1

£ Ethiopia has no records of exports/imports in the CITES database and at present leopards are not hunted there (Hans Bauer, personal communication).

\$ Kenya allow the export of leopard body parts but trophy hunting was outlawed in 1977.

*There were no leopard export records found in the CITES database for the 2006-2010 period in Malawi.

Highlighted countries are those used in our analyses.

5.2.2 Package price variation by administrative boundary and country

We began by performing a series of general linear models to highlight the variations in the duration, daily rate, trophy fee and cheapest available leopard hunt packages offered by hunting outfitters, at (a) at the regional level, using administrative divisions with ≥ 3 outfitters and (b) the country level, using all of the outfitters in our sample. The administrative boundary analysis examines variation within a country between its provinces/regions/districts. We could only use a sample of our outfitters in the administrative level analysis as only four countries featured administrative divisions with ≥ 3 outfitters.

5.2.3 Country level predictors of price

We postulated that leopard package price could also be affected by a number of country level variables, namely: (i) mean number of species included within leopard packages for a particular country (ii) SCI leopard trophy quality, (iii) advertised leopard trophy quality, (iv) relative hunt success, (v) CITES quota, and two closely

linked indices of country attractiveness which we tested separately, namely (via) number of tourists and (vib) a country's failed states index ranking. We therefore created a suite of independent, country-level GLM's which investigated the relationship between each of these predictor variables and mean leopard hunt package price. These are described briefly below.

(i) *Mean number of charismatic species included in leopard packages for a particular country.* We hypothesized that countries with a higher number of charismatic species offered in leopard hunt packages would on average feature more expensive hunts

(ii) *SCI leopard trophy quality.* We obtained information on leopard trophy quality using the approach of Lindsey et al (2012) and Von Brandis & Reilly (2007). These authors obtained antelope and lion trophy sizes from the SCI record book and we replicated this for leopards, calculating the average leopard trophy sizes in inches from the SCI record book for the seven countries in our analysis. We hypothesized that because hunters often seek to shoot the largest individuals, countries with the largest trophies would feature the most expensive packages.

(iii) *Advertised leopard trophy quality.* Leopard trophy quality was also assessed by estimating the ages of leopards displayed on outfitter's online trophy galleries. Balme et al. (2012) demonstrated that leopards could be accurately aged using morphological characteristics (e.g. dewlap size, facial scarring, ear wear; Figure 5.1) featured in photographs. Four assessors, each with extensive leopard aging experience, were asked to assign leopard trophy photographs from outfitter websites to one of four age categories (Balme et al 2012): (1) 1 = leopards of < 2 years (2) 2 =

2-3 years (3) 3 = 4-6 years and (4) 4 = >7 years. Older and larger leopards thus achieve scores closer to 4 on this ordinal scale. We used the median score recorded for each outfitter and then used the median of all outfitters by country. We assessed only those outfitter websites with ≥ 3 leopard trophy photographs. We only included advertised trophy quality as a country-level variable because many outfitters had few or no leopard trophy photographs on their websites.



Figure 5.1: Examples of leopard trophies advertised on outfitter websites in (a) Botswana (b) South Africa (c) Zimbabwe and (d) Tanzania. All images of leopards used in outfitter trophy quality analyses were examined for morphological cues such as ear wear, facial scarring and dewlap size.

(iv) *Relative hunt success*. We hypothesized that the likelihood of securing a leopard trophy may influence hunt package price. We therefore estimated relative leopard hunt success at a national level from 562 post-hunt register forms submitted by hunting clients that hunted with 228 outfitters between 1998-2010 (see

www.huntingreport.com; accessed 1 November 2013). Hunt reports include information on the species hunted, hunting method used, hunt duration, and the success of hunts (Table 5.2). We derived hunting success by dividing the number of successful leopard hunts per country by the total number of leopard hunts reported per country. This would ideally be an outfitter-level variable; however, those outfitters for which we had price data were poorly represented in the hunt return form dataset.

(v) *CITES quota*. We used the 2010 CITES leopard quotas as a primitive measure of leopard availability.

(via) *Number of tourists* and (vib) *Failed states index ranking*. Numerous authors have recognized that political instability is a major driver deterring tourists from visiting sub-Saharan Africa (eg. Beirman, 2003; Sonmez, 1998; Ankomah & Crompton, 1990). Contrastingly, Lindsey et al (2007) suggested hunters are less sensitive to the factors which deter tourists from visiting sub-Saharan Africa. We aimed to examine if country attractiveness and a countries political stability would be important predictors of package price. We used the number of tourist visits (sourced from the United Nations World Tourism Organization tourism highlights, 2013; Table 5.3) as a metric of country attractiveness. We hypothesized that if hunters were to hunt in attractive countries, then price would increase with the number of visits per country (ie. hunters would be drawn to places with more tourist visits). We also hypothesized that package price would be cheaper in countries with more political instability (therefore a higher failed states index). For this we used a country's Failed States Index ranking for the 2010 year (see: fp.statesindex.org/rankings-2010-sortable; accessed 1 November 2013). The Failed States Index is a ranking based

upon 12 indicators of state vulnerability and includes *inter alia* measures of economic decline, criminalization and refugee movements. If the contrary were true (ie. hunters were attracted to countries with less tourists; in line with the suggestion of Lindsey et al., 2007) then we would find an inverse relationship between package price and the number of tourists, and a positive correlation with the failed states index.

Table 5.2: Mean number of wildlife species hunted during a leopard hunt along with mean hunt durations for the seven main leopard hunting countries in Africa.

Country	n*	Mean duration of leopard hunt (days)	Mean number of species hunted
Botswana	15	18.33 ± 1.91	4.6 ± 0.79
Mozambique	20	15 ± 1.34	5 ± 0.64
Namibia	71	13 ± 0.47	5.63 ± 0.42
South Africa	28	14.5 ± 1.17	4.92 ± 0.57
Tanzania	137	21 ± 0.73	8 ± 0.3
Zambia	50	18.32 ± 0.87	7.8 ± 0.45
Zimbabwe	241	15.29 ± 0.43	4.82 ± 0.19
Grand total	562	16.63 ± 3.31	4.99 ± 0.13

*Information obtained from 562 post hunt register forms collected over the 1998-2010 hunting period from 228 outfitters (obtained from the hunting report; www.huntingreport.com).

5.2.4 Outfitter level package price model

We were interested in explaining the variation in total package prices advertised across our sample of leopard hunting outfitters. We therefore hypothesised that package price would be influenced by three variables, one of which has two related parts; namely (i) whether the hunting outfitter was based in hunt country or not, (ii) the number of other animal species included as part of the package; and two measures of outfitter reputation, namely (iiia) the number of leopard trophies the outfitter recorded in the SCI record book – a measure of their leopard hunting reputation and (iiib) the total number of trophy records (of all species) the outfitter recorded in the SCI record book – a measure of their overall hunting reputation.

Each of the potential predictor variables used in our models is described briefly below.

(i) *Foreign or local outfitter*. Many foreign outfitters use local PH's in their hunts, and if this is not possible, they outsource hunts to local outfitters. For this reason we hypothesized that package price would be cheaper amongst local outfitters.

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(ii) *Number of species in package*. As leopard hunts are often sold in combination with other game, and price is likely to increase with the costs of search effort for other game, we hypothesized that package price would increase with the number of other charismatic species offered within the hunt package.

(iiia) *Leopard trophies* and (iiib) *total number of trophies*. We included a measure of outfitter leopard hunting reputation indexed by the total number of leopard trophies, as well as a measure of overall hunting reputation indexed by the wildlife trophies they recorded overall (all species) in the Safari Club International (SCI) record book of big game (period from Dec 1959 – Dec 2010; <http://www.scirecordbook.org>, accessed July 2013). We felt that leopard records was a useful measure of reputation as leopards represent the focal species of the hunts examined in this study. However, as leopard hunt packages are often sold with other species, which may also affect a client's decision (indeed, leopards may not be the primary focus of a safari); hence, we felt it prudent to also include a measure of overall outfitter reputation by recording the total number of trophies they recorded in the SCI record book. Records typically include the hunter's name, hunt location, outfitter and guide information as well as the trophy size of the hunted species recorded in inches (for

leopards, the sum of the length and breadth of the skull; presented in our analysis in decimal inches). We searched for the leopard hunting outfitter and recorded the number of animal trophies they recorded. We hypothesized that outfitter leopard hunting reputation would be an important predictor of package price and this would increase with the number of leopard records recorded by an outfitter. We also hypothesized that general outfitter hunting reputation (as measured by the total number of record wildlife trophies) would be an important predictor of package price, most likely attributed to the broader experience of hunting a variety of species during the duration of the hunt.

We could not include outfitter-specific measurements of leopard trophy quality in our model due to a high frequency of no records. We therefore created a model of trophy quality in our country level analysis (see above).

We created a suite of candidate general linear models using these predictor variables and used Akaike's Information Criterion (AIC) to evaluate our models. We evaluated our models using corrected AIC (AICc) and relative model weight. This process penalises models based upon the number of their parameters and adjusts for low sample sizes (Boyce et al., 2002). We chose the model with the lowest AICc, however if the second ranked model showed a ΔAIC of <2 we used model averaging. All statistical analyses were performed in the "R" statistical package, and where appropriate means with standard error are presented as a measure of precision ($\bar{x} \pm S.E.$).

Table 5.3: The suite of predictor variables used in our individual country-level models to investigate potential drivers of leopard trophy package price.

Country	Mean package price	Quota	Advertised trophy quality (median score)	Mean number of animals in package	Mean country size ^c	Relative hunt success (%)	FSI ranking ^s	Tourists
Botswana	33309.09	130	3	1	15.53	86.67	113	2145
Mozambique	21284.35	120	2.63	1.74	15.68	60	69	1718
Namibia	18155.71	250	2.25	1.29	15.64	50.7	100	984
South Africa	16854	150	2.75	1	15.99	78.57	115	8074
Tanzania	44909.17	500	3	2.67	15.28	85	72	754
Zambia	27456.67	300	2.75	2	15.35	88.24	56	815
Zimbabwe	18623.75	500	3	1.25	15.74	68.44	4	2239

\$FSI (Failed States Index)

£Mean country size refers to mean leopard skull size in decimal inches

5.3 Results

5.3.1 Package price variation by administrative boundary and country

Our regional analysis included a sample of 58 outfitters. Our analysis of daily rate, trophy fee and package price suggested lower variation between administrative boundaries (ie. provinces, regions or districts) within countries (Table 5.4). Mean daily rates were comparable between administrative divisions within Mozambique ($F_{(3, 16)} = 2.01$, $p = 0.15$), Zambia ($F_{(1, 7)} = 0.36$, $p = 0.57$) and Zimbabwe ($F_{(3, 15)} = 0.84$, $p = 0.49$) but differed significantly in Namibia ($F_{(1, 8)} = 17.10$, $p = 0.003$). Trophy fees were comparable between administrative divisions within Mozambique ($F_{(3, 16)} = 0.47$, $p = 0.71$), Zambia ($F_{(1, 7)} = 0.48$, $p = 0.51$), Zimbabwe ($F_{(3, 15)} = 0.32$, $p = 0.81$) and Namibia ($F_{(1, 8)} = 2.83$, $p = 0.13$). Total package price was comparable between administrative divisions within Mozambique ($F_{(3, 16)} = 1.80$, $p = 0.19$), Zambia ($F_{(1, 7)} = 0.25$, $p = 0.63$), Zimbabwe ($F_{(3, 15)} = 0.64$, $p = 0.60$) but differed significantly in Namibia ($F_{(1, 8)} = 10.27$, $p = 0.01$). Advertised hunt duration was comparable between the administrative divisions for the four countries.

Table 5.4: Mean advertised hunt durations, daily rates, trophy fees and total package prices for 58 leopard hunt outfitters across four countries and 12 administrative divisions.

Region	Number of outfitters	Mean advertised duration	Mean daily rate	Mean trophy fee	Mean package price*
Mozambique					
Niassa	4	14	962.50±66.67	3875.00±426.96	17350.00±1357.69
Sofala	6	13.33±0.42	1316.67±112.30	4083.33±374.54	21816.67±1716.67
Tete	7	14	1307.14±104.33	4005.71±291.16	22305.71±1231.77
Zambezia	3	14	1183.33±44.10	4800.00±1274.10	21366.67±1034.94
Namibia					
Caprivi	7	15.14±0.99	1135.71±95.56	4142.86±236.90	21428.57±1903.00
Otjozondjupa	3	13.33±0.67	506.67±29.63	5000.00±577.35	11726.67±563.36
Zambia					
Eastern	5	14	1914.00±211.89	3420.00±566.92	30216.00±3141.79
Lusaka	4	14	1650.00±420.81	3975.00±537.94	27075.00±5948.83
Zimbabwe					
Mashonaland West	10	14	1114±63.82	4090.00±253.95	19686.00±873.73
Matabeleland North	3	14	1033.33±109.29	4583.33±712.00	19050.00±2241.84
Matabeleland South	3	14	930.00±104.40	4100.00±325.32	17120.00±1729.52
Harare	3	14	1000±86.60	4333.33±333.33	18333.33±1510.33

For our country-level analysis we analysed hunt price data from a total of 92 leopard outfitters (106 leopard hunting outfitter points – due to some outfitters hunting in multiple countries) from seven countries. On average the most expensive leopard hunt packages were from Tanzania, followed by Botswana and Zambia, while the cheapest leopard hunts were offered in South Africa. Between the seven countries (Table 5.5), we found significant variation in the mean daily rates ($F_{(6, 99)} = 26.89$, $p < 0.005$; Figure 2), trophy fees ($F_{(6, 99)} = 9.59$, $p < 0.005$; Figure 5.3), total package prices ($F_{(6, 99)} = 36.09$, $p < 0.005$; Figure 5.4) and mean hunt duration ($F_{(6, 99)} = 6.42$, $p < 0.005$; Figure 5.5) Regional variation was described with a smaller sample of 58 outfitters across four countries and 12 administrative divisions (Table 5). The majority of packages (63%) were composed of leopard-only hunts followed by leopard and buffalo combinations (20%; Figure 5.6). Tanzania and Zambia did not offer leopard only hunts.

Table 5. 5: Mean advertised hunt durations, daily rates, trophy fees and total package prices for the 106 leopard hunting outfitters in the seven countries used in our analyses.

Country	Number of outfitter points	Mean advertised duration	Mean daily rate	Mean trophy fee	Mean package price*
Botswana	11	13.64±0.65	2187.27±299.50	5054.55±427.54	33309.09±2871.98
Mozambique	23	13.78±0.15	1230.44±53.97	4301.74±254.90	21284.35±809.58
Namibia	14	14.43±0.51	905±90.77	4871.43±332.40	18155.71±4852.32
South Africa	10	14.00±0.30	651±67.07	7710.00±971.76	16854.00±645.54
Tanzania	12	16.75±0.78	2382.92±136.83	4944.17±334.77	44909.17±2850.68
Zambia	12	13.75±0.46	1722.50±160.04	3687.50±304.33	27456.67±2407.25
Zimbabwe	24	14.08±0.06	1024.17±39.01	4206.25±147.24	18623.75±581.55
Grand total	106	14.27±0.17	1371.56±68.82	4758.21±167.33	24471.89±1034.35

*This is the price calculated for the cheapest package on offer by an outfitter which includes a leopard trophy.

5.3.2 Country-level predictors of price

We analysed 794 leopard trophies (mean number of records per outfitter = 10.59±8.90) from 75 hunter websites (mean number of records per country = 113.43±29.12). Our median scores recorded per country suggested that the oldest leopards were hunted in Botswana, Tanzania and Zimbabwe (median age category = 3) while the youngest leopards appeared on the websites of outfitters advertising hunts in Namibia (median age = 2.25). Our review of leopard records from the SCI record book showed that the largest leopard trophies are found within South Africa (15.99±0.08 inches; $n = 201$ records) while the smallest originate from Tanzania (15.28±0.05 inches; $n = 398$ records). Relative hunt success was highest in Zambia (88.24% of attempted leopard hunts successful; $n = 50$ hunt return forms) and lowest in Mozambique (60% of attempted hunts successful; $n = 20$ hunt return forms; see Table 5.3 for full review).

We found no correlation between mean package price for a country and the quota size for the country ($F_{(1, 5)} = 0.74$, $p = 0.43$), advertised leopard quality ($F_{(1, 5)} = 2.13$, $p = 0.20$), hunt success ($F_{(1, 5)} = 3.34$, $p = 0.13$), failed states index ($F_{(1, 5)} = 0.03$, $p =$

0.87) and the number of tourists visits ($F_{(1, 5)} = 1.27$, $p = 0.31$). However the mean number of animals in hunt package ($F_{(1, 5)} = 4.63$, $p = 0.08$) approached significance and mean country leopard trophy size and package price were negatively correlated ($F_{(1, 5)} = 10.28$, $p = 0.02$; Figure 5.7).

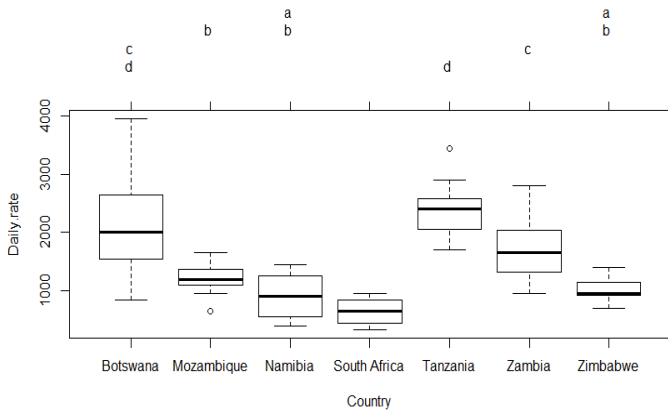


Figure 5.2: Tukey HSD test of daily rate variation between countries. Those countries sharing the same letter are not significantly different from each other.

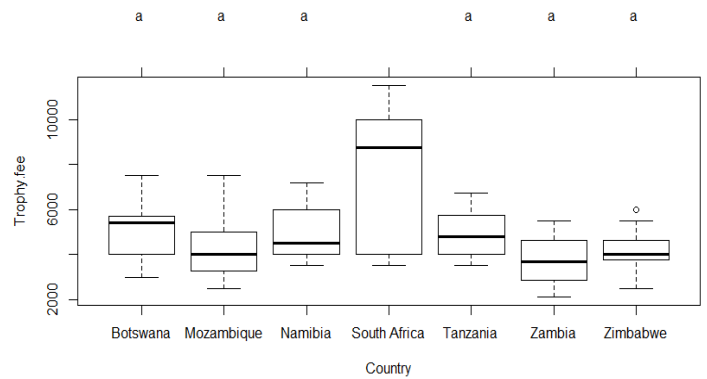


Figure 5.3: Tukey HSD test of trophy fee variation between countries.

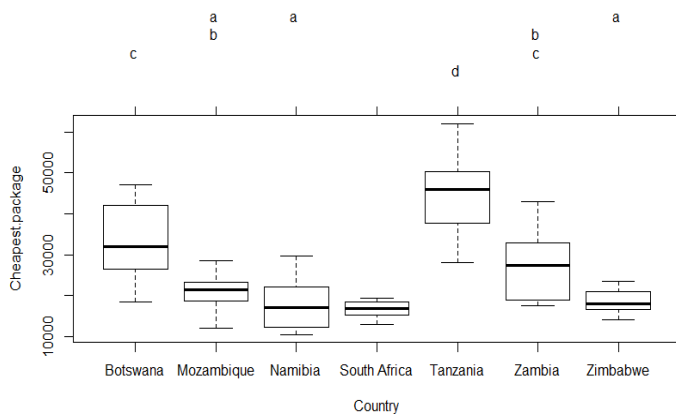


Figure 5.4: Tukey HSD test of cheapest leopard package price variation between countries.

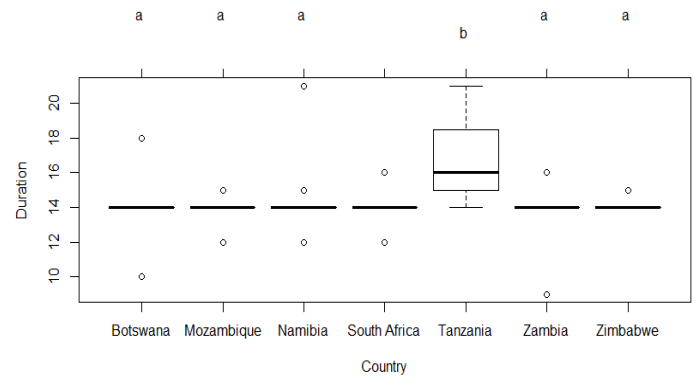


Figure 5.5: Tukey HSD test of hunt duration variation between countries.

5.3.3 Outfitter level package price model

Our most parsimonious GLM examining potential predictors of leopard package price incorporated the predictor variables of number of species within the package, outfitter locality and the total number of trophies for all species that an outfitter had recorded in the SCI record book. The number of leopard trophies in the SCI record book was removed as there was no evidence that it was a useful predictor (Log-likelihood ratio test, $p = 0.36$; see Table 5.6). The most parsimonious model suggested that leopard hunt package price increased with the number of charismatic species included in the hunt package and the total number of trophies recorded in the SCI record book (Table 5.7). Local outfitters featured slightly lower package prices and this approached significance.

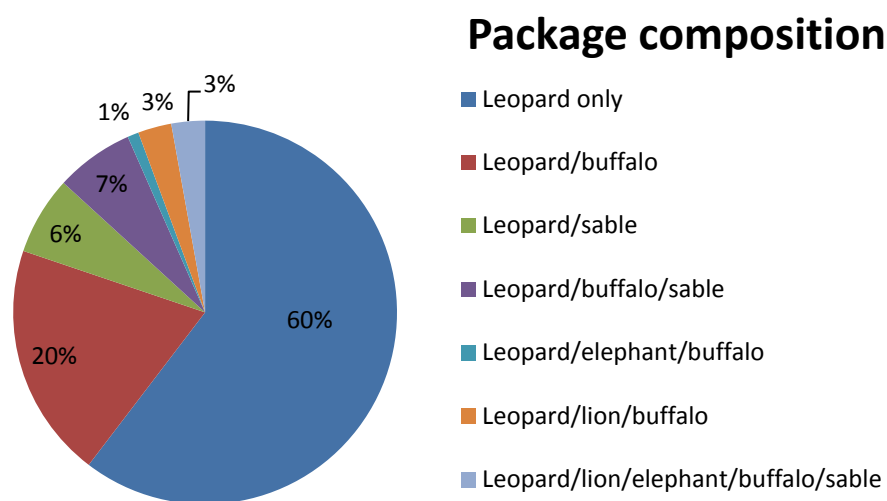


Figure 5.6: Percentage of cheapest hunt packages which included a leopard trophy for the 106 outfitter points in our sample of 92 leopard hunting outfitters.

5.4 Discussion

Our results indicate that leopard hunt package prices vary considerably across African countries, while greater stability is observed in price at the regional level. Most notably, the variation in package price at the country level was not explained by predictors associated with product quality, namely the advertised leopard trophy quality on outfitter websites or those found within the SCI record book. Unexpectedly, package price was inversely correlated with mean country trophy size (SCI record book). This is notable as the prices of wildlife trophies (and even within the felidae) are known to increase with body size (Palazy et al., 2011; Johnson et al., 2010). Our results lend no support for this within a single felid species and contrast with Lindsey et al (2012) who suggested that the price of lion hunts in Botswana's Kalahari are particularly expensive in comparison to other sites, due to the perceived quality of their trophies. Apart from these measures of leopard trophy quality, we also found that an outfitters leopard hunting reputation (as measured by the number of leopard trophies) was not an important predictor of package price in our outfitter model, which goes against our initial hypothesis that this predictor would be positively correlated with price. Package price was also not correlated with product availability (relative success of leopard hunts or the number of CITES tags offered per country (ie. a primitive measure of leopard availability)). There was also no clear trend between the number of tourists or a countries political stability and price.

As expected our outfitter-level model examining package price variation suggested package price increases with the number of charismatic species within a leopard hunt package. However, the package prices used in our analyses only factored in

the leopard component of a given package (ie. duration, daily rate and leopard trophy fee – excluding the trophy fee of other species). Therefore, this increase in package price may also be due to the increased search, recovery and skinning costs involved in hunting these other species. Lions for example are also hunted using a bait and similarly to leopards, suitable older and more attractive males make up only a small fraction of the overall population (Whitman et al, 2004), therefore increasing relative search time for the species. The location of the outfitter base approached significance within our model and the fact that local hunters offered cheaper hunts is in line with our hypothesis that they probably save costs in outsourcing the services of local hunters (usually having hunters of their own).

Interestingly, we also found a positive relationship between outfitter package price and their overall hunting reputation (total wildlife trophies). This result suggests outfitters may be setting their package prices in part due to their trophy hunting track record. Although this has to date not been examined for trophy hunting, there are various studies in the economic literature which suggest reputation and prominence of large firms has significant impact on the price of their products/services (Fombrun & Shanley, 1990). Indeed, Rindova et al (2005) found that the prominence of Business School Faculty's in the US was correlated with the number of premier scholarly journal articles they produced. Similarly numerous authors found that a seller's reputation on the online trading platform "ebay" was an important determinant of the price of their product, and whether they continued to trade over time or closed their business (Cabral & Hortacsu, 2010; Resnick et al., 2006; Melnick & Alm, 2002). Although "ebay" is an online trading platform, it is in some ways similar to the hunting market in that a buyer has only limited information on the hunt he/she

purchases (ie. website photographs, SCI record book records, online hunt reports or word of mouth advertising at a hunt show; see Johnson & Reingen, 1987). The fact that overall outfitter hunting reputation was an important determinant of price is in line with our second hypothesis, which stated that price may be positively correlated with overall reputation due to the overall experience of the hunt. Indeed, leopard hunts are typically over two weeks long, and the hunt itself requires prolonged time (often days) spent by the hunter and his guide in a hunting hide. Our models provide limited evidence for the fact that the overall reputation of the outfitter is more important than the guarantee of a leopard, a high quality trophy or the reputation of the outfitter as a premier supplier of leopard hunts. Instead activities such as tracking, hunting plains game, camping, eating and spending time with the hunting guide may contribute more to overall hunter satisfaction.

Table 5.6: Model components, log-likelihood and weighting scores for the six models incorporating potential predictors of cheapest leopard hunt package price .

Model	D.F	logLik	AICc	Delta AIC	Model weight
Outfitter + Animals in package + All trophies	5	-1096.65	2203.89	0.00	0.51
Outfitter + Animals in package + All trophies + Leopard trophies	6	-1096.20	2205.25	1.36	0.26
Outfitter + Animals in package + Leopard trophies	5	-1098.04	2206.69	2.79	0.13
Animals in package + All trophies + Leopard trophies	5	-1098.28	2207.16	3.26	0.00
Outfitter + All trophies + Leopard trophies	5	-1115.19	2240.98	37.08	0.00

5.4.1 Conservation implications

Our results have some important consequences for the sustainable leopard trophy hunting initiatives recently proposed in the literature (Balme et al., 2012; Packer et al., 2009). They also echo the previous calls of various members of the scientific community for the trophy hunting industry to engage itself in a form of independent certification (Lindsey et al., 2006; Baldus & Cauldwell, 2004). Firstly, population modelling suggests that African leopards may be safely harvested if males > 7 years

of age are targeted by hunters (Packer et al., 2009), as this cohort has sired at least one litter of cubs till independence. Furthermore, there is considerable potential for the application of such an age-based regulation in the field as leopards may be successfully aged by observers, particularly with training on morphological cues (Balme et al., 2012). Leopard cranial size also increases throughout a leopards life (Dusty.Joubert, unpublished data) and older male leopards typically have the most impressive trophies and are sought by hunters (Brackowski et al., submitted). However, our results suggest that the realisation of such an age-based hunting regulation may also have its limitations and our pricing results suggest that product quality may not necessarily be the most important consideration for hunters, and the smallest leopard trophies (as determined by SCI records), fetch the highest prices. Similarly, there was no clear positive relationship between package price and advertised trophies on outfitter websites, despite the fact that Tanzania and Botswana recorded the highest median scores for advertised trophies and had the most expensive packages. Our analysis of outfitter websites also raises concerns over current hunting practices, and median country leopard age scores ranged from 2.25-3, which suggests a high frequency of prime animals with territorial tenure (Bailey, 1993) are being shot by hunters. This is troubling as (a) this is considerably below the “safe-age” limit set by Packer et al (2009) and (b) outfitters typically advertise their best trophies on websites, and it is likely that a high proportion of younger animals are under-represented. The results from our assessment of leopard trophies on outfitter websites lend support to the findings of Spong et al (2000) who also found a high proportion of sub-optimal animals (28.6 % females) in a harvest of leopards in Tanzania. This trend is also observed for lions there (Packer et al., 2011; Packer et al., 2009).

The fact that leopard trophy quality and also leopard outfitter reputation were not important predictors in our models, casts a challenge for the creation of a certification system for leopard hunting, particularly if an age-based regulation is to be the standard of merit upon which outfitters are judged. However, an incentive-based compliance system used in Mozambique's Niassa Reserve on lions, where outfitter quotas increase upon harvest of old individuals is an effective management tool, which has contributed to a stable lion population there (Begg & Begg, 2009; Begg & Begg, 2007).

There is however some hope for explorations of a certification system within the hunting industry, and our finding that package price is positively correlated with overall outfitter hunting reputation may stimulate some interest from a portion of hunting outfitters. Firstly, outfitters with high trophy hunting reputation overall may be a good target audience for conservation authorities for two reasons. Firstly it is plausible that if a sustainable harvest strategy previously developed for large carnivores (eg. Balme et al., 2010; Balme et al., 2009b; Begg & Begg, 2007), was to be tested in the industry, the outfitters with a high hunting reputation may be a key target audience for authorities, as they might set an example for smaller, lesser known ones. Secondly, it is plausible that more reputable hunters perform a higher proportion of overall hunting and dominate a larger share of the hunting market when compared to smaller less reputable outfitters. If this were indeed the case, this could again serve to inspire smaller outfitters to follow the trend of bigger role players.

Finally, our results also suggest that outfitters in other countries could follow the example of the Tanzanian Department of Wildlife and the outfitters it regulates.

Tanzanian leopard hunts have exceptionally high prices when compared to the rest of Africa (despite the fact they record the smallest leopard trophies-as demonstrated by mean country SCI leopard records) and this is owed, a) to longer hunts (typically lasting 16 or 21 days) and b) a government mandate which forces outfitters to set a minimum daily rate of $\geq \$ 850$ to prevent price undercuts (Leader-Williams et al., 1996). This pattern appears consistent for other species (Booth, 2009) and the high price for leopard hunts in Tanzania is also observed for lions which are the most expensive in Africa (Lindsey et al., 2012). It appears that prolonging the duration of a hunt and offering more species within a package may be more profitable than offering leopards alone. South African outfitters could also use the selling point of boasting Africa's largest leopards in their favour, perhaps using this as a marketing ploy.

Table 5.7: Model-averaged coefficients, standard errors and critical values for our outfitter-level model examining potential predictors of leopard hunt package price .

Parameter	Model-averaged coefficient	S.E	Adjusted S.E	z value	Pr (> z)
Intercept (Outfitter foreign)	13552.16	2089.30	2111.52	6.42	<0.005
Outfitter local	-3076.60	1565.22	1583.46	1.94	0.05
Animals in package	6447.65	977.09	988.54	6.52	<0.005
All records	10.32	3.42	3.46	2.99	<0.005
Leopard records	217.32	199.06	200.38	1.09	0.28

5.4.2 Modelling limitations and future research needs

Our results and particularly those from our outfitter-level model should be interpreted with some caution. Most notably, we lacked a number of important predictor variables which may have provided a better fit for our package price data. Most importantly our models did not factor in variations in country GDP, the number of leopard outfitters per country and the running costs of leopard hunts in the respective countries. We also lacked smaller variable information, namely the number of years

an outfitter had hunted and his/her relative advertising effort (particularly at trophy hunting shows in the US), although the number of years hunting and number of records are likely to be highly correlated. A lack of these key predictor variables in the models may have overemphasized the importance of some of our results, particularly the importance of outfitter reputation.

Additionally, many trophy hunters also belong to a formal hunting association of some kind (eg. SCI, Texas Trophy Hunters Association) and the community itself is well connected. It is therefore plausible that word-of-mouth advertising (eg. Chevalier & Mayzlin, 2003; Brown & Reingen, 1987) and personal connections established at hunting conventions between outfitters and clients may also have an important bearing on package price.

Importantly, our analyses of potential leopard hunt package price determinants were implemented from the angle of the outfitter. We recommend that future researchers attempt a similar analysis, however from the angle of the hunters. We recommend a similar semi-structured questionnaire approach to that used by Lindsey et al (2012) where hunters are asked why they choose certain outfitters over others. This paper serves as an important reference for such an exploration, particularly regarding outfitter reputation and whether this is indeed validated by hunter clients. Our aim is to further this research through the incorporation of market information on country-specific GDP's, outfitter numbers and the running costs of leopard hunts (particularly block lease fees). This information is likely to lend further strength to the modelling approach used here.

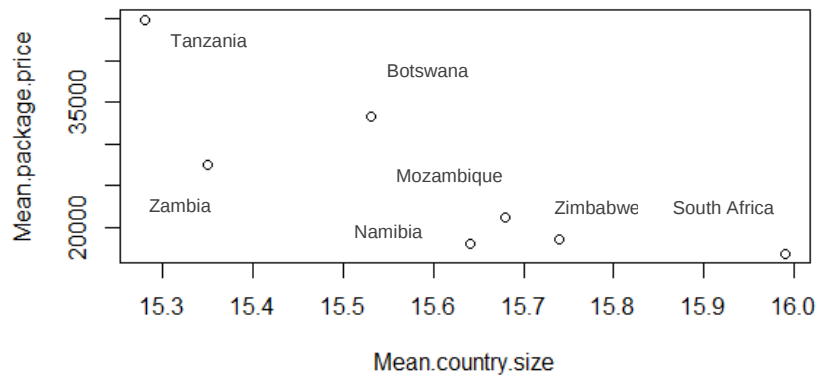


Figure 5.7: Plot of country mean package price and mean country trophy size (in inches). Mean country size was obtained from 1788 leopard skull measurements recorded in the SCI record book.

CHAPTER SIX:

CONCLUSION

6. Conclusion

The trophy hunting of large felids such as lions and leopards has always been controversial and highly debated (Lindsey et al., 2012). However the debate has never been fiercer. Most notably, Zambia recently placed a moratorium on the hunting of leopards and lions, while Botswana has issued an outright trophy hunting ban on state-owned land, which will come into effect in 2014 (Mfula, 2013; Motseta, 2013). The reasons for these bans include *inter alia* limited revenue generation and depletion of wildlife populations (Mfula, 2013; Motseta, 2013). Numerous authors, however (eg. Hunter et al., 2013; Lindsey et al., 2013; Lindsey et al., 2012), continue to support the notion that serious reforms of the practice may be a better alternative to an outright ban. Indeed, a previous ban on lion hunting in Botswana cost the industry 10% of its revenue, while the 2001-2003 ban on trophy hunting in Zambia led to an increased surge in poaching, due to the reduction in conservation incentives (Lindsey et al., 2007; Lewis & Jackson, 2005). Large felids can be harvested in a sustainable manner, particularly if older individuals are targeted (Begg & Begg, 2009; Whitman et al., 2004) or harvest levels are kept to a minimum (eg. Loveridge et al., 2007), and these principles too apply to leopards (Balme et al., 2010; Balme et al., 2009b; Packer et al., 2009).

The data presented in this thesis is likely to be of value for wildlife authorities and biologists alike, particularly if trophy hunting is an elected form of management. Felid research and conservation has always been obstructed by the central question of how many individuals occupy an area, and although recent techniques have made the enumeration of populations more accessible to biologists (eg. Balme et al.,

2009a; Stander, 1998; Karanth, 1995), monitoring the numbers of large felids over wide spatial scales remains a challenge. This is particularly challenging for leopards, the world's most widely distributed but also most persecuted large felid (Hunter & Balme, 2004). Thus, in this thesis we attempted to examine the potential of two useful methods to monitor leopard populations, specifically to aid authorities in monitoring the sustainability of their hunting quotas.

The first method, a lure camera-trap survey (treatment survey), was aimed at increasing the capture rates and precision of traditional leopard camera-trap surveys. Importantly, our treatment survey using lures produced similar density estimates (and estimates of error) to our non-treatment survey and references to previous works (eg. Du Preez, 2014; Grant, 2012) suggest that the use of baits may be a better method to rapidly increase the number of leopard re/captures. The chapter is however useful in serving as a reference to authors interested in the use of lures and their potential in violating the assumptions of population closure and the spatio-temporal patterning of large felids in savanna environments.

Our exploration of the potential use of harvest composition as a monitoring tool in chapter four, suggests the method has considerable promise for application in the field. Most importantly male leopards are the most susceptible cohort to hunting, so we expect adult males to dominate a leopard harvest in an area. Importantly, sub-adults are the least susceptible cohort to hunting and we propose that a high proportion of sub-adults in a hunted harvest may be indicative of a population in decline. Importantly, although our results are promising, they require validation with at least one other method (eg. hunt effort or a change in occupancy). If the method is

validated we plan to promote it amongst numerous African wildlife authorities responsible with the management of leopard quotas (Figure 6.1).

Finally, the results from chapter five serve to illustrate that presumably important factors such as trophy quality, hunt success and the reputation of outfitters in hunting leopards are not necessarily important determinants of leopard hunts. These results cast some doubt over the potential of using age-based hunting regulations for African leopards, as the “safe” cohort for harvest are older males with impressive and large trophy quality. However, with some exposure, particularly in media circles, these results could serve to inform hunting clients that they should place more pressure on outfitters for older, quality leopards. This is motivated by the fact that a significant portion of hunting clients claim to be in favour of “conservation friendly” hunting activities (Lindsey et al., 2006). Exposure of the result that overall reputation was positively correlated with price could be used as a motivator for outfitters to begin an engagement with local wildlife authorities for a preliminary exploration of a incentive-based certification scheme (as recommended by Lindsey et al., 2006).

Envisaged sustainable quota management strategy post verification

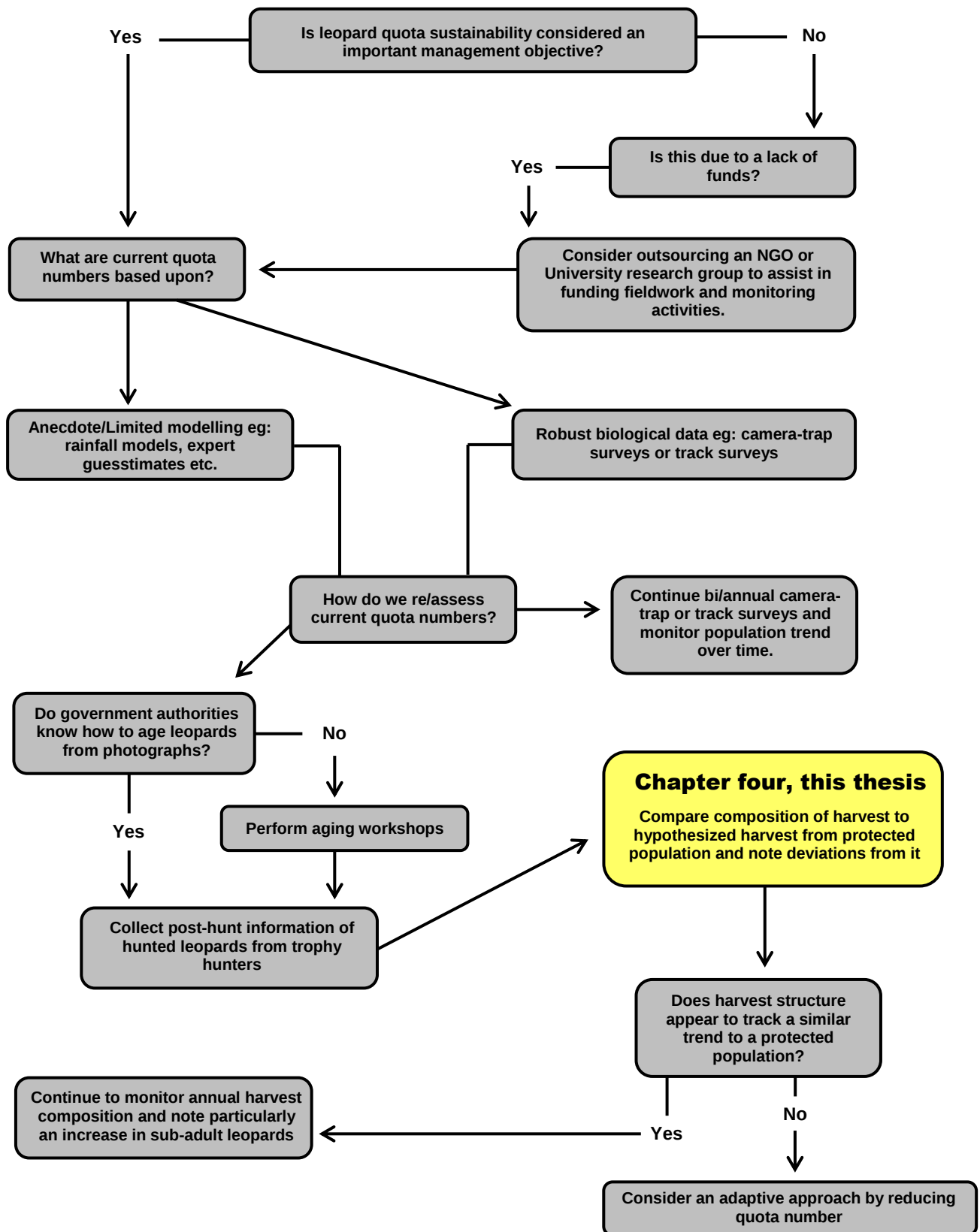


Figure 6.1: Envisaged quota sustainability assessment key and the incorporation of chapter four's results into this framework. Note, that this key and the potential application of the harvest composition monitoring scheme is only envisaged to function post validation of the method.

REFERENCES

- Acoccks, J.P.H. (1988). *Veld types of South Africa*. Memoirs of the Botanical Survey, South Africa, **57**. Pretoria, South Africa.
- Agostinelli, C. (2009). *CircStats package in R*. Version 0.2-4.
- Anderson, C.R. & Lindzey, F.G. (2005). Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. *Wildlife Society Bulletin.*, **33**: 179-88.
- Ankomah, P.K. & Crompton, J.L. (1990). Unrealized tourism potential: The case of sub-Saharan Africa. *Tourism Management.*, **11**(1): 11-28.
- Ariefiandy, A., Purwandana, D., Seno, A., Ciofi, C. & Jessop, T.S. (2013). Can camera-traps monitor komodo dragons a large ectothermic predator? *PloS one.*, **8**(3): e58800.
- Athreya, V., Odden, M., Linnell, J.D., Krishnaswamy, J. & Karanth, U. (2013). Big Cats in Our Backyards: Persistence of Large Carnivores in a Human Dominated Landscape in India. *PloS one.*, **8**(3): e57872.
- Bailey, T.N. (1993). *The African leopard: ecology and behavior of a solitary felid*. Columbia University Press, New York.
- Baldus, R. & Cauldwell, A. (2004). Tourist hunting and its role in development of wildlife management areas in Tanzania. Tanzanian German Development Cooperation. Dar es Salaam, Tanzania. Available from <http://www.wildlife-programme.gtz.de/> (accessed November 2013).
- Balme, G.A., Lindsey, P.A., Swanepoel, L.H. & Hunter, L.T.B. (2013). Failure of research to address the rangewide conservation needs of large carnivores: leopards in South Africa as a case study. *Conservation Letters.*, DOI: 10.1111/conl.12028.

- Balme, G.A. & Hunter, L.T.B. (2013). Why leopards commit infanticide. *Animal Behaviour.*, **86**(4): 791-799.
- Balme, G., Batchelor, A., de Woronin Britz, N., Seymour, G., Grover, M., Hes, L., Macdonald, D.W. & Hunter, L.T.B (2012). Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. *Mammal Review.*, **43** (3): 221-237.
- Balme, G.A., Hunter, L.T.B & Brackowski, A.R. (2012). Applicability of age-based hunting regulations for African leopards. *PloS one.*, **7**(4): e35209.
- Balme, G.A., Slotow, R. & Hunter, L.T.B. (2010). Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. *Animal Conservation.*, **13**(3): 315-323.
- Balme, G.A., Hunter, L.T.B., Goodman, P., Ferguson, H., Craigie, J. & Slotow, R. (2010). An adaptive management approach to trophy hunting of leopards *Panthera pardus*: a case study from KwaZulu-Natal, South Africa. In D.W Macdonald & A.J Loveridge (eds) *Biology and conservation of wild felids*, pp 341-352. Oxford, Oxford University Press.
- Balme, G.A., Hunter, L.T.B & Slotow, R. (2009a). Evaluating methods for counting cryptic carnivores. *The Journal of wildlife management.*, **73**(3): 433-441.
- Balme, G.A., Slotow, R. & Hunter, L.T.B. (2009b). Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation.*, **142**(11): 2681-2690.
- Balme, G., Hunter, L. & Slotow, R. (2007). Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour.*, **74**(3): 589-598.

- Barnhurst, D. (1986). *Vulnerability of cougars to hunting*. Unpublished Msc thesis. Utah State University, Logan.
- Beecham, J. (1980). Some Population Characteristics of Two Black Bear Populations in Idaho. *Bears: Their Biology and Management.*, **4**: 201-204.
- Begg, C.M & Begg, K.S. (2009). Niassa carnivore Project, pp 44. Produced for SRN, Maputo, Mozambique.
- Begg, C.M & Begg, K.S. (2007). *Trophy monitoring in Niassa National Reserve Mozambique: Lion, leopard, buffalo, hippo, and crocodile*, pp 79 SRN, Maputo, Mozambique.
- Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management.*, **59**: 228-237.
- Beirman, D. (2003). *Restoring tourism destinations in crisis: a strategic marketing approach*. Cabi publishing, Wallingford.
- Berger, G. (2007). Fear, human shields and the re-distribution of prey and predators in protected areas. *Biology Letters.*, **3**(6): 620-627.
- Booth, V. (2009). A comparison of the prices of hunting in Southern and Eastern Africa. Joint publication of FAO and CIC, Budapest. CIC, Budapest. Available: www.cic-wildlife.org/fileadmin/Press/Technical_Series/EN/7.pdf via the internet. Accessed August 2013.
- Bond, I., Child, B., De La Harpe, D., Jones, B., Barnes, J. & Anderson, H. (2004). Private land contribution to conservation in South Africa, in B.Child (ed.), *Parks in transition*, pp 29–61. Earthscan, London.
- Botha, G. & Porat, N. (2007). Soil chronosequence development in dunes on the southeast African coastal plain, Maputaland, South Africa. *Quaternary international.*, **162**: 111-132.

- Bothma, J.D.P. & Walker, C. (1999). *Larger carnivores of the African savannas*. Springer, Berlin.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K. (2002). Evaluating resource selection functions. *Ecological modeling.*, **157**(2): 281-300.
- Braczkowski, A., Balme, G.A., Dickman, A., Fattebert, J., Johnson, P., Dickerson, T., Macdonald, D.W. & Hunter, L.T.B. (submitted) Who bites the bullet first? Examining the use of harvest composition as a metric of leopard *Panthera pardus* population trend.
- Braczkowski, A. & Watson, L. (2013). Observations of leopard and caracal responses to novel scents in South Africa. *CAT News.*, **58**: 13-15.
- Braczkowski, A., Watson, L., Coulson, D. & Randall, R. (2012). Diet of leopards in the southern Cape, South Africa. *African Journal of Ecology.*, **50**(3): 377-380.
- Brashares, J., Prugh, L., Stoner, C. & Epps, C. (2010). Ecological and conservation implications of mesopredator release. In *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature* (eds J. Terborgh & J.A. Estes), pp. 221-240. Island Press, Washington, DC.
- Bunnefeld, N., Baines, D., Newborn, D. & Milner-Gulland, E.J. (2009). Factors affecting unintentional harvesting selectivity in a monomorphic species. *Journal of Animal Ecology.*, **78**(2): 485-492.
- Busby, G.B., Gottelli, D., Wacher, T., Marker, L., Belbachir, F., De Smet, K., Belbachir-Bazi, A., Fellous, A., Belghoul, M. & Durant, S.M. (2009). Genetic analysis of scat reveals leopard *Panthera pardus* and cheetah *Acinonyx jubatus* in southern Algeria. *Oryx.*, **43**(3): 412-415.
- Butler, J.R.A., Du Toit, J.T. & Bingham, J. (2004). Free-ranging domestic dogs (*Canis familiaris*) as predators and prey in rural Zimbabwe: threats of

- competition and disease to large wild carnivores. *Biological Conservation.*, **115**(3): 369-378.
- Cabral, L. & Hortacsu, A. (2010). The dynamics of seller reputation: evidence from eBay. *Journal of Industrial Economics.*, **58**(1): 54-78.
- Chapman, S. (2012). Leopard density capture-recapture camera-trap survey results, Hluhluwe-Imfolozi Park. *Unpublished report, Wildlife ACT & NZHO leopard project.*
- Chapman, S. & Balme, G. (2010). An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South African Journal of Wildlife Research*, **40**(2): 114-120.
- Chevalier, J. & Mayzlin, D. (2003). The effect of word of mouth on sales: Online book reviews. *National Bureau of Economic Research*. **10148**.
- Clark, T., Rutherford, M. & Casey, D. (2005). *Coexisting with large carnivores: Lessons from Greater Yellowstone*. Island Press, New York.
- Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003). Undesirable evolutionary consequences of trophy hunting. *Nature.*, **426**(6967): 655-658.
- Conde, D.A., Colchero, F., Zarza, H., Christensen Jr, N.L., Sexton, J.O., Manterola, C. & Ceballos, G. (2010). Sex matters: Modelling male and female habitat differences for jaguar conservation. *Biological Conservation.*, **143**(9): 1980-1988.
- Crosmary, W.G., Loveridge, A.J., Ndaimani, H., Lebel, S., Booth, V., Côté, S.D. & Fritz, H. (2013). Trophy hunting in Africa: long-term trends in antelope horn size. *Animal Conservation.*, **16**(6): 648-660.

- Daly, B., Power, J., Camacho, G., Traylor-Holzer, K., Barber, S., Catterall, S., Fletcher, P., Martins, Q., Martins, N., Owen, C., Thal, T. & Friedmann, Y. (2005). *Leopard Panthera pardus population and habitat viability assessment*. Proceedings of a workshop of the Conservation Breeding Specialist Group. World Conservation Union IUCN Species Survival Commission. Endangered Wildlife Trust, Johannesburg.
- Di Minin, E., Hunter, L.T.B, Balme, G.A., Smith, R.J., Goodman, P.S. & Slotow, R. (2013). Creating Larger and Better Connected Protected Areas Enhances the Persistence of Big Game Species in the Maputaland-Pondoland-Albany Biodiversity Hotspot. *PloS one.*, **8**(8): e71788.
- Di Minin, E., Fraser, I., Slotow, R., & MacMillan, D. C. (2012). Understanding heterogeneous preference of tourists for big game species: implications for conservation and management. *Animal Conservation.*, **16**(3): 249-258.
- Druce, H.C., Pretorius, K. & Slotow, R. (2008). The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biological conservation.*, **141**(12): 3127-3138.
- Du Preez, B. (2014). *The effect of intraguild competition with lion (Panthera leo) on leopard (Panthera pardus) behavioural ecology*. Unpublished PhD thesis. University of Oxford. Oxford.
- Edgaonkar, A. & Chellam, R. (2002). Food habit of the leopard, *Panthera pardus*, in the Sanjay Gandhi National Park, Maharashtra, India. *Mammalia.*, **66**(3): 353-360.
- Efford, M. (2013). *Package secr version 2.6.1*. R language for statistical computing.
- Efford, M.G., Dawson, D.K. & Robbins, C.S. (2004). DENSITY: software for analysing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation.*, **27**(1): 217-228.

- Fattebert, J., Dickerson, T., Balme, G., Slotow, R. & Hunter, L. (2013). Long-distance natal dispersal in leopard reveals potential for a three-country metapopulation. *South African Journal of Wildlife research.*, **43**(1): 61-67.
- Fattebert, J., Balme, G., Robinson, H., Dickerson, T., Slotow, R. & Hunter, L. (submitted) Socio-spatial organisation of a leopard population recovering from over-harvest. *Animal Behaviour*.
- Fattebert et al. (in prep) *Lasting impact of harvest on natal dispersal in leopard (Panthera pardus) in KwaZulu Natal, South Africa*.
- Ferreira, S.M. & Funston, P.J. (2010). Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. *Wildlife Research.*, **37**(3): 194-206.
- Fombrun, C. & Shanley, M. (1990) What's in a name? Reputation building and corporate strategy. *Academy of Management Journal.*, **33**(2): 233-258.
- Funston, P.J., Groom, R.J. & Lindsey, P.A. (2013). Insights into the Management of Large Carnivores for Profitable Wildlife-Based Land Uses in African Savannas. *PloS one.*, **8**(3): e59044.
- Gerber, B.D., Karpanty, S.M. & Kelly, M.J. (2012). Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Population ecology.*, **54**(1): 43-54.
- Gopalaswamy, A.M., Royle, J.A., Delampady, M., Nichols, J.D., Karanth, K.U. & Macdonald, D.W. (2012a). Density estimation in tiger populations: combining information for strong inference. *Ecology.*, **93**(7): 1741-1751.
- Gopalaswamy, A.M., Royle, J.A., Hines, J.E., Singh, P., Jathanna, D., Kumar, N. & Karanth, K.U. (2012b). Program SPACECAP: software for estimating animal

- density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution.*, **3**(6): 1067-1072.
- Grant, T.L. (2012). *Leopard population density, home range size and movement patterns in a mixed landuse area of the Mangwe District of Zimbabwe*. Unpublished PhD thesis. Rhodes University, Grahamstown.
- Gaugris, J.Y. & Van Rooyen, M.W. (2008). A spatial and temporal analysis of Sand Forest tree assemblages in Maputaland, South Africa. *South African Journal of Wildlife Research.*, **38**(2): 171-184.
- Harris, R.B. Cooney, R. & Leader-Williams, N. (2013). Application of the Anthropogenic Allee Effect Model to Trophy Hunting as a Conservation Tool. *Conservation Biology.*, **27**(5): 945-951.
- Harmsen, B.J., Foster, R.J. & Doncaster, C. P. (2011). Heterogeneous capture rates in low density populations and consequences for capture-recapture analysis of camera-trap data. *Population ecology.*, **53**(1): 253-259.
- Hayward, M.W., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G. & Kerley, G.I.H. (2006). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology.*, **270**(2): 298-313.
- Hebblewhite, M., Miquelle, D.G., Murzin, A.A., Aramilev, V.V., & Pikunov, D.G. (2011). Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. *Biological Conservation.*, **144**(10): 2403-2413.
- Henschel, P., Azani, D., Burton, C., Malanda, G., Saidu, Y., Moses, S. & Hunter, L. (2010). Lion status updates from five range countries in West and Central Africa. *Cat News.*, **52**: 34–39.

- Henschel, P., Hunter, L. T. B., Coad, L., Abernethy, K. A. & Mühlenberg, M. (2011). Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. *Journal of zoology.*, **285**(1): 11-20.
- Henschel, P., Hunter, L., Breitenmoser, U., Purchase, N., Packer, C., Khorozyan, I., Bauer, H., Marker, L., Sogbohossou, E. & Breitenmoser-Wursten, C. (2008). *Panthera pardus*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. www.iucnredlist.org. Downloaded on 02 December 2013.
- Henschel, P. & Ray, J. (2003). *Leopards in African rainforests: survey and monitoring techniques*. Wildlife Conservation Society, New York.
- Hunter, L.T.B., Lindsey, P., Balme, G., Becker, M., Begg, C., Brink, H., Chardonnet, P., Dickman, A., Edwards, C., Frank, L., Funston, P., Henschel, P., Ikanda, D., Kissui, B., Loveridge, A.J., Mesochina, P., Midlane, N., White, P. & Whitman-Gelatt, K. (2013). Urgent and comprehensive reform of trophy hunting of lions is a better option than an endangered listing: A science based consensus. *Unpublished report for the United States Fish and Wildlife Service*.
- Hunter, L. & Barrett, P. (2011). *A field guide to the carnivores of the world*. New Holland Publishers, London.
- Hunter, L.T.B., Pretorius, K., Carlisle, L.C., Rickleton, M., Walker, C., Slotow, R. & Skinner, J.D. (2007) Restoring lions *Panthera leo* to northern KwaZulu-Natal, South Africa: short-term biological and technical success but equivocal long-term conservation. *Oryx.*, **41**(2) 196-204.
- Hunter, L. & Balme, G. (2004). Trash or in trouble? – The leopard's predicament. *Africa Geographic.*, 60-67.
- Hunter, L., Balme, G., Walker, C., Pretorius, K. & Rosenberg, K. (2003). The landscape ecology of leopards (*Panthera pardus*) in northern KwaZulu-Natal, South Africa: A preliminary project report. *Ecological Journal.*, **5**: 24-30.

- Hunter, L.T.B. (1998). *The behavioural ecology of re-introduced lions and cheetahs in the Phinda Resource Reserve, northern kwaZulu-Natal, South Africa*. Unpublished PhD thesis. University of Pretoria, Pretoria.
- Ickes, K., Dewalt, S. J. & Appanah, S. (2001). Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. *Journal of Tropical Ecology*., **17**(2):191-206.
- Ickes, K. & Williamson, B. (2000). Edge effects and ecological processes: are they on the same scale? *Trends in ecology & evolution*., **15**(9): 373.
- Jachmann, H. (2002). Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology*., **39**(5): 841-852.
- Johnson, J.B. & Reingen, P.H. (1987). Social ties and word-of-mouth referral behavior. *Journal of Consumer Research*., **14**(3): 350-362.
- Johnson, P. J., Kansky, R., Loveridge, A. J. & Macdonald, D. W. (2010). Size, rarity and charisma: valuing African wildlife trophies. *PLoS One*., **5**(9): e12866.
- Jorge, A.A., Vanak, A.T., Thaker, M., Begg, C., & Slotow, R. (2013). Costs and Benefits of the Presence of Leopards to the Sport-Hunting Industry and Local Communities in Niassa National Reserve, Mozambique. *Conservation Biology*., **27**(4): 832-843.
- Karanth, K.U., Nichols, J.D. & Kumar, S.N. (2011). Estimating tiger abundance camera-trap data: field surveys and analytical issues. In A. O'Connell, J.D. Nichols & K.U. Karanth (Eds). *Camera-traps in animal ecology*, pp. 97-117. Springer, Japan.
- Karanth, K.U. & Nichols, J.D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*., **79**(8): 2852-2862.

- Karanth, K.U. (1995). Estimating tiger *Panthera tigris* populations from camera-trap data using capture—recapture models. *Biological conservation.*, **71**(3): 333-338.
- Lagendijk, D.G., Mackey, R.L., Page, B.R. & Slotow, R. (2011). The Effects of herbivory by a mega-and mesoherbivore on tree recruitment in Sand Forest, South Africa. *PloS one.*, **6**(3): e17983.
- Laundre, J.W., Hernandez, L. & Altendorf, K.B. (2001). Wolves, elk and bison: re-establishing the “landscape of fear” in Yellowstone National Park, USA. *Canadian Journal of Zoology.*, **79**(8): 1401-1409.
- Lazenby, B.T. & Dickman, C.R. (2013). Patterns of detection and capture are associated with cohabiting predators and prey. *PloS one.*, **8**(4): e59846.
- Leader-Williams, N., Smith, R.J., & Walpole, M.J. (2001). Elephant hunting and conservation. *Science.*, **293**(5538): 2203-2204.
- Leader-Williams, N., Kayera, J.A., & Overton, G.L. (1996). *Tourist Hunting in Tanzania: Proceedings of a Workshop Held in July 1993* (No. 14). IUCN Commission, Belgium.
- Lee, J. & Taylor, M. (1994). Aspects of the Polar Bear Harvest in the Northwest Territories, Canada. *Bears: Their Biology and Management.*, **9**(1): 237-243.
- Lewis, D.M. & Alpert, P. (1997). Trophy hunting and wildlife conservation in Zambia. *Conservation Biology.*, **11**(1): 59-68.
- Lewis, D. & Jackson, J. (2005). Safari hunting and conservation on communal land in southern Africa. In R. Woodroffe, S.J. Thirgood, A. Rabinowitz (Eds.), *People and Wildlife: Conflict or Coexistence*, pp. 239–252. Cambridge University Press, Cambridge.

- Lindsey, P.A., Balme, G.A., Funston, P., Henschel, P., Hunter, L., Madzikanda, H., Midlane, N. & Nyirenda, V. (2013). The trophy hunting of African lions: scale, current management practices and factors undermining sustainability. *PloS one.*, **8**(9): e73808.
- Lindsey, P. A., Balme, G., Becker, M., Begg, C., Bento, C., Bocchino, C., Dickman, A., Diggle, R.W., Eves, H., Henschel, P., Lewis, D., Marnewick, K., Mattheus, J., McNutt, J.W., McRobb, R., Midlane, N., Milanzi, J., Morley, R., Murphree, M., Opyene, V., Phadima, J., Purchase, G., Rentsch, D., Roche, C., Shaw, J., van der Westhuizen, H., Van Vliet, N. & Zisadza-Gandiwa, P. (2013). The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. *Biological Conservation.*, **160**: 80-96.
- Lindsey, P.A., Balme, G.A., Booth, V.R. & Midlane, N. (2012). The significance of African lions for the financial viability of trophy hunting and the maintenance of wild land. *PloS one.*, **7**(1): e29332.
- Lindsey, P.A., Roulet, P.A. & Romañach, S.S. (2007). Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation.*, **134**(4): 455-469.
- Lindsey, P.A., Alexander, R., Frank, L.G., Mathieson, A., & Romanach, S.S. (2006). Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. *Animal Conservation.*, **9**(3): 283-291.
- Lindsey, P. A., Frank, L. G., Alexander, R., Mathieson, A., & Romanach, S. S. (2007). Trophy hunting and conservation in Africa: problems and one potential solution. *Conservation biology*, **21**(3), 880-883.
- Little, J.M. & Berrens, R.P. (2008). The Southwestern market for big game hunting permits and services: a hedonic pricing analysis. *Human Dimensions of Wildlife.*, **13**: 147-157.

- Litvaitis, J.A. & Kane, D.M. (1994). Relationship of hunting technique and hunter selectivity to composition of black bear harvest. *Wildlife Society Bulletin.*, **22**: 604–606.
- Livengood, K. R. (1983). Value of big game from markets for hunting leases: the hedonic approach. *Land Economics.*, **59**(3): 287-291.
- Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald, D.W. (2007). The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation.*, **134**: 548-558.
- Loveridge, A.J., Reynolds, J.C. & Milner-Gulland, E.J. (2007). *Does sport hunting benefit conservation?* In D.W. Macdonald & K. Service (eds). *Key topics in Conservation Biology*. Blackwell, Oxford.
- Maciejewski, K. (2012) *Exploring the linkages between biodiversity conservation and ecotourism in Protected Areas*. Unpublished PhD thesis. Nelson Mandela Metropolitan University, Port Elizabeth.
- Macdonald, D.W., Loveridge, A.J. & Nowell, K. (2010). Dramatis personae: an introduction to the wild felids. In D.W Macdonald & A.J. Loveridge (eds) *Biology and Conservation of wild felids*. Oxford University Press, Oxford.
- MacKay, P., Smith, D.A., Long, R. & Parker, M. (2008). *Scat detection dogs. Non-invasive survey methods for carnivores*, pp 183-222. Island Press, Washington,.
- Maffei, L., Noss, A.J., Silver, S.C. & Kelly, M.J. (2011). Abundance/Density case study: Jaguars in the Americas. In A. O'Connell, J.D Nichols & K.U. Karanth (Eds). *Camera-traps in animal ecology Camera-traps in animal ecology*, pp. 119-144. Springer, Japan.
- Maputla, N.W., Chimimba, C.T. & Ferreira, S.M. (2013). Calibrating a camera-trap–based biased mark–recapture sampling design to survey the leopard

- population in the N'wanetsi concession, Kruger National Park, South Africa. *African Journal of Ecology.*, **51**(3): 422-430.
- Marker, L.L. & Dickman, A.J. (2005). Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *South African Journal of Wildlife Research.*, **35**(2): 105-115.
- Marnewick, K., Funston, P.J., & Karanth, K.U. (2008). Evaluating camera-trapping as a method for estimating cheetah abundance in ranching areas. *South African Journal of Wildlife Research.*, **38**(1): 59-65.
- Martin, R.B. & de Meulenaer, T. (1988). *Survey of the Status of the Leopard (Panthera pardus) in Sub-Saharan Africa*. Secretariat for the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Lausanne, Switzerland.
- Martins, Q. & Harris, S. (2013). Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *African Journal of Ecology.*, **51**(4): 571-579.
- Martins, Q., & Martins, N. (2006). Leopards of the Cape: conservation and conservation concerns. *International journal of environmental studies*, **63**(5): 579-585.
- Matthews, W. S. (2007). *Contributions to the ecology of Maputaland, southern Africa, with emphasis on Sand Forest*. Unpublished PhD thesis, University of Pretoria, Pretoria.
- Mcculloch, D.R. (1979). *The George Reserve deer herd-population: ecology of a K selected species*. University of Michigan Press, Ann Arbor.
- McManus., J. (2009). *The Spatial Ecology and Activity Patterns of Leopards (Panthera pardus) in the Baviaanskloof and Greater Addo Elephant National Park, Eastern Cape Province, South Africa*. MSc thesis. Rhodes University, Grahamstown.

- Melnik, M.I. & Alm, J. (2002). Does a seller's ecommerce reputation matter? Evidence from eBay auctions. *The journal of industrial economics.*, **50**(3): 337-349.
- Miller, C.M. & Miller, B. (2005). *Jaguar density in La Selva Maya*. Unpublished report. Wildlife Conservation Society. Gallon Jug, Belize.
- Mills, M.G.L. (1987). Behavioural adaptations of brown and spotted hyaenas in the southern Kalahari. *South African Journal of Science.*, **83**: 595–598.
- Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Csányi, S. & Stenseth, N. C. (2006). Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology.*, **43**(4): 721-734.
- Milner-Gulland, E.J., Bukreeva, O.M., Coulson, T., Lushchekina, A.A., Kholodova, M.V., Bekenov, A.B. & Grachev, I.A. (2003). Reproductive collapse in a harem-breeding ungulate. *Nature.*, **422**: 135.
- Miththapala, S., Seidensticker, J., Phillips, L. G., Fernando, S. B. U. & Smallwood, J. A. (1989). Identification of individual leopards (*Panthera pardus kotiya*) using spot pattern variation. *Journal of Zoology.*, **218**(4): 527-536.
- Mizutani, F. & Jewell, P.A. (1998). Home-range and movements of Leopards (*Panthera pardus*) on a livestock ranch in Kenya. *Journal of Zoology.*, **244**(2): 269-286.
- Moreno, R.S., Kays, R.W. & Samudio Jr, R. (2006). Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *Journal of Mammalogy.*, **87**(4): 808-816.
- Morgan, S. (2010) *Black Rhino (Diceros bicornis) movement and habitat analyses*. Unpublished PhD thesis. University of Kwazulu-Natal, Kwazulu-Natal.

- Mucina, L. & Rutherford, M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia.*, **19**.
- Mysterud, A. (2011). Selective harvesting of large mammals: how often does it result in directional selection? *Journal of Applied Ecology.*, **48**(4): 827-834.
- Noss, A.J., Gardner, B., Maffei, L., Cuéllar, E., Montaña, R., Romero-Muñoz, A., Sollman, R. & O'Connell, A. F. (2012). Comparison of density estimation methods for mammal populations with camera-traps in the Kaa-lya del Gran Chaco landscape. *Animal Conservation.*, **15**(5): 527-535.
- Nowell, K. & Jackson, P. (1996). *The Wild Cats: A Status Survey & Conservation Action Plan*. IUCN. Gland, Switzerland.
- Noyce, K.V., Garshelis, D.L. & Coy, P.L. (2001). Differential Vulnerability of Black Bears to Trap and Camera Sampling and Resulting Biases in Mark-Recapture Estimates. *Ursus.*, **12**: 211-226.
- Obbard, M.E., Howe, E.J., & Kyle, C.J. (2010). Empirical comparison of density estimators for large carnivores. *Journal of Applied Ecology.*, **47**(1): 76-84.
- O'Connell, A., Nichols, J.D. & Karanth, K.U (2011) *Camera-traps in animal ecology*. Springer, Japan.
- Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs.*, **62**:1-135.
- Owen-Smith, N. & Mills, M.G. (2008) .Predator–prey size relationships in an African large-mammal food web. *Journal of Animal Ecology.*, **77**(1): 173-183.

- Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. (2011). Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology*, **1**: 1-12.
- Packer, C., Kosmala, M., Cooley, H.S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Strauss, M., Swanson, A., Balme, G., Hunter, L. & Nowell, K. (2009). Sport hunting, predator control and conservation of large carnivores. *Plos One*, **4**(6): e5941.
- Palazy, L., Bonenfant, C., Gaillard, J. M. & Courchamp, F. (2012). Rarity, trophy hunting and ungulates. *Animal Conservation*, **15**(1): 4-11.
- Palazy, L., Bonenfant, C., Gaillard, J. M. & Courchamp, F. (2011). Cat dilemma: too protected to escape trophy hunting?. *PloS one*, **6**(7): e22424.
- Palomares, F., Roques, S., Chávez, C., Silveira, L., Keller, C., Sollmann, R., do Prado, D.M., Torres, P.C., Adrados, B., Godoy, J.A., de Almeida Jacomo, A.T., Torres, N.M., Furtado, M.M. & López-Bao, J. V. (2012). High Proportion of Male Faeces in Jaguar Populations. *PloS one*, **7**(12): e52923.
- Peres, C.A. & Palacios, E. (2007). Basin-Wide Effects of Game Harvest on Vertebrate Population Densities in Amazonian Forests: Implications for Animal-Mediated Seed Dispersal. *Biotropica*, **39**(3): 304-315.
- Pesenti, E. & Zimmermann, F. (2013). Density estimations of the Eurasian lynx (*Lynx lynx*) in the Swiss Alps. *Journal of Mammalogy*, **94**(1): 73-81.
- Pitman, R. T. (2012). The conservation biology and ecology of the African leopard *Panthera pardus pardus*. *The Plymouth Student Scientist*, **5**(2): 581-600.
- Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, **52**: 703-709.

- Prescott, G.W., Johnson, P.J., Loveridge, A.J. & Macdonald, D. W. (2012). Does change in IUCN status affect demand for African bovid trophies? *Animal Conservation.*, **15**(3): 248-252.
- Quiroga, V.A., Boaglio, G.I., Noss, A.J. & Di Bitetti, M.S. (2013). Critical population status of the jaguar *Panthera onca* in the Argentine Chaco: camera-trap surveys suggest recent collapse and imminent regional extinction. *Oryx.*, 1-8.
- R Development Core Team (2008) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ray, J.C., Hunter, L. & Zigouris, J. (2005). *Setting conservation and research priorities for larger African carnivores* (Vol. 24). Wildlife Conservation Society, New York.
- Ramakrishnan, U., Coss, R.G. & Pelkey, N.W. (1999). Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biological Conservation.*, **89**(2): 113-120.
- Resnick, P., Zeckhauser, R., Swanson, J. & Lockwood, K. (2006). The value of reputation on eBay: A controlled experiment. *Experimental economics.*, **9**(2): 79-101.
- Rindova, V.P., Williamson, I.O., Petkova, A.P. & Server, J.M. (2005). Being good or being known: An empirical examination of the dimensions, antecedents, and consequences of organizational reputation. *Academy of Management Journal.*, **48**(6): 1033-1049.
- Ripple, W.J. & Beschta, R.L. (2008). Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation.*, **141**(5): 1249-1256.
- Ripple, W.J. & Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation.*, **133**(4): 397-408.

- Rivrud, I.M., Sonkoly, K., Lehoczki, R., Csányi, S., Storvik, G.O. & Mysterud, A. (2013). Hunter selection and long-term trend (1881–2008) of red deer trophy sizes in Hungary. *Journal of Applied Ecology.*, **50**(1): 168-180.
- Rogerson, W. (1983). Reputation and Product Quality. *The Bell Journal of Economics.*, **114**(2): 508-516.
- Roseberry, J.R & Klimstra, W.D. (1974). Differential Vulnerability during a Controlled Deer Harvest. *The Journal of Wildlife Management.*, **38**(3): 499-507.
- Royle, J.A., Karanth, K.U., Gopalaswamy, A.M. & Kumar, N.S. (2009). Bayesian inference in camera-trapping studies for a class of spatial capture-recapture models. *Ecology.*, **90**(11): 3233-3244.
- Royle, J.A. & Young, K.V. (2008). A hierarchical model for spatial capture-recapture data. *Ecology.*, **89**(8): 2281-2289.
- Saayman, M., Merwe, P.V.D. & Rossouw, R. (2011) The economic impact of hunting in the Northern Cape province. *South African Journal of Wildlife Research.*, **41**(1): 120-133.
- Samuelsson, E. & Stage, J. (2007). The size and distribution of the economic impacts of Namibian hunting tourism. *South African Journal of Wildlife Research.*, **37**(1): 41-52.
- Skinner, J.D. & Chimimba, C.T. (2005). *The mammals of the Southern African sub-region*. Cambridge University Press, Cambridge.
- Sollmann, R., Tôrres, N.M., Furtado, M.M., de Almeida Jácomo, A.T., Palomares, F., Roques, S. & Silveira, L. (2013). Combining camera-trapping and noninvasive genetic data in a spatial capture–recapture framework improves density estimates for the jaguar. *Biological Conservation.*, **167**: 242-247.

- Sollmann, R., Furtado, M.M., Gardner, B., Hofer, H., Jácomo, A.T.A., Tôrres, N.M. & Silveira, L. (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation.*, **144**: 1017–1024.
- Sönmez, S.F. (1998). Tourism, terrorism, and political instability. *Annals of Tourism Research*, **25**(2): 416-456.
- Spong, G., Hellborg, L. & Creel, S. (2000). Sex ratio of leopards taken in trophy hunting: genetic data from Tanzania. *Conservation genetics.*, **1**(2): 169-171.
- Stander, P.E. (1998). Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology.*, **35**(3): 378-385.
- Stanley, T.R. & Burnham, K.P. (1999). A closure test for time-specific capture–recapture data. *Environmental and Ecological Statistics.*, **6**(2): 197-209.
- Steyn, V. & Funston, P.J. (2006). A case of cannibalism in leopards: short communications. *South African Journal of Wildlife Research*, **36**(2): 189.
- Sunquist, M. & Sunquist, F. (2002). *Wild cats of the world*. University of Chicago Press, Chicago.
- Sunquist, M.E. (1983) Dispersal of three radio-tagged leopards. *Journal of Mammalogy.*, **64**(2): 337-341.
- Swanepoel, L.H., Lindsey, P., Somers, M.J., Hoven, W.V. & Dalerum, F. (2012). Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation.*, **16**(1): 41-50.

- Thomas, P., Balme, G., Hunter, L. & McCabe-Parodi, J. (2005). Using scent attractants to non-invasively collect hair samples from cheetahs, leopards and lions. *Animal Keeper's Forum*, **7/8**: 342-384.
- Thorn, M., Scott, D.M., Green, M., Bateman, P.W. & Cameron, E.Z. (2009). Estimating brown hyaena occupancy using baited camera-traps. *South African Journal of Wildlife Research.*, **39**(1): 1-10.
- Tobler, M.W. & Powell, G.V. (2013). Estimating jaguar densities with camera-traps: Problems with current designs and recommendations for future studies. *Biological Conservation.*, **159**: 109-118.
- Tobler, M.W., Carrillo-Percastegui, S.E., Zúñiga Hartley, A. & Powell, G.V. (2013). High jaguar densities and large population sizes in the core habitat of the southwestern Amazon. *Biological Conservation.*, **159**: 375-381.
- Trollope, W.S., Trollope, L.A., Naylor, S.J. & Goode, R.R. (2011). The Mun-Ya-Wana Private Game Reserve, South Africa—a leader in using a Decision Support System for Prescribed Burning. *Proceedings from the 5th International Wildland Fire Conference*. Sun City, South Africa.
- Tuytens, F.A.M., Delahay, R.J., Macdonald, D.W., Cheeseman, C.L., Long, B. & Donnelly, C.A. (2000). Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *Journal of Animal Ecology.*, **69**(5): 815-828.
- Van Rooyen, N. & Morgan, S.R. (2007). Habitat/Landscapes Phinda Game Reserve. *Unpublished Report. Phinda Private Game Reserve, CCAfrica*, Johannesburg.
- Venables, W.N. & Ripley, B.D. (2002). *Modern Applied Statistics with S*. Springer, New York.

- Von Brandis, R.G. & Reilly, B.K. (2007). A temporal analysis of trophy quality in South Africa: has trophy quality changed over time. *South African journal of wildlife research.*, **37**(2): 153-158.
- Wang, S. W. & Macdonald, D. W. (2009). Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. *Journal of Zoology.*, **277**(4): 275-283.
- Wennergren, E.B., Fullerton, H.H. & Wrigley, J.C. (1977). Quality values and determinants for deer hunting. *The Journal of Wildlife Management.*, **41**(3): 400-407.
- Wenzel, G. W. (2011). Polar bear management, sport hunting and Inuit subsistence at Clyde River, Nunavut. *Marine Policy.*, **35**(4): 457-465.
- Whitman, K., Starfield, A.M., Quadling, H.S. & Packer, C. (2004). Sustainable trophy hunting of African lions. *Nature.*, **428**(6979): 175-178.
- Whittington-Jones, B.M. (2011). *The dispersal of African Wild Dogs Lycaon pictus from protected areas in the northern KwaZulu-Natal province, South Africa.* Unpublished MSc Thesis. Rhodes University, Grahamstown.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002). *Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making.* Academic Press, California.
- Zar, J. H. (1999) *Biostatistical analysis.* Pearson Education, India.

APPENDIX:

COUNTNG CATS: A USER FRIENDLY MANUAL TO PERFORM SPATIALLY EXPLICIT CAPTURE RE-CAPTURE ANALYSES ON WILD FELID POPULATIONS USING SECR AND SPACECAP



Counting cats: a user-friendly manual to perform spatially explicit capture re-capture analyses on wild felid populations using secr and SPACECAP in R



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Foreword and acknowledgements

Since Ullas Karanth and James Nichols' revolutionary work on tigers in the mid-nineties, the suite of analysis techniques available to biologists and managers in order to count wild felids has grown in leaps and bounds. For years biologists have been accustomed to using CAPTURE and MARK; two user-friendly capture recapture programmes. However, more recently catchy names like "SPACECAP", "secr", "DENSITY" and "Jags" have been increasingly thrown around workshops, conferences and classrooms (we can probably all agree that these look even better in the methods section of a new conservation publication). But ultimately, what do these software packages do and how do we use them? After all, once we've collected our camera trap data, we want to be able to count a population of cats using relatively simple methods, and not have to struggle for hours on end, trying to understand tricky algorithms, complex code and intimidating outputs ☹. Wild felids are declining rapidly, and the enumeration of their populations is often required quickly to guide management decisions. We believe conservation biologists and wildlife managers alike should be equipped with the skills in order to achieve this goal and not have to struggle with technical difficulties regarding software or math.

That's why we've come together to create this short, user-friendly tutorial which will help you to analyse camera-trap capture recapture data using two of the most up to date software packages in the R environment: SPACECAP and secr. These packages are freely available on the World Wide Web, use advanced methods of estimation and best of all they don't require you to estimate the effectively sampled area around your camera grid (a tricky user-defined buffer usually based upon mean maximum movements travelled by your study animals). In this guide we provide you with an example dataset from a camera trap survey of leopards conducted in 2011, in the coastal savanna of northern Zululand. We show you how to format the dataset in Excel and how to import it into the R software platform for use by either the SPACECAP or secr packages. We then discuss some of the essentials of wild felid ecology and create a few models which are useful in estimating their densities. Finally, we show you how to analyse the leopard dataset, step by step using SPACECAP and secr, how to interpret the results and how to pick the best model for your final density estimates.

Whether you're working on snow leopards in the rugged mountains of China, jaguars in Brazil's cerrado or tigers in a remote Indian jungle, as long as your species has got stripes or spots which you can use to identify individuals, this manual will help you estimate their populations robustly.

Finally, we'd like to say thanks to a few important people who helped take this manual into its present form. We thank Arjun Gopalaswamy for his comments on technical aspects of this manual. Christos Astaras is thanked for his edits and commentary on previous versions. Cedric Tan is thanked for testing the tutorial and proofing the R code used to run R and the secr/SPACECAP packages.

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The creators of secr and SPACECAP



Dr Murray Efford (PhD) is the creator of the spatially explicit capture-recapture programmes, “DENSITY” as well as the R package “secr”. He is a world leader in the field of density estimation studies, and was the first scientist to incorporate spatial information into capture-recapture models. He has worked on species ranging from brushtail possums *Trichosurus vulpecula* to ship rats *Rattus rattus*. His work on the enumeration of the ovenbird *Seiurus aurocapilla* with Deanna Dawson has revolutionized the field of counting birds, traditionally implemented with mist nets, it can now be achieved using acoustic recordings of bird calls. Dr Efford contributes to a spatially explicit capture-recapture help forum where he addresses user questions, tricky code or software bugs, it is available online at: www.phidot.org/forum. He is a regular contributor to the scientific literature, and has published in journals such as “Ecology”, “Biometrics” and the “Journal of Applied Ecology”.



Arjun Gopaldaswamy (D.Phil student) is a leading tiger biologist based at Oxford University’s Wildlife Conservation Research Unit (WildCRU) and Balliol College. Arjun is lead author and co-creator of the industry’s leading Bayesian spatially-explicit density estimation software package: SPACECAP. He is a regular contributor to the scientific literature, particularly on his density estimation work, and has published on spatially explicit capture-recapture studies in internationally acclaimed journals such as “Ecology”, and the “Journal of Applied Ecology”.

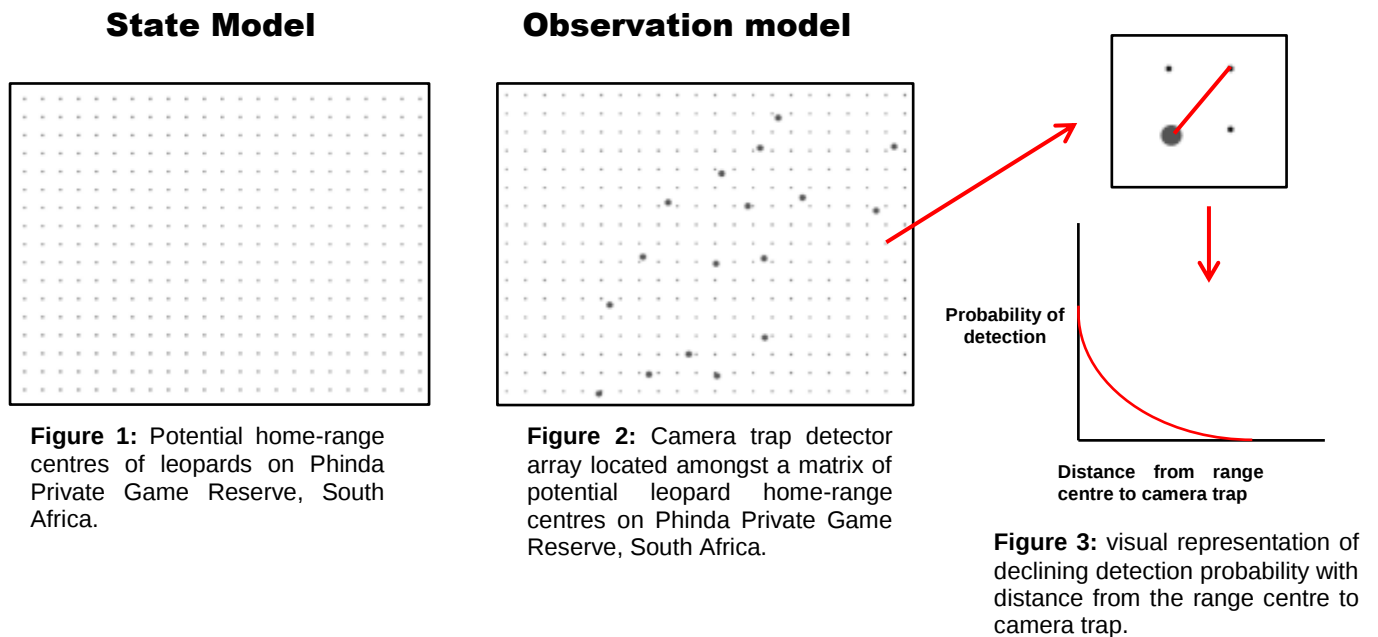
Basics of spatially explicit capture re-capture (SCR)

Important concepts

Spatially explicit capture re-capture (SCR) is a set of modeling techniques used for the estimation of wildlife population densities, and is a rapidly popularizing method used to enumerate wild felids (Athreya et al., 2013; Gopaldaswamy, 2012; Noss et al., 2012). The method uses capture re-capture data collected from a number of detectors, and in the case of enumerating wild felid populations like leopards or tigers, biologists typically make use of camera traps in order to do this (Karanth & Nichols, 1998). The concepts explained in this manual will assume camera-traps as the data collection method and leopards as study animals, in order to frame the basic concepts of SCR.

SCR modeling typically involves a two-fold process of fitting a spatial model (commonly referred to as the State model) to the cat population of interest and an accompanying

observational model which examines their detections or captures (a so termed observation model; Efford, 2014).



The state model describes animal home range distribution (in our case the points represent potential leopard home-range centres) while the observation model relates the probability of capturing a leopard at a particular camera trap to the distance of the camera trap from a central point in each leopards home range (Efford, 2014). The capture probability in the above observation model may be viewed as a declining function of the distance between leopard home range centres and camera traps (Figure 3; Efford et al., 2004), and parallels the detection function observed in distance sampling, a popular method used to estimate animal abundance, particularly that of felid prey species (Efford, 2014; Buckland et al., 1993). SCR makes some assumptions regarding leopard home ranges, mainly that they are approximately circular, and potential home range centres are distributed as a homogenous Poisson point process (Efford, 2014; Noss et al., 2012). Inhomogenous distribution of range centres may also be fitted, and this is particularly useful if the user would like to examine how density changes across varying habitat and soil types, orientation and across other habitat specific-variables (see Efford, 2014). For the purposes of this manual we will explore the former.

Detector types and detection functions

When in the field, one may choose to use a number of detectors (traps) to trap wildlife species, and these include everything from hand-sized Sherman and pitfall traps for capturing small mammals and insects (eg. Umetsuet el., 2006; O'Farrell et al., 1994) to 100 kg mesh box-traps for catching leopards and tigers (Norton, 1987; Smith, 1984). Camera traps (Figure 4) are the most common passive method (Efford et al., 2004) used to detect felids in and ecosystem, and the SCR framework terms camera traps "proximity" detectors. They are useful as they do not restrain the animal from being photographed at another camera, but only record its presence when it passes nearby. Thus camera traps work independently of each other, and also allow for multiple animals to be caught on each trap.

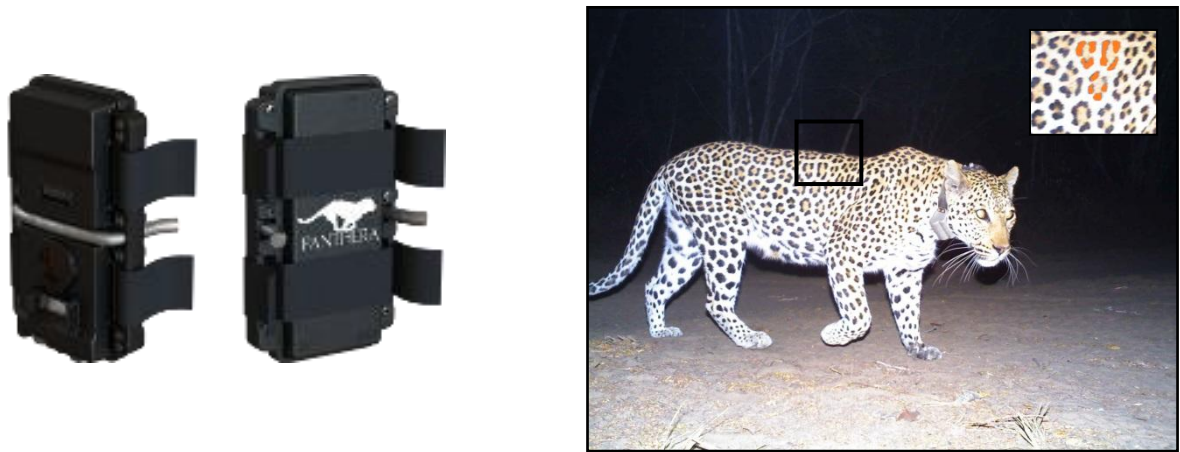


Figure 4: Example of a detection (photograph) of individually recognizable leopard Ngoye recorded using a Panthera IV proximity detector (camera trap) on Phinda Private Game Reserve, South Africa.

Importantly, there are a number of parametric detection functions used in SCR and these describe the decline in capture probability with distance from the animal's home-range centre (Figure 5). Two popularly used functions include the Half-normal and Exponential fits (Figure 5).

Half-normal $g(d) = g_0 \exp\left(\frac{-d^2}{2\sigma^2}\right)$

Exponential $g(d) = g_0 \exp\left(\frac{-d}{\sigma}\right)$

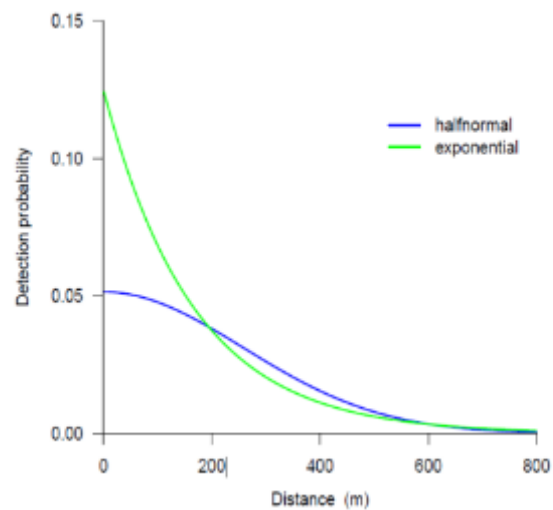


Figure 5: Half-normal and exponential function shapes which relate capture probability to the distance from home range-centre. Detection figure taken from Efford (2014).

Benefits to the user

Efford et al. (2009) assert two key problems associated with traditional non-spatial capture-recapture methods, and term these “edge effects”. The first problem is that camera traps only photograph a proportion of the total animal population in an area. The second is that some animals use the areas beyond the borders of the camera traps in their ranging patterns (Gerber et al., 2012). This second point is one of the biggest challenges faced by authors of many historic capture re-capture studies, and particularly those using the popular software CAPTURE. In essence, the big question is: “how do we calculate the effective

trapping area (ESA)"? One can imagine that this question has far reaching consequences, as the size of the trapping area will directly influence the number of animals reported per hectare or square kilometer (Figure 6). Additionally when we use CAPTURE, our statistical output is given as animals on camera traps and determining the ESA is left totally up to us. Now, the majority of authors have used the prudent approach of applying an animal movement distance buffer to their camera traps (eg. Chapman & Balme, 2010; Soisalo & Cavalcanti, 2006). The method has undergone significant testing and refinement, but the $\frac{1}{2}$ or full mean maximum daily distance moved by an animal, (HMMDM or MMDDM) are typically used. Despite further refinements (eg. Balme et al., 2009a) felid biologists often struggle with the task of defining this ESA, and it may change with environmental conditions and even with the method of data collection (as demonstrated below using telemetry and camera traps to establish buffer length). When it comes down to management scenarios like trying to estimate critically endangered populations of tigers or using camera traps to advise authorities on how to set their leopard hunting quotas, biologists want to be as accurate as possible!

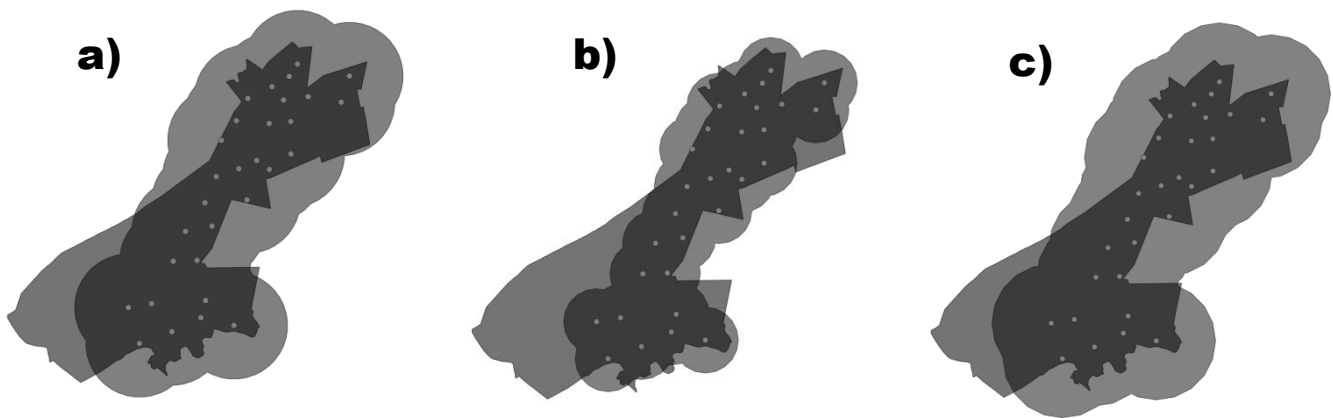


Figure 6: Varying buffer widths applied to camera traps on Phinda Private Game Reserve, South Africa. Note the changes in the size of the effectively sampled area, and also the regions considered by the buffer, a) the MMDDMOSA gives a density estimate of 6.97 ± 1.88 leopards/100km², b) HMMDM as determined from camera traps provides a density of 6.56 ± 1.92 leopards/100km² c) MMDM as determined from radio tracking estimates a density of 3.76 ± 1.10 leopards/100km². Data and figures based upon Balme et al., 2009a.

SCR methods make use of a different approach, and eliminate the animal distance buffer method. Contrastingly to the above, along with recording which animals gets captured and when, SCR also makes use of spatial information, and identifies where the individual was caught. Similarly to the traditional animal movement buffer method, we also apply a buffer to our camera traps, in order to decrease the chance of photo trapping animals who reside beyond the extent of camera traps. This buffer width is recommended to be five times the estimated home-range diameter of the target species, and in the case of larger felids like tigers, leopards and jaguars 15 km is a commonly used figure, while for smaller species such as ocelots 6 km is recommended (Noss et al., 2012; Gopalaswamy et al., 2012). There is no risk in making this buffer too big (this only increases computational time) – but if it is made too small one risks overinflating population estimates (Gopalaswamy et al., 2012).

Recent applications in wild cat research

There has been a mass shift towards the use of SCR in wild felid studies over the past 5-8 years. We've identified a few of the most recent and interesting applications to wild felid populations. Take a look below and check out a short summary on why each paper may be useful in the context of your study, and an accompanying link to its pdf:

- 1) Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N., & Karanth, K. U. (2012). Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution*, 3(6), 1067–1072.

Why is this a useful reference? Arjun and co-authors eloquently explain the fundamentals of the SPACECAP package in R, Bayesian approach to spatially-explicit capture re-capture and use tigers as a model. This short six page paper summarizes the key steps involved in the modelling process, briefly explains Markov-Chain Monte-Carlo and the process of data augmentation. Make sure to use it as an accompaniment to this tutorial. Get it here: <http://onlinelibrary.wiley.com/doi/10.1111/j.2041-210X.2012.00241.x/full>

- 2) Borah, J., Sharma, T., Das, D., Rabha, N., Kakati, N., Basumatary, A., Ahmed, M.F & Vattakaven, J (2013) Abundance and density estimates for common leopard *Panthera pardus* and clouded leopard *Neofelis nebulosa* in Manas National Park, Assam, India. *Oryx*, 1-7. Get it here: http://70.38.52.75/sites/default/files/articles/Co_predator_Manas.pdf

Why is this a useful reference? Jimmy Borah and his team bring us one of the first spatially explicit estimates on the rare and poorly studied clouded leopard. They don't use secr but make use of the similar GUI based DENSITY programme (also created by Murray Efford). This paper is great in that it nicely represents what it means to have a good camera-trapping effort (75 camera sites with an effort of 4 275 camera days). Read this to get an idea on what it takes to get captures for species that are notoriously difficult to detect.

- 3) Karki, J. B., Pandav, B., Jnawali, S. R., Shrestha, R., Pradhan, N. M. B., Lamichane, B. R., Khanal, P., Subedi, N & Jhala, Y. V. (2013) Estimating the abundance of Nepal's largest population of tigers *Panthera tigris*. *Oryx*, 1-7. University access is available here: <http://journals.cambridge.org/action/displayAbstract?fromPage=online&aid=9061313>

Why is this a useful reference? Ever wondered if you could come up with a density estimate for a very large area, or maybe even a whole national park? Well, this massive field effort by Jhamak Karki and co-authors in Chitwan has shown it may be possible. 61 days, 310 camera-traps, 1261 km² and a whole lot of field effort suggests this park is one of the most important source populations in Nepal.

- 4) Athreya, V., Odden, M., Linnell, J. D., Krishnaswamy, J. & Karanth, U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PloS one*, 8(3), e57872. Get it here for free: <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0057872>

Why is this a useful reference? If you're interested in working in non-protected landscapes then this paper led by Vidya Athreya is a great reference. She uses a SCR approach in estimating the densities of leopard and hyena in a landscape with 177 people/km².

- 5) Noss, A. J., Gardner, B., Maffei, L., Cuéllar, E., Montañó, R., Romero-Muñoz, A., Sollman, R & O'Connell, A. F. (2012) Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape. *Animal Conservation*, 15(5), 527-535. Get it here: [file:///C:/Users/Radek_000/Downloads/Noss%20et%20al.%202012.%20Comparison%20of%20density%20estimation%20methods%20for%20mammal%20populations%20with%20camera%20traps%20in%20the%20Kaa-Iya%20del%20Gran%20Chaco%20landscape%20\(2\).pdf](file:///C:/Users/Radek_000/Downloads/Noss%20et%20al.%202012.%20Comparison%20of%20density%20estimation%20methods%20for%20mammal%20populations%20with%20camera%20traps%20in%20the%20Kaa-Iya%20del%20Gran%20Chaco%20landscape%20(2).pdf)

Why is this a useful reference? If you're interested in taking a look at how the new SCR approaches compare to previous non-spatial methods and what this means for density estimates, Andrew Noss and colleagues paper investigate how density estimates from secr, SPACECAP and non-spatial CAPTURE methods compare to each other for jaguar, puma, ocelot and tapirs in 11 sites across the Kaa-Iya landscape in the Bolivian Chaco.

Analysis Rationale

Now before we jump into looking at our dataset, formatting it for our two packages and creating a suite of models, let's take a step back and examine what we are about to do in its entirety. Here are the six essential steps commencing with data collection and culminating with the interpretation of key model outputs:

1. Camera trap survey

- Usually 40-60 days in length (eg. Balme et al 2009a).
- Period usually ensures assumption of demographic closure and geographic (Williams et al., 2002; Otis et al., 1978).
- Camera spacing ensures individual animals have similar capture probability (Karanth & Nichols., 1998) – rule of thumb = smallest theoretical female home-range.
- Adequate number of camera traps.



2. Data examination

- Individual animal photographs examined in photo viewing software (Microsoft picture viewer, Adobe Photoshop etc.)
- Animals assigned unique id, age, sex (if possible)
- Capture occasions noted, camera-specific covariates noted
- Camera malfunctions noted ie. When did my cameras fail in the field eg. elephant damage or battery failure (Gopalaswamy et al., 2012)

A screenshot of a data table with columns for ID, sex, age, and capture occasions. The table contains multiple rows of data, likely representing individual animals and their capture history.

3. Data formatting for secr

- Creation of detector (camera trap) location and leopard detection (photo captures) txt files for secr (Efford, 2013) or trap deployment and animal capture csv files for SPACECAP (Gopalaswamy et al., 2012).
- Creation of habitat suitability mask in Geographic Information System (Quantum, R, or Arc etc.)- only if required otherwise in secr.

Two screenshots of data tables. The left table shows detector locations with columns for ID, x, y, and other spatial coordinates. The right table shows animal captures with columns for ID, sex, age, and capture occasions.

4. Data input into secr (within R)

- Install the secr and SPACECAP packages within the R statistical environment (download and install R if necessary – both free!).
- Load secr txt or SPACECAP csv files as well as the habitat mask (if necessary) and create a capture history object.



5. Analysis

- Come up with an explicit set of a priori hypotheses and consider which predictor variables may be used in addressing these.
- Fit a suite of biologically meaningful models (do not just load the secr workspace with every combination of predictors!), SPACECAP currently runs two key models – one with no trap response and one with a trap response present (Gopalaswamy et al., 2012).



6. Interpret secr and SPACECAP model outputs

- Examine models using AIC criteria, and model averaging using AIC weight in secr. Consider the robustness of models, and specifically examine the co-variance matrix.
- If algorithms fail consider a different model fitting method
- Examine Bayesian p-value and Geweke diagnostic statistics to ascertain whether model is adequate in SPACECAP

A screenshot of model output showing AIC criteria and other statistics. The table lists various models and their corresponding AIC values, weights, and other diagnostic statistics.A screenshot of model output showing Bayesian p-value and Geweke diagnostic statistics. The table lists various models and their corresponding Bayesian p-values and Geweke diagnostic statistics.

Phinda leopard camera trap dataset

Background to the project

The data used in this tutorial are a small camera trapping component of Panthera's Mnyawana leopard project, a twelve year conservation and monitoring programme focused on a population of leopards residing in the mesic coastal savanna of South Africa's Kwazulu-Natal province (Figure 6). The project was initiated by Luke Hunter (Figure 7) and Guy Balme (Figure 8) in 2001, and aimed to address the decline of leopards in and around the Phinda Private Game Reserve, a 27 000 hectare wildlife preserve. Leopards in the region declined mainly through unsustainable levels of trophy hunting offtake, illegal hunting and retaliatory killings by farmers due to livestock losses. However, after a series of conservation interventions and policy reforms, including a more equitable distribution of hunting permits amongst landowners, the population recovered. Details on the decline of the population, the conservation interventions and trophy hunting reforms as well as the subsequent recovery of the population may be found in Hunter et al (2003), Balme et al. (2004), Balme et al (2009b) and Balme et al (2010).

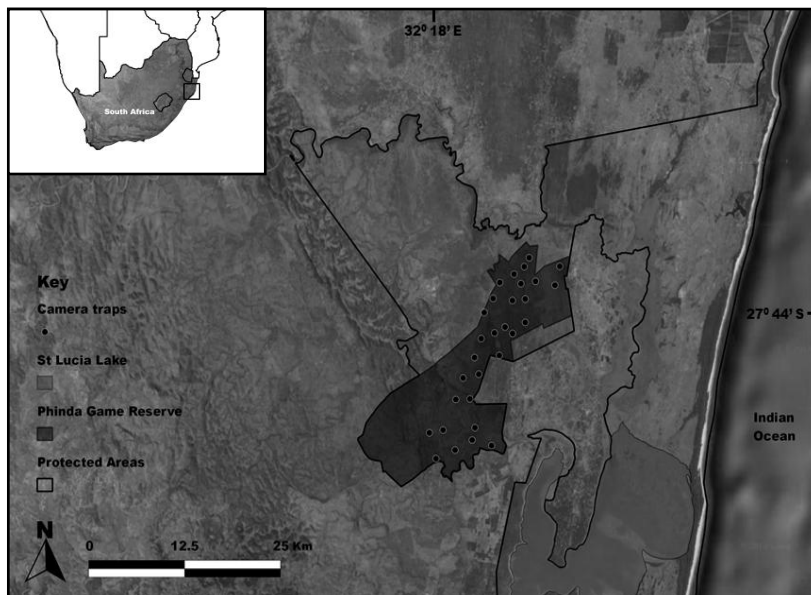


Figure 6: The location of Phinda Private Game Reserve, its camera trap array and the adjoining Mkhuze and St Lucia protected reserves located to the West and East respectively. Cattle ranches, game ranches and community lands comprise the broader non-protected matrix around Phinda.



Figure 7: Project leader Luke Hunter takes morphometrics from an anaesthetized leopard.



Figure 8: Leopard programme director Guy Balme, attaches a radio collar to an immobilized leopard.

The camera trap data in this tutorial were collected in the dry season of 2011, between the 13 April-22 May. They were collected after conservation interventions had been applied and the subsequent population recovery had occurred. The population is thought to represent a population near ecological capacity as density estimates between 2009 and 2011 were comparable (Balme et al., 2009b). The survey made use of 60 Panthera IV digital camera traps set up in a paired format at 30 locations. Similarly to other studies, the survey period was limited to 40 days in order to meet the assumption of population closure (Balme et al., 2009a). Mean camera spacing was limited to 1.67 km (well within the limits of the smallest female leopard home-range on Phinda which is 30 km²; Fattebert et al., 2013) in order to

reduce the heterogeneity of capture probability amongst individuals (Karanth & Nichols, 1998). Cameras were checked every three days to ensure functionality. The authors also only counted a leopard once on a camera trap in a 24 hour period in order to maintain temporal independence between individual captures. These protocols have ensured repeatability and comparisons between a total of six surveys implemented between 2005-2012. As the majority of the study animals were radio-collared over the survey period, the age and sex of leopards was also noted.

Critical numbers

The survey recorded a total of 55 temporally independent leopard photographs over the 20 sampling sessions. A total of 16 individual leopards were photographed with 13 of these comprising adult animals (three sub adults), nine females and seven males (Figure 9). In terms of photographic events, 29 photographs were of females, 26 were of males while 47 were of adults and eight were of sub adults (Figure 10).



Figure 9: Percentages of unique leopards photographed, in terms of males, females, adults and sub adults.

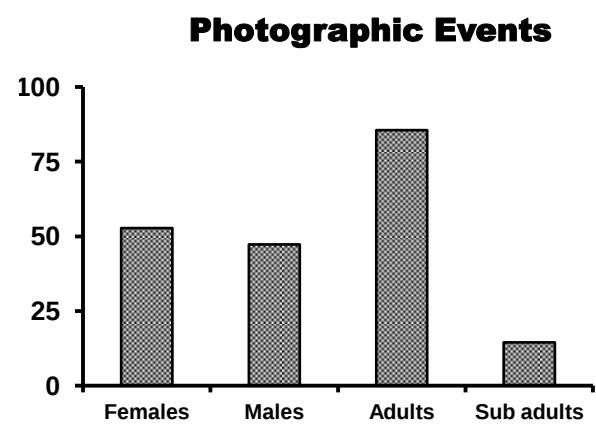


Figure 10: Percentages of temporally independent leopard photographs, in terms of males, females, adults and sub adults.

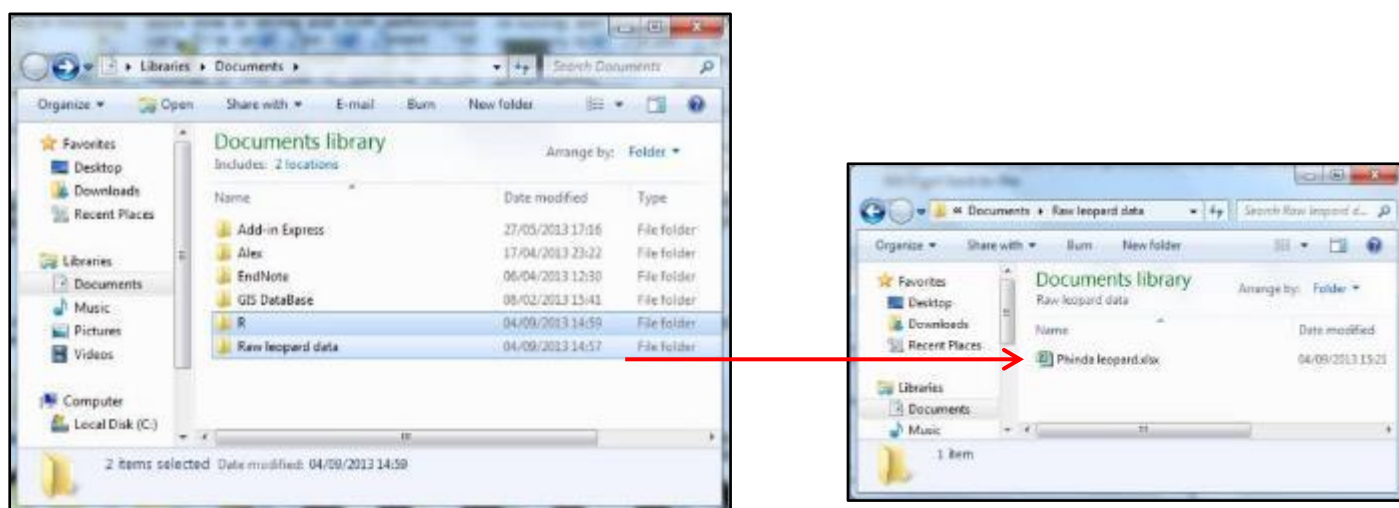
Data formatting and input into secr

Now that you have some understanding to the background of the Phinda data set, let's move onto a few simple explanations on how to format the raw data into workable formats for the secr package in R. We'll be relying on the spreadsheet processing software Excel and wordpad. The process is really simple, and in this tutorial we'll guide you through it, step by step. Let's start off by opening the downloaded "Phinda leopard" zip file, and unzipping it to your desktop or other easily accessible location. If you do not have winzip, you can access an open source version of "j zip", at: <http://lp.jzip.com/?sysid=102&appid=100>

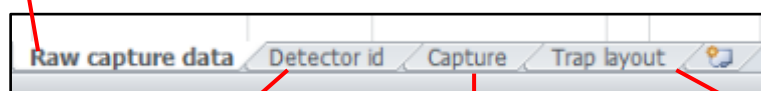
Getting started

Let's start by creating two files where we can easily store our data spreadsheets, one for our Excel spreadsheet and another for our R files.

1. Start by clicking on your documents directory in the windows startup. Alternatively click on "My computer" or "Computer" either in the startup tab or on your desktop to access the documents folder. Once you are inside your documents directory, go on and create one folder called "Raw leopard data", and another called "R" (if you're a regular R user you'll undoubtedly already have the latter). We'll dump the unzipped "Phinda leopard" Excel spreadsheet into the "Raw leopard data" folder. We'll get back to the R folder later.



2. Now that we have our two working folders, let's go into our "Raw leopard data" folder and click on the "Phinda leopard secr.xlsx" spreadsheet. Once it's open, let's make sure that we have all the necessary components for our data formatting and try understand what these spreadsheet components mean. The excel spreadsheet should comprise four sheets and we can examine these at the bottom of the screen. The first sheet is titled "Raw capture data" and includes the raw leopard capture data (eg. Individual name, animal code etc.). The second sheet is called "Detector id" and includes the abbreviations of the camera names used in the "Raw capture data" sheet as well as the camera codes we will use in our "Capture" and "Trap layout" files. Finally there should be a "Capture" and "Trap layout" sheet. The "Capture" sheet contains information on the id of animals, trapping occasion etc. while the "Trap layout" file contains the detector code, the spatial co-ordinates of detectors and several trap covariates. If all of the above are present we can proceed onto understanding what the components of these four sheets mean.

Detector id sheet

#	Session	Id	Occasion	Detector	Sex	Age	Covariates
1	2011	4	1	6	m	a	
2	2011	4	1	6	m	a	
3	2011	10	1	13	f	a	
4	2011	6	2	26	m	a	
5	2011	4	3	8	m	a	
6	2011	7	3	21	f	sa	
7	2011	4	4	2	m	a	
8	2011	4	4	8	m	a	
9	2011	11	4	27	f	a	
10	2011	12	4	27	f	sa	
11	2011	15	4	28	m	a	
12	2011	6	5	29	m	a	
13	2011	10	5	13	f	a	
14	2011	12	5	27	f	a	
15	2011	4	6	7	m	a	
16	2011	10	6	13	f	a	
17	2011	11	6	26	f	a	

Capture sheet

#	Session	Id	Occasion	Detector	Sex	Age	Covariates
1	2011	4	1	6	m	a	
2	2011	4	1	6	m	a	
3	2011	10	1	13	f	a	
4	2011	6	2	26	m	a	
5	2011	4	3	8	m	a	
6	2011	7	3	21	f	sa	
7	2011	4	4	2	m	a	
8	2011	4	4	8	m	a	
9	2011	11	4	27	f	a	
10	2011	12	4	27	f	sa	
11	2011	15	4	28	m	a	
12	2011	6	5	29	m	a	
13	2011	10	5	13	f	a	
14	2011	12	5	27	f	a	
15	2011	4	6	7	m	a	
16	2011	10	6	13	f	a	
17	2011	11	6	26	f	a	

File Home Insert Page Layout Formulas				
Clipboard		Font		Calibri 11
6/29				
	A	B	C	D
1	Detector	X	Y	Covariates
2	1	4327992	6934735	/North Sand
3	2	438693	6933715	/North Sand
4	3	430067	6935531	/North Sand
5	4	430622	6936481	/North Sand
6	5	440365	6933080	/North Sand
7	6	442615	6933571	/North Sand
8	7	445166	6935579	/North Sand
9	8	448184	6942074	/North Sand
10	9	448417	6942464	/North Sand
11	10	447749	6938496	/North Sand
12	11	435667	6938411	/North Sand
13	12	436239	6936060	/North Sand
14	13	434136	6927034	/North Sand
15	14	434460	6930617	/North Sand
16	15	436885	6929075	/North Sand
17	16	437719	6931913	/North Sand
18	17	436254	6935828	/North Sand
19	18	434485	6940177	/North Sand
20	19	444478	6935621	/South Clay
21	20	432671	6936023	/South Clay
22	21	433870	6924034	/South Clay
23	22	432866	6921411	/South Clay
24	23	431247	6921337	/South Clay
25	24	433466	6918344	/South Clay
14 4 6 Pi Have sample data - Detector ID - C				

What do these datasheet components mean?

1. Raw capture data

The “Raw Capture data” sheet is an example of a typical table in which you will store your non-formatted leopard capture data. It is simply a neat, orderly way to store your data and includes information on individual leopards, their sex and age (if possible), an id code and when they were caught. This is NOT an input file but it does contain critical information that will be used in our input sheets later.

secur/SPACECAP code

This is the unique code we will assign each leopard in our “Capture” sheet.

Date and Sampling occasion

The dates upon which we photographed an individual leopard, compounded into one 48 hour sampling occasion. This is used in our “Capture” sheet

Events

This provides the number of temporally independent leopard captures (photographs) recorded during the 20 sampling occasions.

Date					13/14	15/16	17/18	19/20	21/22	23/24	25/26	27/28	29/30	1/2	3/4	5/6	7/8	9/10	11/12	13/14	15/16	17/18	19/20	21/22	Events
Sampling occasion					1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Individual	Animal code	secur/SPACECAP code	Sex	Age class																					
Ngove	AF1	1	F	Adult								Mkh											Sun		2
Nombi	AF2	2	F	Adult										Buf				Pan	BB			BB	CA		4
Charoalale male	AM1	3	M	Adult				CA				CA		CA											5
Meras	AM2	4	M	Adult	CL		CC	CC		Res			Wie	CL				BB	Tor						8
Charoalaleas female	AF4	5	F	Adult									CC	Ngu											2
Zaphyr	AM3	6	M	Adult			Fou		Ubo				Mgo	Nar	Ubo			Mgo					Nar		7
Red dam sub adult female	SAF1	7	F	Sub									RD												3
Red dam adult female	AF5	8	F	Adult									RD	RD									RD	Mgo	4
Red dam adult male	AM4	9	M	Adult																					1
Forest adult female	AF6	10	F	Adult	SFC				SFC	SFC		WH													6
Sepi	AF7	11	F	Adult					Tam															Tam	3
Ubombo sub adult female	SAF2	12	F	Sub					Tam	Tam															3
Eve	AF8	13	F	Adult														Tam							2
Mara	SAF11	14	M	Sub											Nar								Tsh		2
Blue-eyed male	AM5	15	M	Adult					Tsh						Ubo										2
Fourtops adult male	AM6	16	M	Adult							Fou														1



Individual

We try and provide photographed leopards with a simple identity name, in this case the “Blue-eyed male” is an easily identifiable leopard, by his one blue eye. Where you can, try give your animals useful names or codes so you don’t get confused later.

Sex and Age class

We’ll use this sex and age information in the “Capture” sheet. These are simple animal-specific covariates. If you can think of more, in the context of your own study, be sure to include a few more columns.

Detector location (abbreviated)

We place an abbreviation for each detector which recorded a leopard at a specific occasion. We’ll use this abbreviation in our “Detector id” sheet which matches a numeric detector code (this is what we will use in our “Capture” sheet).

2. Detector Id

Detector name	Detector abbreviation	Detector code	X	Y	Orientation	Soil type
Ndulamithi	Ndl	1	437892	6934735	North	Sand
Charcoal Alley	CA	2	438693	6933715	North	Sand
Buffalo Beat	Buf	3	439067	6935534	North	Sand
Overgrown Pan	Ove	4	439622	6936481	North	Sand
Bushbaby	BB	5	440365	6933980	North	Sand
Coucal Lane	CL	6	442615	6933571	North	Sand
Reservoir	Ries	7	443166	6935579	North	Sand
Charcoal Clearings	CC	8	439189	6932074	North	Sand
Ngulubeni Pans	Ngu	9	439212	6929594	North	Sand
Mkhombe Loop	Mkh	10	437749	6928396	North	Sand
Sun! Loop	Sun	11	435667	6928441	North	Sand
Bushcamp	BC	12	436239	6926060	North	Sand
SFCLINE	SFC	13	434136	6927834	North	Sand
Tortillas	Tor	14	434469	6930617	North	Sand
Bateleur	Bat	15	436885	6929075	North	Sand
Kudu Pans	KP	16	437719	6931913	North	Sand
Pano Rama Circle	Pan	17	436254	6933828	North	Sand
Woolnecked Haven	WH	18	435485	6932122	North	Sand
Vlei Rd	Vle	19	433378	6925821	South	Clay
Red Dam	RD	20	432071	6923623	South	Clay
Mbondwe	Mbo	21	433870	6924034	South	Sand
Mgoti (Crow alley)	Mgo	22	432866	6921411	South	Clay
Tracker's Rd	Tra	23	431247	6921337	South	Clay
Narina	Nar	24	433466	6918344	South	Clay

3. Capture

# Session	Id	Occasion	Detector	Sex	Age
2011	4	1	6	m	a
2011	10	1	13	f	a
2011	6	2	26	m	a
2011	4	3	8	m	a
2011	7	3	21	f	sa
2011	4	4	2	m	a
2011	4	4	8	m	a
2011	11	4	27	f	a
2011	12	4	27	f	sa
2011	15	4	28	m	a
2011	6	5	29	m	a
2011	10	5	13	f	a
2011	12	5	27	f	a
2011	4	6	7	m	a
2011	10	6	13	f	a
2011	11	6	26	f	a
2011	9	7	20	m	a
2011	16	7	26	m	a
2011	1	8	10	f	a
2011	3	8	2	m	a
2011	6	8	22	m	a
2011	7	8	20	f	sa
2011	10	8	18	f	a
2011	4	9	19	m	a

The “Capture” sheet provides us with the name of our camera session (in this case we ran only one survey ie. 2011). The Id, occasion number, sex and age are column information taken from the “Raw capture data” sheet. The “Detector” column makes use of the “Detector code” from the “Detector Id” sheet.

The screenshot shows a Microsoft Excel spreadsheet with a list of countries and their GDP values. The columns are labeled 'Country' and 'GDP'. The data is as follows:

Country	GDP
USA	14.5
China	12.1
Germany	3.5
France	2.7
UK	2.5
Japan	4.6
India	1.9
Canada	1.6
Italy	1.8
Spain	1.4
South Korea	1.2
Sweden	0.5
Norway	0.4
Denmark	0.3
Finland	0.2
Switzerland	0.2
Austria	0.2
Netherlands	0.2
Belgium	0.2
Luxembourg	0.1
Ireland	0.1
Portugal	0.1
Greece	0.1
Poland	0.1
Czech Republic	0.1
Slovakia	0.1
Hungary	0.1
Slovenia	0.1
Croatia	0.1
Serbia	0.1
Bulgaria	0.1
Romania	0.1
Ukraine	0.1
Belarus	0.1
Latvia	0.1
Lithuania	0.1
Estonia	0.1
Malta	0.1
Cyprus	0.1
Singapore	0.1
Hong Kong	0.1
Taiwan	0.1
South Korea	0.1
Japan	0.1
China	0.1
India	0.1
USA	0.1

Red arrows point to the following cells:

- Cell A1 (Country: USA)
- Cell B1 (GDP: 14.5)
- Cell A2 (Country: China)
- Cell B2 (GDP: 12.1)
- Cell A3 (Country: Germany)
- Cell B3 (GDP: 3.5)
- Cell A4 (Country: France)
- Cell B4 (GDP: 2.7)
- Cell A5 (Country: UK)
- Cell B5 (GDP: 2.5)
- Cell A6 (Country: Japan)
- Cell B6 (GDP: 4.6)
- Cell A7 (Country: India)
- Cell B7 (GDP: 1.9)
- Cell A8 (Country: Canada)
- Cell B8 (GDP: 1.6)
- Cell A9 (Country: Italy)
- Cell B9 (GDP: 1.8)
- Cell A10 (Country: Spain)
- Cell B10 (GDP: 1.4)
- Cell A11 (Country: South Korea)
- Cell B11 (GDP: 1.2)
- Cell A12 (Country: Sweden)
- Cell B12 (GDP: 0.5)
- Cell A13 (Country: Norway)
- Cell B13 (GDP: 0.4)
- Cell A14 (Country: Denmark)
- Cell B14 (GDP: 0.3)
- Cell A15 (Country: Finland)
- Cell B15 (GDP: 0.2)
- Cell A16 (Country: Switzerland)
- Cell B16 (GDP: 0.2)
- Cell A17 (Country: Austria)
- Cell B17 (GDP: 0.2)
- Cell A18 (Country: Netherlands)
- Cell B18 (GDP: 0.2)
- Cell A19 (Country: Belgium)
- Cell B19 (GDP: 0.2)
- Cell A20 (Country: Luxembourg)
- Cell B20 (GDP: 0.1)
- Cell A21 (Country: Ireland)
- Cell B21 (GDP: 0.1)
- Cell A22 (Country: Portugal)
- Cell B22 (GDP: 0.1)
- Cell A23 (Country: Greece)
- Cell B23 (GDP: 0.1)
- Cell A24 (Country: Poland)
- Cell B24 (GDP: 0.1)
- Cell A25 (Country: Czech Republic)
- Cell B25 (GDP: 0.1)
- Cell A26 (Country: Slovakia)
- Cell B26 (GDP: 0.1)
- Cell A27 (Country: Hungary)
- Cell B27 (GDP: 0.1)
- Cell A28 (Country: Slovenia)
- Cell B28 (GDP: 0.1)
- Cell A29 (Country: Croatia)
- Cell B29 (GDP: 0.1)
- Cell A30 (Country: Serbia)
- Cell B30 (GDP: 0.1)
- Cell A31 (Country: Bulgaria)
- Cell B31 (GDP: 0.1)
- Cell A32 (Country: Romania)
- Cell B32 (GDP: 0.1)
- Cell A33 (Country: Ukraine)
- Cell B33 (GDP: 0.1)
- Cell A34 (Country: Belarus)
- Cell B34 (GDP: 0.1)
- Cell A35 (Country: Latvia)
- Cell B35 (GDP: 0.1)
- Cell A36 (Country: Lithuania)
- Cell B36 (GDP: 0.1)
- Cell A37 (Country: Estonia)
- Cell B37 (GDP: 0.1)
- Cell A38 (Country: Malta)
- Cell B38 (GDP: 0.1)
- Cell A39 (Country: Cyprus)
- Cell B39 (GDP: 0.1)
- Cell A40 (Country: Singapore)
- Cell B40 (GDP: 0.1)
- Cell A41 (Country: Hong Kong)
- Cell B41 (GDP: 0.1)
- Cell A42 (Country: Taiwan)
- Cell B42 (GDP: 0.1)
- Cell A43 (Country: South Korea)
- Cell B43 (GDP: 0.1)
- Cell A44 (Country: Japan)
- Cell B44 (GDP: 0.1)
- Cell A45 (Country: China)
- Cell B45 (GDP: 0.1)
- Cell A46 (Country: India)
- Cell B46 (GDP: 0.1)
- Cell A47 (Country: USA)
- Cell B47 (GDP: 0.1)

4. Trap Layout

#Detector	X	Y	Covariates
1	437892	6934735	/North Sane
2	438093	6933715	/North Sane
3	439067	6935534	/North Sane
4	439622	6936481	/North Sane
5	440365	6933980	/North Sane
6	442615	6933571	/North Sane
7	443166	6935579	/North Sane
8	439189	6932074	/North Sane
9	439212	6929594	/North Sane
10	437749	6928396	/North Sane
11	435667	6928441	/North Sane
12	436239	6926060	/North Sane
13	434136	6927834	/North Sane
14	434469	6930617	/North Sane
15	436885	6929075	/North Sane
16	437719	6931913	/North Sane
17	436254	6933828	/North Sane
18	435485	6932122	/North Sane
19	433378	6925821	/South Clay
20	432071	6923623	/South Clay
21	433870	6924034	/South Sane
22	432866	6921411	/South Clay

The “Trap Layout” sheet provides us with a column labelled “#Detector” and this is the “Detector code” from the “Detector Id sheet”. This sheet also contains the X and Y spatial co-ordinates of each detector as well as two camera site covariates. You can find all of these in the “Detector Id” sheet.

Optional extra
Trap specific covariates for
density surface modeling

Covariates
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/North Sand
/South Clay
/South Clay
/South Sand
/South Clay
/South Clay

As you may notice, our “Trap Layout” sheet contains a column with trap-specific covariates. Note that the layout of the trap covariates is a little different to those of the animal covariates in the “Capture” sheet, which were simply extra columns. These covariates are added in a single cell, but are preceded by one forward slash /. Also note that multiple covariates like “North/South” and “Sand/Clay” are added into the same cell, merely separated by a single space. Note these are not essential and you don’t have to add these. However these are crucial to density surface models (see Efford, 2013).

/North Sand
/North Sand
/North Sand
/North Sand

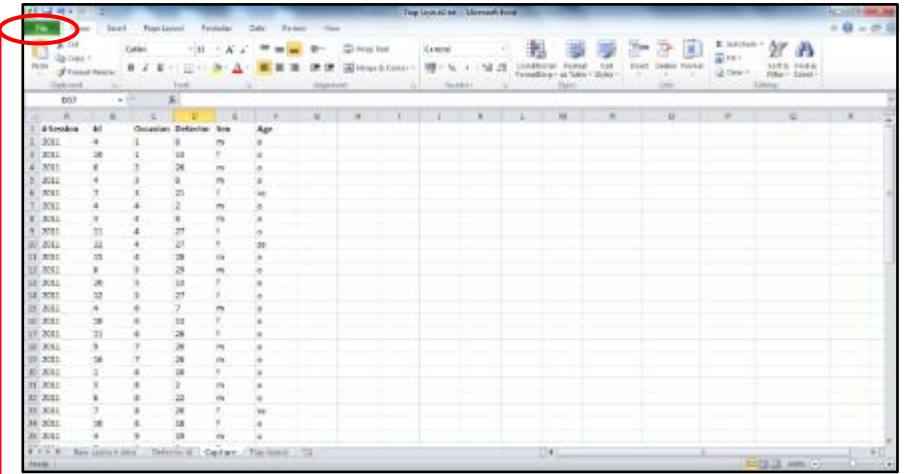
Be careful here! Remember, one forward slash in a new cell, then your first covariate, one space and then your second, and so on and so on.

Excel datasheet conversion for secr

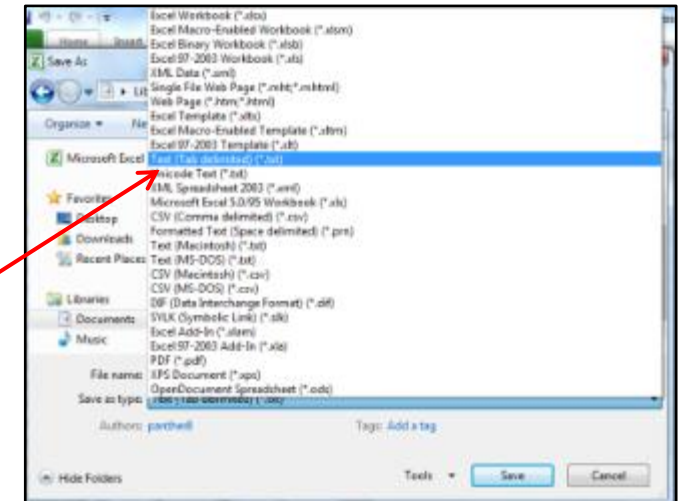
Now that we've got a grasp on what our four data sheet components mean, we'll convert two of these into R readable formats. Let's go ahead and convert the "Capture" and "Trap layout" sheets into txt format.

1. Start off by selecting the "Capture" sheet, and click on the file tab at the top of the Excel browser.
2. Select the "Save as" tab.
3. Then go ahead and click the "Documents" tab and select the "R" folder we created earlier (This is where we'll store our files for secr and later SPACECAP).
4. Finally, click the "Save as type" tab and select the "Text (Tab delimited) (*.txt)" option.
5. Give the file a meaningful name: "Capture".
6. Click "Save" and repeat this step for the "Trap Layout" sheet.

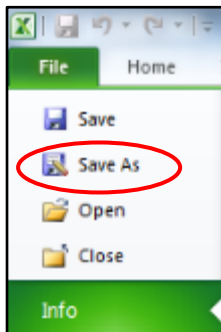
1.



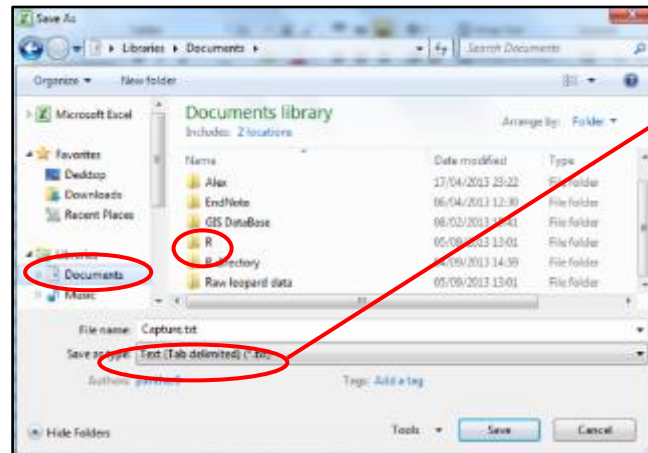
4.



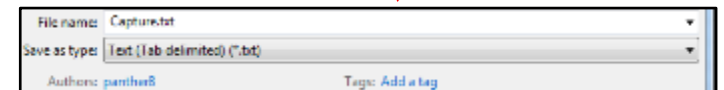
2.



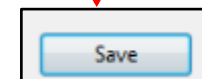
3.



5.



6.



Data import and secr package installation in R

Now that we have our txt files within our R folder, let's go ahead and open R. If you do not have R, you can download it for free at: <http://www.r-project.org/>. It's quick, free and easy, just choose an R Mirror (the country nearest to you) and make sure you have 52 mb of space on your hard disk. You can also download the "R studio", a user friendly R gui which works with multiple windows for you to paste your R code, display graphics and even make use of some useful drop down keys. You can also get it for free at: <http://www.rstudio.com/ide/>. We'll assume that for this tutorial, you have the standard R gui. Now the code pasted for the tutorial below has been tested and if you have performed everything up until this point correctly and copy and paste the code as is, it should work correctly.

Let's get started with installing secr and SPACECAP and importing our data:

1. Open the R gui in your windows startup. It should be under the "Programmes" tab, and will have its own folder "R".
2. Let's start by setting our work directory for our R session. This will allow R to access the "Capture" and "Trap Layout" txt files we stored in our R folder.

Code: `setwd("~/R")`

3. Now let's install the "secr" package

Code: `install.packages("secr")`

4. Now let's load "secr"

Code: `library(secr)`

5. Great, now let's get those "Capture" and "Trap layout" files into R for secr and create a capture history object. Notice how we specify exactly what the animal and trap-specific covariates are within the command.

Code: `leopard=read.caphist("Capture.txt", "Trap layout.txt",
detector="proximity",fmt="trapID", noccasions=20, covnames=c("Sex","Age"),
trapcovnames=c("Orientation", "Soil"))`

6. If this is successful you'll get the following output: `No errors found :-)`
7. We're real close to running our first analysis but we have to make a decision on whether we want to create a habitat suitability mask. Remember that this is likely to be a case-specific decision, and if you are located in a large, well-protected reserve this may not be necessary. However in the context of Phinda, we know that there are many human settlements beyond Phinda's eastern fence, and the 15km recommended buffer (Gopalaswamy et al., 2012; Noss et al., 2012) extends well into community land. Therefore it would be prudent to exclude some regions out of our analysis, as we know leopards probably won't have their home-range centres in densely populated regions (ie. they may move through a settlement but probably won't reside there). For the purpose of this tutorial, we'll assume that our entire area is suitable leopard habitat (however we've provided you with an example of a habitat

suitability mask in the “Phinda leopard” zip folder as well as the shapefiles to create your own using R spatial code). Even without eliminating some unsuitable habitat (assuming everything is suitable) we still have to create a mask, albeit a simple one which considers a totally homogenous spread of potential leopard home-range centres (remember the buffer from the “Benefits to the user” section...we still have to add this to our camera traps, so let’s do this).

8. Right, let’s assign our trap layout a name that secr can use in the creation of the mask, detector type is proximity (see Basic concepts section).

Code: `traps=read.traps ('Trap layout.txt', detector='proximity')`

9. Let’s specify a few essentials: the buffer width is recommended at 15 km, but let’s make it a little bigger (30 km; this only increases computational time), next let’s specify the grid spacing (580 m is within the recommended limit and recommended for SPACECAP ie. 0.336 km², so let’s go with that), next let’s select “trapbuffer” as the buffer type.

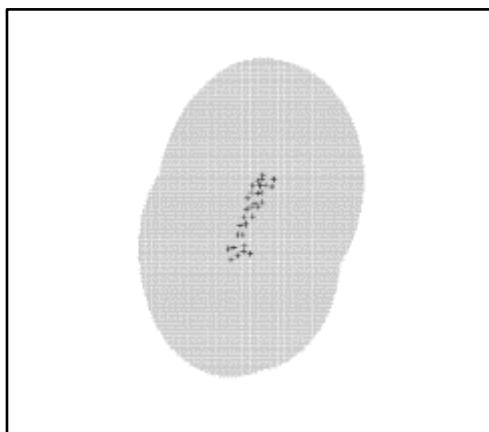
Code: `mask1=make.mask(traps, buffer = 30000, spacing = 580, type = "trapbuffer", poly = NULL)`

10. Let’s plot the mask.

Code: `plot(mask1)`

11. Let’s add our traps (you should see the following image displayed below).

Code: `plot(traps, detpar = list(col = "black"), add = TRUE)`



12. With our capture history and habitat mask constructed, we can go on and proceed with our analyses but let’s finish off by writing this mask to our R folder for later use in SPACECAP (currently one cannot create a mask in the SPACECAP programme).

Code: `write.csv(mask1, file = "C:/Users/panther8/Documents/R/Spacemmask.csv")`

Analysis in secr

Biologically meaningful models

The secr package considers three key parameters in its modelling framework. The density of animals per hectare (D), the encounter rate at an animal's activity centre (g_0) and the scale parameter (σ) which describes the decline of encounter rate with increased distance from an animal's activity centre (Efford, 2014). When maximizing our models with conditional likelihood, as we will do, there are a number of predictors that we can use in our models. These range from the learned response and site learned response to heterogeneity variables (Table 1). Moreover the user may specify his/her own suite of animal and trap-specific covariates (like the "Sex" and "Age" covariates we created). These covariates really give the user the freedom to answer a variety of questions, but they can be equally overwhelming, begging the question of what predictor works best for my data? It is therefore important to identify a series of explicit questions, and frame these in the context of wild felids. For the purposes of the tutorial we'll fit a few simple and biologically meaningful models, but many more examples may be found in the literature (eg. Noss et al., 2012; Efford, 2011; Borchers & Efford, 2008).

Table 1: secr generated default as well as animal and trap-specific predictor variables used in the construction of leopard density models on Phinda in the 2012 control and baited surveys. (Adapted from Efford, 2014)

Variable	Description	Variable function
1	Constant	Parameter kept constant across sessions and occasions
t	Time factor	One level for each occasion
T	Time trend	Linear trend over occasions on a link scale
b	Learned response	Step change in parameter after initial detection of animal
B	Transient response	Parameter dependent on previous occasion detection
bk	Animal x site response	Site-specific step change
Bk	Animal x site response	Site-specific transient response
k	Site learned response	Site effectiveness changes once animal is caught
K	Site transient response	Site effectiveness depends on preceding occasion
H2	2-class mixture	Finite mixture model with two latent classes
A*	Age of animal	Adult or sub-adult
S*	Sex of animal	Male or female
O [£]	Orientation	Camera trap located in North or South of reserve
SO [£]	Soil type	Clay or sand

*Animal-specific covariate

£Trap-specific covariate

Let's start by thinking about felid ecology and what we'd like to examine. Firstly, wild felids are territorial, and are likely to patrol a certain area over our camera trapping period, secondly, they are intelligent and may be wary of humans and camera traps, sometimes walking around them or avoiding them altogether. Thirdly, their behavioural ecology is influenced by their age and sex and this has important bearing on the way they move. Let's try consider these factors in the selection of a suite of models for analysis of density.

Model varieties for wild felids in secr

Below are a few model fitting options you might consider in your future analyses. For the purposes of the tutorial we will fit models (1.), (2.), (2a.), (2b.), (3.) & (4.). We'll then have a look at the performance of these models according to their AIC criteria, Δ AIC values and if necessary we'll use model averaging to assess our most competitive candidate models.

Base model



Capture probabilities are homogenous among individual leopards.

Sometimes the simplest model fits the data best and when it comes to capture re-capture statistics there is no better analogy in the literature than that of Otis et al (1978) who compare the capture probability of this model to a jar of marbles, where the size, colour and distribution of marbles in the jar is exactly the same. However if we think about this in terms of leopards, this is highly unlikely and capture probability is likely to vary with age, sex, condition etc. However let's fit the model **(1.)** and see how it fares against our other candidates.

Trap happy/shy



Capture probabilities differ between previously caught and uncaught leopards due to trap response behaviour.

There is evidence that some felids (eg. tigers, Wegge et al., 2004) may exhibit a trap shy response towards cameras, and it is plausible that this may be the case with leopards. It's worth fitting a model that will examine a behavioural response **(2.)**. The behavioural models Bk **(2a.)** and bk **(2b.)** are also suggested by Efford (2014).

Age/sex

Research suggests detection probability may vary between different sex (Braczkowski et al., 2013; Maputla et al., 2013; Martins & Harris, 2013) classes in leopards. It may be useful to examine sex-specific density amongst classes by factoring in sex-specific estimates of detection probability at a home-range centre **(3.)** as well as sex-specific sigma **(3a.)**.

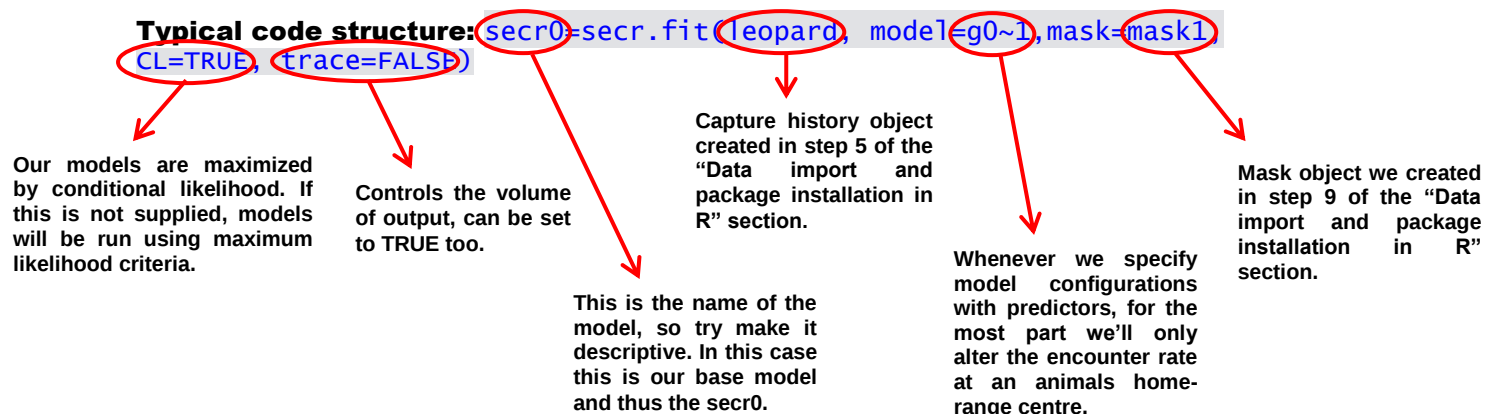


Capture probabilities differ between sexes/sexes.

What if I can't tell the sex/age of my study animals?

This is indeed a possibility. Balme et al (2012) for example showed that female and sub-adult leopards are difficult to distinguish from photographs. This is a problem as we know that varying sex classes often have different capture probabilities (eg. Females often avoid trails; Palomares et al., 2012). Now if you can't identify these sex/age classes there is a very good chance that unmodelled heterogeneity in capture probabilities remains. Luckily, there is a Finite mixture model with two latent classes which you can run in secr. This model will attempt to deal with this heterogeneity. In our model list it is model 4 (sechr).

Model fitting and interpretation in secr

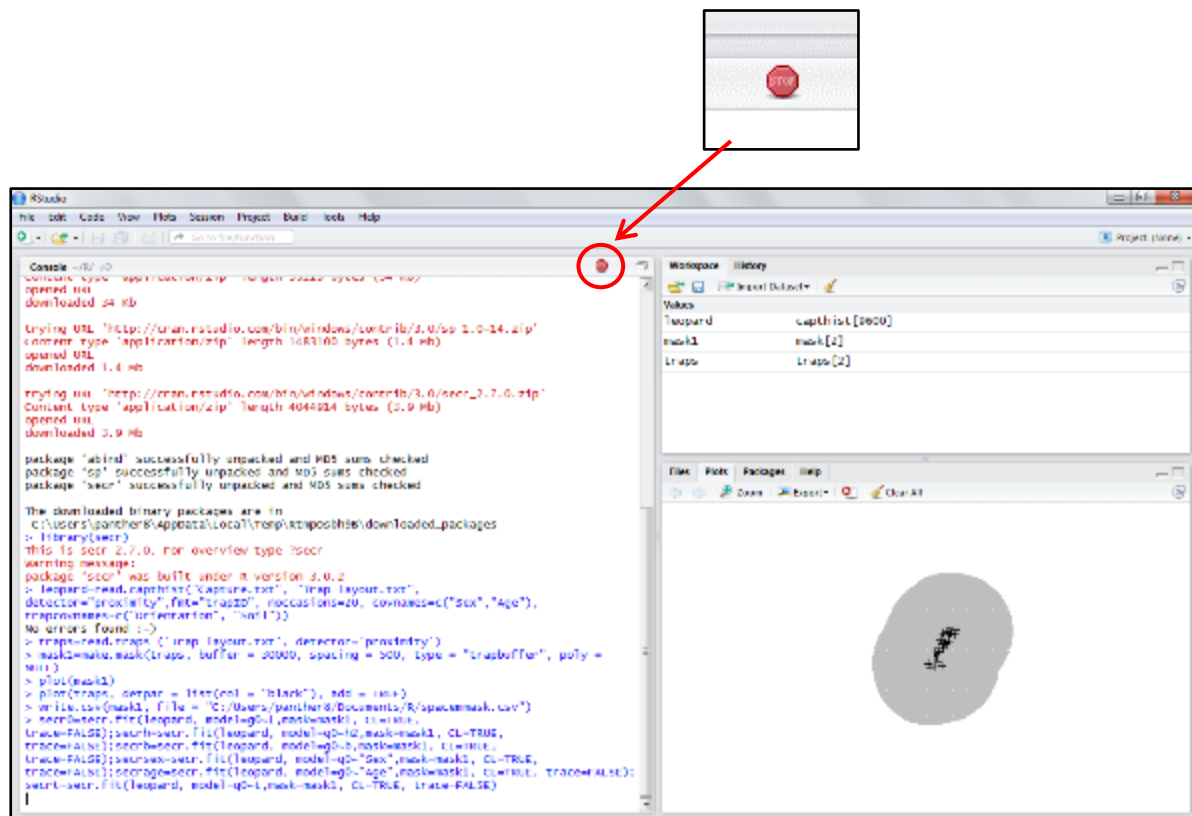


Now that we've outlined a few biologically meaningful models for the estimation of leopard density on Phinda and have an idea of what the model structure looks like, let's go ahead and fit these within the secr package in R. The models will take a few minutes to run, but we can fit them simultaneously and list their respective outputs once they're done. Run these, make a cup of coffee and comeback (they should be done in ~ 20 minutes, you'll notice however that when you play with these other covariates, model run time can take substantially longer).

1. Let's fit the six models we outlined in the above section simultaneously. Remember the tip about giving your models meaningful names? So secr0 is model 1. (our base), secrb is model 2. (behavioural response), secrBk is model 2a (transient response), secrbk is model 2b (step-change), secrsex is model 3. (using the "Sex" covariate only to examine differences in g0), 3a. incorporates "Sex" into g0 and sigma and finally secrh is model 4. (our mixture model). P.S: Once you've entered this code and hit enter, don't worry about the fact that you see nothing in the R window, there is a small red icon in the top right corner which shows you R is working (see below).

Code:

```
secr0=secr.fit(leopard, model=g0~1, mask=mask1, CL=TRUE,
trace=FALSE);secrb=secr.fit(leopard, model=g0~b, mask=mask1, CL=TRUE,
trace=FALSE);secrBk=secr.fit(leopard, model=g0~Bk, mask=mask1,
CL=TRUE, trace=FALSE);secrbk=secr.fit(leopard,
model=g0~bk, mask=mask1, CL=TRUE,
trace=FALSE);secrsex=secr.fit(leopard, model=g0~"Sex", mask=mask1,
CL=TRUE, trace=FALSE);
secrsex2=secr.fit(leopard, model=list(g0~"Sex", sigma~"Sex"), mask=mask1, CL
=TRUE, trace=FALSE);secrh=secr.fit(leopard, model=g0~h2, mask=mask1,
CL=TRUE, trace=FALSE)
```



- Let's have a look at the output of one of our models, to make sure everything's there.

Code: `secur0`

- If this is successful you'll get the following model details in the output window:

```
secur.fit(capthist = leopard, model = list(D ~ 1, g0 ~ 1, sigma ~
  1), mask = mask1, CL = TRUE, trace = FALSE)
secur 2.7.0, 14:25:36 13 Jan 2014

Detector type      proximity
Detector number    30
Average spacing    1677.312 m
x-range            428214 443166 m
y-range            6915025 6936481 m
N animals          : 16
N detections       : 55
N occasions        : 20
Mask area          : 463850 ha

Model              : g0~1 sigma~1
Fixed (real)       : none
Detection fn       : halfnormal
N parameters       : 2
Log likelihood     : -273.3234
AIC                : 550.6468
AICC               : 551.5699

Beta parameters (coefficients)
      beta      SE.beta      lcl      ucl
g0    -3.115831 0.2301811 -3.566978 -2.664685
sigma  7.938248 0.1327411  7.678080  8.198415

variance-covariance matrix of beta parameters
      g0      sigma
g0    0.05298335 -0.01297419
sigma -0.01297419 0.01762021

Fitted (real) parameters evaluated at base levels of covariates
      link      estimate SE.estimate      lcl      ucl
g0    logit 4.245893e-02 9.358283e-03 2.746542e-02 6.508968e-02
sigma  log  2.802445e+03 3.736444e+02 2.160467e+03 3.635186e+03
```

- The output window details everything from your model structure to the AIC values we will require in our model evaluation analysis. It also includes useful information on the mask area we created, the average spacing of our camera traps and the number of parameters in the model. One thing you'll notice is that we don't have a density estimate in this window, and this is because of the conditional likelihood we specified to be true in our model structure.

Important components before density reporting!

```
Fitted (real) parameters evaluated at base levels of covariates
link      estimate SE.estimate      lcl      ucl
g0    logit 4.245893e-02 9.358283e-03 2.746542e-02 6.508968e-02
sigma    log 2.802445e+03 3.736444e+02 2.160467e+03 3.635186e+03
```

Take a look at the fitted (real) parameters section at the bottom of the output window. The first component is g0 which if you remember is the detection probability at the home-range centre. The second estimates is sigma – the scale parameter which describes the decline of encounter rate with increased distance from the animals home-range centre. These are critical values and are typically reported in your paper/publication (see results reporting on pg 25).

- Let's get our density estimate using the “derived” command in R.

Code: `derived(secr0)`

- You'll get the following output:

```
> derived(secr0)
      estimate SE.estimate      lcl      ucl CVn      CVa
esa 4.097007e+04          NA          NA          NA  NA      NA
D   3.905289e-04 0.0001155874 0.0002213032 0.0006891579 0.25 0.1584365
      CVD
esa      NA
D   0.2959766
```

- There's that golden number we were after, the density of animals. Presented here in animals/hectare. In this case that means 0.00039 leopards/hectare. If we want this number in leopards/100 km² then we multiply it by 10000 (3.9 leopards/100 km²). We also have the lower and upper confidence limits, so secr estimates we have 3.9 leopards/100km², but this figure could be as low as 2.2/100km² and as high as 6.9/100 km². With wild felids these CL's aren't bad!
- Now that we've taken a look at our output and know how to obtain our density estimate, let's evaluate our eight models head to head using the AIC method discussed above.

Code: `AIC(secr0,secrb,secrBk,secrbk,secrsex,secrsex2,secrh)`

	model	detectfn	npar	logLik	AIC	AICc	dAICc	AICcwt
secrsex2	g0~Sex sigma~Sex	halfnormal	4	-264.0456	536.091	539.728	0.000	0.9687
secrbk	g0~bk sigma~1	halfnormal	3	-269.2976	544.595	546.595	6.867	0.0313
secrBk	g0~Bk sigma~1	halfnormal	3	-270.9103	547.821	549.821	10.093	0.0000
secr0	g0~1 sigma~1	halfnormal	2	-273.3234	550.647	551.570	11.842	0.0000
secrb	g0~b sigma~1	halfnormal	3	-272.2682	550.536	552.536	12.808	0.0000
secrsex	g0~Sex sigma~1	halfnormal	3	-273.1393	552.279	554.279	14.551	0.0000
secrh	g0~h2 sigma~1 pmix~h2	halfnormal	4	-273.3234	554.647	558.283	18.555	0.0000

9. The output gives you a list of model structure, the detection function used, number of parameters as well as the important AIC weight value. As in a lot of cases in statistical analysis, the most parsimonious model often fits the data the best, and here we see that our model which factors in sex-specific detection at home-range centre and sigma has overwhelming support. When we look at the density estimate from our winning model using the derived code, we can see that it's a bit higher than our base model ie. 4.99 leopards/100 km², and that's what we'll report.

Not familiar with AIC?

Developed by Japanese scientist Hirotugu Akaike in 1974 (Figure 11), the Akaike Information Criterion (AIC) is a method used to measure the relative quality of a model against a set of other models developed from a given set of data. It assesses the number of parameters that a model uses and also the goodness of fit of the model (it is rooted in the law of parsimony). Importantly, the AIC method only provides an assessment of model fitness from the set of candidate models. It does not tell the user anything about the quality of the model itself! So if one puts garbage in one will get garbage out (GIGO)!

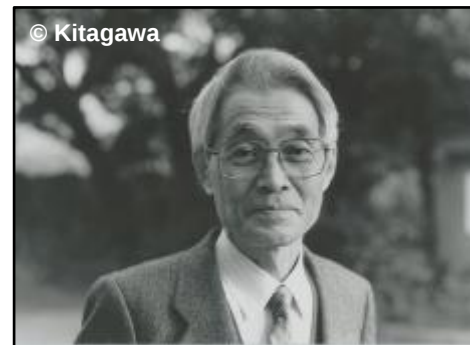


Figure 11: Professor Hirotugu Akaike.

10. Finally let's vary the buffer and spacing of our chosen model (secrsex2) mask buffer (mask1) and make sure the likelihood estimates remains stable.

Code: `mask.check(secrsex2)`

```
Computing log likelihoods...
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
spacing
buffer 336 252 168
29856 1e+10 1e+10 1e+10
44784 1e+10 1e+10 1e+10
59712 1e+10 1e+10 1e+10
```

Critical Analysis Point

Chase-Grey et al (2013) show the importance of checking that the state-space (potential home-range centre buffer) is large enough. In their paper a 10 km buffer produced a density estimate of 25 leopards/100 km² (range = 17-34) but buffers of 15, 20 & 25 km produced the same estimate of 10 leopards/100 km². It is this stabilization of estimates that is critical to reporting accurate estimates of density. Remember that a massive buffer will only increase analysis time – it does not have a negative effect on your estimates unless this buffer extends into areas of non-suitable leopard habitat. See the full paper here: <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0082832>

11. The estimates appear stable and neither narrower spacing nor wider buffer adjustments would have affected our density estimates. Don't forget that making too big a buffer will only increase your computational time, it won't affect your results (see an example of this in Chase-Grey, 2013) unless the buffer extends into areas which are not likely to encompass a leopard's home-range centre.
12. Finally, out of interest let's take a look at density estimates by "Sex", but first let's see how the model using sex-specific detection probability estimated total population density.

Code: `derived(secrsex2)`

```
> derived(secrsex2)
      estimate SE.estimate      lcl      ucl      CVn      CVa
esa 3.204689e+04      NA      NA      NA      NA      NA
D   4.992684e-04 0.000157996 0.0002725009 0.0009147453 0.2869551 0.133419
      CVD
esa      NA
D   0.3164551
```

13. You can also use the "derived" function to look at density by sex. The same could also be done for "Age" if this was a parameter of interest.

Code: `derived(secrsex2, groups="Sex")`

14. You can see that the confidence limits are considerably narrower for females when compared to males, and this is probably owed to the higher number of re-captures for females. If you realistically want to examine sex or age specific densities, you'll need a lot of good re-capture data.
15. Finally, just for interest sake, let's see how our base model would have performed with the inclusion of the habitat suitability map generated for Phinda.
16. Let's bring in the habitat suitability mask.

Code: `habmask=read.mask(file="NS test.csv")`

17. Let's plot the habitat suitability mask.

Code: `plot(habmask)`



How do I know if I need a detailed habitat suitability mask?

Remember! You've got to make the call on whether you need a detailed habitat mask or not. If you're working in a large protected reserve, chances are you will not (and the steps outlined in creating a mask in the preceding section will suffice). However if you're working in a modified landscape with tracts of land which support palm oil, human villages or farmland, you may need a more detailed mask which omits non-suitable patches of land. We'll show you how to make a detailed mask later in this document ☺

18. Let's run the same base model ie. secr0, but use the habitat suitability mask instead of our own, which specifies all range centres to be located within suitable habitat.

Code: `secrmask=secr.fit(leopard, model=g0~1,mask=habmask, CL=TRUE, trace=FALSE)`

Code: `derived(secrmask)`

	estimate	SE.estimate	lcl	uc1	cvn	Cva	CVD
esa	3.615808e+04	NA	NA	NA	NA	NA	NA
D	4.425014e-04	0.0001237417	0.0002584339	0.0007576692	0.25	0.125297	0.2796414

19. You can see that in the case of the density estimates produced are higher when we factor in the habitat suitability mask for leopards on Phinda and its surrounds. This makes sense as large tracts to the southeast of Phinda are unsuitable for leopards to establish a home-range centre within.

Further secr reading and the Phidot help forum

If you've managed to receive the above outputs then you've successfully run a few basic and relevant models to determine the density of your wild cat population. However the scope of secr is very wide and we've outlined the most important material to guide you further in your future analyses below. Additionally be sure to make use of the fantastic online forum serviced by Murray Efford and other users at <http://www.phidot.org/forum/viewforum.php?f=36>. There are literally hundreds of queries on the secr package, accompanying solutions and even useful code entries.

- 1) Efford, M (2014) Package "secr" manual. Get it here: <http://cran.r-project.org/web/packages/secr/secr.pdf>

Why is this a useful reference? Murray has created a detailed manual for his "secr" package and it is full of useful functions, code segments and help queries which will assist you in running your analyses.

- 2) Efford, M (2014) Package "secr" overview. Get it here: <http://www.otago.ac.nz/density/pdfs/secr-overview.pdf>

Why is this a useful reference? If you're interested in a simple, quick overview of the package, its key components and a model example this is the document you need!

Data formatting for SPACECAP

Start off by opening the “Raw leopard data” folder located in your “Documents”. If you haven’t created this folder or the “R” folder we’ll be using to store our formatted files, take a quick look at the “Getting started” section of “Data formatting for secr”. We’ll start by assuming that these two folders are created. Click on the “Phinda leopard SPACECAP.xlsx” spreadsheet located in the “Raw leopard data” folder. Examine the spreadsheet components carefully.

Raw capture data	Detector id	Animal capture	Trap deployment
1	2	3	4
5	6	7	8
9	10	11	12
13	14	15	16
17	18	19	20
21	22	23	24
25	26	27	28
29	30	31	32
33	34	35	36
37	38	39	40
41	42	43	44
45	46	47	48
49	50	51	52
53	54	55	56
57	58	59	60
61	62	63	64
65	66	67	68
69	70	71	72
73	74	75	76
77	78	79	80
81	82	83	84
85	86	87	88
89	90	91	92
93	94	95	96
97	98	99	100

Raw capture data	Detector id	Animal capture	Trap deployment
------------------	-------------	----------------	-----------------

Detector name	Detector abbreviation	Detector code
Ndulamithi	Ndl	1
Charcoal Alley	CA	2
Buffalo Beat	Bul	3
Overgrown Pan	Ove	4
Bushbaby	BB	5
Coucal Lane	CL	6
Reservoir	Res	7
Charcoal Clearings	CC	8
Ngulubeni Pass	Ngp	9
Mkhombe Loop	Mkh	10
Sun Loop	Sun	11
Bushcamp	BC	12
SFCline	SFC	13
Tortoise	Tor	14
Bateleur	Bat	15
Kudu Pans	KP	16

Detector id

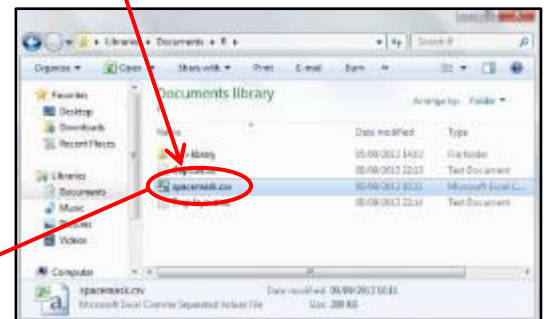
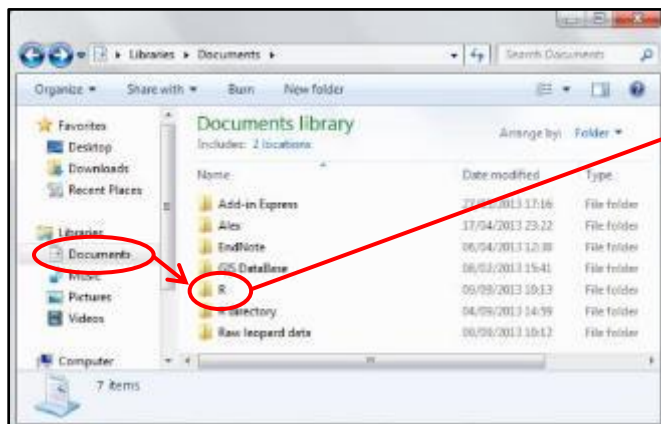
LOC_ID	ANIMAL_ID	SO
1	6	4
2	13	10
3	26	6
4	8	4
5	21	7
6	7	4
7	8	4
8	27	11
9	27	12
10	28	15
11	29	6
12	13	10
13	27	12
14	7	4
15	13	10
16	26	11

Animal capture

LOC_ID	X_Coord	Y_Coord	1	2
1	437892	6934735	1	1
2	438693	6933715	1	1
3	439067	6935594	1	1
4	439622	6936481	1	1
5	440365	6933980	1	1
6	442615	6933571	1	1
7	443186	6935579	1	1
8	439189	6932074	1	1
9	439212	6929594	1	1
10	437749	6928396	1	1
11	435667	6928441	1	1
12	436239	6926060	1	1
13	434136	6927834	1	1
14	434469	6930617	1	1
15	436885	6929075	1	1
16	437719	6931513	1	1

Trap deployment

You'll notice that similarly to secr, the spreadsheet has a few components drawn upon from the "Raw capture data" table (this is exactly the same as that provided for the secr exercise). Except for a few name changes to the headings in the spreadsheet components, the information format is essentially the same. The only thing we still have to do before we format our data is get the habitat mask we created in secr. We do this as a habitat mask cannot currently be created in the SPACECAP package itself (a function available in secr). We'll therefore use the habitat mask we created in step nine, and exported from secr in step twelve of the "Data import and package installation in R" section of "Data formatting for secr". Start off by opening the "Spacemask.csv" file.



	A	B
1	x	y
2	425464	6885275
3	425964	6885275
4	426464	6885275
5	426964	6885275
6	427464	6885275
7	427964	6885275
8	428464	6885275
9	428964	6885275
10	429464	6885275
11	429964	6885275
12	430464	6885275
13	430964	6885275
14	431464	6885275
15	431964	6885275
16	432464	6885275
17	432964	6885275

Spacemask.csv file in R folder (Potential home-range centres file)

Have a look at the "spacemask.csv", you can see that it's missing a habitat value. Go on and change the headings of "x" and "y" to "X_Coord" and "Y_Coord" and also add a column labeled "Habitat". Fill the "Habitat" columns with 1's. Remember, for the purpose of the exercise, we assume that all potential home-range centres are suitable for leopards.

	A	B	C
1	X_Coord	Y_Coord	Habitat
2	425464	6885275	1
3	425964	6885275	1
4	426464	6885275	1
5	426964	6885275	1
6	427464	6885275	1
7	427964	6885275	1
8	428464	6885275	1
9	428964	6885275	1
10	429464	6885275	1
11	429964	6885275	1
12	430464	6885275	1
13	430964	6885275	1
14	431464	6885275	1
15	431964	6885275	1
16	432464	6885275	1
17	432964	6885275	1

Spacemask.csv file with added habitat suitability (Potential home-range centres file)

Your end product should look like this. Hit the save button and close the file, we'll come back to it later.

Now let's take a quick look at how each of the components from the "Raw leopard data" sheet are integrated into the three spreadsheet components. We'll also save these as csv. files, the standard format accepted by the SPACECAP package.

[illegible]

The screenshot shows an Excel spreadsheet with the following data:

	A	B	C
1	Detector name	Detector abbreviation	Detector code
2	Ndulamethi	ND	3
3	Charcoal Alley	CA	5
4	Buffalo Beat	BB	5
5	Overgrown Pan	OP	6
6	Bushbushy	BB	5
7	Coccol Lane	CL	6
8	Reservoir	Res	7
9	Charcoal Clearings	CC	8
10	Ngalubeni Pans	Ngp	9
11	Mkhombe Loop	Mkh	10
12	Sunil Loop	Sun	11
13	Bushcamp	BC	12
14	SFCline	SFC	13
15	Tortillas	Tor	14
16	Bateleur	Bat	15
17	Kudu Pans	KP	16

Red circles highlight the cell 'CA' in column B, row 3, and the cell '5' in column C, row 3. A red arrow points from the 'CA' cell to the '5' cell.

Detector id

The screenshot shows an Excel spreadsheet with the following data:

	A	B	C	D
1	LOC_ID	ANIMAL_ID	SO	
2	6	4	1	
3	13	10	1	
4	26	6	2	
5	8	4	3	
6	21	7	3	
7	2	4	4	
8	8	4	4	
9	27	11	4	
10	27	12	4	
11	28	15	4	
12	29	6	5	
13	13	10	5	
14	27	13	5	
15	7	4	6	
16	15	10	6	
17	26	11	6	

Red circles highlight the following cells: (2, 6), (2, 4), (2, 2), (2, 1), and (2, 5). A red line connects these points, illustrating a sequence of visits for animal 2.

Animal capture

The screenshot shows an Excel spreadsheet with the following data:

	A	B	C	D	E
1	LOC_ID	X_Coord	Y_Coord	1	2
2	1	437892	6934733	1	1
3	2	438693	6933715	1	1
4	3	439067	6935534	1	1
5	4	439622	6936483	1	1
6	5	440365	6933540	1	1
7	6	442615	6933171	1	1
8	7	443186	6935779	1	1
9	8	439189	6920704	1	1
10	9	439212	6925994	1	1
11	10	437749	6928396	1	1
12	11	435667	6928441	1	1
13	12	436239	6926060	1	1
14	13	434136	6927834	1	1
15	14	434465	6930617	1	1
16	15	436889	6929075	1	1
17	16	437719	6931911	1	1

Trap deployment

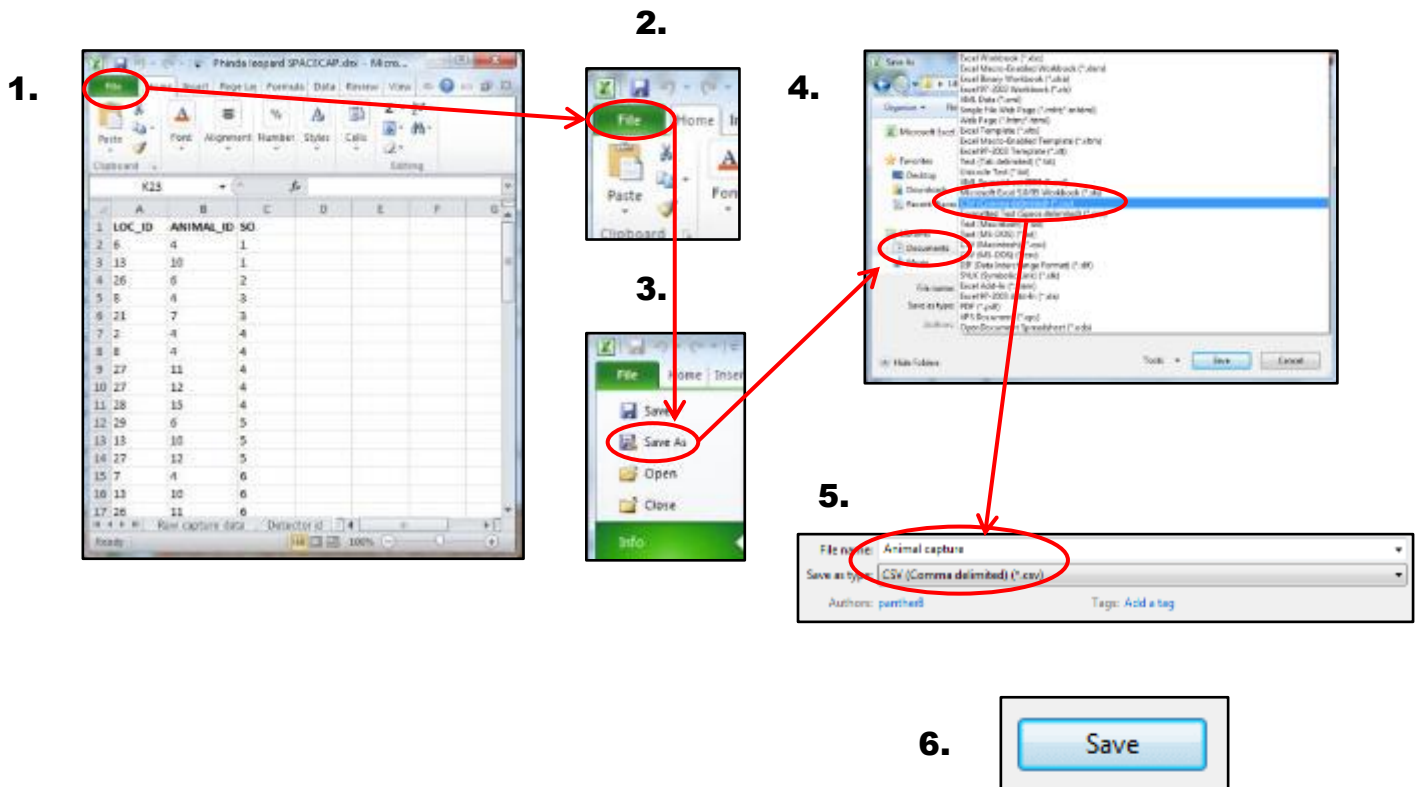
The “Detector id” is the same as that used in the secr section and it holds information on the camera location, an abbreviation which we use in the “Raw leopard data” table, and the important detector code. In the “Animal capture” spreadsheet we use the detector code in the “LOC_ID” column, we obtain the “ANIMAL_ID” from the “secr/SPACECAP code” and the “SO” is obtained from the “Samplingoccasion” row.

This is the camera trap functionality column. It denotes whether your camera trap was operational. If you had a failure for a particular camera at a sampling occasion, place a 0 in the column. If the camera worked during the sampling occasion then place a 1 in the column. As you can see during the Phinda survey all the camera traps were functional for the full 20 sampling occasions. Although we did not include this in the secr tutorial, this is similarly possible.

Excel datasheet conversion for SPACECAP

Now that we have an understanding of how we obtained these different information components let's go ahead and convert the "Animal capture" and "Trap deployment" sheets into csv format.

1. Start of by selecting the "Animal capture" sheet, and click on the file tab at the top of the Excel browser.
2. Select the "Save as" tab.
3. Then go ahead and click the "Documents" tab and select the "R" folder we created earlier (This is where we'll store our files for SPACECAP).
4. Finally, click the "Save as type" tab and select the "CSV(Comma delimited) (*.csv)" option.
5. Give the file a meaningful name: "Animal capture".
6. Click "Save" and repeat this step for the "Trap deployment" sheet.



You can check you have all three csv files saved in your R folder. If you do, let's jump into installing the SPACECAP package in R and importing our data!

Data import and SPACECAP package installation in R

Now that we have our txt files within our R folder, let's go ahead and open R. If you do not have R, have a look at the "Data import and secr package installation in R" section. Let's get started with installing SPACECAP and importing our data:

1. Open the R gui in your windows startup. It should be under the "Programmes" tab, and will have its own folder "R".
2. Let's start by setting our work directory for our R session. This will allow R to access the "Animal capture" and "Trap deployment" csv files we stored in our R folder.

Code: `setwd("~/R")`

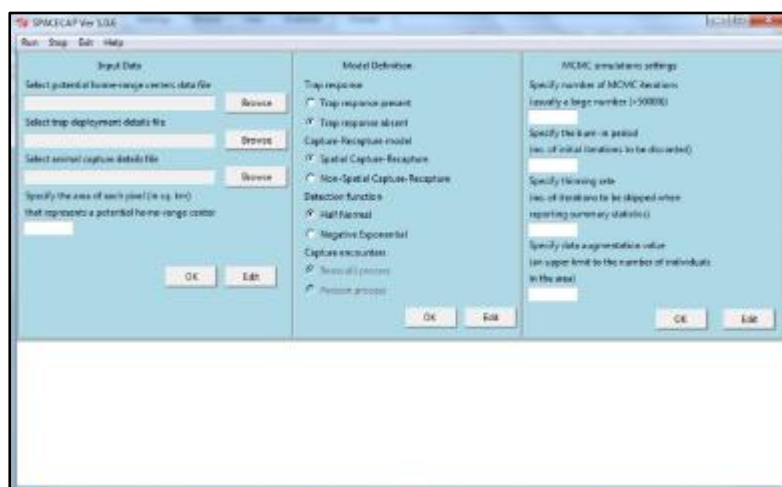
3. Let's install the "SPACECAP" package

Code: `install.packages("SPACECAP")`

4. Now let's load "SPACECAP"

Code: `library(SPACECAP)`

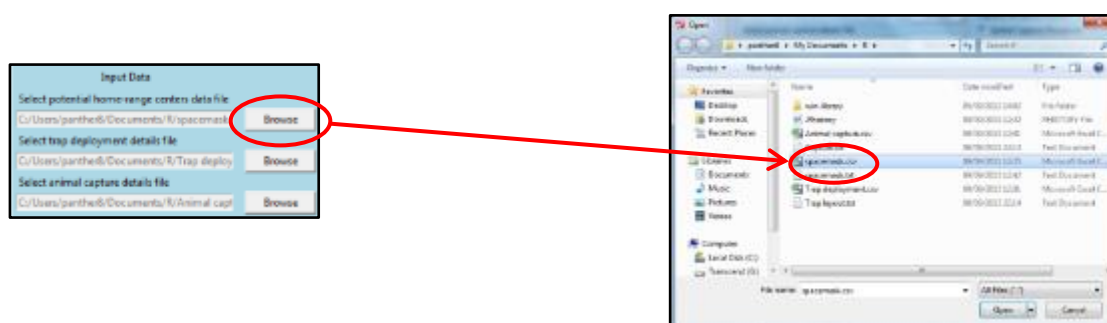
Code: `SPACECAP()`



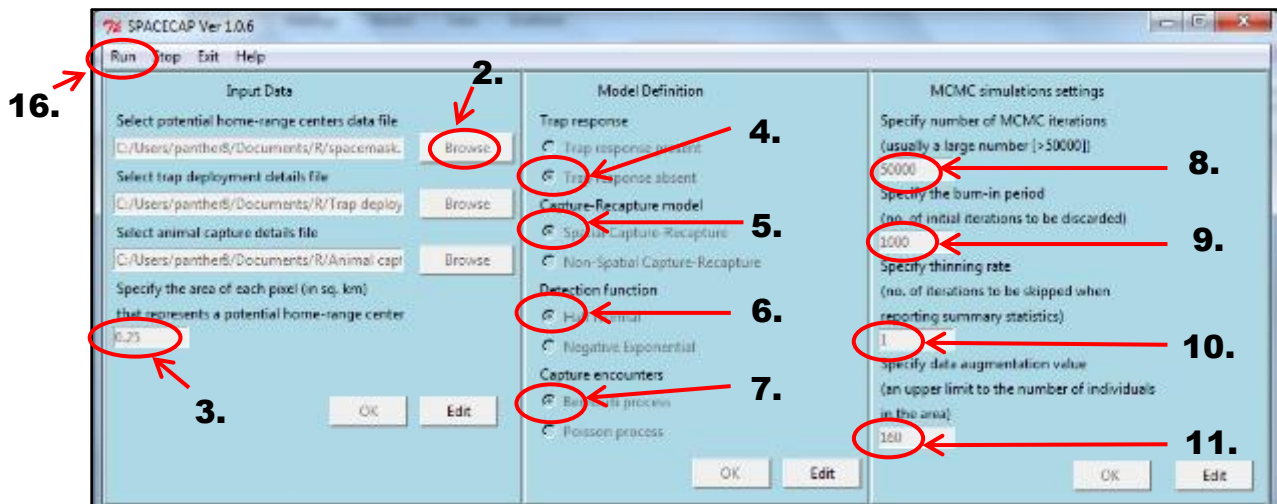
No code here! Arjun and his team have made a user-friendly drop down gui! It couldn't be easier for you to load your files and set your model preferences! ☺

Model fitting and interpretation in SPACECAP

1. Great, now that we've got the SPACECAP gui up and running let's get those "Animal capture", "Trap deployment" and potential home-range centres ("Spacemask") files into R for SPAECAP.
2. Start off by clicking the browse tabs for each section of the "Input data" section within the gui (ie.our three csv files located within our "R" folder).

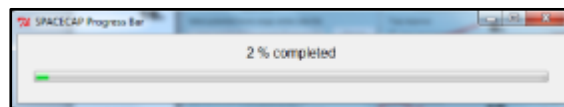


3. Once these have been selected, go on and specify the area of each pixel that represents a home-range (it's in km^2 , so in our case this means 0.336 km^2 – remember our initial spacing was in metres and this was 580 m). Then hit the "OK" button.
4. Under the model definition section we have two key model varieties available to us, namely the "Trap response absent" which is similar to our base model and the "Trap response present" which factors in a trap-specific behavioural response. For the purpose of this tutorial let's run the base model.
5. As we are interested in spatially explicit capture re-capture modeling, go on and select the "Spatial Capture-Recapture" tab.
6. Select the half-normal detection function, the same function used to run models in secr.
7. The Bernoulli process is automatically selected for you and hit the "OK" tab.
8. Usually in the Markov-Chain Monte Carlo (MCMC) section you will specify a high number of iterations ie. > 50 000 (Gopalaswamy et al., 2012).
9. The burn-in period (this is what the model "trains" on) should usually be set to about 10 000.
10. Set the thinning rate to 1.
11. The data augmentation value is recommended to be 5-10 times the number of animals photographed (in our case 16 leopards, so that's 160 – again, don't make this too small – but there is no danger in making it large ie. Just increases run time).



12. The above tab is what your typical analysis figures should look like (except for the area of each pixel which in our case is 0.336 and the data augmentation value which will change dependent on your number of unique individuals photographed). Once you've hit run, you'll see the SPACECAP output window fill up with text and you'll also get a progress bar showing how far the analysis has progressed.

```
Input data read successfully
Model definition complete
MCMC simulation settings complete
Input Summary
-----
```



13. Now the SPACECAP analysis will take some time. A typical 50-60 000 iteration analysis will take you about 24-36 hours. In the long run this is worth it as this Bayesian-based analysis is robust and if you think about it even a busy project running two or three camera surveys a year will only need a few days to complete their analyses.

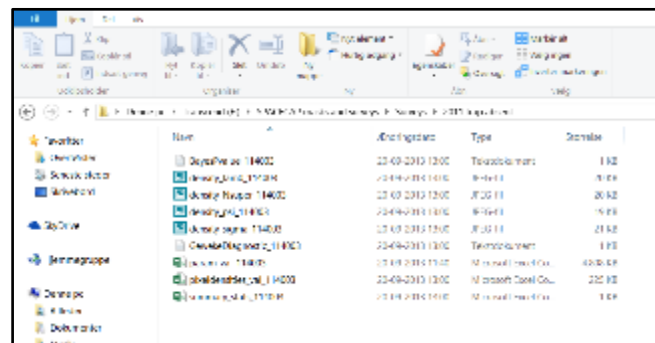
14. Once the analysis has finished running, you will receive a summary table in the SPACECAP gui. This gives you your critical values including lam0, sigma, psi, beta and density in individuals/100km². You can see that in our case the estimate of density is similar to that generated by secr. Summary stats, pixel densities (used to generate a density surface map) and density graphs are stored in our R folder automatically (useful for table creation).

Input Summary				
Area of each pixel representing a potential home-range center: 0.25 sq km				
Model selected: Trap response absent, Spatial Capture-Recapture, Half-normal detection function, Bernoulli detection process				
MCMC simulation settings: Iterations - 50000 Burnin - 1000 Thinning - 1 Data Augmentation - 160				
	Posterior_Mean	Posterior_SD	95%_Lower_HPD_Level	95%_Upper_HPD_Level
sigma	3.0333	0.4253	2.293	3.8742
lam0	0.0449	0.0106	0.028	0.0666
psi	0.8113	0.1347	0.5583	1
Nsuper	143.3812	23.4727	100	176
Density	3.0911	0.506	2.1559	3.7943

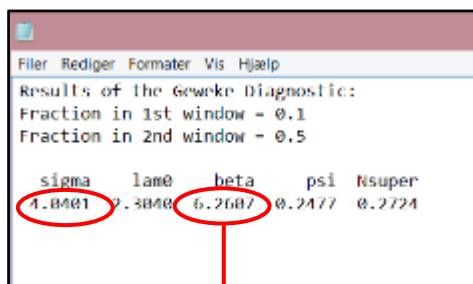
Model outputs and assessing model performance

Now that we have completed our analysis, SPACECAP provides us with further, neatly packaged outputs beyond the framework of the GUI. Let's access some of these and have a look at how to gauge the performance of a particular model.

1. Open up your R folder and have a look for a file beginning with the word "Output" followed by some numbers. This is where you'll find a series of "txt" and Excel files with information on how our model performed.



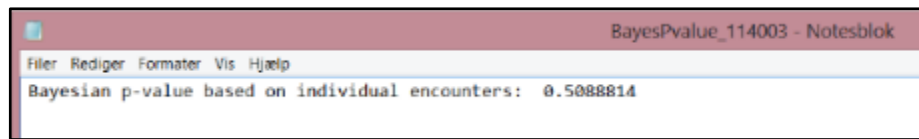
2. Let's start by clicking on the Geweke Diagnostic txt file.



Remember when we selected the 50 000 iterations tab in the R GUI? Well this is where we see if that number of repetitions converged around a solution using the Markov Monte Carlo Chains. These numbers should not exceed a value of 1.6 but if they do, as shown in the example to the left, try increase the number of iterations (to 60 or 70 000). If your Geweke Diagnostic statistics continue to exceed the 1.6 value then compare the density estimates from the 50 000 run. If these are not significantly different (by about a decimal place then go ahead and report them).

Both these values indicate that MCMC convergence has not taken place. Re-run the analysis with more iterations.

3. For the purpose of this tutorial let's assume that our Geweke Diagnostic statistics all indicated chain convergence around a solution (ie. were all ≤ 1.6), the next thing we have to look at is the Baye's P value. Click on the Bayes P value txt file.



4. You can see that the reported value here is 0.50, and according to Gopalaswamy et al (2012) this indicates very good model adequacy. If this value is close to 0 or 1 then the implemented model is regarded as inadequate. Remember that the Geweke Diagnostic statistics and the Bayes P values examine different things but both are important in gauging the performance of your model.
5. There are several other outputs provided by SPACECAP, the foremost of which is the "summary_stats" and "pixeldensities_val" Excel files. The summary stats file is a clone of the GUI output we have at the top of this page. The pixeldensities file is a neat way of graphically representing the differences in density across the state space landscape. You can load this as a shapefile into either Arcview or Quantum equivalent GIS package and then assign a colour gradient to each pixel. This is made possible because each pixel has a pixel density. See Gopalaswamy et al (2012) for a graphic example.

Reporting results in scientific publications and reports

Let's take a look at two recent scientific publications which report SCR-based results of felid density. We'll look at Gray & Prum (2012), published in the Journal of Wildlife Management and Chase-Grey et al (2013) published in PloS One. The hyperlink to Gray & Prum (2012) is: <http://onlinelibrary.wiley.com/doi/10.1002/jwmg.230/abstract?deniedAccessCustomisedMessage=&userIsAuthenticated=false>, while the other hyperlink may be found in the "Recent applications in wild cat research" section on page eight.

Let's jump straight into Gray & Prum (2012) and their density estimate on leopards in eastern Cambodia. We like this paper as it has great management relevance, in the context of population status after a human conflict situation. If we take a look at the top of the "Results" section we see that the authors clearly describe camera effort, the number of leopards photographed and capture frequencies. This is a great thing to do as it is transparent and replicable to reviewers and other authors. Now let's jump to the leopard densities section. Although the authors have used the DENSITY programme in the analysis of their data this is analogous to secr and is still SCR. What we're interested in here are the g0 and sigma parameters reported at the bottom of this section. g0 and sigma are both reported with a measure of error (SE) and each is explained briefly.

RESULTS

We photographed 12 individually identified leopards, 5 male and 7 female, during the 3,738 camera-trap night survey period. The number of encounters with individually identified leopard was 60; the number of sampling occasions (24-hr periods) in which each individual was encountered varied between 1 and 23 (mean $5 \pm \text{SE } 1.9$). Capture frequencies were 23, 10, 9, 8, and 1 for the 5 males and 2, 2, 1, 1, 1, and 1 for the 7 females.

secr

Fitted (real) parameters evaluated at base levels of covariates
Link: estimate SE estimate 1e1 uc1
g0: 2.802445e+01 7.726144e+02 2.180467e+03 1.835188e+03
sigma: 2.802445e+01 7.726144e+02 2.180467e+03 1.835188e+03

Take a look at the Fitted (real) parameters section at the bottom of your model output on page 22 – this is where you obtain your g0 and sigma estimates.

SPACECAP

	g0	sigma	Posterior_Mean	Posterior_SD	95%_Lower_CrI	95%_Upper_CrI
1	27.729	0.0005	0.0004	0.0004	0.0001	0.0009
2	0.0005	0.0004	0.0004	0.0004	0.0001	0.0009
3	0.0005	0.0004	0.0004	0.0004	0.0001	0.0009
4	0.0005	0.0004	0.0004	0.0004	0.0001	0.0009
5	0.0005	0.0004	0.0004	0.0004	0.0001	0.0009
6	0.0005	0.0004	0.0004	0.0004	0.0001	0.0009
7	0.0005	0.0004	0.0004	0.0004	0.0001	0.0009

Click on the "summary_stats" Excel file and turn your attention to the lam0 (the Posterior_Mean with SD) and sigma columns.

Leopard Densities

We captured 6 individual leopards, 4 male and 2 female, at different locations. Maximum distance moved between captures were between 4.8 km and 16.8 km (mean $10.3 \pm \text{SE } 2.1$); total study area, based on HMMDM, was therefore $560 \text{ km}^2 \pm \text{SE } 77.12$. Leopard density estimates were $2.9 \pm \text{SE } 0.9$ individuals/100 km^2 based on model Mh (Jack-knife) in CAPTURE, $3.8 \pm \text{SE } 1.9$ individuals/100 km^2 based on model Mh (Chao) in CAPTURE, and $3.9 \pm \text{SE } 2.9$ individuals/100 km^2 based on model-averaged abundance estimates from MARK. In SECR analysis in DENSITY, we estimated leopard density at $3.6 \pm \text{SE } 1.0$ individuals/100 km^2 . Capture probability at home-range center (G_0) was estimated as $0.04 \pm \text{SE } 0.01$ (males) and $<0.01 \pm \text{SE } <0.01$ (females) and sigma (a function of movement) was $700 \text{ m} \pm \text{SE } 60 \text{ m}$ (males) and $4,900 \text{ m} \pm \text{SE } 1,050 \text{ m}$ (females).

Where do I get this info from?

metres & kilometres

In SPACECAP sigma is reported in kilometres while in secr it is reported in metres. g0 in both packages is reported in the same decimal format.

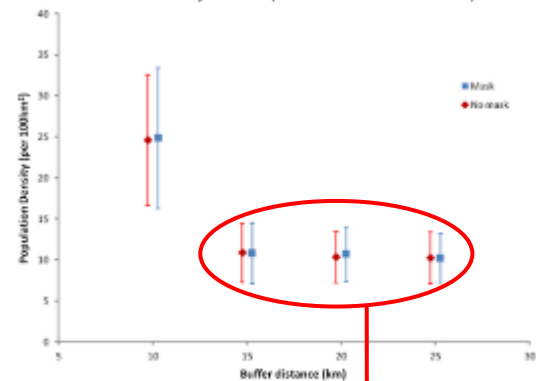
Now that we've looked at Gray and Prum (2012), let's compare the result reporting to Chase-Grey et al (2013). Open up this paper and jump down to the results section. The most important components here are the density estimates from SPACECAP, the size of the state space and also the changes (and stabilization) in density estimates as a result thereof. This paper emphasizes the point of truncating the state space and overestimating the density estimate (see also Figure 2).

Results

Leopard density

103 photographs (53 left flanks and 50 right flanks) of 10 individual adult leopards (7 females and 3 males) were obtained over 819 trap nights, alongside 31 photographs (15 left flank and 16 right flank) of 4 juvenile individuals (2 males and 2 females) (Table 1). Capture histories of individually identified leopards were used to calculate capture frequencies. The number of captures and recaptures ranged from 1 to 19. Only adult leopards were used to calculate leopard densities as cubs of solitary felids (age <1 year) have been found to have low capture probabilities and sub-adults may be transient individuals and therefore not part of the resident population [54]. Spatially explicit capture recapture via SPACECAP provided a density estimate of 25 adults per 100km² (SD 8.54) with a buffer of 10km. The density estimates then stabilised between 10.85 (SD 3.68) and 10.22 (SD 3.00) for buffers between 15km and 25km (Figure 2). The removal of unsuitable leopard habitat had little effect on the final result. Since a buffer of 20km is larger than the home range of a female leopard collared in the western Soutpansberg (14km²) [55], this buffer was selected to ensure that the buffer area was large enough such that no individual animal outside of the buffered region had any probability of being photo-captured by the camera traps during the survey. With a 20km buffer the mean density estimate was 10.73 adult leopards per 100 km² with a standard deviation of 3.32 (Table 2). Without unsuitable habitat removed from the state space area, the density was 10.41 adult leopards per 100 km² with a standard deviation of 3.13 suggesting that the unsuitable habitat did not significantly influence the density estimates. The density estimate obtained with a 20km buffer and unsuitable habitat removed is thus robust and a Bayesian P value of 0.60 confirmed the adequacy of the model with z scores from the Geweke diagnostic confirming that chain convergence had been achieved for all parameters (Table 2). The encounter probabilities (posterior means) for individuals pre- and post-initial encounter were $p_1 = 0.0286$ and $p_2 = 0.649$ indicating a positive trap response. This is unlikely to reflect "trap-happiness", however, but instead indicates non-dependence among encounters due to leopards favouring certain trails in moving through their territories [47].

Figure 2. Graph showing the effect of buffer increase and use of a habitat mask on the SPACECAP density estimate (mean and standard deviation).



Chase-Grey JN, Kord VT, Hill RA (2013) Evidence of a High Density Population of Heterotyped Leopards in a Mountain Environment. PLoS ONE 8(12): e69632. doi:10.1371/journal.pone.0069632



This paragraph is critical and lists the change and stabilization in density estimates with varying buffer widths.

Where do I get this info from?

```
Computing log likelihoods...
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
beta vector : -2.551295 7.258018
spacing
buffer 336 252 168
29856 1e+10 1e+10 1e+10
44704 1e+10 1e+10 1e+10
59712 1e+10 1e+10 1e+10
```

Code: `mask.check(secrsex2)`

Table 2. Posterior summary statistics and z scores from the SECR model fitted to the leopard camera trapping data in the western Soutpansberg Mountains, South Africa.

Parameter	Mean	SD	95% lower HPD level	95% upper HPD level	Z scores
D	10.73	3.32	4.68	17.38	
λ_0	0.029	0.099	0.013	0.047	-0.86
ϕ	1.89	0.28	1.25	2.23	-0.71
β_1	1.10	0.32	0.46	1.72	-0.32
W	0.54	0.17	0.23	0.87	0.22
N ₀	206.16	63.81	88.00	332.00	0.22

Only adult leopards were included. D is density/100 km². λ_0 is the expected encounter rate; $\phi = \exp(1/\lambda^2)$ is the scale parameter of a bivariate normal encounter function and may also be viewed as a range parameter of an animal; β_1 is the regression coefficient measuring the behavioural response; W is the ratio of the number of animals actually present within the state space to the maximum allowable number; N₀ is N_{auger} and equals the population size for the state space.

doi: 10.1371/journal.pone.0069632.t002

If you are running SPACECAP, you can run your analysis with varying buffer widths – again if all of your habitat is suitable then we can specify this with a very easy command (see below). In secr we can use the “mask.check” command (see pg 24).

When using SPACECAP it's also important to report the measures of model fitness discussed on page 34 & 35.

References

- Athreya, V., Odden, M., Linnell, J. D., Krishnaswamy, J., & Karanth, U (2013) Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. *PloS one*, 8(3), e57872.
- Balme, G. A., Slotow, R., & Hunter, L. T. (2009b) Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Pantherapardus*) population. *Biological Conservation*, 142(11), 2681-2690.
- Balme, G. A., Hunter, L. T., & Slotow, R. (2009a) Evaluating methods for counting cryptic carnivores. *The Journal of wildlife management*, 73(3), 433-441.
- Balme, G., & Hunter, L. (2004) Mortality in a protected leopard population, Phinda Private Game Reserve, South Africa: a population in decline. *Ecological Journal*, 6, 1-6.
- Borah, J., Sharma, T., Das, D., Rabha, N., Kakati, N., Basumatary, A., Ahmed, M.F & Vattakaven, J (2013) Abundance and density estimates for common leopard *Panthera pardus* and clouded leopard *Neofelis nebulosa* in Manas National Park, Assam, India. *Oryx*, 1-7.
- Borchers, D. L & Efford, M. G. (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, 64(2), 377-385.
- Brackowski, A.R (2013) The susceptibility of leopards *Panthera pardus* to trophy hunting. MSc thesis. University of Oxford, Oxford.
- Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L (1993) *Distance sampling: estimating abundance of biological populations*. Chapman & Hall.
- Chapman, S. & Balme, G (2010) An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South African Journal of Wildlife Research*, 40(2), 114-120.
- Efford (2014) Package “secr”, version 2.8.1, for spatially explicit capture-recapture modelling in R. *R language for statistical computing*.
- Efford, M. G (2011) Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. *Ecology*, 92(12), 2202-2207.
- Efford, M. G., Dawson, D. K. & Borchers, D. L (2009) Population density estimated from locations of individuals on a passive detector array. *Ecology*, 90(10), 2676-2682.
- Efford, M. G., Dawson, D. K. & Robbins, C. S (2004) DENSITY: software for analysing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation*, 27(1), 217-228.
- Fattebert, J (2013) Spatial ecology of a leopard population recovering from over-harvest. PhD thesis. University of Kwazulu-Natal, Kwazulu-Natal.
- Grey, J. N. C., Kent, V. T., & Hill, R. A (2013) Evidence of a High Density Population of Harvested Leopards in a Montane Environment. *PloS one*, 8(12), e82832.

- Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. & Karanth, K. U (2012) Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution*, 3(6), 1067-1072.
- Hunter, L., Balme, G., Walker, C., Pretorius, K. & Rosenberg, K (2003) The landscape ecology of leopards (*Panthera pardus*) in northern KwaZulu-Natal, South Africa: A preliminary project report. *Ecological Journal*, 5, 24-30.
- Karanth, K. U., & Nichols, J. D (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, 79(8), 2852-2862.
- Karki, J. B., Pandav, B., Jnawali, S. R., Shrestha, R., Pradhan, N. M. B., Lamichane, B. R., Khanal, P., Subedi, N & Jhala, Y. V (2013) Estimating the abundance of Nepal's largest population of tigers *Panthera tigris*. *Oryx*, 1-7.
- Maputla, N. W., Chimimba, C. T., & Ferreira, S. M (2013) Calibrating a camera trap–based biased mark–recapture sampling design to survey the leopard population in the N'wanetsi concession, Kruger National Park, South Africa. *African Journal of Ecology*, 51(3), 422-430.
- Martins, Q., & Harris, S (2013) Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *African Journal of Ecology*, 51(4), 571-579.
- Norton, P. M & Henley, S. R (1987) Home range and movements of male leopards in the Cedarberg Wilderness Area, Cape Province. *S. AFR. J. WILDL. RES.* 17(2), 41-48.
- Noss, A. J., Gardner, B., Maffei, L., Cuéllar, E., Montañó, R., Romero-Muñoz, A., Sollman, R & O'Connell, A. F. (2012) Comparison of density estimation methods for mammal populations with camera traps in the Kaa-lya del Gran Chaco landscape. *Animal Conservation*, 15(5), 527-535.
- O'Farrell, M. J., Clark, W. A., Emmerson, F. H., Juarez, S. M., Kay, F. R., O'Farrell, T. M., & Goodlett, T. Y (1994) Use of a mesh live trap for small mammals: are results from Sherman live traps deceptive?. *Journal of Mammalogy*, 692-699.
- Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, 62, 3–135.
- Smith, J.L.D (1984) *Dispersal, communication and conservation strategies for the tiger (Panthera tigris) in Royal Chitwan, National Park, Nepal*. PhD thesis. University of Minnesota, St Paul.
- Soisalo, M. K., & Cavalcanti, S (2006) Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, 129(4), 487-496.
- Umetsu, F., Naxara, L., & Pardini, R (2006) Evaluating the efficiency of pitfall traps for sampling small mammals in the Neotropics. *Journal of Mammalogy*, 87(4), 757-765.
- Wegge, P., Pokheral, C. P., & Jnawali, S. R (2004) Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Animal Conservation*, 7(3), 251-256.

Williams, B.K., Nichols, J.D.&Conroy, M.J (2002) *Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making*.Academic Press, San Diego, California, USA.

