THE APPLICATION OF SPATIAL CAPTURE-RECAPTURE MODELS TO INVESTIGATE LEOPARD ECOLOGY AND CONSERVATION IN SOUTH AFRICA

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ABSTRACT

Population monitoring is essential to wildlife conservation and management. Rare and elusive species are difficult to observe, and hence monitor, in wild populations. Leopards (*Panthera pardus*) are an iconic and threatened species whose conservation is hampered by a lack of robust population data, in part due to their sparse populations and cryptic nature. I used camera-trap surveys from 28 protected areas in northeastern South Africa to make inferences about the status and conservation needs of leopards. I first evaluated the relationship between leopard density and proportion of area used within protected areas to determine if the latter could serve as a more efficient yet robust proxy for the former. I found that the relationship was too imprecise to be informative, that many populations of varying density used all the space available, and that the scale of individual movement strongly influenced the proportion of area used regardless of density. I then fit multisession spatial capture-recapture models to time series data from seven of these leopard populations to assess their threat level based on the estimated probability of population declines. I found some evidence of decline in six of the seven populations and found that the population at one site has a 75% chance of declining by 80% over three leopard generations. Lastly, I investigated the relative influence of bottom-up ecological factors and top-down anthropogenic factors as possible determinants of leopard density to identify what conditions are most suitable for conserving leopard populations. I found that while habitat and management characteristics of protected areas matter, human impacts around and within protected areas are the primary drivers of variation in leopard density. Based on these analyses, I conclude that South African protected areas are not conferring sufficient protection to leopard populations and that more must be done to mitigate human impacts inside protected areas. I also show that the leopard monitoring program would benefit from longer surveys with more sampling locations to increase the statistical power for detecting changes. This thesis demonstrates the capacity for large-scale monitoring programs to greatly expand our understanding of the conservation needs of a cryptic species.

DECLARATION

I, Matthew Schaffer Rogan, hereby declare that this thesis was carried out in accordance with the regulations of the University of Cape Town; that the work on which this thesis is based is my original work (except where expressly indicated otherwise); and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree at this or any other university. I grant the university free license to reproduce for research in whole or in part, for research purposes. I am presenting this thesis for examination toward the Degree of Doctor of Philosophy in Biological Sciences.

I hereby acknowledge that this work was conducted as part of a larger, ongoing collaboration between the Institute for Communities and Wildlife in Africa (iCWild) and Panthera. While I contributed to data collection, the majority was conducted by Panthera's Leopard Monitoring Program for Southern Africa. The project was conceived and supervised by Dr. Guy Balme, and implemented by Dr. G. Mann, Dr. R. Pitman, and G. Whittington-Jones, with assistance from others (see Acknowledgements below). Panthera was primarily responsible for collecting, managing, and processing the raw data as described in the thesis.

I further acknowledge that much of the content of chapters 3 & 4 have been published or are being prepared for publication in peer-reviewed journals (See Rogan et al. 2019, "The influence of movement on the occupancy-density relationship at small spatial scales," doi: 10.1002/ecs2.2807).

This thesis has been submitted to the Turnitin module and I confirm that my supervisors have seen my report and that any concerns raised therefrom have been resolved between myself and my supervisors.

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For my teachers…

CHAPTER 1

INTRODUCTION

1.1 The status and conservation of large carnivores

The decimation of wildlife and disruption of ecosystem function have become hallmarks of the Anthropocene and the sixth mass extinction (Pimm and Raven 2000, Ceballos et al. 2017). Though iconic and charismatic, large carnivores have fared especially poorly and have been extirpated from vast areas (Riggio et al. 2013, Brugière et al. 2015, Jacobson et al. 2016, Durant et al. 2017, Wolf and Ripple 2017). With range loss came population collapse. Large carnivores' high trophic levels, sparse populations, and relatively slow life history render them especially vulnerable to extinctions (Purvis et al. 2000, Cardillo et al. 2005). For example, tiger, giant panda, and wild dog populations have dwindled to a few thousand individuals and, in the case of the former, three subspecies have gone extinct (Weber and Rabinowitz 1996, Woodroffe and Sillero-Zubiri 2012, Goodrich et al. 2015, Swaisgood et al. 2016). Lions have lost 75% of their African range and are on pace to lose half their west, central, and east African populations; a single remnant population persists outside the continent despite lions once being widespread across Europe and Asia (Riggio et al. 2013, Bauer et al. 2015). Cheetahs have lost 90% of their range, and retain only 2% of their historical range in Asia (Durant et al. 2017). Outside Amazonia, every jaguar subpopulation is small and declining (De La Torre et al. 2018). Polar bears' future is uncertain as their habitat melts away (Regehr et al. 2016) while brown bears, wolves, and pumas were virtually exterminated in western Europe and the continental USA, though these populations have begun to recover or recolonize (Miller 1989, Clark et al. 1996a, Chapron et al. 2014, Mech 2017). These declines will continue unless wholesale changes are made to the way we manage land and wildlife (Di Minin et al. 2016b).

The decline of large carnivores has far-reaching consequences for human and ecological communities. Defaunation pulls at the foundations of our society: the food we eat, the air we breathe, the water we drink, and the places we live (Young et al. 2016). Apex predators in particular play pivotal roles in community dynamics. The loss of this guild, which includes all large carnivores, drives trophic cascades (Miller et al. 2001, Ripple et al. 2014), with adverse consequences for animals lower down the food chain (Crooks and Soulé 1999) and for ecosystems as a whole (Redford 1992, Soulé and Terborgh 1999, Galetti and Dirzo 2013). Population declines are consequential even where the risk of extinction or extirpation is minimal; the loss of abundance can still negatively impact ecosystems (Baker et al. 2019). More diverse wildlife communities generate greater financial benefits for local economies (Naidoo et al. 2011). Sustaining large carnivores therefore can be beneficial for people, especially because these iconic species drive demand for photographic tourism (Di Minin et al. 2013a), which in turn creates jobs and spurs developing economies (Makochekanwa 2010, Snyman and Spenceley 2012). Large carnivores also help contain disease vectors, thus improving human health (Young et al. 2014, Braczkowski et al. 2018). They are vital to conservation (Sergio et al. 2008), and may act as ambassador or umbrella species that extend conservation to less charismatic ones (Caro 2003, Caro and Riggio 2013, Thornton et al. 2016). The presence of large carnivores indicates limited human impacts, at least a modest degree of biodiversity preservation, and general ecosystem function (Noss et al. 1996, Morrison et al. 2007). In summary, carnivores are critical indicators of broad-scale conservation programs and socio-ecological systems (Soulé and Terborgh 1999, Cardillo et al. 2004, Macdonald et al. 2010).

Underpinning the plight of large carnivores is a deep-rooted societal ambivalence towards wild animals (Bruskotter and Wilson 2014). Large carnivores in particular spark controversy (Clark et al. 1996b, Edge et al. 2011, Figari and Skogen 2011, Chapron et al. 2014, Dickman et al. 2014). On the one hand, society, through policies implemented at both the multinational (e.g., IUCN, UNESCO) and national levels, unquestionably identifies some degree of responsibility to preserve biodiversity and iconic species as a public trust (Bruskotter et al. 2011, Treves et al. 2017). Moreover, social attitudes often celebrate iconic species, whether via money spent to view wildlife or social media campaigns against hunting them (Wilson 1997, Macdonald et al. 2016). Attitudes towards carnivores are generally improving in developed western countries (Chapron et al. 2014, Gompper et al. 2015).

On the other hand, management of large carnivores has historically revolved around eradication and persecution (Mech 1996, Riley et al. 2004, Treves 2009, Treves et al. 2017). People fear large carnivores (Bruskotter and Wilson 2014) even where the risk from large carnivores is extremely low (Bruskotter and Wilson 2014), in part because people tend to paint species with one broad, tarnishing brush (Dickman et al. 2014). These animals kill humans and harm livestock farmers' livelihoods through depredation (Clark et al. 1996b, Sillero-Subiri and Laurenson 2001). Poor and disadvantaged communities may also associate iconic species such as large carnivores with inequality and exclusive land policies (Clark et al. 1996b, Muth and Bowe Jr. 1998, Peterson et al. 2017). Persecution of large carnivores and other animals often stems from broader conflicts among human communities (Dickman 2010). These attitudes result in widespread legal and illegal killing of large carnivores (St. John et al. 2012). Reconciling such conflicting perspectives remains a challenge.

Beyond conflict with humans, habitat loss and prey depletion threaten nearly all large carnivores (Ripple et al. 2014, Wolf and Ripple 2017). Human density remains one of the best indicators of large carnivore prevalence (Woodroffe 2000, Riggio et al. 2013), especially for high-trophic species that occur sparsely (Cardillo et al. 2004). Land sparing is thus of particular concern for managing large carnivores. Currently, however, only small, fragmented areas of these species' historical ranges are protected (Crooks *et al*. 2011).

Furthermore, even where populations occur within protected areas, they are exposed to detrimental edge effects such as conflict with humans, which can ultimately result in extinctions within protected areas (Woodroffe and Ginsberg 1998). Populations within small protected areas surrounded by humans are least protected (Parks and Harcourt 2002) but are common throughout sub-Saharan Africa (Harcourt et al. 2001) and are the focus of this thesis. Resourcing protected area management is as important as gazettement (Lindsey et al. 2018, Coad et al. 2019). Too often, reserves act as mere "paper parks", nominally protected areas that confer little additional protection for biodiversity (Bruner et al. 2001, Joppa et al. 2008, Craigie et al. 2010).

Large carnivores inside and outside of protected areas are subject to trophy hunting (Packer et al. 2009), targeted and incidental snaring (Becker et al. 2013), and retaliatory or preemptive killings because of livestock predation (Pitman et al. 2015, van Eeden et al. 2018a) or attacks on humans (Packer et al. 2005, Athreya et al. 2011). Many species are also traded illegally for fur or traditional medicine, which drives targeted poaching (Loveridge et al. 2010, Dickman et al. 2015, Williams et al. 2017b, Nijman et al. 2019, Coals et al. 2020, Naude et al. 2020b). In some cases, humans outcompete large carnivores for limited prey (Henschel et al. 2011, Rogan et al. 2017). Consequently, many existing protected areas do not necessarily protect large carnivores with populations having been extirpated from dozens of reserves in west Africa

(Brugière et al. 2015). Lions, Africa's most iconic apex predator are generally declining throughout protected areas except for the most intensively managed that have fences and the financial resources to minimize edge effects (Packer et al. 2013, Bauer et al. 2015).

Conservation interventions beyond the creation of reserves are thus imperative for the effective conservation of large carnivores. Globally, conservationists aim to reduce poaching and illegal trade in large carnivores (Trouwborst 2015, Carter et al. 2017), mitigate livestock predation and retaliatory killings (Treves and Karanth 2003, Lennox et al. 2018, van Eeden et al. 2018b, 2018a), make trophy hunting more sustainable (Balme et al. 2010a, Loveridge et al. 2016, Miller et al. 2016), facilitate coexistence between humans and large carnivores (Carter and Linnell 2016), and boost the effectiveness of protected areas (Wikramanayake et al. 2011, Lindsey et al. 2017, 2018). Determining the success of such interventions, however, depends on effective monitoring of populations (Weber and Rabinowitz 1996, Yoccoz et al. 2001). Whether prioritizing populations for conservation (e.g., Bottrill et al. 2008), measuring the effect of an intervention within an experimental framework (e.g., Adams and Sandbrook 2013), or engaging in adaptive management (e.g., Westgate et al. 2013), information on population status and health is essential to management and conservation.

Although we know that the animal kingdom is contracting, we lack robust data to quantify the rate and severity of decline for most vertebrate species (Dirzo et al. 2014). Our knowledge of large carnivore populations varies substantially by species. Some, such as lions, are carefully monitored and populations are regularly inventoried (Bauer and Van Der Merwe 2004, Riggio et al. 2013, Bauer et al. 2015, 2016). In North America, population estimates and management policies for carnivores have even been scrutinized in courts and legislatures (Bruskotter et al. 2011, Artelle et al. 2014, Treves et al. 2017, Darimont et al. 2018). Tigers, snow leopards, and cheetahs have all been the subject of censuses for all or large portions of their ranges (Goodrich et al. 2015, McCarthy et al. 2016, Durant et al. 2017, Weise et al. 2017, Jhala et al. 2019). In the case of leopards, however, most research has focused on ecological studies in protected areas, despite most of their range being unprotected (Balme et al. 2014). Only recently has the full extent of their range loss been documented (Jacobson et al. 2016). Furthermore, not all wildlife population estimates are reliable (Allen et al. 2017). Often, they become politicized and more representative of stakeholder interests than rigorous sampling (Darimont et al. 2018). These interests, both against and in support of conserving large carnivores, often drive policy debates far more than scientific consensus (Treves and Karanth 2003). Unreliable methodologies for collecting and analyzing survey data exacerbate this issue; they fuel controversy within the scientific community, provide ammunition to interest groups, and undermine effective management (Hayward et al. 2015).

Underpinning these issues is the plain fact that counting carnivores is difficult. They are rare. They move over large areas and are generally secretive and shy around humans. Sampling regimes must therefore be both extensive to cover the large areas in which they move and intensive to compensate for the difficulty in detecting their presence. Fortunately, new technologies and analytical advances are providing unprecedented insights into large-carnivore populations.

1.2 Advances in monitoring large carnivores

Monitoring populations and ecosystems is a cornerstone of conservation, in part because when done effectively, it can achieve several aims. Legg and Nagy (2006) describe three overarching goals for monitoring programs: indicating when systems depart from a desired state, measuring success of interventions, and detecting volatility in systems. Stem et al. (2005) report four primary motivations for monitoring: basic research, accounting and certification, status assessment, and effectiveness measurement. Mascia et al. (2014) identify five key approaches to monitoring: ambient monitoring, management assessment, performance measurement, impact evaluation, and systematic review. Effective, continual monitoring is thus essential to adaptive management, a structured process for making and updating decisions under uncertainty (Lyons et al. 2008). At the heart of these conceptual frameworks is the need to surveil for problems and facilitate successful interventions. The more sensitive monitoring programs are for measuring these key concepts, the more successful they will be. In addition, monitoring should always be integrated into conservation and management (Nichols and Williams 2006). In the case of large carnivores, this means ensuring that monitoring programs yield sufficient information to better secure these species' futures.

The search for better monitoring tools remains an ongoing process in carnivore ecology. Abundance has conventionally been the central metric for assessing wildlife population status (Nichols and MacKenzie 2004). Early methods for counting animals included direct observation, recording indirect signs, and the use of radioactive dyes to mark individuals (Sanderson 1966). Tracking spoor is one of the oldest methods (Murie 1936) that remains common (Balme et al. 2009a, Sanei et al. 2011, Bauer et al. 2014, Midlane et al. 2014). The invention of telemetry collars (Craighead Jr. et al. 1963) and many subsequent advances to remote tracking devices (Tucker et al. 2018) continue to transform our capacity to monitor individuals' movement. Telemetry, however, has its shortcomings. It is expensive and difficult to scale, impossible to know how representative the sample is, and most importantly, it is invasive and poses significant risk to animals' welfare through catching, anesthetizing, and wearing the devices (Zemanova 2020).

The application of non-invasive motion-triggered cameras to census carnivore populations (Karanth 1995) arguably did more to transform population monitoring than telemetry because it provided a more representative sample of populations and communities using non-invasive methods. DNA extracted from hair or scat has offered an alternative means of sampling species or individuals within a population (Gardner et al. 2009, Riley et al. 2017). Though each method has its advantages, a consensus has emerged that remote cameras are among the most effective and versatile methods (Silveira et al. 2003, Srbek-Araujo and Chiarello 2005, Riley et al. 2017, Davis et al. 2020), particularly for species that are individually recognizable from pelage patterns. They have proven especially effective for sampling multiple species and yielding high rates of detection (Wearn and Glover-Kapfer 2019).

Perhaps more important than innovations in field methods have been developments in analytical techniques and computational capacity. All methods for estimating abundance depend on a relationship between the number of observed individuals and the probability of observing them (Nichols et al. 2000). Capture-recapture (also known as mark-recapture) models for estimating abundance from repeat observations of individuals within a population date back decades (Hammersley 1953, Darroch 1958, Otis et al. 1978, Burnham and Overton 1979). These models were later adapted to estimate vital rates of open populations – populations in which individuals exit via death or immigration and enter via birth and immigration – such as apparent survival and recruitment (Williams et al. 2002). One challenge these models faced, however, was heterogeneous capture probability among individuals (Seber 1986). Otis et al. (1978) developed a widely used capture-recapture model formulation that treated individual heterogeneity in detection as a random effect (model M_h in classical CR parlance). Following Karanth's (1995) seminal study of tigers, capture-recapture analyses of remote-camera survey data for large carnivores with distinct markings became increasingly prominent, with an emphasis on models that accounted for individual heterogeneity (Karanth and Nichols 1998, Silver et al. 2004, Jackson et al. 2006, Karanth et al. 2006, Balme et al. 2009a, Stein et al. 2011). Individual heterogeneity, however, remained a major source of bias in classical CR models (Harmsen et al. 2011).

Chapter 1: Introduction

In the early 2000s, rapid advances in computing power and software development allowed the efficient processing of more complex hierarchical models – models with two or more functions related conditionally. As a result, statistical models of population-level phenomena erupted. In 2002, Mackenzie and his colleagues introduced occupancy models, which were an extension of closed-population capture-recapture models (MacKenzie et al. 2002). Rather than estimate the abundance of the population when detection is imperfect, however, they modeled the probability of a species occurring at each sampling location when detection is imperfect. Occupancy models were quickly extended to include estimating local colonization and extinction over multiple sampling periods (MacKenzie et al. 2003), local abundance of unmarked species (Royle and Nichols 2003), resource selection (MacKenzie 2006), species interactions (Rota et al. 2016), and community assemblages (Dorazio and Royle 2005). Occupancy models have become an important analytical tool for monitoring large carnivores with applications to tigers (Karanth et al. 2011), wolves (Miller et al. 2013), jaguars (Zeller et al. 2011), leopards (Thorn et al. 2011, Pitman et al. 2017a, Miller et al. 2018), and even the large carnivore guild at a global scale (Rich et al. 2017).

Density estimation, however, has always had advantages over occurrence estimation because it measures not only where populations occur but at what intensity. As such, it is at the core of population ecology (Buckland et al. 1993, Efford 2004). It is, however, considerably more difficult to measure due to the need to estimate both the number of individuals and the area within which they occur (Thompson 2004, Keiter et al. 2017). Classical capture-recapture models could be used to estimate abundance, but transforming abundance to density required ad hoc surrogates for approximating the effective sampling area (ESA), whereby sampling locations were buffered according to the maximum observed distance between detection locations of individuals (Wilson and Anderson 1985, Karanth and Nichols 1998). This mean-maximum-distance-moved (or sometimes half-mean-maximum-distance-moved) parameter became standard practice for the next decade (Balme et al. 2009a, but see Efford 2004 for a summary of alternative ad hoc approaches).

The ad-hoc approximation of the ESA was always flawed. Specifically, it was prone to underestimating the scale of movement, thus underestimating the ESA and overestimating density (Obbard et al. 2010, Sollmann et al. 2011, Noss et al. 2012, Ivan et al. 2013). To address this problem, Efford (2004) developed a means of estimating the ESA directly, while simultaneously introducing a more sophisticated approach to modeling individual heterogeneity in the capture process. By borrowing a fundamental assumption of distance sampling – the detection probability of an animal is a function of the distance between it and the observer – Efford suggested that individual heterogeneity in capture probabilities could be modeled as a function of the distance between detector locations and an animal's activity center. Not only would these spatially-explicit capture-recapture (SCR) models account for the reduced probability of capturing animals the farther they are from detectors, but this distance function could also estimate the area around detectors within which individuals were likely to be detected – the ESA. Even where classical CR models provide reliable estimates, SCR models were found to be more accurate (Ivan et al. 2013) and precise (Blanc et al. 2013). SCR models also allow for greater flexibility in modeling variation in density in response to spatial covariates (Ivan et al. 2013). With further developments of maximum likelihood estimators (Borchers and Efford 2008) and Bayesian analysis using Markov-chain Monte Carlo algorithms with data augmentation (Royle and Young 2008), in addition to the development of supporting open-source software (e.g., R packages "secr", Efford 2010; "SPACECAP", Gopalaswamy et al. 2012; and "oSCR", Sutherland et al. 2019), SCR models became widely applicable, available, and used (Green et al. 2021).

Though occupancy and SCR remain especially prominent analytical tools for monitoring large carnivores, numerous other approaches have emerged in the last decade. In cases where individuals are not identifiable, models including N-mixture models (Royle 2004), spatial count models (Chandler and Royle 2013), random encounter models (Rowcliffe et al. 2008, Nakashima et al. 2018), time-to-event models (Moeller et al. 2018), and count-per-frame models (Campos-Candela et al. 2018) are more applicable. In other cases, researchers aim to address more expansive questions, such as spatially-explicit population viability (Campbell et al. 2018) or the newly emergent family of integrated population models (Plard et al. 2019). Together with novel sampling techniques such as remote camera trapping, these spatial models are revolutionizing our ability to reliably monitor wildlife populations including large carnivores.

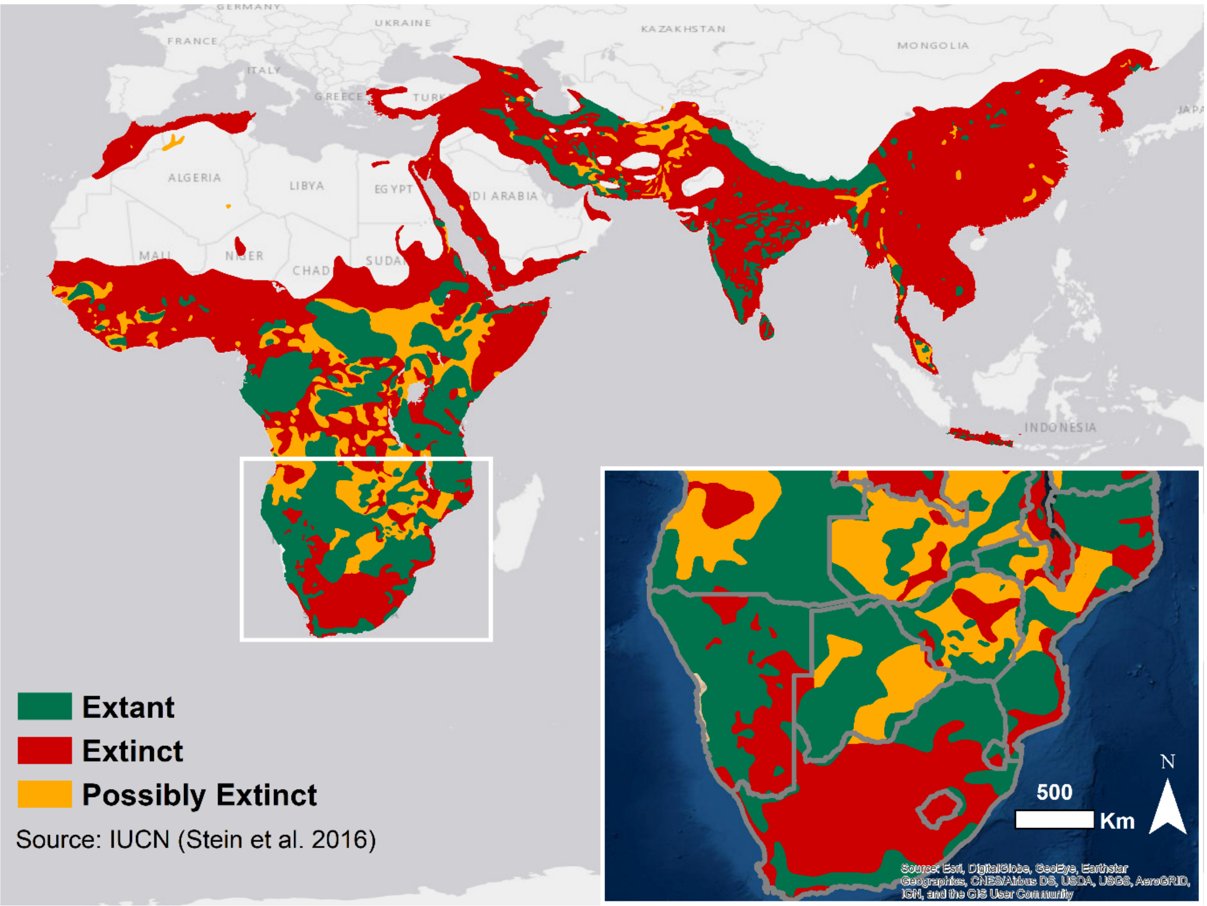
1.3 Leopard ecology and conservation

Leopards (*Panthera pardus*) face all the challenges of living in the Anthropocene common to the large carnivore guild. They are quintessential generalists, living in deserts and tropical forests (Wang and Macdonald 2009) across a large range that spans three continents and extends from sea level to the tops of mountains (Stein et al., 2016; Fig. 1). They are also notorious for their catholic diet, consuming everything from insects, reptiles, and birds to juvenile megafauna. In most areas, however, leopards predominantly consume small to medium sized antelope such as impala (Hayward et al. 2006). Of particular interest to conservationists, leopards persist even in some human-dominated landscapes (Athreya et al. 2013, Odden et al. 2014, Carter et al. 2015, Lamichhane et al. 2019). This adaptability makes them good bellwethers for management and conservation; they persist under such diverse conditions that their status can be compared across land uses and management regimes (see Chapter 5 for further discussion of leopard ecology and distribution).

Their adaptability, however, has not spared them from the ravages of the Anthropocene. Leopard range has contracted at least 60% globally and by more than 90% for four Asian subspecies; in sub-Saharan Africa, range contraction has been less pronounced but still severe: at least half and likely 60% lost (Jacobson et al. 2016). Despite some tolerance for humans, leopard range contraction has been severest in the most heavily populated regions. Often, they require a protected refuge such as mountains to persist around human settlements (Farhadinia et al. 2018, Mann et al. 2020). Leopards have even been extirpated from within protected areas (Rasphone et al. 2019, Gaynor et al. 2021).

Leopards are also subject to the full range of threats that large carnivores face. Farmers persecute them to preempt or retaliate for livestock killings, which is exacerbated by the loss of natural prey (Kissui 2008, Abade et al. 2014a, Khorozyan et al. 2015, Swanepoel et al. 2015a, Koziarski et al. 2016, Harmsen et al. 2017). Leopards are among the top trophy species in sub-Saharan Africa (Di Minin et al. 2016a). Mismanagement of leopard trophy hunting can suppress populations through unsustainable off-take (Balme et al. 2009b). Leopards are also harvested illegally for their fur and other body parts (Loveridge et al. 2010, Dickman et al. 2015, Mondol et al. 2015) for religious (Kumalo and Mujinga 2017), medicinal (Williams et al. 2017b), aesthetic (Nijman et al. 2019), and cultural purposes (Harries 1993). People further kill leopards through vehicle collisions, problem animal control, and incidental snaring (Loveridge et al. 2010, Pitman et al. 2015). Leopards are also at risk from diseases such as rabies and canine distemper spread via domestic dogs (Butler et al. 2004). Our understanding of the spatial distribution of these threats is especially poor because many of these activities are cryptic. We can assess habitat characteristics based on patterns in vegetation and biophysical characteristics, but prediction surfaces for anthropogenic threats are rare and only applicable locally. As a result, evaluation of habitat quality typically ignores anthropogenic threats.

Despite the severity of threats and ongoing range contraction, research on leopards is scarce relative to many large carnivores, and especially relative to other *Panthera* species. Research within South Africa accounts for a disproportionate number of leopard studies, with most of these investigating behavior (e.g., diet studies) in areas of high leopard suitability rather than topics of immediate conservation concern (Balme et al. 2014). Perhaps because of their broad historic range and versatility, leopards have garnered relatively little conservation attention for an apex predator. Yet recent evidence indicates a combination of range collapse and population declines.



Source: IUCN (Stein et al. 2016)

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

***Figure 1.1**: Current and historic global extent of leopard (Panthera pardus) range.*

In Asia, many leopard subspecies are on the brink of extinction (Jacobson et al. 2016). African leopards are not yet as imperiled. Some populations have declined sharply however, particularly outside of protected areas (Swanepoel et al. 2015c). Within protected areas, declines have been attributed to excessive trophy hunting in both South Africa (Balme et al. 2009a) and Tanzania (Packer et al. 2011) and to illegal human killings in the Soutpansberg Mountains of South Africa (Swanepoel et al. 2015a, Williams et al. 2017a). In the Limpopo province of South Africa, a combination of trophy hunting and problem animal control has led to unsustainable rates of offtake (Pitman et al. 2015). Arguably more striking than the multiple indicators of decline is the paucity of population monitoring data throughout their range.

1.4 Estimates of leopard densities and space use

Despite a general lack of population estimates for leopards across their range, efforts have been made to estimate densities within some areas. Martin and de Meulenaer (1988) presented 23 density estimates from sub-Saharan Africa of 1.2 – 40 leopards per 100 km^2 with a strong linear relationship to annual rainfall, though the robustness of these estimates is debatable. Subsequently, Chase Grey et al. (2013) reported density estimates of 0.6 – 30.3 leopards per 100 km^2 in Africa, though only Kruger National Park’s riverine areas exceeded a density of 13; density in that park’s more extensive savanna habitat was only 3.5 (Bailey 1986). More recent studies from the greater Kruger ecosystem found densities of approximately 12 leopards per 100 km^2 in the national park (Maputla et al. 2013) and an adjacent private reserve (Balme et al. 2019). These estimates are comparable to density estimates from Laikipia, Kenya (O’Brien and Kinnaird 2011). Allen et al. (2020) reported 33 “rigorous density estimates” from sub-Saharan African that ranged from the aforementioned high in Kruger to as low as 0.25 leopards per 100 km^2 in Kalahari rangelands (Boast and Houser 2012). Noack et al. (2019) reported the highest published SCR estimate of leopard density: 14.5 leopards per 100 km^2 on a small, fenced Namibian reserve.

Central to estimates of leopard density is measuring space use to determine the area over which abundance is distributed. For tracked individuals, near-saturated information on space use is available (Wilmers et al. 2013, Hubel et al. 2018). Telemetry indicates that leopards exhibit a wide range of space use, from as little as 8 km^2 in India to >2000 km^2 in the Kalahari Desert (Table 1.1). However, telemetry typically monitors only a small portion of a population, with most studies having tracked fewer than 10 leopards. By far, the most comprehensive and intensive analysis of leopard home-range size was Fattebert et al.’s (2016) study of 67 individuals in the Phinda-uMkhuze Complex. They found that in a population recovering from overharvest, female home-range size shrank, and home-range fidelity decreased, but male home-range size remained large.

In contrast to telemetry studies, camera traps effectively sample entire populations, but provide few data on each individual’s movement. Nevertheless, recent applications of SCR models include a parameter that indicates the spatial rate of decay in detection probability (σ) around individuals’ activity centers. Studies have found estimates of σ ranging from as little as 1000 m for females in Limpopo Province, South Africa to nearly 9200 m for males and females in the same province (Table 1.2). One study reported an uninformative credibility interval for σ of 2643 – 158124 m (Noor et al. 2020), which may indicate a transient population without stable home ranges (in addition to a general lack of data from the study). Assuming the combined area of all detections is representative of home ranges (see Dey et al. 2021, Chapter 3 for more on the validity of this assumption), home range size can be estimated from SCR model parameters (Royle et al. 2013, but see Efford et al. 2016 for an example of how home-range size can be directly linked to density). Given credible estimates of σ consistent with the known biology of the species, SCR models suggest mean home-range sizes within populations of as little as 20 km^2 and as large as 920 km^2.

Table 1.1*: Published estimates of leopard home range size (in km^2), with the number of individuals in the sample in parentheses. (A)KDE = (autocorrelated) kernel density estimator, MCP = minimum convex polygon.*

Reference	**Male home range**	**Female home range**	**Region**	**Method**
Bothma et al. 1997	2182 ± 492 (3)	489 ± 293 (5)	Kalahari, South Africa	KDE
Devens et al. 2018	72 – 490 (12)	29 – 136 (9)	The Cape region, South Africa	KDE
Farhadinia et al. 2018	103.4 ± 51.8 (3)		Northeastern Iran	AKDE
Fattebert et al. 2016	74 ± 7.5 (25)	29.5 ± 1.6 (42)	KwaZulu-Natal, South Africa	KDE
Jenny 1996	86 (1)	22, 29 (2)	Cote d’Ivoire	MCP
Le Roux and Skinner 1989		23 (1)	Mpumalanga, South Africa	grid-cell occupancy
Mizutani and Jewell 1998	32.75 ± 7.35 (4)	13.98 ± 7.38 (5)	Laikipia District, Kenya	MCP
Norton and Henley 1987	51 ± 15.7 (3)		Cedarberg Mountains, South Africa	MCP
Odden and Wegge 2005	47.5 ± 0.7 (2)	17 (1)	Nepal	KDE
Odden et al 2014*	42 (1)	65 (1)	Maharashtra and Himachal Pradesh, India	KDE
Odden et al. 2014	8 (1)	13 ± 2.8 (2)	Maharashtra and Himachal Pradesh, India	KDE
Stein et al. 2011	108 (1)	53 ± 18 (2)	North-central Namibia	MCP
Weilenmann et al. 2010	645 ± 129 (2)	513 ± 215 (3)	Kalahari, Botswana	KDE
Weise et al. 2015	187 ± 76 (8)	78 ± 38 (9)	Namibia	KDE

*Translocated individuals

***Table 1.2**: Estimates of σ (in meters) from selected studies using spatial capture-recapture models to estimate leopard density. A range of values implies multiple surveys or models while equivalent estimates for males and females implies studies did not model variation between sexes.*

Reference	**Male σ**	**Female σ**	**Region**
Balme et al. 2019	1810	1660	Greater Kruger, South Africa
Borah et al. 2014	4210	4210	Assam, India
Braczkowski et al. 2016	4370	2540	KwaZulu-Natal Province, South Africa
Chase Grey et al. 2013	1690	1690	Soutpansberg Mountains, South Africa
Davis et al. *in press*	3447	3447	Kasungu Plateau, Malawi
Farhadinia et al. 2019	2000-3900	620-4340	Northeastern Iran (3 surveys)
Goldberg et al. 2015	2000	1200	Sarpang and Zhemgang Districts, Bhutan
Gray and Prum 2012	4700	4900	eastern Cambodia
Havmøller et al. 2019	1149-2440	1149-2440	Udzungwa Mtns., Tanzania (6 surveys)
Hedges 2015	2249-4016	2699-5950	Terengganu, Malaysia (2 models)
Kalle et al. 2011	2190	2190	Western Ghats, India
Kandel et al. 2020	4013	4013	Terai Arc, Nepal
Kumar et al. 2019	1660-2980	780-1640	Madhya Pradesh, India (16 surveys)
Lamichhane et al. 2019	7000	7000	Terai Arc, Nepal
Miller et al. 2018	2542-9156	2542-9156	KwaZulu-Natal and Limpopo Provinces, South Africa (19 surveys)
Ngoprasert et al. 2017	2604	2604	Greater Tenasserim Landscape, Thailand
Noack et al. 2019	2379	1585	Otjozondjupa Region, Namibia
Noor et al. 2020	55579	55579	Western Himalaya, India
O'Brien and Kinnaird 2011	1062	1062	Laikipia, Kenya
Ramesh et al. 2017	1942-4949	1942-4949	KwaZulu-Natal Province, South Africa (4 surveys)
Rich et al. 2019	3200	2400	Okavango Delta, Botswana
Rostro-García et al. 2018	3850	3850	Eastern Plains, Cambodia
Strampelli et al. 2018	1963	1963	Limpopo, Mozambique
Swanepoel et al. 2015b	1040-5620	1580-3550	Limpopo, South Africa (2 surveys)
Thapa and Kelly 2017	3080	3080	Terai Arc, Nepal
Thapa et al. 2014	2880	2880	Terai Arc, Nepal
Wang et al. 2017	5780-6970	3390-4650	Jilin and Heilongjiang Provinces, China
Webb et al. 2020	2100	1200	Central highlands, Sri Lanka
Yang et al. *in press*	2960-3020	1760-2000	Shaanxi Province, China (2 models)

1.5 Improving monitoring of leopards and other large carnivores

Conserving leopards and other large carnivores demands that we redouble efforts to gather robust data on population-level patterns so that the efficacy of PAs and management interventions can be assessed (Hayward et al. 2015). Carnivore ecology must move beyond small-scale short-term snapshots of populations or individuals and instead build the scientific infrastructure for longitudinal studies that track populations over longer periods and latitudinal studies that track them across larger, more complex, and more diverse landscapes. Achieving this goal requires greater cooperation among scientists and practitioners and advances in gathering, processing, and analyzing data.

1.6 Thesis outline

In this thesis, I present and analyze data from a long-term, extensive leopard monitoring program. I use recently developed modeling approaches to provide a more comprehensive understanding of leopard population status across protected areas in South Africa. The data presented here represent one of the largest aggregations of population-level survey data ever compiled for a large carnivore species, totaling nearly 10,000 observations of more than 1,300 individuals.

In **Chapter 2,** I provide background on the camera-trap survey methodology and a description of how data were collected for this thesis. I also describe the sites in northeastern South Africa where data were collected. I then explain the general analytical framework used for this thesis.

In **Chapter 3,** I present density estimates for leopard populations at 24 sites in South Africa, estimated using single-session SCR models. I examine the relationship between density and proportion-of-area-used to assess the efficacy of occupancy modeling as a proxy for density in highly fragmented landscapes. Furthermore, I use the relationship between occurrence and density to explore how leopard space use and movement influence the way individuals encounter detectors in camera-trap surveys. This work has also been published in a peer-reviewed article (Rogan et al. 2019).

In **Chapter 4,** I investigate whether leopard populations are declining within study sites. I use a probabilistic Bayesian framework to fit multi-session SCR models to data from sites that were surveyed for at least five consecutive years. I represent expected density using a log-linear trend over time and assess the conservation risk of leopard populations at each site.

In **Chapter 5,** I use multi-site, multi-session SCR models to delve deeper into differences in density among sites to identify the underlying factors that drive variation in leopard density in select South African protected areas. Specifically, I use an information theoretic approach to test multiple working hypotheses about how leopard density responds to bottom-up ecological variables and top-down anthropogenic factors. Based on the relative statistical support for each hypothesis and estimated effects of individual predictor variables, I draw conclusions on what conditions in and around protected areas promote dense populations.

Finally, in **Chapter 6**, I summarise my findings and offer general conclusions regarding the use of SCR models to assess large-carnivore populations in protected areas. I describe the contribution of the research presented in this thesis to our knowledge of leopard population status and its implications for conserving the species. Additionally, I offer some recommendations for how to improve leopard monitoring in South Africa and suggest avenues for future research.

CHAPTER 2

GENERAL METHODS

2.1 Study area description

The data presented here were collected in collaboration with Panthera's long-term Leopard Monitoring Program (LMP) for Southern Africa. The LMP was implemented to address a lack of data on leopard populations in South Africa and to propagate non-invasive monitoring tools that would reduce the harm of invasive field methods on leopards. The LMP began in 2013 with surveys in KwaZulu-Natal and Limpopo provinces. In 2015, the program was extended to include reserves in the Lubombo Transfrontier Conservation Area in Mozambique and the Kingdom of eSwatini. The following year, LMP extended its surveys into South Africa's Northwest, Gauteng, and Mpumalanga provinces.

Data for this thesis were collected within 28 protected areas or networks of small contiguous reserves within those five provinces of South Africa (Table 2.1, Fig. 2.1). Study sites were located between 23.0^{o} and 32.6^{o} longitude and 22.2 - 28.5^{o} southern latitude. LMP selected research sites in partnership with national, provincial, and local stakeholders to address data deficiencies and prioritize areas of greatest conservation concern. Leopard habitat is widespread but fragmented in South Africa (Swanepoel et al. 2013) and, apart from the Kruger National and Kgalagadi Transfrontier Parks, most protected areas are relatively small, seldom exceeding a few hundred square kilometers.

Habitat types among study sites were highly diverse. Sites were located predominantly within savanna and grassland biomes, with some eastern KZN sites occupy sub-tropical forest biomes (Olson et al. 2001). One site, Khamab Kalahari Game Reserve, was located in the dry shrublands biome. The majority of vegetation within the study areas were classified as various types of bushveld complemented with other mixed savanna habitat (SANBI 2012). Other common vegetation types included montane, riverine, or coastal forests; various types of thickets; and montane or wooded grasslands.

***Table 2.1**: Twenty-eight LMP study sites in protected areas of northeastern South Africa.*

Site	**Province**	**Survey years**	**Area (km^2)**	**Authority**	**Activities**
Atherstone Nature Reserve	Limpopo	2013-2018	230	State	Photo-tourism
Barberton Nature Reserve	Mpumalanga	2016	276	Private*	Mixed
Blyde River Canyon Nature Reserve	Mpumalanga	2016	257	State	Hiking
Dinokeng Game Reserve	Gauteng	2016	191	Private	Photo-tourism
Eastern Shores Section of iSimangaliso Wetlands Park	KZN[#]	2014-2018	264	State	Photo-tourism
Hluhluwe-iMfolozi Park	KZN	2013-2018	904	State	Photo-tourism
Ithala Game Reserve	KZN	2013-2018	292	State	Photo-tourism
Khamab Kalahari Game Reserve	North West	2016-2018	887	Private	Photo-tourism
KwaZulu-Natal Private Reserves (KZNPRs): KwaZulu Private Game Reserve, Amakhosi/Zeekoepan Game Reserve, Mkuze Falls Game Reserve, Mahlalela Game Ranch	KZN	2015, 2017[†]	377	Private	Trophy hunting
Lajuma Research Center and adjacent private properties	Limpopo	2014-2018	308	Private	Mixed
Lapalala Wilderness	Limpopo	2016-2018	436	Private	Photo-tourism
Loskop Dam Nature Reserve	Mpumalanga	2016	229	State	Photo-tourism
Madikwe Game Reserve[‡]	North West	2016-2018	614	State	Photo-tourism
Makalali Game Reserve	Limpopo	2016-2018	234	Private	Photo-tourism
Manyoni Private Game Reserve	KZN	2015, 2017	217	Private	Photo-tourism
Mapesu Private Game Reserve	Limpopo	2018	153	Private	Photo-tourism
Munyawana Private Game Reserve	KZN	2014, 2016-2018	232	Private	Photo-tourism
Ophathe Game Reserve	KZN	2014	297	State	Photo-tourism
Pilanesberg National Park	North West	2016-2018	490	State	Photo-tourism
Somkhanda Game Reserve	KZN	2013-2017	313	Private	Photo-tourism
Songimvelo Game Reserve	Mpumalanga	2016	318	State	Photo-tourism
Tembe Elephant Park	KZN	2015-2018	301	State	Photo-tourism
Timbavati Private Nature & Game Reserve	Limpopo, Mpumalanga	2013-2018	543	Private	Mixed
uMkhuze Game Reserve	KZN	2013-2018	355	State	Photo-tourism
Venetia Limpopo Nature Reserve	Limpopo	2014-2017	321	Private	Mixed
Welgevonden Game Reserve	Limpopo	2013-2018	339	Private	Photo-tourism
Wonderkop Nature Reserve	Limpopo	2013-2015	149	State	Photo-tourism
Zingela Nature Reserve	Limpopo	2016-2018	221	Private	Photo-tourism

*A provincial reserve that is predominantly leased to and managed by private entities.

[#] KwaZulu-Natal Province.

[†] 2017 survey included only KPGR and Amakhosi/Zeekoepan.

[‡] Sampled using a clustered array with four stations per cluster.

Average annual precipitation varied from 308 – 1060 mm (Hijmans et al. 2005) and elevation ranged from sea level to nearly 2000 m (USGS 2006). Provincial parks agencies managed 13 sites, private enterprises managed another 14, and a community owned one site with management support from a non-governmental organization. All sites provided varying levels of protection to wildlife (IUCN categories II – VI; Dudley 2008), with sporadic leopard trophy hunting permitted at five sites prior to a nation-wide moratorium implemented in 2016.

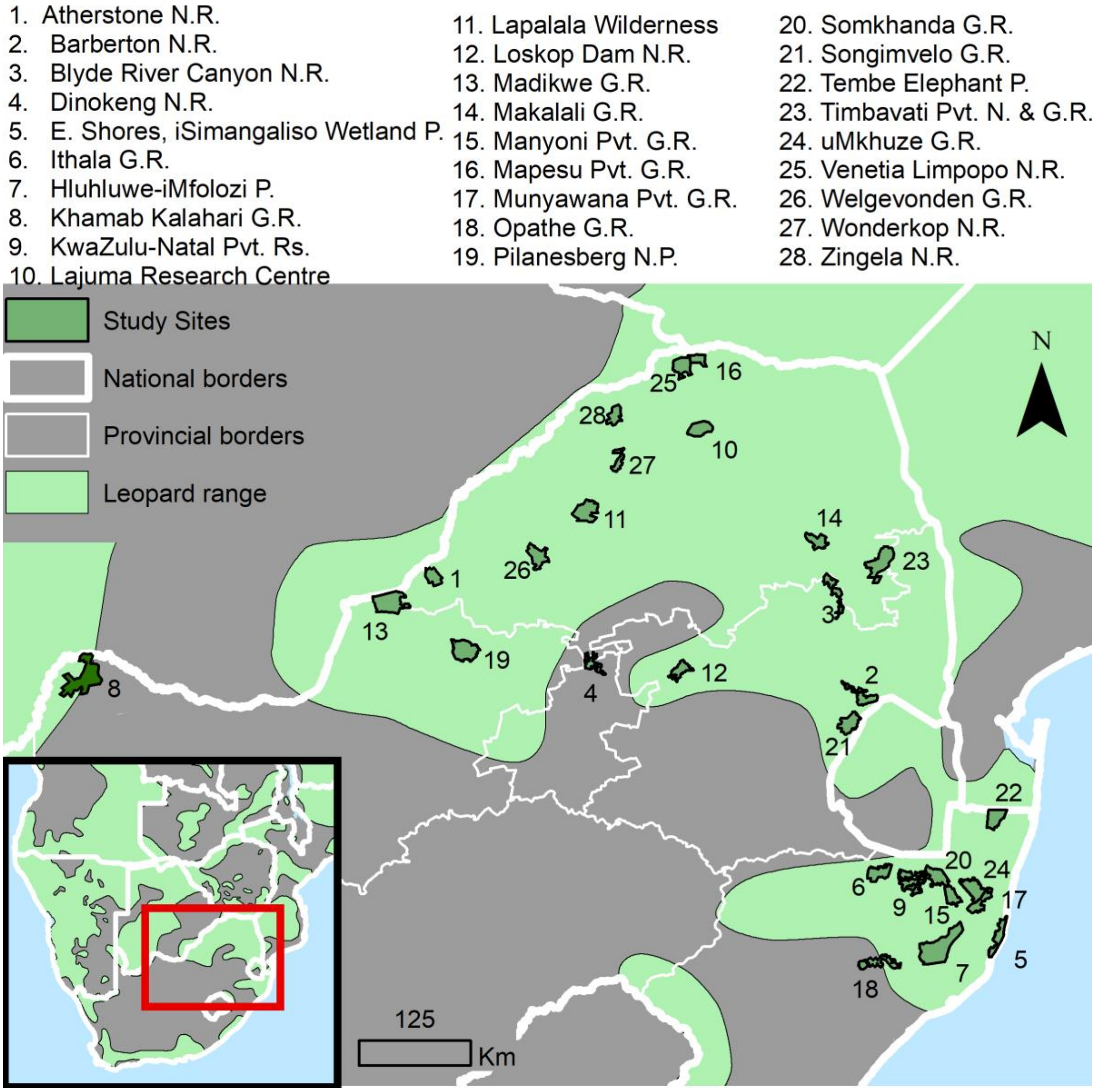


Figure 2.1: *Twenty-eight LMP study sites in protected areas of northeastern South Africa.*

2.1.1 Leopard management within the study area

Leopard management and conservation in and around the study sites, and indeed, throughout southern Africa, typically revolve around five prominent issues: 1) non-consumptive tourism (Di Minin et al. 2013a), 2) trophy hunting (Balme et al. 2010a, Braczkowski et al. 2015, Di Minin et al. 2016), 3) conflict with livestock farmers and game ranchers (Constant et al. 2015, Pitman et al. 2017b), 4) incidental snaring and loss of prey due to illegal bushmeat hunting (Fig. 2.1), and 5) the targeted harvest and trade of leopard furs (Dickman et al. 2015, Naude et al. 2020b). Leopard populations at all 28 study sites are actively or potentially affected by at least four of these five challenges. Historically, leopards were extirpated from most of South Africa, though they persisted around the country's periphery (Jacobson et al. 2016, Stein et al. 2016). However, habitat loss is not generally a major factor in South African leopard management currently, and indeed, wildlife-based land uses have proliferated on South African private land over the last half-century (Carruthers 2008, Cousins et al. 2008).

2.1.1.1 Non-consumptive tourism

Photographic safaris are a major industry in South Africa. As a charismatic apex predator, leopards have strong appeal for tourists and reserves that sustain leopard and other large carnivore populations have proven to be the most profitable (Clements et al. 2016). Some private reserves thus constitute an important refuge for leopards beyond state protected areas.

2.1.1.2 Trophy hunting

Until 15 years ago, trophy hunting of leopards was loosely regulated and was common in most state and private protected areas within South Africa. Leopards were listed as Least Concern from 1996 until 2008 (Stein et al. 2016), at which point South Africa was issued 150 CITES export permits for the year (Balme et al. 2010a). In the mid-2000s, provincial wildlife authorities in KZN established leopard hunting zones and other protocols to better manage the spatial distribution of trophy hunting and reduce locally intensive offtake. They also placed additional restrictions on destruction permits (see below), and limited the trophy hunting to fewer individuals, all of whom had to be adult male leopards. By 2015, all provinces followed similar trophy hunting protocols. Yet concerns persisted. In 2016 and 2017, South Africa's Department of Environmental Affairs, in consultation with the Scientific Authority, issued a zero-quota due to the scarcity of robust data for sustainably allocating permits. The department resumed issuing permits in 2018 with 7 permits allocated nationally for male leopards that were seven years or older and limited to leopard hunting zones for which survey data confirmed populations were not declining (Department of Environmental Affairs 2018).

2.1.1.3 Conflict

Conflict between farmers and large carnivores is apparent nearly everywhere they co-occur (Treves and Karanth 2003). South African leopards are no exception (Seoraj-Pillai and Pillay 2017). In South Africa, this conflict manifests in illegal killing of large carnivores and through destruction permits that grant livestock and game ranchers permission to kill animals that attack their stock. The value of ranched game poses particular issues for managing human-leopard conflict (Pitman et al. 2017b). In the past, destruction permits could also be used for lucrative trophy hunts, thus incentivizing land owners to request permits with little oversight (Balme et al. 2009b). While the trophy hunting industry has experienced major regulatory overhauls, little attention has been paid to conflict-induced killings.

Figure 2.2*: Camera-trap images of leopards with snares from Blyde RCNR, Eastern Shores, and Lajuma RC.*

2.1.1.4 Incidental snaring

Illegal bushmeat hunting is common throughout Africa, with snaring and dogs being among the most common and widespread hunting methods (Lindsey et al. 2013). Data on bushmeat hunting in South Africa are scarce but it unquestionably occurs widely (Hayward 2009, Lindsey et al. 2013, Nieman et al. 2019). LMP surveys recorded cases of snared animals, including leopards (Fig. 2.2), as well as men accompanied by packs of dogs (Panthera *unpublished data*). Besides the direct risk of leopards encountering snares or hunters, unchecked bushmeat hunting may also deprive South African carnivores of their prey base, though surveys of leopard populations are rare in protected areas with depleted wildlife (Balme et al. 2014).

2.2 Data collection

Surveys consisted of 29 – 62 camera stations. Each station comprised two cameras straddling roads, drainages, or game trails such that animals walking along these features were photographed on both flanks. Sampling such features with multiple cameras increases rates of detections for many large carnivores (Sollmann et al. 2011, Cusack et al. 2015, Pease et al. 2016, Kolowski and Forrester 2017, O'Connor et al. 2017). Stations were spaced an average of 1.1 – 3.2 km apart such that any theoretical leopard home range located within the sampling array would encompass multiple stations based on a minimum female home range size of 16 km^2 (Fattebert et al. 2015a). Each survey ran for 44 – 65 days to ensure the assumption of population closure was not unduly violated during each annual survey period (Dupont et al. 2019). Field teams recorded when cameras at each station were active or inactive due to disturbance or mechanical failure. A station was designated as active if at least one camera was working on each calendar day during the survey.

Photo classification and leopard identification were conducted by the LMP team. Data were subsequently provided for the purposes of this thesis as individual capture histories of leopards and records of photos for non-leopards classified by species and number of individuals. Photos were classified by species and number of individuals through a combination of research team members, citizen scientists (Pitman 2016), and a machine learning algorithm (Willi et al. 2018). LMP research team members confirmed records of priority species such as leopards and manually classified photos that machine learning algorithms could not classify with high confidence. A single observer from the LMP team manually identified individual leopards from unique pelage patterns with the aid of pattern recognition software (Crall et al. 2013). Such software offers high specificity in matching but is sensitive to the quality of images (Nipko et al. 2020). Male leopards were sexed from the presence of testes, larger head and body size, and the presence of a dewlap (Balme et al. 2012). Not all photographs were of sufficient quality to reliably detect these traits and some leopards could not be accurately sexed.

I conducted an exploratory validation of leopard IDs from Welgevonden for seven surveys conducted from 2013 to 2019. I found 10% of photos and 30% of IDs were misidentified mirroring estimates of single-observer error from (Johansson et al. 2020). These errors most likely resulted from the low sensitivity of pattern recognition algorithms and less rigorous data management protocols in the early years of the LMP. However, error rates were not random and almost all errors occurred in “splitting” of IDs between sessions, but not within sessions. Within-session error had no effect on model estimates because the difference was far less than the sampling variance. However, the between-session misidentification error precluded open-population models. As data from all sites were handled in a similar fashion and reflected independent estimates of single-observer error from Johansson et al. (2020), I concluded that the error rates in the Welgevonden data were likely representative of all surveys.

2.3 Spatial capture-recapture models for closed populations

Spatial capture-recapture (SCR) models (Royle et al. 2013b) are a form of hierarchical models with a “state process” representing the ecological state of the study population and a “detection process” that describes the probability of animals being observed and is conditionally related to the state process (Buckland et al. 2004). In the case of SCR, the state process is leopard density and it is represented as the intensity of a point process across a state space. The “points” in this state process are unobserved animal activity centers, which theoretically represent the mean location of animals during the survey duration but can also be interpreted to represent the centroid of a home range (Royle et al. 2013b, Efford et al. 2016). For the purposes of this thesis, the distribution of activity centers is assumed to be fixed during the sampling period and the population is assumed to be closed (i.e., no births, deaths, immigration, or emigration, but open-population extensions of SCR are available). The state space is a user-defined area that encompasses all possible activity center locations for which an individual would have a non-zero probability of being detected. As density is the number of individuals per unit area, it is directly estimated in SCR models as the estimated number of activity centers per unit area. Since the actual locations of these activity centers cannot be observed, we instead estimate the intensity with which they occur as a latent random effect (Borchers 2012).

The detection process in SCR is designed to account for individual variation in detection probability caused by the way individuals are distributed in space. In this respect, the detection process in SCR is much like the random effect on detection in the classical M_h model in non-spatial capture-recapture (Otis et al. 1978), but it uses the location of captures to provide structure to the latent variation. This structure resolves issues with non-identifiability in classical capture-recapture models (Royle et al. 2013b). Unlike in classical capture-recapture where recaptures occur in time, SCR is predicated on multiple recaptures in space such that detections can be recorded during a single sampling occasion or across multiple secondary sampling occasions. Using multiple occasions allows for modeling variation in detection over time, for example variation resulting from behavioral responses to trapping (Royle et al. 2011), and may be necessary for some detector types such as live traps.

To account for a degree of inherent randomness in observations, we assume that detections are the result of probability distributions. The distribution must be appropriate for the detector type. For example, in the case of live trapping, each individual can only be detected at a single location on a given occasion and multiple occasions are therefore necessary to record spatial recaptures. In the case of genetic identification of fur samples from hair snares, individuals can be detected at multiple detectors, but it cannot be determined how many times they visited those detectors. Remote cameras, on the other hand, are an especially flexible type of detector; individuals can be observed repeatedly at multiple detectors during a single session. As a result, observations in camera-trap surveys can reasonably be modelled using several probability distributions.

The means of those probability distributions (i.e., expected probability or number of captures) are determined by the detection model (sometimes referred to as the "encounter model") which describes the probability distribution of captures for each individual-detector dyad. The detection model has its origins in distance sampling and is founded on the same fundamental assumption, namely that the farther an organism is from a detector, the less likely it is to be observed (Buckland et al. 1993, Royle et al. 2013b). Thus, the detection model describes the spatial decay of the probability of detecting an individual as the distance between its activity center and a detector increases.

The most common formulation of the detection model for SCR applied to remote camera surveys is a Bernoulli distribution with probability determined using a half-normal decay function (Noss et al. 2012, Williams et al. 2017a), but the relationship can theoretically be described using any function that estimates the probability of detection as a function of distance. That said, studies uniformly use functions that assume detection probability decreases as distance increases; assuming detection is constant over distance has been shown to be unreliable (Efford 2004). All detection models include at least two parameters: a baseline detection probability (typically denoted g_0 or p_0) that represents the probability of observing an individual with its activity center located at the detector, and a spatial decay parameter (denoted σ in most detection models) that describes the rate of decline in detection probability in relation to distance of the activity center from the detector. These two parameters can be directly linked if the model assumes a compensatory relationship (i.e., the further an individual moves, the less likely it is to occur in any one place (Efford and Mowat 2014). Although the Bernoulli process is flexible because it allows for varying detection probabilities among secondary sampling occasions, it is computationally inefficient because it requires separate calculations for each occasion. An alternative approach therefore is to aggregate observations using either a binomial distribution with k trials equivalent to the number of occasions a station was active (e.g., Gardner et al. 2018), or a Poisson count distribution (e.g., Sollmann et al. 2011, Rich et al. 2019) with an alternative measure of independence than secondary occasions. In the latter case, baseline detection is represented as a rate (denoted λ_0) that determines the expected number of captures per temporal sampling unit and can be incorporated into a multi-occasion framework to model variation among occasions.

Model fitting can occur within a Bayesian framework using data augmentation and Markov-Chain Monte-Carlo simulations (Royle and Young 2008), or using maximum likelihood estimation (Borchers and Efford 2008). Models can incorporate covariates for both the state and the detection processes. Covariates for density are modelled using an inhomogeneous point process. Covariates for detection can influence the baseline detection probability or the spatial decay parameter, and can reflect variation in detector or station characteristics, traits intrinsic to individuals in the population (e.g., sex), or temporal variants. Models can also account for variation in detector usage, for example when detectors are inactive or sample for unequal durations.

2.3.1 Extensions of SCR models

The SCR models described above are founded on several important assumptions: 1) activity centers occur independently, 2) the detection model is radially symmetrical, 3) populations are closed during survey periods without entrants or emigrants, and 4) individuals are perfectly recognizable. SCR models can be extended to account for violations of all of these assumptions. Reich and Gardner (2014) developed a model that treats activity centers as dependently distributed in space to reflect territoriality among individuals. Other studies have considered non-Euclidean distance in the detection model to reflect resource selection (Royle et al. 2013a) or highly-structured landscapes (Sutherland et al. 2015). SCR models with non-Euclidean detection do not assume that detection probabilities are radially symmetrical. Open-population SCR models record individuals across multiple primary sampling sessions; they allow estimates of population vital rates and rates of change (e.g., Gardner et al. 2010, Ergon and Gardner 2014, Schaub and Royle 2014). SCR models have been broadened to account for partially-identifiable (Rich et al. 2014, Augustine et al. 2018, Jiménez et al. 2021), categorically identifiable (Augustine et al. 2019), or even unidentifiable individuals (Chandler and Royle 2013, Burgar et al. 2018). SCR models have also been generalized to incorporate additional sources of information such as telemetry data (Linden et al. 2018), and presence data (Chandler and Clark 2014, Sun et al. 2019), but can be modified to fit multiple observation processes in general (Tourani et al. 2020).

CHAPTER 3

THE RELATIONSHIP BETWEEN OCCUPANCY AND DENSITY OF LEOPARDS AT FINE SPATIAL SCALES

Abstract

Population density is one of the most vital metrics for monitoring populations and informing conservation. However, it is notoriously difficult to estimate for rare, cryptic, and far-ranging species. Proxies for density can be more efficiently derived but are typically sensitive to variation in target species' detectability or scale of movement. The relationship between proportion of area occupied and population density is widely observed but highly variable. Occupancy modeling, and associated Royle-Nichols abundance models, offer substantial promise as a proxy for density because of this underlying relationship and because they directly account for imperfect detection. I used data from 88 camera-trap surveys of leopard populations in northeastern South African protected areas to investigate whether the proportion of area used and Royle-Nichols abundance estimates were effective proxies for leopard density estimated via spatial capture-recapture models. Although I did find evidence of a positive association between proportion of area used and density (with less evidence of a relationship between Royle-Nichols abundance and density), the relationship was highly uncertain and did not extend to the 40% of surveys where leopard occupancy was saturated. I further show how differences in the scale of leopard movement distorts estimates of occupancy and abundance at fine sampling scales. Although occupancy and Royle-Nichols abundance are not suitable proxies for density when comparing leopard populations with varying scales of movement, they may still be informative when such sources of variation are absent or coarse sampling is used to preserve independence among sampling locations.

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3.1 Introduction

In Chapter 1, I described the importance of reliable estimates of density for informing conservation of wildlife populations, as well as how difficult these estimates are to obtain in the case of rare, cryptic species. In particular, most methods for estimating density have strict data requirements such as telemetry data from a representative sample of the population (Fuller and Snow 1988), observations of marked or distinguishable individuals (Otis et al. 1978), reliable estimates of the speed of movement (Rowcliffe et al. 2008), or precise measurements of the area surveyed by detectors (Campos-Candela et al. 2018, Nakashima et al. 2018). Gathering data to satisfy model assumptions or requirements and meet minimum sample sizes is also expensive. A consequence of these requirements is that sample sizes in most published studies are small. For example, spatial capture-recapture (SCR) models typically estimate the spatial decay of detection from only a handful of spatial recaptures per individual (Efford and Boulanger 2019) while telemetry studies of large carnivores are often limited to fewer than 10 individuals (see Table 1.1). While some of the newest methods hold considerable promise (e.g., space to event models and count-per-frame models), many of these methods have been shown to be unreliable under common field conditions (e.g., Gerber and Parmenter 2015, Bellier et al. 2016, Chauvenet et al. 2017, Barker et al. 2018).

Due to these constraints, ecologists have repeatedly turned to proxies of density rather than attempting to estimate density directly. One common type of proxy is relative abundance indices (RAIs), the simplest of which use naïve capture rates, often derived from remote camera surveys (Carbone et al. 2001, O'Brien et al. 2003, Parsons et al. 2017). The advantage of such approaches is their broad applicability to a variety of data collection techniques including low-cost methods such as the recording of field signs (Burgar et al. 2018) and their applicability when individuals are not recognizable. Capture rates, however, are unreliable estimators of density, due largely to differences in detectability, home range size, and movement patterns (Carbone et al. 2001, Tobler et al. 2008, Sollmann et al. 2013).

Occupancy, measured by the extent of occurrence or proportion of area occupied, is also widely used as an indicator of density and abundance (Wilson 2008). The relationship between occupancy and abundance is one of the most widely observed patterns in ecology, with a mean effect size of 0.655 (Blackburn et al. 2006). It is, however, rarely straightforward. Latham et al. (2014) found that the relationship between wolf occupancy and abundance was sensitive to wolf movement behavior and pack cohesiveness. More generally, Wilson (2008) found that sampling scales and sampling techniques commonly distort the occupancy-abundance relationship. Alternatively, area occupied may correlate with density at low or moderate densities but stagnate for dense populations (Nielsen et al. 2005) and changes in occurrence may temporally lag changes in density (Royle and Kéry 2007). In other words, while occupancy is generally correlated with abundance and density, the shape and robustness of the relationship depend strongly on local circumstances and sampling methodologies.

Occupancy models are an especially useful framework for investigating the relationship between occurrence and density because they directly account for the detectability issues that may confound naïve RAIs. As a result, such studies have proliferated over the past decade (e.g., Tempel and Gutiérrez 2013, Clare et al. 2015, Wilson and Schmidt 2015, Linden et al. 2017, Parsons et al. 2017, Schmidt et al. 2017, Steenweg et al. 2018). Occupancy models (Hoeting et al. 2000, MacKenzie et al. 2002) directly estimate species detection as conditional on occurrence. Occupancy modeling and SCR are similar in the way they improve on classical models by accounting for variation in detectability, however occupancy does not necessitate individual identification, spatial recaptures, or a formal estimation of the sampling area and is thus more widely applicable. Shortly after the inception of occupancy models, the proportion of area occupied (i.e., mean occupancy across sampling sites) was proposed as a cost-effective “surrogate” for density (MacKenzie and Nichols 2004). Royle and Nichols (2003) extended occupancy models to estimate localized abundance by estimating the probability of detecting an individual at a given sampling location rather than a single detection probability among all individuals present. Local abundance is thus estimated based on how many individuals would be present to maximize the likelihood of the observed number of detections. Both models are fit to detection/non-detection observations of unmarked individuals. They control for movement via an assumption that observations are independent among sampling locations (i.e., the same individual is not recorded at multiple sites). This assumption, however, is frequently violated and animals that move among sites are subject to double-counting which confounds the relationship between occupancy and density (Efford and Dawson 2012, Parsons et al. 2017, Neilson et al. 2018, Steenweg et al. 2018).

The reason this double counting is noteworthy is because density relates directly to abundance and inversely to the area of occupancy (Clare et al. 2015, Keiter et al. 2017). Variation in individual movement adds uncertainty and influences the process by which individuals encounter detectors (Webb and Merrill 2012, Parsons et al. 2017, Neilson et al. 2018). The farther individuals in a population range, the more extensive the population's distribution will be, with occupancy saturating when individual home ranges are larger than the scale of the sampling array (Efford and Dawson 2012). Animal movement can be a greater determinant of the detection process and detection rates than the underlying state process of abundance or occurrence (Stewart et al. 2018). This issue is especially acute for studies in which occupancy represents probability of use rather than occurrence (MacKenzie 2006), due to violating the assumption of independence between sampling units (Parsons et al. 2017). Furthermore, density and occupancy may respond differently to ecological processes and conditions, such that the relationship will not persist across large, diverse landscapes (Parsons et al. 2017).

The movement of individuals among sampling units is also a concern in when modeling local abundance of unmarked animals. Such models must resolve both where animals occur without being detected and the relationship between multiple detections and local abundance (Gilbert et al. 2020). When animals move freely among sampling units, the relationship between detections and population abundance becomes muddied.

Despite these challenges, some studies have found compelling evidence that occupancy is an accurate and precise index for carnivore density. Clare et al. (2015) found a strong linear relationship (R^2=0.95) between bobcat occupancy and density at nine study sites where density estimates ranged between 0.45 – 5.13 bobcats per 100 km^2. Linden et al. (2017) found a similarly strong relationship ($R^2 > 0.94$) for fishers in a continuous landscape. Critically, however, neither of these studies produced occupancy estimates above 0.73 and thus were not subject to a saturating relationship such as Nielsen et al. (2005) found for moose.

Here I examine whether estimates of the probability of use and mean abundance derived from single-season occupancy and Royle-Nichols abundance models are a reliable proxy for leopard density within the small protected areas where we surveyed leopards. I further consider the effects of saturated occupancy and of varying leopard movement among surveys on the underlying occupancy-density relationship to better understand how measuring probability of use (i.e., violating independence) affects the utility of occupancy estimates as a proxy for density. I conducted this analysis to provide insights on two related management questions: 1) could Panthera's long-term Leopard Monitoring Program (LMP) use surveys of leopard sign to estimate relative density outside protected areas where the risk of camera theft precludes remote camera surveys, and 2) could reserve managers with limited resources and training in statistical modeling reliably track leopard density on their reserves using relatively efficient occupancy surveys?

3.2 Methods

Throughout this chapter, I adhere to standard capture-recapture nomenclature such that "Station" defines a point location at which a pair of camera traps sampled leopard occurrence and identity (equivalent to "site" in conventional occupancy nomenclature), and "site" refers to a protected area, or a cluster of small contiguous protected areas, where one or more closed-population surveys occurred. "Survey" indicates a continuous primary sampling period of a closed population by a set of stations at a single site in a given year. Each survey is subdivided into a set of occasions, secondary temporal units over which sampling is replicated.

3.2.1 Density estimation

Data for this analysis consisted of 88 LMP surveys from 24 study sites (Table 3.1, Appendix 3.1). Some surveys/sites were excluded because they produced too few observations to fit SCR models. I fit SCR models for each survey with package "secr" v. 3.2.0 (Efford 2019) in R x64 versions 3.5.2 or later (R Core Team 2019) using maximum likelihood estimation of the full likelihood (Borchers and Efford 2008). I modeled density ("D") as a homogenous Poisson point process within the state space, which I defined using a 15-km buffer around each station (Chase Grey et al. 2013, Braczkowski et al. 2016). I discretized the state space using a 500 m × 500 m (0.25 km^2) grid that defined the possible locations of all activity centers (Braczkowski et al. 2016, Williams et al. 2017a), excluding cells that were classified as "water" or "urban" land uses (Plummer et al. 2017). Station locations were recorded in the WGS84 datum and projected into a custom equidistant conic projection with parallels at 20^{o} S and 27^{o} S.

The probability of detecting leopard i at station j on occasion k was modeled as a Bernoulli process conditional on a station being active during occasion k. Each occasion was defined as one calendar day. I adopted the commonly-used half-normal detection function (Efford 2004, Noss et al. 2012), which consists of a distance parameter, σ; and a baseline detection parameter, g_0, to describe the inverse relationship between detection probability and the distance from an individual's activity center to a station, respectively.

Table 3.1*: Study sites, including their size, management type, the province in which they are situated, and the years they were surveyed, used to investigate the occupancy-density relationship (see Appendix 3.1 for further details).*

Site	**Province**	**Survey years**	**Area (km^2)**	**Management authority**
Atherstone Nature Reserve	Limpopo	2013-2018	230	Provincial
Blyde River Canyon Nature Reserve	Mpumalanga	2016	257	Provincial
Eastern Shores Section of iSimangaliso Wetlands Park	KwaZulu-Natal	2014-2018	264	Provincial
Hluhlwe-iMfolozi Park	KwaZulu-Natal	2013-2018	904	Provincial
Ithala Game Reserve	KwaZulu-Natal	2013-2018	292	Provincial
KwaZulu Private Game Reserve, Amakhosi/Zeekoepan Game Reserve, Mkuze Falls Game Reserve, Mahlalela Game Ranch	KwaZulu-Natal	2015, 2017†	377	Private
Lajuma Research Center and adjacent private properties	Limpopo	2014-2018	308	Private
Lapalala Wilderness	Limpopo	2016-2018	436	Private
Loskop Dam Nature Reserve	Mpumalanga	2016	229	Provincial
Madikwe Game Reserve‡	North West	2016-2018	614	Provincial
Makalali Game Reserve	Limpopo	2016-2018	234	Private
Manyoni Private Game Reserve	KwaZulu-Natal	2015, 2017	217	Private
Mapesu Private Game Reserve	Limpopo	2018	153	Private
Molopo Game Reserve	North West	2016-2018	887	Provincial
Munyawana Private Game Reserve	KwaZulu-Natal	2014, 2016-2018	232	Private
Pilanesberg National Park	North West	2016-2018	490	Provincial
Somkhanda Game Reserve	KwaZulu-Natal	2013-2017	313	Community
Tembe Elephant Park	KwaZulu-Natal	2015-2018	301	Provincial
Timbavati Private Nature & Game Reserve	Limpopo, Mpumalanga	2013-2018	543	Private
uMkhuze Game Reserve	KwaZulu-Natal	2013-2018	355	Provincial
Venetia Limpopo Nature Reserve	Limpopo	2014-2017	321	Private
Welgevonden Game Reserve	Limpopo	2013-2018	339	Private
Wonderkop Nature Reserve	Limpopo	2013-2015	149	Provincial
Zingela Nature Reserve	Limpopo	2016-2018	221	Private

†2017 survey included only KPGR and Amakhosi/Zeekoepan
‡Sampled using a clustered array with four stations per cluster

I fit four SCR models per survey. In addition to a null model (no variation in g_0, σ, or D), I fit models with partially-observed sex classifications as a covariate for g_0, σ, or both, as variation in large felid movement and detection between sexes in camera-trap surveys has been clearly established (Sollmann et al. 2011, Swanepoel et al. 2015b, Miller et al. 2018). We compared models using AIC corrected for small sample sizes (“AICc”; Hurvich and Tsai 1989) due to the small ratio of observations to model parameters.

3.2.2 Occupancy and abundance estimation

The purpose of the occupancy and abundance models was to create the simplest possible index of occurrence/abundance, while accounting for imperfect detection without relying on individual identification. I therefore treated each station as a unique sampling unit such that the spatial resolution of sampling was equivalent to the distance between stations (Steenweg et al. 2018). As in the case of density, I did not include any station-level covariates for the state process as my goal was to derive a single estimate per site.

I fit single-season occupancy and RN abundance models (MacKenzie et al. 2002, Royle and Nichols 2003) for each survey with R package “unmarked” version 0.12-3 (Fiske and Chandler 2011) using a maximum likelihood framework. Both models consist of a detection process and a state process. In occupancy models, the detection parameter, p, and the state parameter, Ψ, are defined as Bernoulli random variables. Given that surveys were designed primarily to estimate leopard density, camera stations were spaced at a scale intended to produce multiple captures of individuals. The distribution of stations thus violated the assumption of independence among sampling locations, rendering Ψ an estimate of “probability of use” rather than occurrence (MacKenzie 2006). In RN abundance models, the state process, abundance, is modeled as a Poisson random variable, N, with a log link. The detection parameter, r, defines the detection probability of an individual at station j such that the probability of detecting any individual at station j is given by the formula $p_j = 1-(1-r_j)^{N_j}$ where N_j is the number of individuals occurring at station j and r_j is the detection probability of a single individual at station j.

The optimal number of sampling occasions to maximize accuracy and precision varies depending on detection probability and Ψ (MacKenzie and Royle 2005). As study populations exhibited a wide range of detection probabilities and Ψ, I let occasion length vary among 3, 5, 9, and 15 days and accounted for variation in detection based on effort, defined as the number of days per occasion a station was active. In cases with few detections, the models cannot reliably distinguish between species that are widespread but rarely captured, and species with limited occurrence but high detection probability. I therefore rejected models where $p < 0.15$ as recommended by O'Connell et al. (2006). I chose a cutoff of $r < 0.1$ for RN abundance models on the basis that a mean local abundance of 1.5 would represent a relatively sparse population (e.g., one male overlapping two female home ranges). No surveys exhibited signs of the inverse case: low PAU (i.e., $\Psi < 0.2$) and near-perfect detection. I then selected the best performing model for each survey using chi-square goodness of fit tests to estimate the probability of the observed capture histories given the expected distribution (MacKenzie and Bailey 2004). Expected distributions were generated via 400 parametrically bootstrapped simulations with the package "AICcmodavg" v 2.2-1 (Mazerolle 2019). To allow direct comparison of detection parameters derived from varying occasion lengths, I converted p and r to daily detection probability such that $p_{daily} = 1 - (1 - p)^{1/l}$ where l is the occasion length in days.

3.2.3 The occupancy-density relationship

As Ψ and N were constant across all stations, I treated the parameter estimates for each survey as an approximation of the proportion of area used (PAU) in the case of Ψ and the mean abundance among stations in the case of N. I plotted the relationship between D and the state variables, Ψ and N, to explore the utility of these parameters as indices of density. I further plotted the relationship between density and both p and r to explore the relationship between density and the detection process.

I investigated the effect of home-range size on the occupancy-density relationship by plotting density against occupancy and RN abundance after relativizing the latter two parameters by a survey-specific proxy for home-range size (HR) derived for SCR models with half-normal detection functions: $HR = \pi \times (2.447\sigma)^2$ (Royle et al. 2013b, Havmøller et al. 2019). For surveys with sex-specific σ (n = 57), I calculated home-range size based on mean σ for males and females weighted by the estimated proportion of the partially observed mixture. However, there can be a compensatory relationship between σ and g_0 (Efford and Mowat 2014), and I found that models with very low estimates of g_0 (i.e., $g_0 \leq 0.01$) sometimes compensated with ecologically-implausible, inflated estimates of σ. I therefore limited these comparisons by excluding surveys with sex-weighted mean σ values above 4000 m (~300 km^2 home ranges), well above sex-averaged σ from other SCR analyses of leopards in Limpopo and KwaZulu-Natal Provinces (Chase Grey et al. 2013, Swanepoel et al. 2015b, Braczkowski et al. 2016).

3.3 Results

3.3.1 Density

Surveys recorded 21 – 279 captures of 7 – 50 individuals, for a total of 9270 captures of 1367 individuals (or 2231 session-specific capture histories) across the 88 surveys. Spatial recaptures per survey ranged between 5 and 84 (median = 33.5). Surveys recorded between 0 and 15 leopards that could not be reliably sexed (median = 3), which accounted for up to 45% of the total number of individuals in a survey (median = 8%; see Appendix 3.1 for capture summaries). Survey effort was 1246 – 2722 (median: 1857) trap-days. SCR models including sex as a covariate for σ exhibited the lowest AICc score for 44 surveys, followed by a model without covariates for 20 surveys. A model with sex as a covariate for both g_0 and σ performed best for 13 surveys, while 11 models with sex as a covariate for only g_0 were selected. Median estimated density for the 88 surveys was 6.3 leopards per 100 km^2 (range: 0.24 – 15.0; Appendix 3.2). Density estimates were imprecise: standard errors were equivalent to 27% of the density estimate on average (range: 15 – 110%).

Among the 31 selected models with no variation in σ among the sexes, estimates of σ ranged from 1579 – 8057 m. Where models accounted for sex-based variation in σ, male σ was greater than female σ for 54 surveys and less in three surveys. Among these 57 models, female σ ranged from under 1000 m for three surveys to 3200 m, with one outlier of 6590 m for the 2017 Pilanesberg survey. Male σ among these 57 models varied from 1631 – 7872 m. Median sex-weighted home-range size was 85 km^2 but was above 300 km^2 for six surveys, which were subsequently excluded from the comparison of density with relativized PAU and RN abundance.

3.3.2 Occupancy

Occupancy mode with 15-day occasions provided the best fit for 41 surveys, followed by 9-day occasions for 32 surveys, and 5-day occasions for 15 surveys. Models exhibited adequate fit (i.e., MacKenzie-Bailey GOF p-value > 0.05) for 84 of the 88 surveys (see Appendix 3.3 for details). The interquartile range for GOF tests was 0.25 – 0.68. Estimated PAU ranged from 0.35 to 1 (median = 0.90). Thirty-five surveys exhibited saturated occupancy, with another three producing PAU estimates above 0.99. Daily detection probabilities ranged from 0.019 to 0.145 (median: 0.053).

3.3.3 Royle-Nichols abundance

Eighty-five surveys produced individual detection rates (*r*) above 0.1. RN models with 15-day occasions provided the best fit to the data for 37 surveys, followed by 35 for 9-day occasions, 12 for 5-day occasions, and one for 3-day occasions. RN models fit the data better than occupancy models; the minimum GOF p-value was 0.09, with an interquartile range of 0.41 – 0.75. Mean abundance estimates ranged from 0.5 – 5.1 individuals (median: 2.4). Precision of mean abundance was lower than for density but less varied; standard error was equivalent to 37% of the estimate on average (range: 19 – 93%). Individual detection probability ranged from 0.10 – 0.55. Daily detection probabilities for individuals were 0.009 – 0.068.

3.3.4 The relationship between density and abundance indices

I found clear evidence of a relationship between density and PAU; however, the association did not extend to cases where PAU was saturated (Fig. 3.1a). Detection probability, *p*, was more consistently, though weakly associated with density but it too exhibited evidence of a non-linear saturating effect (Fig. 3.2a). Sites with mean RN abundance below 1.5 individuals also exhibited low densities, but above 1.5 individuals, no relationship was apparent (Fig. 3.1c). Individual detection, *r*, exhibited no association with density (Fig. 3.2b). Relativizing PAU and RN abundance by home-range size had similar effects on their relationship to density. Both showed clear linear relationships, but they remained imprecise (Fig. 3.1b&d). Relativizing by home-range size corrected the saturating effect in the density-PAU relationship.

3.4 Discussion

I investigated whether proportion of area used by leopards within a protected area is a useful proxy for leopard density. Although I found evidence of a relationship, the relationship was weak and heavily influenced by variation in animal movement and detectability. Furthermore, the relationship did not extend to cases where PAU was saturated (40% of sites). As a result, PAU is not a reliable indicator of density when comparing variable populations, such as ones exhibiting differing home-range sizes, or when sampling techniques yield divergent detection probabilities. Despite this, these findings provide robust estimates of population density across an entire region (northeastern South Africa) for a threatened species for which relatively few estimates of density are available (Jacobson et al. 2016) and for which no total abundance estimates exist (Stein et al. 2016). These results will serve as an important baseline for ongoing long-term monitoring of the conservation status of leopards.

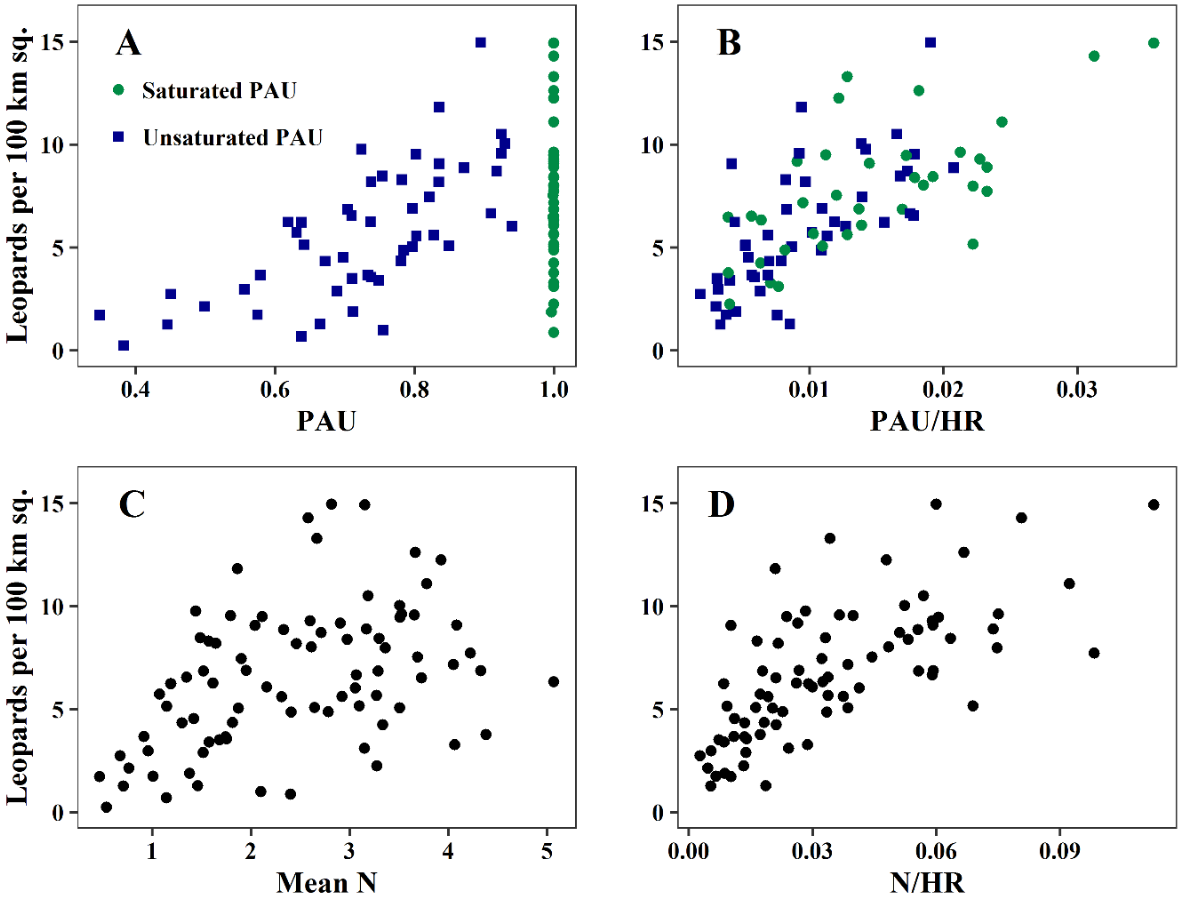

***Figure 3.1**: Leopard density in relation to A) proportion of area used (PAU, n = 88); B) PAU relativized by approximate home-range size (PAU/HR, n = 82); C) mean Royle-Nichols abundance (N, n = 85); and D) N relativized by HR (N/HR, n = 80) among camera-trap surveys of leopard populations at 24 sites in northeastern South Africa, with each site surveyed 1-6 times.*

PAU was weakly associated with density among leopard populations in South Africa. This finding contrasts with previous research on small carnivores that found strong relationships between occupancy probability and density (Clare et al. 2015, Linden et al. 2017). As other recent studies demonstrated (e.g., Efford and Dawson 2012, Parsons et al. 2017, Neilson et al. 2018), when home ranges encompass multiple stations, PAU and local abundance become disentangled from the underlying density of the population. PAU can saturate at varying densities and relativising the state process in occupancy models (e.g., Ψ or N) by the scale of movement (e.g., home-range size) accounts for the lack of a relationship between saturated occupancy and density. The leopard populations we surveyed exhibited marked variation in the scale of movement as denoted by the wide range of σ estimates among surveys. When sampling scale is fixed and finer than an individual's home range (as required for SCR), the farther that individual moves, the greater the number of sampling units it is likely to encounter.

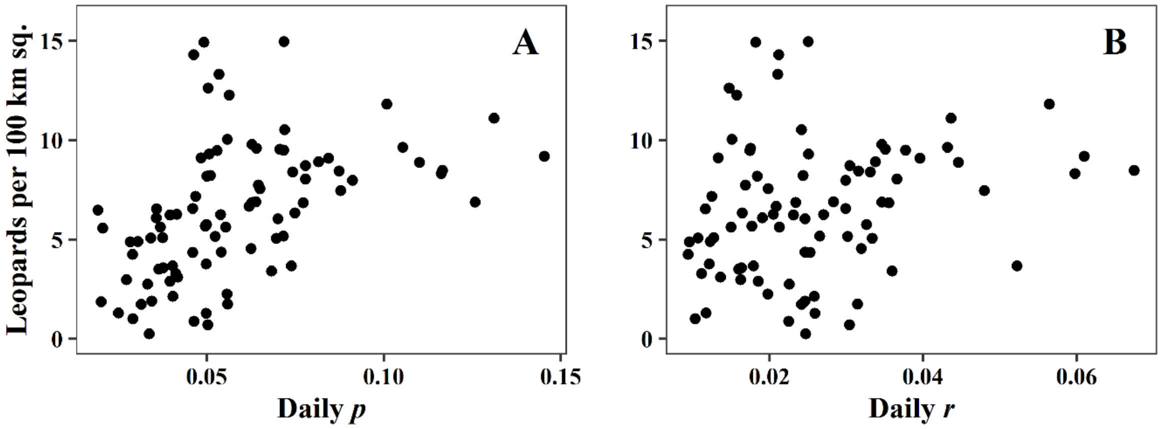

Figure 3.2: Leopard density among leopard populations at 24 sites surveyed 1-6 times in northeastern South Africa in relation to A) detection probability (p) from occupancy models and B) individual detection probability (r) from Royle-Nichols abundance models, scaled per day according to the formula: $p_{daily} = 1 - (1 - p)^{1/l}$ *where l is the occasion length in days.*

The PAU for each individual is thus dependent on its scale of movement (Efford and Dawson 2012). Hence, some populations with similar densities but dissimilar home-range sizes exhibited widely divergent PAUs. For example, the 2015 survey of Atherstone Game Reserve yielded a moderate estimate of AOU ($\Psi = 0.64$) and a moderate estimate of overall density (6.2 leopards per 100 km^2) but a small mean approximate home-range size (41 km^2). In comparison, the 2017 survey at uMkhuze Game Reserve was estimated to have a similar density (6.3 leopards per 100 km^2) but saturated occupancy and large mean home-ranges (156 km^2) The effect of movement is especially acute for RN abundance estimates; animals encountering multiple sampling units will be double counted, with each such incident further distorting the association of RN abundance to density.

Even after controlling for home-range size, however, the relationships between density and PAU/RN abundance were still weak and of limited utility for inferring density. Partly, this is a result of greater variability in leopard density with increasing Ψ or N, as is evident from Fig. 3.2. However, factors other than the scale of movement and the mean-variance relationship also distort the observed occupancy-density relationship. Typically, individuals were detected infrequently and thus sampling error of the density models was high. Imprecise density estimates and uncertainty blur any underlying density-use or density-abundance relationships. This pattern is especially evident in the variation in estimates of σ from year to year. Atherstone

GR (2015-2016), Khamab Kalahari GR (2016-2017), Madikwe GR (2017-2018), and Zingela NR (2016-2017), among other sites, exhibited increases in σ of several-fold from one year to the next. As doubling σ translates to quadrupling the implied home-range size, this degree of variation in space use is not biologically plausible and cannot be explained by behavioral responses to changes in leopard density. Most likely it is the result of excess sampling variance due to low detection probabilities (see Chapter 6 for further discussion). Fattebert et al. (2016) found female home-range size shrunk by less than a third and male home-range size remained constant after four years of recovery from overharvest. Similarly, Naude et al. (2020a) found no difference in home range sizes between a high-density population free from anthropogenic mortality and an overharvested one. It is far more likely that this variation is the product of high sampling variance resulting from low baseline detection (see Chapter 6). No study has formally validated the robustness of using σ to estimate home-range size but there is some evidence that it is sensitive to misspecification of the detection function (Dey et al. 2021). While σ is an informative parameter and may often be a useful proxy for home-range size, it is not always reliable and should be interpreted with caution.

The relationship between density and PAU/RN abundance is further confounded because much of the variation in density is reflected in the detection process of occupancy models rather than the state process. As expected, there was a relationship between cumulative detection probability (p) and density, but not between individual detection probability (r) and density. Greater density dictates more individuals available for detection in a given area, and thus cumulative detection of all individuals is also greater (Neilson et al. 2018). When measuring detection probabilities for individuals, however, this cumulative effect disappears and detection probability reflects the magnitude or speed of movement, trap shyness, or trap characteristics (Sollmann et al. 2013, Wearn et al. 2013, Neilson et al. 2018, Stewart et al. 2018).

Ultimately, the relationship between density and PAU depends on three factors: the number of individuals in the population, the amount of space each individual uses, and the degree of spatial overlap among individuals. Occupancy models lack a component to measure degree of overlap. RN abundance models directly estimate localized overlap among individuals, but do not account for individual space use when individuals are detected at multiple sites. So long as all three factors play a role (e.g., when independence among sampling units is violated), error will always exist in the occupancy-density and RN abundance-density relationship limiting the ability to generalize from these estimates to density.

The scale (spatial extent and temporal replicates) of this leopard monitoring program is unprecedented in Africa and illustrates the challenges inherent in monitoring a rare, cryptic, and far-ranging species. Even with years of data for some sites, imprecise density estimates mean that we lack statistical power to detect trends from single-session SCR models (see Chapter 4 for a discussion of multisession trend models). Some surveys (n = 8) not presented here produced too few leopard captures to apply SCR models (see Chapter 5). In the case of other surveys, sampling was constrained by camera theft or unsafe field conditions, limiting monitoring in human-affected landscapes where population status may be of particular concern. We thus have the least information from the most vulnerable sites.

Alternative approaches that facilitate more efficient and versatile monitoring inside and outside protected areas, such as sampling indirect signs rather than using remote cameras, would greatly expand the capacity of this monitoring program and other similar programs. Unfortunately, occupancy and RN abundance were not as informative as density when sampling small protected areas to measure population status. Relationships that are strong under one set of circumstances (e.g., sampling at a grain equivalent to one home range) may not hold when assumptions are violated, or populations vary widely. Directly estimating density of rare cryptic species continues to pose a challenge for wildlife managers but applying models in inappropriate contexts is not a reliable strategy for improving our knowledge of population status. PAU cannot be relied on to robustly compare population density between populations nor to estimate density with any meaningful level of precision.

However, I would not go so far as to categorically reject the two goals of this analysis. In some instances, occupancy surveys could be an effective approach for tracking changes in density *within* a single population. For reserves where the proportion of area used is below 0.75 (i.e., the range of occupancy probabilities reported by Clare et al. 2015), occupancy could reveal changes over time that might indicate a need for more intensive sampling. Alternatively, occupancy surveys might be an effective strategy for monitoring spatial variation in density within large continuous populations (e.g., the greater Kruger ecosystem) using a survey design that more closely resembles Linden et al.’s (2017) coarser survey design than those presented here. Lastly, I continue to see promise for occupancy surveys conducted outside protected areas. Such areas are unlikely to exhibit saturated occupancy. Furthermore, sampling both in and around protected areas implies that the surveys will not be constrained by the issues accompanying fine-scale surveys that I found for these study sites. Ultimately, the relationship between occupancy and density will remain noisy and imperfect (Blackburn et al. 2006, Wilson

2008), but reinforces how integral the spatially explicit detection process in SCR is to robustly estimating density of highly mobile species.

Appendix 3.1: Summaries of 88 camera-trap surveys of leopard populations in northeastern South Africa.

Site	Year	Duration (days)	Stations	Mean trap spacing (m)	Effort (trap-days)	No. of captures	No. of individuals	No. of spatial recaptures	No. of females	No. of males	No. of unsexed leopards	Naive occupancy
Atherstone GR	2013	52	50	1500	2600	98	20	44	9	8	3	0.6
Atherstone GR	2014	54	40	2040	2160	63	21	19	13	7	1	0.65
Atherstone GR	2015	53	39	1990	2067	68	22	14	15	3	4	0.51
Atherstone GR	2016	50	40	2030	1873	33	17	13	10	4	3	0.6
Atherstone GR	2017	43	40	2070	1647	51	19	16	10	3	6	0.5
Atherstone GR	2018	49	40	2040	1823	29	15	10	6	5	4	0.42
Blyde RCNR	2016	45	31	2100	1316	21	7	5	2	4	1	0.26
Hluhluwe-iMfolozi P.	2013	45	30	3150	1343	40	23	6	11	11	1	0.57
Hluhluwe-iMfolozi P.	2014	46	46	2240	2035	162	36	49	22	13	1	0.89
Hluhluwe-iMfolozi P.	2015	45	46	2250	2040	112	29	39	16	12	1	0.74
Hluhluwe-iMfolozi P.	2016	45	46	2250	2031	59	20	19	12	7	1	0.61
Hluhluwe-iMfolozi P.	2017	53	46	2240	2133	84	25	29	15	9	1	0.63
Hluhluwe-iMfolozi P.	2018	58	46	2080	2219	84	23	32	10	12	1	0.8
Ithala GR	2013	45	36	1990	1545	253	50	62	27	18	5	0.94
Ithala GR	2014	45	31	2390	1340	224	44	46	24	13	7	0.97
Ithala GR	2015	45	31	2340	1349	246	39	51	20	15	4	0.94
Ithala GR	2016	45	30	2310	1345	138	32	40	21	9	2	0.93
Ithala GR	2017	53	30	2290	1479	126	30	34	18	9	3	0.87
Ithala GR	2018	53	30	2290	1455	149	33	36	18	9	6	0.87
iWP. E. Shores	2014	45	40	1520	1775	185	19	48	15	4	0	0.75
iWP. E. Shores	2015	45	41	1490	1831	204	31	72	15	10	6	0.83
iWP. E. Shores	2016	45	41	1450	1810	149	24	55	14	8	2	0.83
iWP. E. Shores	2018	57	41	1480	2104	200	24	53	12	4	8	0.73

Site	**Year**	**Duration (days)**	**Stations**	**Mean trap spacing (m)**	**Effort (trap-days)**	**No. of captures**	**No. of individuals**	**No. of spatial recaptures**	**No. of females**	**No. of males**	**No. of unsexed leopards**	**Naive occupancy**
Khamab Kalahari GR	2016	45	40	3030	1781	40	7	10	2	5	0	0.28
Khamab Kalahari GR	2017	51	40	3030	1672	51	10	12	2	5	3	0.4
KZNPRs	2015	44	62	1730	2644	158	35	48	23	10	2	0.68
KZNPRs	2017	52	36	1950	1785	119	38	33	24	9	5	0.83
Lajuma RC	2014	47	39	1850	1805	157	38	42	22	7	9	0.9
Lajuma RC	2015	55	39	1850	2131	120	24	38	14	8	2	0.85
Lajuma RC	2016	53	40	1860	1889	148	27	47	15	8	4	0.88
Lajuma RC	2017	59	40	1860	2202	140	27	46	16	7	4	0.95
Lajuma RC	2018	60	40	1820	2190	143	33	40	17	9	7	0.88
Lapalala Wld.	2016	53	40	2450	2014	71	22	19	9	12	1	0.55
Lapalala Wld.	2017	63	40	2460	2455	91	29	23	13	16	0	0.68
Lapalala Wld.	2018	53	40	2450	2030	70	28	16	8	16	4	0.65
Loskop Dam NR	2016	61	34	1930	1898	115	26	33	11	15	0	0.68
Madikwe GR[#]	2017	43	40	1100	1632	26	15	9	4	11	0	0.32
Madikwe GR[#]	2018	51	40	1200	1910	65	21	21	5	9	7	0.55
Makalali GR	2014	59	50	1760	2722	87	25	34	14	8	3	0.6
Makalali GR	2015	65	40	1880	2241	138	37	60	15	13	9	0.9
Makalali GR	2016	53	40	1880	2001	103	32	27	15	11	6	0.7
Makalali GR	2017	57	40	1880	2205	118	37	41	20	14	3	0.88
Makalali GR	2018	50	40	1880	1949	97	33	34	10	8	15	0.88
Manyoni PGR	2015	45	40	1920	1793	72	8	23	2	6	0	0.52
Manyoni PGR	2017	54	39	1840	1916	40	7	13	2	5	0	0.36
Mapesu PGR	2018	50	35	1810	1559	58	13	18	4	7	2	0.51
Munyawana PGR	2014	45	42	1770	1863	197	28	68	15	10	3	0.93
Munyawana PGR	2016	57	42	1770	2286	194	33	64	18	9	6	0.88

Site	Year	Duration (days)	Stations	Mean trap spacing (m)	Effort (trap-days)	No. of captures	No. of individuals	No. of spatial recaptures	No. of females	No. of males	No. of unsexed leopards	Naive occupancy
Munyawana PGR	2017	50	42	1780	2006	75	21	27	8	9	4	0.69
Pilanesberg NP	2016	45	40	1990	1784	76	32	22	12	14	6	0.65
Pilanesberg NP	2017	47	40	2000	1708	81	42	17	18	17	7	0.7
Pilanesberg NP	2018	50	40	1960	1827	100	40	33	16	15	9	0.75
Somkhanda GR	2014	45	39	2070	1665	50	12	30	7	5	0	0.51
Somkhanda GR	2015	45	40	2050	1732	57	14	24	6	7	1	0.57
Somkhanda GR	2016	45	29	1960	1246	43	8	18	4	4	0	0.52
Somkhanda GR	2017	58	33	2040	1701	63	12	20	5	7	0	0.58
Tembe EP	2015	45	32	1940	1392	120	17	37	12	5	0	0.88
Tembe EP	2016	45	32	1910	1427	130	26	37	16	7	3	0.81
Tembe EP	2017	44	32	1950	1359	118	27	31	16	11	0	0.91
Tembe EP	2018	54	32	1950	1610	167	30	51	14	12	4	0.94
Timbavati PGNR	2013	60	40	1920	1887	95	38	26	17	18	3	0.78
Timbavati PGNR	2014	56	40	1930	2141	155	50	42	27	20	3	0.88
Timbavati PGNR	2015	60	40	1930	2301	123	46	41	24	18	4	0.8
Timbavati PGNR	2016	50	40	1940	1936	105	30	40	10	15	5	0.8
Timbavati PGNR	2017	55	40	1930	2109	129	44	43	25	17	2	0.9
Timbavati PGNR	2018	47	40	1940	1841	119	40	26	23	14	3	0.8
uMkhuze GR	2013	45	41	1720	1827	146	34	52	16	15	3	0.88
uMkhuze GR	2014	45	40	1710	1740	144	28	51	18	8	2	0.88
uMkhuze GR	2015	45	40	1710	1759	104	23	43	12	10	1	0.85
uMkhuze GR	2016	45	40	1670	1784	95	22	36	12	9	1	0.75
uMkhuze GR	2017	56	40	1680	2004	177	32	67	19	9	4	0.98
uMkhuze GR	2018	50	40	1680	1901	279	27	84	12	9	6	0.98
Venetia-Limpopo GR	2014	49	40	2000	1850	61	26	21	15	10	1	0.7

Site	Year	Duration (days)	Stations	Mean trap spacing (m)	Effort (trap-days)	No. of captures	No. of individuals	No. of spatial recaptures	No. of females	No. of males	No. of unsexed leopards	Naive occupancy
Venetia-Limpopo GR	2015	47	40	2210	1694	36	16	13	8	8	0	0.48
Venetia-Limpopo GR	2016	49	40	2220	1934	85	27	18	14	12	1	0.57
Venetia-Limpopo GR	2017	48	40	2260	1848	80	23	28	8	11	4	0.72
Welgevonden GR	2013	53	51	1430	2545	138	19	60	11	8	0	0.73
Welgevonden GR	2014	58	40	1900	1957	94	25	37	14	11	0	0.88
Welgevonden GR	2015	52	40	1940	1845	116	18	52	9	9	0	0.85
Welgevonden GR	2016	44	40	1900	1292	56	16	23	7	9	0	0.65
Welgevonden GR	2017	57	40	1870	2150	88	22	36	6	9	7	0.72
Welgevonden GR	2018	52	40	1740	1971	88	23	38	9	5	9	0.75
Wonderkop NR	2013	50	52	1270	2528	41	12	20	9	3	0	0.4
Wonderkop NR	2014	55	40	1690	1887	85	13	40	8	4	1	0.72
Wonderkop NR	2015	51	37	1810	1603	29	12	12	7	4	1	0.41
Zingela NR	2016	45	40	2030	1716	36	14	10	5	8	1	0.42
Zingela NR	2017	46	40	2950	1778	21	10	10	4	6	0	0.38
Zingela NR	2018	50	40	2060	1932	69	24	28	7	8	9	0.7

*2017 survey included only KPGR and Amakhosi/Zeekoepan reserves

#Sampled using a clustered array with four stations per cluster

Appendix 3.2: Detailed results of top-ranked (AICc) spatial capture-recapture models for 88 camera-trap surveys of leopard populations at 24 sites in South Africa.

Site	Year	g_0	σ	Density* (SE)	Female g_0 (SE)	Male g_0 (SE)	Female $\sigma^{\#}$ (SE)	Male $\sigma^{\#}$ (SE)	Prop. male	Sex-weighted $\sigma^{\#}$	Home-range size[†]
Atherstone GR	2013		~ Sex	6.26 (1.45)	0.022 (0.004)	0.004 (0.004)	2059 (172)	1631 (138)	0.56	1820	62
Atherstone GR	2014			4.24 (1.04)	0.015 (0.003)	0.003 (0.003)	2895 (325)	2895 (325)	0.35	2895	157
Atherstone GR	2015	~ Sex	~ Sex	6.23 (1.48)	0.047 (0.011)	0.007 (0.007)	1241 (114)	4214 (1491)	0.08	1488	41
Atherstone GR	2016	~ Sex		6.47 (3.13)	0.002 (0.001)	0.005 (0.005)	3679 (714)	3679 (714)	0.11	3679	254
Atherstone GR	2017			3.5 (1.00)	0.013 (0.003)	0.003 (0.003)	3499 (508)	3499 (508)	0.23	3499	230
Atherstone GR	2018			5.57 (1.69)	0.011 (0.004)	0.004 (0.004)	1949 (304)	1949 (304)	0.45	1949	71
Blyde RCNR	2016			1.72 (0.76)	0.06 (0.026)	0.026 (0.026)	1579 (307)	1579 (307)	0.67	1579	46
Hluhluwe-iMfolozi P.	2013			5.73 (1.48)	0.026 (0.008)	0.008 (0.008)	1821 (250)	1821 (250)	0.50	1821	62
Hluhluwe-iMfolozi P.	2014		~ Sex	6.03 (1.05)	0.049 (0.006)	0.006 (0.006)	1738 (113)	2583 (200)	0.29	1986	74
Hluhluwe-iMfolozi P.	2015	~ Sex		5.05 (1.00)	0.021 (0.005)	0.009 (0.009)	2218 (159)	2218 (159)	0.37	2218	92
Hluhluwe-iMfolozi P.	2016	~ Sex	~ Sex	3.56 (0.89)	0.011 (0.004)	0.014 (0.014)	3008 (471)	1820 (229)	0.36	2579	125
Hluhluwe-iMfolozi P.	2017	~ Sex		4.53 (1.06)	0.01 (0.003)	0.008 (0.008)	2615 (227)	2615 (227)	0.27	2615	128
Hluhluwe-iMfolozi P.	2018		~ Sex	3.28 (0.83)	0.024 (0.005)	0.005 (0.005)	1970 (330)	4154 (504)	0.35	2738	141

Site	**Year**	**g_0**	**σ**	**Density (SE)**	**Female g_0 (SE)**	**Male g_0 (SE)**	**Female σ (SE)**	**Male σ (SE)**	**Prop. male**	**Sex-weighted σ**	**Home-range size (km^2)**
Ithala GR	2013	~ Sex	~ Sex	9.17 (1.39)	0.047 (0.007)	0.01 (0.01)	2194 (146)	2926 (193)	0.31	2418	110
Ithala GR	2014		~ Sex	11.1 (1.75)	0.107 (0.012)	0.012 (0.012)	1312 (75)	2010 (132)	0.26	1494	41
Ithala GR	2015	~ Sex	~ Sex	9.62 (1.61)	0.077 (0.013)	0.016 (0.016)	1426 (102)	1911 (108)	0.33	1587	47
Ithala GR	2016		~ Sex	8.43 (1.58)	0.062 (0.008)	0.008 (0.008)	1473 (105)	2412 (214)	0.21	1667	52
Ithala GR	2017		~ Sex	8.90 (1.80)	0.051 (0.007)	0.007 (0.007)	1251 (99)	2728 (229)	0.18	1519	43
Ithala GR	2018		~ Sex	8.87 (1.66)	0.082 (0.011)	0.011 (0.011)	1269 (97)	2295 (206)	0.23	1501	42
iWP. E. Shores	2014	~ Sex	~ Sex	8.47 (2.00)	0.119 (0.017)	0.009 (0.009)	1322 (75)	2974 (265)	0.14	1556	45
iWP. E. Shores	2015	~ Sex	~ Sex	11.81 (2.31)	0.053 (0.008)	0.005 (0.005)	1601 (102)	4368 (510)	0.21	2182	89
iWP. E. Shores	2016		~ Sex	9.49 (2.06)	0.042 (0.005)	0.005 (0.005)	1752 (136)	3640 (278)	0.23	2181	89
iWP. E. Shores	2018	~ Sex	~ Sex	8.30 (1.92)	0.071 (0.01)	0.007 (0.007)	1672 (108)	4979 (431)	0.18	2254	95
KZNPRs	2015	~ Sex		6.84 (1.21)	0.019 (0.003)	0.011 (0.011)	2134 (106)	2134 (106)	0.24	2134	85
KZNPRs	2017	~ Sex	~ Sex	14.92 (2.74)	0.054 (0.011)	0.008 (0.008)	964 (81)	3401 (464)	0.11	1237	28
Lajuma RC	2014	~ Sex	~ Sex	10.51 (1.88)	0.031 (0.006)	0.012 (0.012)	1580 (134)	2997 (266)	0.11	1729	56
Lajuma RC	2015		~ Sex	5.61 (1.23)	0.034 (0.005)	0.005 (0.005)	1747 (156)	2907 (236)	0.25	2039	78
Lajuma RC	2016		~ Sex	6.85 (1.41)	0.045 (0.006)	0.006 (0.006)	1487 (107)	2850 (210)	0.21	1773	59
Lajuma RC	2017		~ Sex	7.72 (1.60)	0.041 (0.005)	0.005 (0.005)	1273 (87)	2836 (257)	0.16	1525	43

Site	Year	g_0	σ	Density (SE)	Female g_0 (SE)	Male g_0 (SE)	Female σ (SE)	Male σ (SE)	Prop. male	Sex-weighted σ	Home-range size (km^2)
Lajuma RC	2018		~ Sex	9.29 (1.79)	0.042 (0.006)	0.006 (0.006)	1243 (91)	3098 (277)	0.16	1536	44
Lapalala Wld.	2016	~ Sex		4.33 (1.10)	0.011 (0.004)	0.01 (0.01)	2263 (206)	2263 (206)	0.44	2263	96
Lapalala Wld.	2017	~ Sex		5.60 (1.18)	0.008 (0.002)	0.004 (0.004)	2527 (200)	2527 (200)	0.45	2527	120
Lapalala Wld.	2018		~ Sex	4.88 (1.15)	0.018 (0.004)	0.004 (0.004)	1730 (272)	3477 (465)	0.47	2552	122
Loskop Dam NR	2016		~ Sex	9.53 (2.27)	0.032 (0.005)	0.005 (0.005)	1009 (113)	2658 (225)	0.33	1549	45
Madikwe GR	2017			2.74 (1.00)	0.007 (0.003)	0.003 (0.003)	3613 (785)	3613 (785)	0.73	3613	245
Madikwe GR	2018		~ Sex	6.55 (4.69)	0.029 (0.006)	0.006 (0.006)	940 (490)	2761 (324)	0.29	1460	40
Makalali GR	2014		~ Sex	5.14 (1.15)	0.018 (0.003)	0.003 (0.003)	2209 (232)	3617 (481)	0.25	2558	123
Makalali GR	2015		~ Sex	10.04 (1.79)	0.025 (0.004)	0.004 (0.004)	1590 (129)	2549 (208)	0.32	1899	67
Makalali GR	2016		~ Sex	9.77 (1.88)	0.03 (0.005)	0.005 (0.005)	1455 (150)	2050 (210)	0.32	1646	51
Makalali GR	2017		~ Sex	9.57 (1.75)	0.015 (0.002)	0.002 (0.002)	2071 (207)	2803 (305)	0.33	2316	100
Makalali GR	2018		~ Sex	9.46 (1.85)	0.03 (0.005)	0.005 (0.005)	1430 (134)	2666 (270)	0.27	1763	58
Manyoni PGR	2015			0.69 (0.36)	0.061 (0.032)	0.032 (0.032)	4651 (945)	4651 (945)	0.75	4651	406
Manyoni PGR	2017			1.27 (0.53)	0.045 (0.011)	0.011 (0.011)	2665 (362)	2665 (362)	0.71	2665	133
Mapesu PGR	2018			3.66 (1.08)	0.036 (0.008)	0.008 (0.008)	2120 (213)	2120 (213)	0.64	2120	84
Molopo GR	2016			0.24 (0.09)	0.041 (0.011)	0.011 (0.011)	8057 (745)	8057 (745)	0.71	8057	1221

Site	**Year**	***g_0***	**σ**	**Density (SE)**	**Female *g_0* (SE)**	**Male *g_0* (SE)**	**Female σ (SE)**	**Male σ (SE)**	**Prop. male**	**Sex-weighted σ**	**Home-range size (km^2)**
Molopo GR	2017		~ Sex	1.29 (1.41)	0.078 (0.026)	0.026 (0.026)	935 (576)	7872 (656)	0.16	2037	78
Munyawana PGR	2014		~ Sex	7.97 (1.61)	0.069 (0.007)	0.007 (0.007)	1262 (81)	2314 (138)	0.27	1547	45
Munyawana PGR	2016	~ Sex	~ Sex	8.71 (1.67)	0.061 (0.009)	0.005 (0.005)	1292 (80)	3959 (393)	0.15	1678	53
Munyawana PGR	2017	~ Sex	~ Sex	6.66 (1.60)	0.066 (0.018)	0.005 (0.005)	1067 (131)	2307 (357)	0.48	1667	52
Pilanesberg NP	2016	~ Sex	~ Sex	8.20 (1.64)	0.041 (0.014)	0.003 (0.003)	1322 (172)	2998 (432)	0.42	2020	76
Pilanesberg NP	2017		~ Sex	8.18 (1.87)	0.006 (0.001)	0.001 (0.001)	6590 (1047)	3167 (460)	0.75	4039	306
Pilanesberg NP	2018	~ Sex		9.07 (1.89)	0.005 (0.002)	0.003 (0.003)	3258 (318)	3258 (318)	0.34	3258	199
Somkhanda GR	2014			1.86 (0.62)	0.011 (0.002)	0.002 (0.002)	4295 (624)	4295 (624)	0.42	4295	347
Somkhanda GR	2015		~ Sex	2.89 (0.84)	0.032 (0.007)	0.007 (0.007)	1903 (213)	3176 (393)	0.4	2414	109
Somkhanda GR	2016			1.74 (0.67)	0.039 (0.01)	0.01 (0.01)	2847 (349)	2847 (349)	0.5	2847	152
Somkhanda GR	2017			1.88 (0.59)	0.045 (0.009)	0.009 (0.009)	2906 (312)	2906 (312)	0.58	2906	158
Tembe EP	2015	~ Sex	~ Sex	5.15 (1.32)	0.055 (0.014)	0.02 (0.02)	1440 (145)	2006 (136)	0.21	1560	45
Tembe EP	2016		~ Sex	7.45 (1.57)	0.049 (0.007)	0.007 (0.007)	1542 (113)	2806 (251)	0.19	1784	59
Tembe EP	2017		~ Sex	8.02 (1.63)	0.052 (0.008)	0.008 (0.008)	1444 (116)	2246 (187)	0.31	1696	54
Tembe EP	2018		~ Sex	8.38 (1.62)	0.053 (0.006)	0.006 (0.006)	1440 (92)	2289 (184)	0.35	1739	56
Timbavati PGNR	2013		~ Sex	12.62 (2.32)	0.021 (0.004)	0.004 (0.004)	1398 (142)	2228 (250)	0.39	1723	55

Site	**Year**	g_0	**σ**	**Density (SE)**	**Female g_0 (SE)**	**Male g_0 (SE)**	**Female σ (SE)**	**Male σ (SE)**	**Prop. male**	**Sex-weighted σ**	**Home-range size (km^2)**
Timbavati PGNR	2014		~ Sex	14.95 (2.27)	0.032 (0.004)	0.004 (0.004)	1313 (90)	2224 (174)	0.3	1591	47
Timbavati PGNR	2015		~ Sex	13.30 (2.15)	0.015 (0.002)	0.002 (0.002)	1817 (164)	2472 (229)	0.35	2048	78
Timbavati PGNR	2016		~ Sex	7.16 (1.43)	0.021 (0.003)	0.003 (0.003)	2022 (207)	2693 (301)	0.51	2363	105
Timbavati PGNR	2017	~ Sex		12.25 (2.03)	0.013 (0.003)	0.006 (0.006)	2093 (140)	2093 (140)	0.33	2093	82
Timbavati PGNR	2018		~Sex	14.29 (2.59)	0.039 (0.006)	0.039 (0.006)	1042 (95)	2229 (201)	0.22	1308	32
uMkhuze GR	2013		~ Sex	9.09 (1.75)	0.054 (0.008)	0.008 (0.008)	1348 (93)	3261 (269)	0.3	1917	69
uMkhuze GR	2014		~ Sex	7.54 (1.60)	0.037 (0.005)	0.005 (0.005)	1755 (124)	4226 (627)	0.14	2100	83
uMkhuze GR	2015		~Sex	5.66 (1.38)	0.036 (0.007)	0.036 (0.007)	1674 (154)	4026 (656)	0.26	2282	97
uMkhuze GR	2016		~ Sex	6.88 (1.58)	0.029 (0.005)	0.005 (0.005)	1658 (155)	2662 (267)	0.32	1975	73
uMkhuze GR	2017		~ Sex	6.32 (1.26)	0.031 (0.004)	0.004 (0.004)	2510 (191)	4657 (660)	0.17	2883	156
uMkhuze GR	2018		~ Sex	6.86 (1.42)	0.074 (0.007)	0.007 (0.007)	1606 (98)	2797 (159)	0.31	1980	73
Venetia-Limpopo GR	2014	~ Sex		6.52 (1.69)	0.006 (0.002)	0.005 (0.005)	3059 (396)	3059 (396)	0.31	3059	176
Venetia-Limpopo GR	2015			4.86 (1.35)	0.017 (0.005)	0.005 (0.005)	1961 (255)	1961 (255)	0.5	1961	72
Venetia-Limpopo GR	2016	~ Sex		6.23 (1.45)	0.007 (0.002)	0.006 (0.006)	2737 (276)	2737 (276)	0.33	2737	140
Venetia-Limpopo GR	2017		~ Sex	5.06 (1.14)	0.025 (0.005)	0.005 (0.005)	1812 (211)	2629 (242)	0.48	2200	91
Welgevonden GR	2013	~ Sex		3.40 (0.85)	0.013 (0.003)	0.007 (0.007)	3129 (214)	3129 (214)	0.35	3129	184

Site	Year	g_0	σ	Density (SE)	Female g_0 (SE)	Male g_0 (SE)	Female σ (SE)	Male σ (SE)	Prop. male	Sex-weighted σ	Home-range size (km^2)
Welgevonden GR	2014		~ Sex	3.76 (0.86)	0.016 (0.003)	0.003 (0.003)	3200 (377)	4588 (625)	0.34	3665	252
Welgevonden GR	2015			2.24 (0.57)	0.04 (0.006)	0.006 (0.006)	3619 (288)	3619 (288)	0.5	3619	246
Welgevonden GR	2016		~ Sex	3.10 (1.05)	0.031 (0.008)	0.008 (0.008)	1665 (288)	5787 (1014)	0.24	2636	130
Welgevonden GR	2017		~ Sex	4.35 (1.25)	0.03 (0.006)	0.006 (0.006)	1423 (192)	4636 (563)	0.27	2297	99
Welgevonden GR	2018		~ Sex	6.07 (1.49)	0.023 (0.004)	0.004 (0.004)	1632 (157)	4453 (656)	0.11	1956	72
Wonderkop NR	2013			2.13 (0.70)	0.019 (0.006)	0.006 (0.006)	2962 (388)	2962 (388)	0.25	2962	165
Wonderkop NR	2014			0.87 (0.25)	0.028 (0.006)	0.006 (0.006)	6307 (550)	6307 (550)	0.33	6307	748
Wonderkop NR	2015			2.97 (1.16)	0.01 (0.003)	0.003 (0.003)	3060 (624)	3060 (624)	0.36	3060	176
Zingela NR	2016			3.65 (1.10)	0.012 (0.003)	0.003 (0.003)	2623 (373)	2623 (373)	0.62	2623	129
Zingela NR	2017			1.00 (0.48)	0.006 (0.003)	0.003 (0.003)	6283 (1536)	6283 (1536)	0.6	6283	742
Zingela NR	2018		~ Sex	5.08 (1.43)	0.011 (0.002)	0.002 (0.002)	2209 (301)	5815 (1089)	0.21	2948	163

*Leopards per 100 km^2
$^{\#}$Measured in meters
†Measured in km^2

Appendix 3.3: Details of top-ranked (by GOF) occupancy and Royle-Nichols abundance models for 88 camera-trap surveys of leopard populations at 24 sites in northeastern South Africa.

		OCCUPANCY					**ROYLE-NICHOLS ABUNDANCE**				
.Site	**Year**	**Occasion length (days)**	**Ψ (SE)**	**P (SE)**	**P-value**	**Daily P**	**Occasion length (days)**	**N (SE)**	**R (SE)**	**P-value**	**Daily r**
Atherstone GR	2013	15	0.74 (0.08)	0.47 (0.06)	0.30	0.042	15	1.6 (0.5)	0.27 (0.08)	0.32	0.020
Atherstone GR	2014	15	1.00 (NA)	0.36 (0.04)	0.77	0.029	15	3.3 (1.7)	0.13 (0.07)	0.88	0.009
Atherstone GR	2015	15	0.64 (0.1)	0.46 (0.07)	0.11	0.040	15	1.2 (0.4)	0.30 (0.09)	0.09	0.023
Atherstone GR	2016	15	1.00 (0.02)	0.25 (0.04)	0.09	0.019	Excluded due to r < 0.1				
Atherstone GR	2017	9	0.71 (0.13)	0.28 (0.06)	0.25	0.036	9	1.7 (0.9)	0.14 (0.07)	0.30	0.016
Atherstone GR	2018	9	0.8 (0.21)	0.17 (0.05)	0.09	0.021	Excluded due to r < 0.1				
Blyde RCNR	2016	15	0.35 (0.13)	0.38 (0.14)	0.73	0.031	15	0.5 (0.3)	0.31 (0.15)	0.47	0.024
Hluhluwe-iMfolozi P.	2013	Excluded due to p < 0.05					15	1.1 (0.4)	0.39 (0.12)	0.20	0.033
Hluhluwe-iMfolozi P.	2014	9	0.94 (0.05)	0.48 (0.04)	0.80	0.070	9	3.1 (0.9)	0.20 (0.06)	0.84	0.025
Hluhluwe-iMfolozi P.	2015	5	0.80 (0.07)	0.3 (0.03)	0.08	0.070	15	1.9 (0.6)	0.40 (0.11)	0.66	0.033
Hluhluwe-iMfolozi P.	2016	9	0.74 (0.1)	0.29 (0.05)	0.31	0.038	9	1.8 (0.7)	0.14 (0.06)	0.42	0.016
Hluhluwe-iMfolozi P.	2017	5	0.70 (0.08)	0.28 (0.03)	0.43	0.063	5	1.4 (0.4)	0.15 (0.04)	0.70	0.032
Hluhluwe-iMfolozi P.	2018	15	1.00 (<0.001)	0.47 (0.05)	0.73	0.041	15	4.1 (1.2)	0.16 (0.05)	0.85	0.011
Ithala GR	2013	5	1.00 (NA)	0.54 (0.03)	0.59	0.145	5	2.9 (0.8)	0.27 (0.07)	0.76	0.061
Ithala GR	2014	5	1.00 (NA)	0.51 (0.03)	0.27	0.131	15	3.8 (1.3)	0.49 (0.15)	0.67	0.044
Ithala GR	2015	15	1.00 (NA)	0.81 (0.04)	0.20	0.105	9	3.5 (1.1)	0.33 (0.10)	0.64	0.043
Ithala GR	2016	9	1.00 (NA)	0.56 (0.04)	0.41	0.087	9	3.3 (1.2)	0.25 (0.09)	0.72	0.032
Ithala GR	2017	15	1.00 (NA)	0.72 (0.05)	0.53	0.082	15	3.2 (1.2)	0.40 (0.14)	0.82	0.034

		OCCUPANCY					**ROYLE-NICHOLS ABUNDANCE**				
Site	**Year**	**Occasion length (days)**	**Ψ (SE)**	**P (SE)**	**P-value**	**Daily P**	**Occasion length (days)**	**N (SE)**	**r (SE)**	**P-value**	**Daily r**
Ithala GR	2018	5	0.87 (0.06)	0.44 (0.03)	0.65	0.110	5	2.3 (0.8)	0.20 (0.06)	0.83	0.045
iWP. E. Shores	2014	5	0.75 (0.07)	0.46 (0.03)	0.33	0.117	9	1.5 (0.3)	0.47 (0.07)	0.45	0.068
iWP. E. Shores	2015	15	0.84 (0.06)	0.8 (0.04)	0.50	0.101	3	1.9 (0.4)	0.16 (0.03)	0.58	0.056
iWP. E. Shores	2016	5	1.00 (NA)	0.31 (0.03)	0.06	0.072	5	2.1 (0.7)	0.18 (0.05)	0.60	0.038
iWP. E. Shores	2018	5	0.78 (0.07)	0.46 (0.03)	0.85	0.116	9	1.6 (0.4)	0.43 (0.07)	0.86	0.060
Khamab Kalahari GR	2016	15	0.38 (0.11)	0.4 (0.12)	0.44	0.034	15	0.5 (0.2)	0.31 (0.13)	0.21	0.025
Khamab Kalahari GR	2017	15	0.67 (0.16)	0.32 (0.08)	0.39	0.025	15	1.5 (1.0)	0.16 (0.11)	0.17	0.012
KZNPRs	2015	5	0.70 (0.06)	0.33 (0.03)	0.25	0.077	15	1.5 (0.4)	0.42 (0.09)	0.26	0.036
KZNPRs	2017	15	1.00 (NA)	0.53 (0.05)	0.31	0.049	15	3.2 (1.4)	0.24 (0.10)	0.62	0.018
Lajuma RC	2014	15	0.93 (0.05)	0.67 (0.05)	0.74	0.072	15	3.2 (1.2)	0.31 (0.11)	0.70	0.024
Lajuma RC	2015	9	1.00 (NA)	0.4 (0.03)	0.74	0.055	9	2.9 (1.0)	0.18 (0.06)	0.90	0.021
Lajuma RC	2016	15	1.00 (NA)	0.62 (0.05)	0.63	0.063	15	3.3 (1.2)	0.30 (0.11)	0.77	0.023
Lajuma RC	2017	9	1.00 (NA)	0.45 (0.03)	0.64	0.065	9	4.2 (1.1)	0.14 (0.04)	0.80	0.017
Lajuma RC	2018	15	1.00 (NA)	0.54 (0.04)	0.17	0.051	15	2.6 (0.8)	0.32 (0.09)	0.67	0.025
Lapalala Wld.	2016	15	0.67 (0.09)	0.51 (0.07)	0.64	0.046	15	1.3 (0.4)	0.32 (0.10)	0.32	0.025
Lapalala Wld.	2017	Excluded due to $p < 0.05$					9	2.3 (0.8)	0.13 (0.05)	0.12	0.015
Lapalala Wld.	2018	15	1.00 (NA)	0.37 (0.05)	0.08	0.031	15	2.8 (1.5)	0.17 (0.09)	0.29	0.012
Loskop Dam NR	2016	9	0.80 (0.08)	0.48 (0.04)	0.90	0.071	9	1.8 (0.5)	0.28 (0.07)	0.78	0.035
Madikwe GR	2017	5	0.45 (0.11)	0.16 (0.04)	0.49	0.033	5	0.7 (0.3)	0.11 (0.05)	0.58	0.023
Madikwe GR	2018	15	0.71 (0.09)	0.51 (0.07)	0.22	0.046	5	1.4 (0.4)	0.14 (0.04)	0.10	0.030
Makalali GR	2014	5	0.64 (0.08)	0.24 (0.03)	0.83	0.052	5	1.1 (0.3)	0.14 (0.03)	0.92	0.030
Makalali GR	2015	9	0.93 (0.05)	0.4 (0.04)	0.42	0.056	15	3.5 (1.2)	0.20 (0.07)	0.47	0.015
Makalali GR	2016	9	0.72 (0.08)	0.44 (0.05)	0.12	0.063	9	1.4 (0.4)	0.27 (0.06)	0.40	0.035
Makalali GR	2017	9	0.93 (0.05)	0.45 (0.04)	0.97	0.064	9	3.7 (1.3)	0.15 (0.05)	0.97	0.018

		OCCUPANCY					**ROYLE-NICHOLS ABUNDANCE**				
Site	**Year**	**Occasion length (days)**	**Ψ (SE)**	**P (SE)**	**P-value**	**Daily P**	**Occasion length (days)**	**N (SE)**	**r (SE)**	**P-value**	**Daily r**
Makalali GR	2018	15	1.00 (NA)	0.56 (0.05)	0.56	0.053	15	3.5 (1.4)	0.23 (0.09)	0.75	0.017
Manyoni PGR	2017	15	0.45 (0.09)	0.54 (0.09)	0.64	0.050	5	0.7 (0.2)	0.12 (0.04)	0.38	0.026
Mapesu PGR	2018	15	0.58 (0.09)	0.68 (0.08)	0.71	0.074	15	0.9 (0.3)	0.55 (0.11)	0.22	0.052
Munyawana PGR	2014	5	1.00 (NA)	0.38 (0.03)	0.30	0.091	5	3.4 (1.0)	0.14 (0.04)	0.67	0.030
Munyawana PGR	2016	9	0.92 (0.05)	0.52 (0.04)	0.19	0.078	9	2.7 (0.7)	0.24 (0.06)	0.61	0.030
Munyawana PGR	2017	15	0.91 (0.06)	0.62 (0.06)	0.56	0.062	9	3.1 (1.2)	0.17 (0.06)	0.65	0.021
Pilanesberg NP	2016	Excluded due to $p < 0.05$					9	1.6 (0.6)	0.20 (0.07)	0.30	0.024
Pilanesberg NP	2017	15	0.84 (0.09)	0.54 (0.07)	0.85	0.050	15	2.5 (1.1)	0.24 (0.11)	0.85	0.018
Pilanesberg NP	2018	9	0.84 (0.07)	0.55 (0.05)	0.28	0.084	9	2.0 (0.6)	0.31 (0.08)	0.41	0.040
Somkhanda GR	2014	15	1.00 (0.07)	0.26 (0.05)	0.96	0.020	Excluded due to $r < 0.1$				
Somkhanda GR	2015	9	0.69 (0.11)	0.31 (0.05)	0.69	0.040	9	1.5 (0.7)	0.16 (0.07)	0.73	0.019
Somkhanda GR	2016	15	0.58 (0.11)	0.58 (0.09)	0.98	0.056	9	1.0 (0.4)	0.25 (0.08)	0.68	0.031
Somkhanda GR	2017	15	0.71 (0.11)	0.41 (0.08)	0.21	0.034	9	1.4 (0.4)	0.20 (0.06)	0.14	0.025
Tembe EP	2015	Excluded due to $p < 0.05$					15	3.1 (1.1)	0.33 (0.12)	0.19	0.027
Tembe EP	2016	9	0.82 (0.07)	0.56 (0.05)	0.73	0.088	5	1.9 (0.5)	0.22 (0.05)	0.66	0.048
Tembe EP	2017	9	1.00 (NA)	0.52 (0.05)	0.32	0.078	9	2.6 (0.8)	0.29 (0.08)	0.69	0.037
Tembe EP	2018	15	1.00 (NA)	0.69 (0.05)	0.13	0.074	5	3.0 (0.8)	0.16 (0.04)	0.46	0.033
Timbavati PGNR	2013	5	1.00 (NA)	0.23 (0.02)	0.68	0.050	9	3.7 (1.6)	0.13 (0.05)	0.83	0.015
Timbavati PGNR	2014	9	0.90 (0.05)	0.49 (0.04)	0.55	0.072	9	2.8 (1.0)	0.20 (0.07)	0.65	0.025
Timbavati PGNR	2015	9	1.00 (NA)	0.39 (0.03)	0.12	0.053	5	2.7 (1.1)	0.10 (0.04)	0.64	0.021
Timbavati PGNR	2016	9	1.00 (NA)	0.35 (0.04)	0.44	0.047	9	4.1 (1.2)	0.11 (0.03)	0.65	0.012
Timbavati PGNR	2017	9	1.00 (NA)	0.41 (0.03)	0.75	0.056	9	3.9 (1.3)	0.13 (0.04)	0.79	0.016
Timbavati PGNR	2018	15	1.00 (NA)	0.51 (0.05)	0.31	0.046	15	2.6 (1.1)	0.28 (0.11)	0.67	0.021
uMkhuze GR	2013	15	1.00 (NA)	0.53 (0.05)	0.70	0.048	15	4.1 (1.3)	0.18 (0.06)	0.80	0.013

		OCCUPANCY					**ROYLE-NICHOLS ABUNDANCE**				
Site	**Year**	**Occasion length (days)**	**Ψ (SE)**	**P (SE)**	**P-value**	**Daily P**	**Occasion length (days)**	**N (SE)**	**r (SE)**	**P-value**	**Daily r**
uMkhuze GR	2014	9	1.00 (NA)	0.45 (0.04)	0.49	0.065	9	3.7 (1.2)	0.17 (0.06)	0.62	0.020
uMkhuze GR	2015	15	1.00 (NA)	0.53 (0.05)	0.34	0.050	15	3.3 (1.4)	0.24 (0.10)	0.61	0.018
uMkhuze GR	2016	9	0.80 (0.08)	0.45 (0.05)	0.33	0.064	9	2.0 (0.6)	0.23 (0.07)	0.45	0.028
uMkhuze GR	2017	15	1.00 (<0.001)	0.69 (0.05)	0.59	0.075	15	5.1 (1.0)	0.22 (0.05)	0.73	0.016
uMkhuze GR	2018	9	1.00 (NA)	0.70 (0.03)	0.17	0.126	9	4.3 (1.0)	0.27 (0.06)	0.75	0.035
Venetia-Limpopo GR	2014	5	1.00 (NA)	0.17 (0.02)	0.51	0.036	15	3.7 (1.5)	0.16 (0.07)	0.28	0.012
Venetia-Limpopo GR	2015	15	0.79 (0.18)	0.35 (0.1)	0.45	0.028	15	2.4 (2.2)	0.13 (0.13)	0.60	0.010
Venetia-Limpopo GR	2016	9	0.62 (0.09)	0.39 (0.05)	0.37	0.054	15	1.2 (0.4)	0.34 (0.10)	0.19	0.027
Venetia-Limpopo GR	2017	15	1.00 (NA)	0.41 (0.05)	0.40	0.034	15	3.5 (1.7)	0.15 (0.07)	0.44	0.011
Welgevonden GR	2013	9	0.75 (0.07)	0.47 (0.04)	0.91	0.068	9	1.6 (0.4)	0.28 (0.06)	0.78	0.036
Welgevonden GR	2014	9	1.00 (NA)	0.37 (0.04)	0.39	0.050	9	4.4 (1.2)	0.10 (0.03)	0.48	0.012
Welgevonden GR	2015	15	1.00 (NA)	0.58 (0.05)	0.24	0.056	15	3.3 (1.4)	0.26 (0.11)	0.46	0.020
Welgevonden GR	2016	15	1.00 (NA)	0.47 (0.06)	0.47	0.042	9	3.2 (1.7)	0.12 (0.07)	0.56	0.014
Welgevonden GR	2017	9	0.78 (0.08)	0.39 (0.04)	0.17	0.054	9	1.8 (0.6)	0.20 (0.06)	0.35	0.025
Welgevonden GR	2018	15	1.00 (NA)	0.42 (0.05)	0.28	0.036	15	2.2 (0.9)	0.25 (0.10)	0.67	0.019
Wonderkop NR	2013	15	0.50 (0.09)	0.46 (0.08)	0.94	0.040	9	0.8 (0.3)	0.21 (0.07)	0.98	0.026
Wonderkop NR	2014	15	1.00 (NA)	0.51 (0.06)	0.42	0.046	15	2.4 (1.1)	0.29 (0.13)	0.63	0.022
Wonderkop NR	2015	9	0.56 (0.13)	0.22 (0.06)	0.92	0.027	9	1.0 (0.5)	0.14 (0.07)	0.86	0.016
Zingela NR	2016	9	0.73 (0.11)	0.31 (0.05)	0.92	0.040	9	1.7 (0.8)	0.15 (0.07)	0.85	0.018
Zingela NR	2017	9	0.76 (0.16)	0.23 (0.06)	0.64	0.029	15	2.1 (1.8)	0.14 (0.12)	0.58	0.010
Zingela NR	2018	15	0.85 (0.1)	0.44 (0.07)	0.11	0.038	15	2.6 (1.4)	0.18 (0.09)	0.19	0.013
Manyoni PGR	2015	15	0.64 (0.09)	0.54 (0.07)	0.66	0.050	15	1.1 (0.4)	0.37 (0.11)	0.59	0.030

CHAPTER 4

ESTIMATING TRENDS AND ASSESSING CONSERVATION STATUS FROM TIME SERIES DATA

Abstract

Temporal trends in population abundance or density are usually better indicators of population status and vulnerability than estimates at specific moments in time. Reliably detecting and estimating population-level trends typically requires a decade or more of monitoring. However, delaying action until trends are definitive is at odds with the conservation ethos. An alternative approach is to estimate relative probabilities of key population parameters for a range of outcomes and to manage populations accordingly. Here I use multi-session spatial capture-recapture models within a Bayesian framework to estimate the probability that seven leopard populations within South African protected areas are declining at rates that meet or exceed declines of 30%, 50% or 80% over three leopard generations. Of the seven sites, one (Hluhluwe-iMfolozi Park) had a 0.75 probability of declining by 80% over three generations. At another three sites, declines of at least 50% over three generations were more likely than not (0.56 – 0.76 probability). Only one site (Makalali) had a high probability of positive growth. Overall, the three sites in KwaZulu-Natal Province appeared to fare worse than the four sites in Limpopo province. Together these findings suggest that South African protected areas do not inherently confer protection on leopard populations and that KZN leopards likely face serious threats that must be identified, measured, and addressed.

4.1 Introduction

Declining wildlife populations are a hallmark of the Anthropocene and the associated 6th mass extinction (Young et al. 2016, Ceballos et al. 2017). Population declines lay the foundation for extinction (Purvis et al. 2000), but declines are also inherently ecologically harmful even when the risk of extinction is vanishingly small. The loss of abundance in populations and ecosystems can have widespread cascading effects on ecosystem processes and services (Baker et al. 2019).

Preventing declines is thus a central tenet of biodiversity conservation (Fournier et al. 2019). Population monitoring allows us to assess population status and dictate conservation strategies. Monitoring is most useful when it informs how the study population is changing. For reserve managers and conservationists, the trajectory of a population is more informative for planning and a better measure of conservation success than a snapshot of the status of a population at any given point in time (Rosenblatt et al. 2014). Changes in populations are especially important for guiding sustainable population harvest (Linnell et al. 2010), determining whether a population is at risk of extirpation (Staples et al. 2004), and “impact evaluation” of interventions (Mascia et al. 2014). Long-term monitoring studies that track changes over time can also improve cooperation among scientists and managers, leading to better decision-making and outcomes (Durant et al. 2007).

Determining population trends, however, poses considerable challenges (Fournier et al. 2019). Gathering data repeatedly through time requires substantial resources and necessitates delays in drawing inferences. These difficulties are exacerbated in long-lived species for which changes in populations occur slowly (Morant et al. 2020). In the case of rare, far-ranging, and cryptic species such as large felids, gathering sufficient data requires especially intensive monitoring, with commensurately high demands on resources. Data scarcity is therefore common for these species and population models derived from sparse data often lack sufficient statistical power and are prone to sampling and survey error (Yoccoz et al. 2001, Staples et al. 2004).

Furthermore, trend analyses often assume linear or log-linear relationships between density or abundance and time. However, linear processes, even on the link scale, are the exception, not the rule, to population trends (Clark and Luis 2020) and underlying patterns are typically obscured by stochastic population processes, often referred to as “process variance” or “process error” (Holmes 2001, Staples et al. 2004). Accounting for this variance is essential for accurate trend estimation (Green 2003). As a result, most populations – and especially those of cryptic long-lived species – require at least 10 years (and often 16) of monitoring to achieve sufficient statistical power to confidently detect trends (White 2019).

These demands for intensive, long-term monitoring pose an enormous dilemma – the time needed to reliably measure population trends is often at odds with the acute threats that many species face in the Anthropocene. Conservation science is a crisis discipline and “in crisis disciplines, one must act before knowing all the facts” (Soulé 1985). In statistical terms, conservation is more concerned with type II errors (i.e., failing to detect an effect) than more conventional disciplines (Legg and Nagy 2006). In practical terms, by the time we reliably measure a population in decline, it may be too late to save the population (McDonald-Madden et al. 2010, Authier et al. 2020). How then do we reconcile needing to know the trend in populations when we cannot wait to find out? One approach is adherence to the precautionary principle (Myers 1993), which stipulates that when the potential for harm is especially egregious or irreversible (as is the case when confronting the potential extirpation of a population), we should act even if we are uncertain whether that harm would be realized (Bodansky 2004, Braunisch et al. 2015). This principle demands embracing uncertainty to quantify and plan for a range of possible outcomes (Schindler and Hilborn 2015, Falcy 2016).

The need for the precautionary principle is evident in the management of South Africa’s leopard populations. Long-term analyses of leopard population dynamics are extremely rare (Jacobson et al. 2016). We have very little data on the efficacy of conservation interventions, though Balme et al. (2009) provide an example of how effective interventions can be for leopards when coupled with long-term monitoring. Unlike with other members of the *Panthera* genus (e.g., Antonio De La Torre et al., 2018; Bauer et al., 2015; Goodrich et al., 2015; McCarthy et al., 2017; Riggio et al., 2013), no range-wide assessment of leopard population status exists. As discussed in earlier chapters, leopards face numerous threats such as conflict with livestock farmers and incidental snaring throughout their range and in South Africa specifically. Of particular relevance and concern regionally is the poorly quantified threat from the illegal trade in leopard skins, likely amounting to the harvest of thousands of leopards each year (Naude et al. 2020b). The potential for egregious and irreversible harm to regional populations is obvious. Less obvious is whether South Africa’s network of protected areas sufficiently protects populations from such threats (see Chapter 5). Regionally, a few estimates of leopard density trends exist (Balme et al. 2009b, 2017, Williams et al. 2017a) but they offer no indication of the extent to which the observed trends reflect broader regional patterns versus localized conditions at the respective study sites.

Here I provide a broader investigation of trends in leopard populations in northeastern South Africa. I use probabilistic Bayesian analyses to quantify the probability of declines (Bauer et al. 2015, Falcy 2016) in selected populations in KwaZulu-Natal and Limpopo provinces. I contextualize these results using globally accepted threat assessment standards with the goal of providing novel insights into the long-term status of leopard populations in northeastern South Africa.

4.2 Methods

4.2.1 Data description

I modeled trends in leopard density at seven long-term monitoring sites (protected areas) in Limpopo and KwaZulu-Natal (KZN) provinces that were surveyed at least five times between 2013 and 2018 (7 sites; Table 4.1). Six of the sites were sampled in all six years while Makalali was sampled from 2014 to 2018. Each survey consisted of 30 – 51 camera stations that operated for 43 – 65 days resulting in sampling effort of 1292 – 2721 trap-days per survey (Table 4.1). Study site descriptions and details of data collection and processing are available in Chapter 2.

To avoid duplicating individuals with unmatched left and right flanks within a single session, I arbitrarily included only individuals with an identified left flank. Thus, individuals for whom only a right flank was observed were excluded from analyses. While it is more common to preferentially select the flank with most captures, doing so introduces bias (Augustine et al. 2018). To avoid greater preferential bias in some surveys relative to others within the same model, I used the standardized left-flank approach. I recorded captures as a count of the number of independent observations of each individual at each station (i.e., a “count” trap formulation in *secr* parlance) during each survey (i.e., no independent occasions within each survey as in Chapter 3). I measured trapping effort for each station as the number of trap-days at least one camera was active. Following standard SCR nomenclature, I use “session” to denote each survey, which is assumed to occur at a single point in time defined as the midpoint between when stations were first and last active for each survey. I measured time between each survey in years and use “study period” to denote the entire duration of sampling at each site from the midpoint of the first survey to the midpoint of the last survey. The annual timing of surveys sometimes varied from year to year. Each site thus had a unique study period. To facilitate comparisons of population densities among sites, I recentered time measurements at each site such that time 0 represented the midpoint of each site's study period.

Captures of each individual at each trap were recorded as independent observations if they were non-consecutive or if they occurred at least 8 hours apart, such that leopards could be observed in consecutive crepuscular periods but not, for example, repeatedly observed in the same night. I modeled sex-specific detection functions using a partially observed finite mixture.

***Table 4.1**: Summary of camera-trap surveys at seven long-term leopard monitoring sites (protected areas) in two provinces of northeastern South Africa. Sites were sampled once per year with effort defined as the number of trap-days stations were active.*

Site	**Area (km^2)**	**Province**	**Management**	**Years**	**Stations**	**Effort**
Atherstone	229	Limpopo	State	2013-2018	39-50	1647-2550
Hlulhuwe-iMfolozi (HiP)	904	KZN	State	2013-2018	30-46	1343-2217
Ithala	292	KZN	State	2013-2018	30-36	1340-1545
Makalali	233	Limpopo	Private	2014-2018	40-50	1933-2721
Timbavati	543	Limpopo	Private	2013-2018	40-40	1841-2299
uMkhuze	359	KZN	State	2013-2018	40-41	1740-1992
Welgevonden	339	Limpopo	Private	2013-2018	40-51	1292-2515

The number and locations of stations often varied among sessions at each site as more cameras became available or in response to reserve managers' requests. I therefore treated stations as unique to each survey and constructed an activity matrix that recorded in which session each station was active, with stations being unavailable to capture leopards during sessions when they were inactive.

I projected traps into the custom equidistant conic projection (see Chapter 2) and then converted spatial units from meters to kilometers for computational efficiency. I represented the state space as a continuous rectangle with area A that buffered minimum and maximum X and Y trap coordinates by 12 km for five sites and by 16 kilometers for two sites to ensure that in all cases the buffer was at least 4σ, which corresponds to an expected detection rate approximately three ten-thousandths the magnitude of the baseline detection rate. While I did not exclude non-habitat for these models in the interest of computational efficiency, the extent of non-habitat within these study sites was negligible (see Table S4.4.1).

4.2.2 Model formulation

In contrast to other chapters in this thesis which rely on frequentist statistical inference, here I apply a probabilistic Bayesian framework to estimate the probability that study populations are declining at biologically meaningful rates. Frequentist modeling (i.e., maximum likelihood estimation) for trend analyses determines whether to reject a null hypothesis. It relies on an initial assumption that the population is stable and then quantifies the frequency with which the observed data would occur given that assumption. However, this classical approach poorly represents ecological reality where populations are always in flux. More importantly, studies of wild populations typically lack the statistical power to reliably reject the null hypothesis at time scales suitable for intervening (Authier et al. 2020). Bayesian modelling, on the other hand, allows for calculating the probability that model parameters take certain values. As a result, we can estimate the probability that a population is declining (McBride 2019) or that it is changing at a specified rate (Falcy 2016). Here I take the latter approach. I assume that the observed quantity – in this case leopard density – always exhibits a trend (McBride 2019). While sampling and process error preclude knowing what the trend is with certainty, Bayesian methods allow me to estimate the probability that the trend in leopard density meets a set of standard threat levels. This approach is intended to inform management in the face of uncertainty by quantifying a range of potential outcomes (Schindler and Hilborn 2015).

I applied Bayesian multi-session SCR models for closed populations (Royle and Converse 2014) using data augmentation to define the parameter space (Royle and Young 2008). I adapted the model specification from R package “scrbook” (Royle et al. 2013b). Although individual leopards typically recur in the population from year to year, leopard IDs were not always verified between years. I therefore treated leopards as independent individuals for each year (i.e., individuals observed in multiple years were assigned multiple IDs). Admittedly, the reoccurrence of some individuals in the population can lead to underestimating the variance because capture histories of the same individual in different sessions are treated as independent even though they are not truly (Royle et al. 2013b). However, following the assumptions of Royle et al. (2013, section 14.5), I assume that this effect will be too limited to bias inferences based on interannual and seasonal shifts in individuals’ home range behavior, and in response to life history changes such as breeding behavior.

Unlike in other chapters of this thesis where the state process is defined as a point process with intensity, D, here the state process is an abundance model with density subsequently derived from estimated abundance within the predefined area of the state space. I modeled the expected abundance of leopards within the state space during session t, Λ_t, as a log-linear model such that $\ln \Lambda_t = \beta_0 + \beta_1 \times Time_t$ where e^{β_0} represents the mean (on the log scale) expected abundance during the continuous study period and e^{β_1} represents an annual rate of change in the population. I accounted for process variance around the expected trend using a stochastic realization of population abundance during session t, N_t, according to a multinomial distribution with probability Π_t. The probability, Π_t, that individual i occurred in the population during session t was derived from the expected abundance according to the formula $\Pi_t = \frac{\Lambda_t}{\sum \Lambda}$. In other words, the realized abundance during session t is assumed to deviate from the expected abundance according to the variance of a multinomial process such that $var(N_t) = \Pi_t(1 - \Pi_t) \times \sum \Lambda$.

I specified the size of the augmented population, M, for each site to ensure it exceeded maximum estimated densities reported in Chapter 3 and I ran posterior checks to confirm that all posterior samples for abundance were well below M (see Table S4.4.2). Each individual i in the augmented population M was counted towards the "true" population N following a Bernoulli distribution, Z_i, with probability Ψ derived from the cumulative expected population according to the formula $\Psi = \frac{1}{M} \sum \Lambda$. Each individual in the true population has a latent activity center distributed within the state space independently of other individuals with location S_i. I included a partially observed $Year$ variable of length M in the model to designate which session each year-unique individual occurred in the population, with $Year_i$ known for observed individuals and estimated for unobserved individuals. The realized abundance, N_t, was derived from the number of individuals for which $Year_i = t$ and $Z_i = 1$. Leopard density per 100 km^2 was calculated as $100 \times \frac{N_t}{A}$ where A is the area of the state space.

Following the methodology and assumptions of Rocha et al. (2016) and Satter et al. (2019), I assumed that the detection process and underlying behavioral processes were constant from year to year for each sex at each site on the basis that ecological conditions were largely consistent and pooling data across sessions reduces the influence of sampling error (Mohamed et al. 2013). In other words, I assumed that while individual space use (home range size and speed of movement) varied from year to year, the population mean remained constant. I modeled the expected number of captures of leopard i at station j as a zero-inflated Poisson process. Individuals were not detected at most stations either because individual i was not in the "true" population (i.e., $Z_i = 0$) or because individual i occurred in the population during a session when station j was not operational. I used the zero-inflated Poisson process to efficiently account for these "structural zeroes" by negating the need to calculate the expected number of captures when captures were structurally impossible (Turek et al. 2021). In the absence of a structural zero, the number of observations of individual i at station j was modeled as a Poisson process with an expected number of captures, $\lambda_{i,j}$, that decreased as a function of the distance between station j and leopard i's latent activity center, $d_{i,j}$, following a hazard half-normal detection function with a spatial decay parameter, σ, measured in kilometers and a baseline detection rate, λ_0. I included station effort, K_j, as a linear term on the detection model and estimated separate σ and λ_0 values for males and females. Unsexed or unobserved individuals were estimated as female or male following a Bernoulli distribution with probability ψ_{sex}. The detection model in the case of non-structural zeroes was thus specified as:

$$\lambda_{ij} = K_j \times \lambda_{0,Sex_i} \times e^{\left(\frac{-d_{ij}{}^2}{2\sigma_{Sex_i}{}^2}\right)}$$

I set uninformed or slightly informed priors for all model parameters. β_0 was drawn from a uniform distribution with limits based on the mean number of observed individuals in each session and the maximum theoretical population M. β_1 was drawn from a normal distribution with mean 0 and standard deviation of 1. I accounted for the 0 bound on λ_0 by defining the prior distribution for the baseline detection rate using a log-transformation such that $\alpha_0 = \ln \lambda_0$, with α_0 drawn from an uninformed diffuse prior for males and females. I defined σ using a uniform prior distribution between 0 and 12 kilometers and ψ_{sex} was defined as uniformly distributed between 0 and 1. Latent activity centers for each individual were uniformly distributed across the state space (see Appendix 4.3 for details of the model code).

4.2.3 Model implementation and evaluation

I fit models using Markov-chain Monte Carlo simulations in R package *nimble* v. 0.9.1 (de Valpine et al. 2017, 2020). I set slice samplers for β_0, β_1, σ, ln λ_0, ψ_{sex}, and S to reduce autocorrelation within chains, but retained the default binary samplers for Z and Sex and a categorical sampler for $Year$ (Anton 2020). I randomly generated initial values for unobserved variables. In the case of variables with uninformed priors, I drew initial values from distributions based on previous models of leopard populations (see Appendix 4.3 for details). For each site I ran three MCMC chains for 30000 iterations, of which I discarded the first 5000 as burn-in samples, thus retaining a total of 75000 posterior samples. I confirmed that chains converged adequately using the Gelman-Rubin statistic (Gelman and Rubin 1992) in R package *coda* v. 019-3 (Plummer et al. 2006) and by manually checking posterior distributions. I evaluated trace plots to ensure burn-in samples were sufficient.

4.2.4 Trend assessment

I derived biologically meaningful thresholds of decline based on the IUCN Red List criteria for identifying populations or species of conservation concern (IUCN Species Survival Commission 2000). One criterion is based on population trends over ten years or three generations, whichever is greater, to account for differences in life history among species. Stein et al. (2016) reported a three-generation duration of 22.3 years (7.42 years per generation) based on reproductive histories of leopards in a protected population free from human-induced mortality (Balme et al. 2013). I therefore evaluated conservation concern based on the cumulative expected change in density over 22.3 years.

IUCN criteria further distinguish between declines resulting from threats that “are clearly reversible and understood and ceased” versus those stemming from threats that “have not ceased or may not be understood or may not be reversible” (IUCN Species Survival Commission 2000). As snaring (Becker et al. 2013, Loveridge et al. 2020), habitat loss (Jacobson et al. 2016), conflict with livestock farmers (Pitman et al. 2017b, Williams et al. 2017a), and the illegal trade in leopard furs (Dickman et al. 2015, Williams et al. 2017b, Naude et al. 2020b) are ongoing threats to leopards in southern Africa (see Chapter 2), I applied thresholds of decline based on threats that have not ceased according to the A.2. criterion for each category: critically endangered (“Cr”, ≥80% reduction), endangered (“En”, ≥50% reduction), and vulnerable (“Vu”, ≥30% reduction). Population reductions of these magnitudes over three generations (i.e., 22.3 years) correspond to annual growth rates of 0.930, 0.969, and 0.984 for Cr, En, and Vu, respectively, and values of -0.072, -0.031, and -0.016, respectively, for the log-linear slope parameter, β_1. I report the probability that the true population rate of change at each site meets the criterion for each of the three categories based on the proportion of the posterior distributions for β_1 for each site that exceed the aforementioned thresholds on the log-linear scale. I offer conservation recommendations commensurate with the threat assessment of each site.

4.3 Results

4.3.1 Data summary

Individual surveys recorded between 14 and 41 individuals (median = 23; Table 4.2). Atherstone and Welgevonden consistently recorded the fewest individuals, while other sites were more variable. Spatial recaptures per survey varied between 6 and 88 (median = 38). The number of independent captures per survey varied between 29 (15 individuals) and 279 (25 individuals), corresponding to 1.9 – 11.2 captures per individual (median = 4.2). Capture rates at some sites were highly variable among years. For example, Hluhluwe-iMfolozi (hereafter "HiP") recorded 44 independent captures of 23 individuals with just 6 spatial recaptures in 2013 when the survey consisted of 30 stations, and 58 – 156 independent captures of 17 – 35 individuals with 19-49 spatial recaptures in subsequent years when surveys included 46 stations. Atherstone was more consistent, with between 14 and 18 individuals observed per year, but the number of captures still varied three-fold and spatial recaptures varied four-fold, from 96 captures and 43 spatial recaptures in 2013 to 29 and 10, respectively, in 2018 (see Appendix 4.2 for details). Four out of every five surveys recorded more females than males, however, Timbavati recorded five more males than females in both 2013 and 2016. By comparison, some surveys at Ithala recorded twice as many females as males. Thirty-three surveys recorded at least one individual for which sex could not be identified with certainty. The number of unsexed individuals was typically five or fewer, except for the Makalali 2018 survey which recorded 12 unsexed individuals.

Table 4.2*: Summary of the number of individual leopards, independent captures, spatial recaptures, and observed males and females recorded at each site across multiple surveys.*

Site	No. Surveys	No. Individuals	No. Captures	No. Spatial Recaptures	No. Females	No. Males
Atherstone	6	14-18	29-96	10-43	6-13	2-7
Hluhluwe-iMfolozi	6	17-35	44-156	6-49	8-22	7-13
Ithala	6	25-38	124-267	33-58	16-22	6-15
Makalali	5	19-31	79-139	26-62	9-16	7-13
Timbavati	6	22-41	82-146	24-42	10-22	8-18
uMkhuze	6	20-32	94-279	36-88	11-17	7-13
Welgevonden	6	15-23	57-136	22-60	7-13	5-10

4.3.2 Posterior evaluation

Models for all seven sites converged adequately and trace blots were stable, indicating adequate burn-in. Gelman-Rubin statistics were all below 1.01 and maximum estimates of N were below 65% of the augmented population, M, for all sites. Effective sample size exceeded 1500 for all monitored variables, with an interquartile range across all sites and parameters of interest between 3975 and 8656. State spaces for each site included less than 1% non-habitat and the state space buffer was at least three times greater than the maximum σ estimate for each site except uMkhuze, where the buffer was 2.96 times maximum σ (see Appendix 4.4 for additional details of posterior checks, Appendix 4.5 for trace plots, and Appendix 4.6 for posterior distributions).

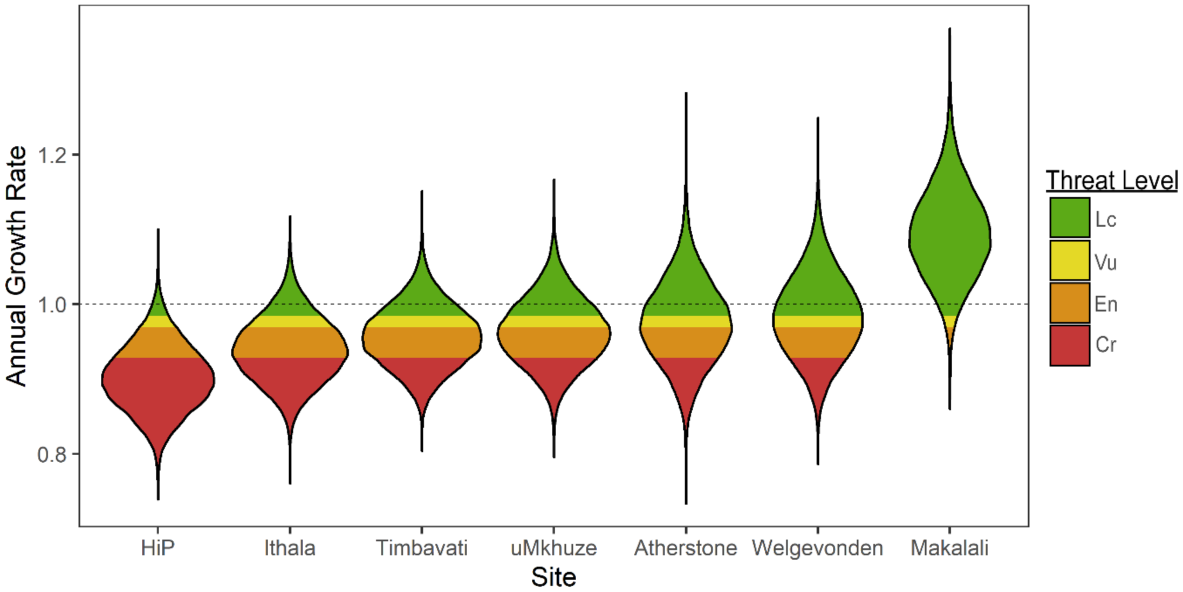

Figure 4.1*: Posterior distributions of the expected annual growth rate and corresponding threat levels for seven long-term monitoring sites: Least concern (“Lc”), Vulnerable (“Vu”), Endangered (“En”), and Critically endangered (“Cr”). Annual growth rates are derived from the slope parameter, β_1, in the log-linear temporal trend models. A growth rate of 1 (dashed line) corresponds to constant density.*

4.3.3 Population trends

Posterior means of the annual growth rates were less than 1 for six of the seven sites (see Table 4.3 for details). As expected, uncertainty in population growth rates was high and only one site, HiP, exhibited a 95% HPD that did not overlap 0. The posterior distributions of β_1 were especially diffuse for the scarcely populated sites of Welgevonden and Atherstone, but also for Makalali (Fig. 4.1). The latter site exhibited strong evidence of population growth, with a mean annual growth rate of 1.092 and a 95% HPD of 0.98 – 1.22. Among the other six sites, mean posterior growth rates were between 0.983 at Welgevonden and 0.901 at HiP, with greater than 95% confidence that the latter population declined during the study period (95% HPD: 0.82 – 0.99). Although I could only ascertain the direction of the trend for HiP with a high degree of certainty, posterior distributions for β_1 indicated at least a 60% chance that four of the populations viz., HiP, Ithala, Timbavati, and uMkhuze, declined during the study period at rates exceeding the threshold for "Vulnerable" populations and for all of those sites, except uMkhuze, at least 60% of their posterior samples met the "Endangered" threshold. HiP, however, was the only site more likely than not ($p_{Cr} = 0.74$) to have declined at a rate commensurate with the "Critically Endangered" classification.

***Table 4.3**: Posterior statistics (mean and 95% highest posterior density, "HPD") of expected leopard abundance within the state space and cumulative probabilities of threat categories. Mean state-space abundance (i.e., at the midpoint of the sampling period) and annual growth rate are derived from the parameters of the log-linear trend in expected population, β_0 and β_1. Threat probabilities represent the cumulative probability that annual growth rates exceed the thresholds of decline over three leopard generations for critically endangered (>80%, "Cr"), endangered (>50%, "En"), and vulnerable (>30%, "Vu") threat levels.*

	STATE-SPACE ABUNDANCE	**ANNUAL GROWTH RATE**	**THREAT PROBABILITY**		
Site	**Mean (95% HPD)**	**Mean (95% HPD)**	**Cr**	**En**	**Vu**
Hluhluwe-iMfolozi	117 (98-138)	0.90 (0.82-0.99)	0.74	0.93	0.96
Ithala	125 (107-144)	0.94 (0.86-1.03)	0.42	0.76	0.85
Timbavati	159 (138-183)	0.96 (0.88-1.04)	0.26	0.62	0.75
uMkhuze	96 (81-113)	0.96 (0.88-1.05)	0.23	0.56	0.69
Atherstone	95 (77-118)	0.97 (0.87-1.09)	0.21	0.47	0.57
Welgevonden	85 (69-104)	0.98 (0.88-1.10)	0.17	0.41	0.51
Makalali	112 (94-134)	1.09 (0.98-1.22)	<0.001	0.02	0.03

4.3.4 Population density

Three sites (Welgevonden, Atherstone, and HiP) exhibited sparse densities of approximately 4 leopards per 100 km^2 (Figs. 4.2, 4.3), three other sites – Makalali, uMkhuze, and Ithala – exhibited moderate density of approximately 7 leopards per 100 km^2, while Timbavati hosted a markedly denser population than other sites of approximately 9 leopards per 100 km^2. Although Atherstone and Welgevonden might be expected to host sparser populations because their climates are more xeric than the other study sites, that would not be the case for HiP, which has a similar climate to the moderate and high-density sites.

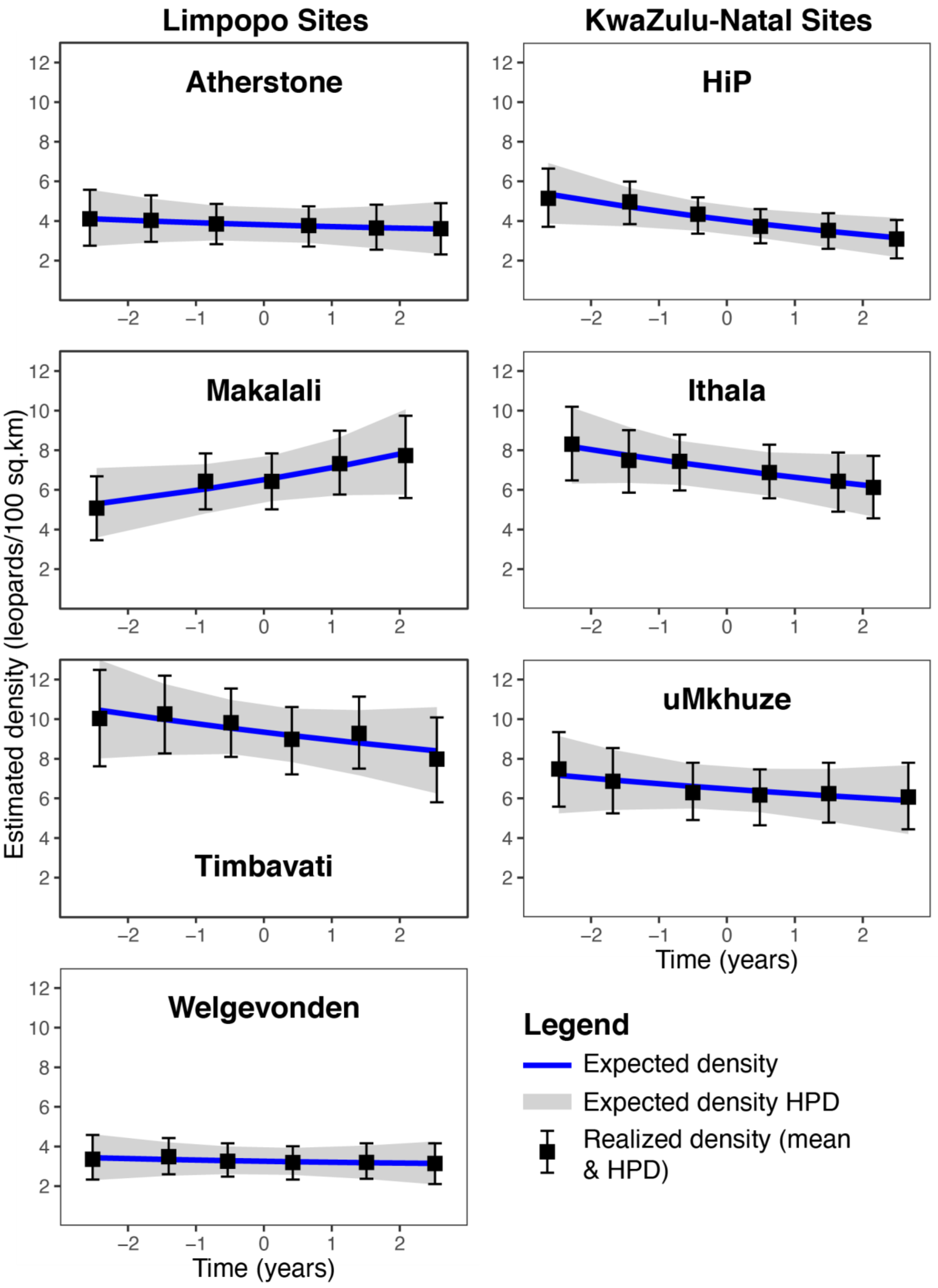

Figure 4.2: *Posterior means and 95% highest posterior densities (HPDs) of expected (lines and shaded regions) and realized (dot and whisker plots) leopard population density per 100 km^2 over time at seven long-term leopard monitoring sites in northeastern South Africa. Time is measured in years from the temporal midpoint of the study period at each site. Expected density is derived from Λ_t and the area of the state space. Realized density is the reported posterior distribution derived from N_t.*

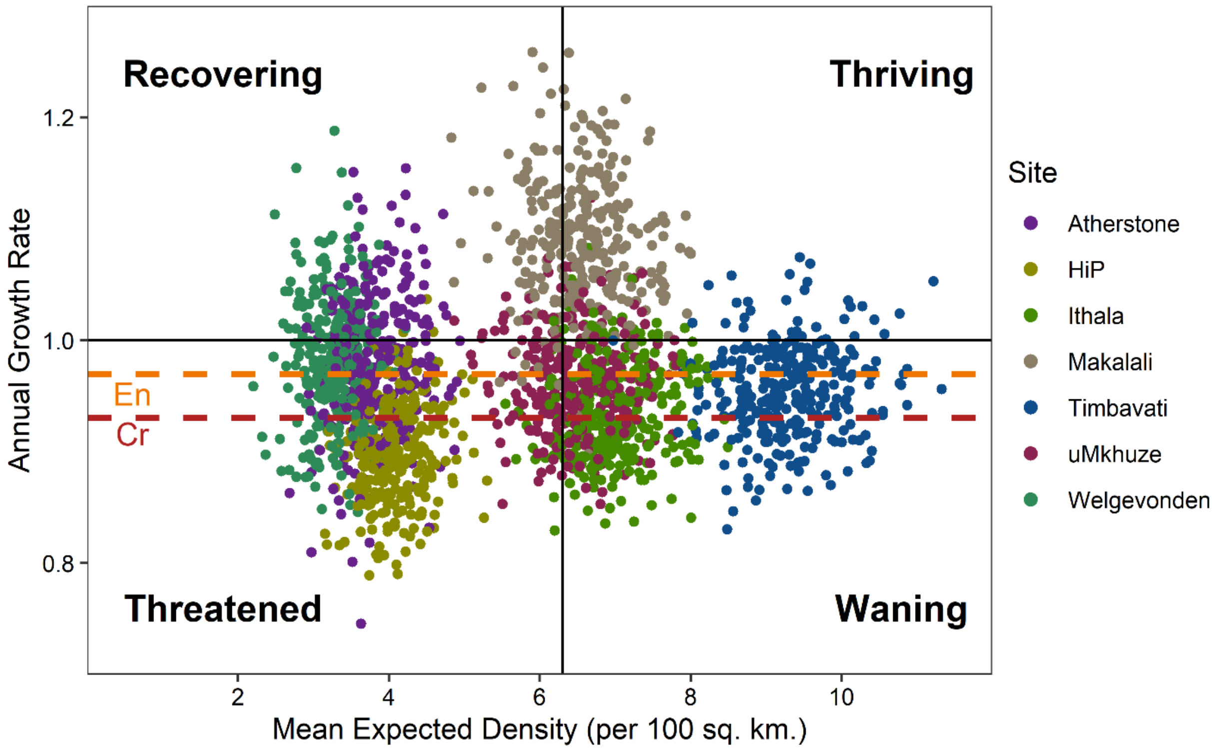

Figure 4.3*: Conservation status of posterior distributions of annual growth rates and mean expected densities (i.e., at the temporal midpoint of the study periods) for seven long-term leopard monitoring sites in northeastern South Africa. Mean expected density and annual growth rates were derived from the intercept and slope parameters of the log-linear model of expected abundance such that mean expected density was calculated as $e^{\beta_0} \div Area \times 100$ and the annual growth rate was calculated as e^{β_1}. Endangered ("En") and Critically Endangered ("Cr") correspond to population declines of at least 50% and at least 80% over three leopard generations (22.3 years), respectively. The threshold of 6.3 leopards per 100 km^2 for low vs. high densities was based on the median density for all 88 surveys reported in Chapter 3. Posterior samples were thinned by 250 for display purposes, yielding 300 posterior samples for each site included in the plot.*

Despite the likelihood of declines at most of these sites, HiP accounted for half of the cumulative expected net loss in leopard abundance within PAs across all seven sites (Table 4.4). The combination of a large PA (904 km^2) and a severe negative growth rate translated into substantial estimated losses in abundance (-18 individuals) for HiP. Changes in mean leopard abundance at Welgevonden and Atherstone, two small reserves with sparse populations and modest estimated negative growth rates, were trivial at -0.5 and -1.1 leopards, respectively.

4.3.5 Detection

Males exhibited greater σ estimates than females at all seven sites with a mean difference ranging from 0.5 km at HiP to 1.6 km at uMkhuze (Fig. 4.4). Female σ ranged from 1.6 ± 0.1 km at Ithala, Timbavati, and uMkhuze to 2.5 ± 0.1 km at Welgevonden, while male σ ranged from 2.2 ± 0.1 km at Timbavati to 4.0 ± 0.2 km at Welgevonden (Table 4.5). Differences in baseline detection rates between the sexes were less consistent, with males more detectable than females at three sites (i.e., $\Delta\lambda_0 > 0.01$) and equally detectable at the remaining four sites (i.e., $|\Delta\lambda_0| < 0.005$). Posterior means for female baseline detection rates varied between 0.02 captures per day at Atherstone, Makalali, Timbavati, and Welgevonden, and 0.07 per day at Ithala. Male baseline detection rates were more varied, with posterior means between 0.015 at Atherstone and 0.087 at Ithala. Males accounted for a quarter to two-fifths of each population.

__Table 4.4__: Expected change in abundance of leopards with activity centers located within each protected area (N_{PA}) from 2013 to 2018 (2014-2018 for Makalali, which was not sampled in 2013) for seven long-term leopard monitoring sites. Density is reported as the posterior mean for the respective years. N_{PA} is derived from posterior density and the area of each PA. ΔN_{PA} is summarized for all posterior samples.

Site	**Area (km^2)**	**Density ($100\ km^{-2}$)**		**Mean N_{PA}**		**ΔN_{PA}**		
		2013	2018	2013	2018	Median	1st quartile	3rd quartile
HiP	904	5.1	3.1	46	28	-18	-25	-12
Timbavati	543	10.0	8.0	54	43	-11	-18	-4
Ithala	292	8.3	6.1	24	18	-6	-9	-4
uMkhuze	359	7.5	6.1	27	21	-5	-8	-2
Atherstone	229	4.1	3.6	9	8	-1	-3	1
Welgevonden	339	3.4	3.1	11	10	-1	-3	1
Makalali	233	*5.1	7.7	*12	18	6	4	8

*2014 estimates for Makalali

Table 4.5: Posterior estimates (mean and standard deviation) of detection parameters α_0, λ_0, and σ for adult male and female leopards at seven long term leopard monitoring sites. α_0 represents a log transformation of the baseline detection rate, λ_0. ψ_{sex} represents the estimated sex ratio of the population.

Site	**Female α_0**	**Male α_0**	**Female λ_0**	**Male λ_0**	**Female σ**	**Male σ**	**ψ_{sex}**
Atherstone	-3.94 (0.12)	-4.21 (0.16)	0.019	0.015	2.2 (0.1)	3.0 (0.3)	0.27 (0.05)
HiP	-3.68 (0.11)	-3.25 (0.09)	0.025	0.039	2.1 (0.1)	2.6 (0.1)	0.34 (0.04)
Ithala	-2.67 (0.07)	-2.44 (0.06)	0.069	0.087	1.6 (0.1)	2.4 (0.1)	0.26 (0.03)
Makalali	-3.86 (0.11)	-3.65 (0.09)	0.021	0.026	1.9 (0.1)	2.7 (0.1)	0.33 (0.04)
Timbavati	-3.76 (0.10)	-3.60 (0.09)	0.023	0.027	1.6 (0.1)	2.2 (0.1)	0.39 (0.04)
uMkhuze	-3.02 (0.07)	-3.12 (0.08)	0.049	0.044	1.6 (0.1)	3.2 (0.2)	0.25 (0.03)
Welgevonden	-3.97 (0.12)	-3.43 (0.08)	0.019	0.032	2.5 (0.1)	4.0 (0.2)	0.31 (0.05)

4.4 Discussion

Preventing population declines is a central aim of biodiversity conservation. Monitoring is a critical tool for assessing population trends and crafting interventions, but the time scales necessary for measuring population trends of long-lived species are at odds with the urgency

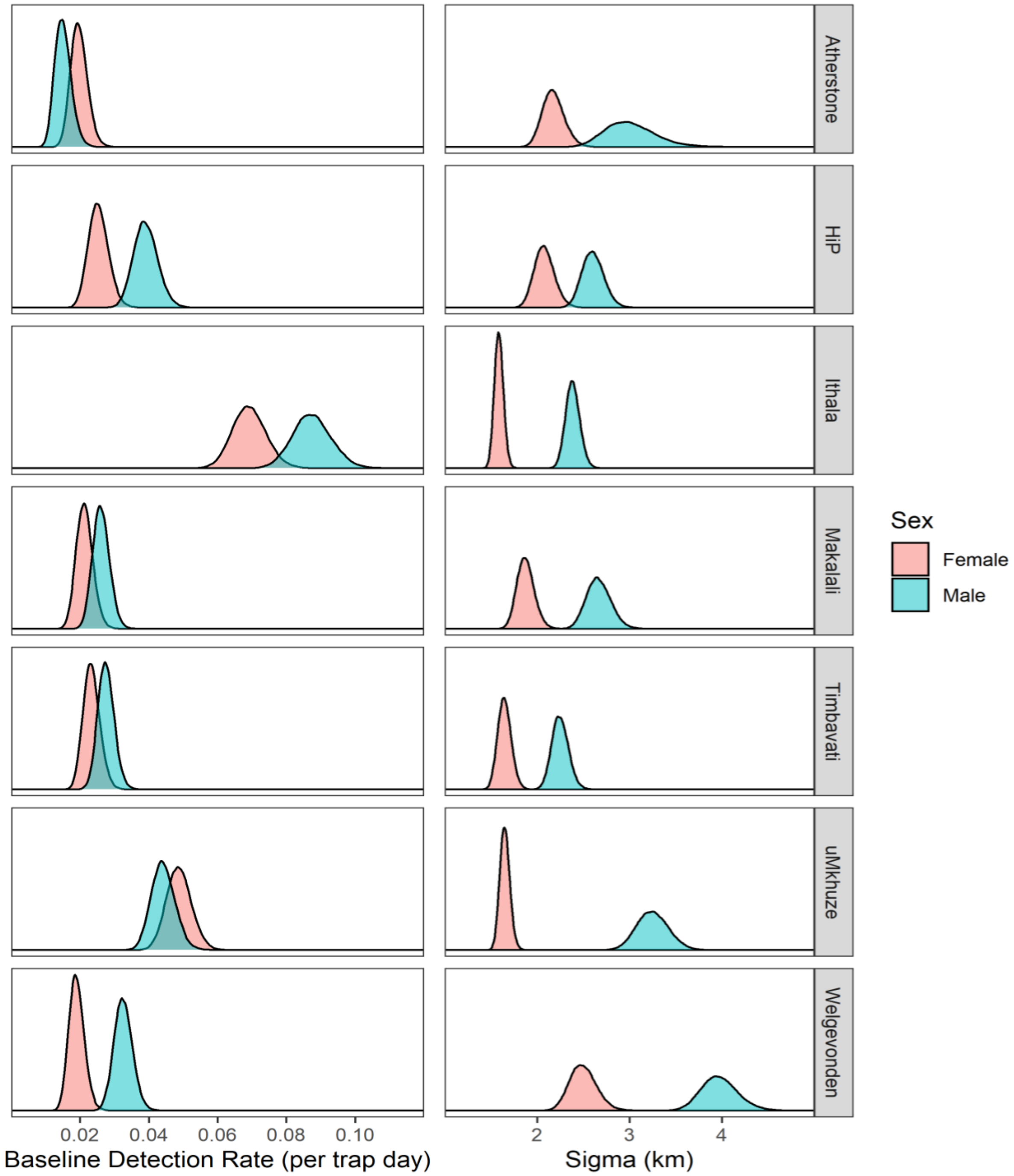

Figure 4.4*: Posterior densities of the detection parameters for males and females. Baseline detection rate (λ_0) represents the expected number of captures of an individual at a trap located at the individual's activity center. σ represents the spatial decay parameter in the hazard half-normal detection model.*

of conservation. Large-carnivore populations have repeatedly exhibited vulnerability to anthropogenic threats, even populations that occur inside protected areas (Brugière et al., 2015; Watson et al., 2013; Woodroffe, 1998). South Africa's leopard populations are no different (Balme et al. 2010b, Swanepoel et al. 2015c, Williams et al. 2017a). I investigated temporal trends in leopard density at seven prominent state or private reserves in northeastern South Africa to determine the conservation status of these populations. I aimed to quantify the probability of a range of outcomes in the hopes that conservationists and PA managers can better prioritise the need for immediate interventions versus ongoing monitoring. The data presented here comprise an unprecedented long-term (i.e., 5+ years) multi-site monitoring dataset for leopards in southern Africa. For a species generally lacking in robust population estimates (Balme et al. 2014; Jacobson et al. 2016), these data are an important contribution to our understanding of leopard population status in the region.

Although the monitoring period was long relative to other studies for this species, it was nevertheless too short to be confident of definitively detecting or estimating trends for a relatively long-lived species (White 2019). Thus, it is no surprise that estimates of temporal trends in density were highly uncertain and, except for Hlhluwe-iMfolozi Park, confidence that populations truly declined was low (i.e., < 90%). Managing such uncertainty remains a core component of ecological decision making and adaptive management (Artelle et al. 2013). Overall, I found sufficient evidence of decline among most sites to warrant concern. As a preliminary finding to guide current management of leopards in South Africa, these results point to widespread loss of leopards within select South African protected areas, including flagship provincial reserves (e.g., HiP).

Leopard populations in the three KwaZulu-Natal provincial reserves appeared to fare poorly compared to their Limpopo counterparts. The mean estimates of decline were 4-10% per year with greater than two-thirds probability that populations at the three sites declined at rates that exceed a 30% loss over three leopard generations. At HiP, which meets the “Vulnerable” criterion with greater than 95% confidence, the population was estimated to have already declined by 30% after just five years of monitoring. While these rates are not as severe as the decline reported for a population in the Soutpansberg Mountains (Williams et al. 2017a), these populations exhibited lower initial densities when the sampling period began. In accordance with the precautionary principle, I would urge KZN wildlife managers to develop interventions directed at leopard conservation.

In contrast, the Limpopo study sites exhibited some signs for optimism. Densities at Atherstone and Welgevonden were sparse but essentially stable and Makalali exhibited strong evidence of a thriving population (i.e., reasonably dense and growing, Fig. 4.3). It is unsurprising that

Atherstone and Welgevonden host sparse leopard populations because of their relatively xeric landscapes. I therefore do not consider these populations to be highly threatened.

While Timbavati declined more likely than not during the study period, it started with a high density and the estimated decline may be the result of density-dependent fluctuations rather than systematic loss of leopards (Knape and de Valpine 2012), with monitoring coinciding with a period of temporary decline or reversion to a long-term mean (Fournier et al. 2019). Timbavati is also part of one of the largest contiguous leopard populations in the world in the greater Kruger ecosystem and its population may be especially transient; immigration rates may be higher than in more fragmented populations. As a result, it might be unusually variable. Evidence for this can be found in Chapter 3, where density was mostly estimated between 12 and 15 leopards per 100 km^2, but dipped to an estimated 7.2 leopards per 100 km^2 in 2016 before rebounding in 2017 and 2018. The multisession model presented here smoothed some of that variability. Timbavati remained the most densely populated site among the seven investigated here, with a considerably higher population density than in most other parts of the greater Kruger system (L. Smyth, unpublished data). It was, however, slightly sparser than the nearby, similarly managed Sabi Sands Game Reserve, which serves as a baseline population for leopards free from anthropogenic mortality (Balme et al. 2019). Monitoring should continue, but there is currently no evidence that the population is in jeopardy.

The same clearly cannot be said for HiP. It was the only site with posterior distributions that fell almost entirely within the “Threatened” quadrant (Fig. 4.3). Despite the evidence of declines in density at uMkhuze and Ithala, leopard populations at those sites remain at or slightly above the regional median. They are sufficiently abundant that the persistence of their populations in the short term does not currently seem in doubt. That HiP’s leopard population is two thirds as dense and declining twice as fast as the uMkhuze and Ithala populations despite their similar habitats and management regimes crystalizes just how poorly that population is faring. I conclude that HiP’s leopard population should be deemed critically endangered. Its extirpation is a distinct possibility.

The models presented here achieved the goal of quantifying probabilistic outcomes for select leopard populations and identifying where population declines were highly probable. However, they are still founded an assumption of linearity (on the log scale) and constant trends. The deviance between realized abundance and expected abundance was trivial and unquestionably understates how erratic populations can be in response to short-term variation (Werner et al.

2020). As the monitoring program accumulates more data, more sophisticated models will be necessary to better understand population processes. Non-linear responses to ecological thresholds (Qi et al. 2020) could be investigated. Open-population SCR models that track outcomes for individuals from year to year (Gardner et al. 2010, Schaub and Royle 2014) or time-series models that directly estimate variance components (Winker et al. 2018) could offer additional insights from future analyses. Additionally, errors in trend detection are especially sensitive to variance in the observation process (Nuno and Bunnefeld 2014). More robust survey designs could greatly improve the leopard monitoring programs capacity for detecting and measuring trends (see Chapter 6).

4.4.1 Implications for management

Although estimated trends were uncertain, I have attempted to quantify that uncertainty and then offer recommendations accordingly (Reckhow 1994, Artelle et al. 2013). Crucially, we must consider the socio-ecological context within which these populations persist. While this study did not directly investigate threats to these populations and sources of mortality, those threats have been clearly established elsewhere (Balme et al. 2010a, Pitman et al. 2015, Swanepoel et al. 2011, Swanepoel et al. 2015b, Williams et al. 2017a, and see Chapter 1 for further details). Though leopards are renowned for being widespread and adaptable, they are vulnerable, including within protected areas (Swanepoel et al. 2014, Brugière et al. 2015, Jacobson et al. 2016). The mere presence of a protected area has not been sufficient to conserve other large felids (Craigie et al. 2010, Bauer et al. 2015, Durant et al. 2017), and that appears to be the case for leopards, too. Stakeholders need more focused efforts to address the threats facing leopards in order to safeguard these populations and the ecosystems in which they live.

In Chapter 5 I investigate the environmental conditions and management characteristics that are most conducive to maintaining high leopard densities within PAs. Here I show that the results of temporal trends reveal that the HiP leopard population needs immediate intervention to halt and ultimately reverse its decline. HiP leopards are clearly facing sustained threats that have not been adequately measured or addressed. Data on retaliatory killings and destruction permits due to conflict with farmers and game ranchers (Swanepoel et al. 2014, Pitman et al. 2015) are scarce for KZN province. Even more concerning is the demand for leopard furs from followers of the Shembe Church whose support base is greatest in KZN (Naude et al. 2020b). Almost certainly some of the demand for leopard skins has been met from what would once have been the largest leopard population in the province (HiP), as well as from the nearby Ithala and uMkhuze populations. Precaution dictates that actions be taken to further protect leopards in KZN’s provincial reserves while simultaneously addressing the illegal demand for leopard skins as religious symbols. Measuring this loss and reducing its harm should be considered the most pressing issue in KZN leopard conservation, and possibly for South African leopards generally.

Appendix 4.1: Survey summary

Site	Year	No. of Stations	*Effort	#Sampling duration
Atherstone	2013	50	2550	51
Atherstone	2014	40	2160	54
Atherstone	2015	39	2067	53
Atherstone	2016	40	1852	50
Atherstone	2017	40	1647	43
Atherstone	2018	40	1815	48
HiP	2013	30	1343	45
HiP	2014	46	2035	46
HiP	2015	46	2040	45
HiP	2016	46	2031	45
HiP	2017	46	2120	53
HiP	2018	46	2217	57
Ithala	2013	36	1545	45
Ithala	2014	31	1340	45
Ithala	2015	31	1349	45
Ithala	2016	30	1345	45
Ithala	2017	30	1473	51
Ithala	2018	30	1438	53
Makalali	2014	50	2721	59
Makalali	2015	40	2231	65
Makalali	2016	40	1982	51
Makalali	2017	40	2205	56
Makalali	2018	40	1933	50
Timbavati	2013	40	1882	60
Timbavati	2014	40	2139	56
Timbavati	2015	40	2299	60
Timbavati	2016	40	1935	50
Timbavati	2017	40	2104	55
Timbavati	2018	40	1841	47
uMkhuze	2013	41	1827	45
uMkhuze	2014	40	1740	45
uMkhuze	2015	40	1759	45
uMkhuze	2016	40	1784	45
uMkhuze	2017	40	1992	56
uMkhuze	2018	40	1897	50
Welgevonden	2013	51	2515	51
Welgevonden	2014	40	1951	58
Welgevonden	2015	40	1838	51
Welgevonden	2016	40	1292	44
Welgevonden	2017	40	2149	56
Welgevonden	2018	40	1961	51

*Number of trap-days

#Maximum number of trap-days for a single station

Appendix 4.2: Capture summary

Site	Year	Individuals	Captures	Spatial recaptures	Females	Males
Atherstone	2013	16	96	43	8	7
	2014	18	62	19	13	4
	2015	16	61	14	11	2
	2016	16	32	13	10	4
	2017	14	43	14	7	3
	2018	15	29	10	6	5
HiP	2013	23	44	6	11	11
	2014	35	156	49	22	13
	2015	28	113	39	15	12
	2016	19	58	19	12	7
	2017	22	81	29	13	8
	2018	17	75	31	8	8
Ithala	2013	38	236	58	22	12
	2014	29	185	40	18	10
	2015	33	267	52	18	15
	2016	30	134	38	19	9
	2017	28	124	33	18	8
	2018	25	138	35	16	6
Makalali	2014	19	79	33	10	7
	2015	31	139	62	16	10
	2016	23	89	26	10	11
	2017	31	109	39	16	13
	2018	28	90	33	9	7
Timbavati	2013	29	82	26	12	17
	2014	41	146	42	22	18
	2015	40	113	38	21	17
	2016	29	106	40	10	15
	2017	40	122	41	21	17
	2018	22	90	24	13	8
uMkhuze	2013	32	138	50	15	13
	2014	25	133	50	17	7
	2015	20	97	40	11	8
	2016	21	94	36	11	9
	2017	25	168	65	14	7
	2018	25	279	88	13	9
Welgevonden	2013	17	136	60	9	8
	2014	23	91	37	13	10
	2015	18	113	52	9	9
	2016	15	57	22	7	8
	2017	19	86	37	7	8
	2018	18	84	38	8	5

Appendix 4.3: NIMBLE model code

```
###Randomly generate over dispersed initial values


initFun <- function(){
 yr_obs <- which(is.na(data$yrid) == F) #rows for observed individuals
 yr_st <- sample(1:constants$nt, constants$bigM, replace = T) #randomly assign year to…
 yr_st[yr_obs] = NA                                          #…unobserved individuals


 Zst <- rbinom(constants$bigM, 1, 0.5) #randomly assign individuals to “true” population
 Zst[yr_obs] <- NA


 sex_obs <- which(is.na(data$Sex) == F) #individuals with known sex
 Sex_st <- rbinom(constants$bigM, 1, 0.5) #randomly assign sex to unsexed individuals
 Sex_st[sex_obs] <- NA


 S_obs <- do.call(rbind, S.list) #mean capture locations of observed individuals
 S_st <- cbind(runif(constants$bigM, constants$xmin, constants$xmax),
             runif(constants$bigM, constants$ymin, constants$ymax)) #randomly generate…
               #...activity centers within state space
 for(i in 1:length(yr_obs)){
  S_st[yr_obs[i], 1:2] <- S_obs[i, 1:2] #replace random activity centers of observed
                                         individuals with mean #capture location
 }


 init_out <- list(
  psi = runif(1, exp(constants$bmin)*constants$nt/constants$bigM, 1), #randomly generate
       psi … #... init value between minimum observed proportion of M and 1
  psi.sex = runif(1, 0.1, 0.8), #proportion male init between 0.1 and 0.8
  alpha0 = rnorm(2, -3.5, 1),
  sigma = runif(2, 1, 7), #sigma inits of between 1 and 7 kilometers
  beta0 = runif(1, constants$bmin, constants$bmax), #randomly generate init for mean
       expected #abundance between minimum number of observed individuals and
       augmented population size
  beta1 = rnorm(1, 0, 0.1), #slightly informed prior based on ecological plausibility
  z = Zst,
```

```
    yrid = yr_st,
    S = S_st,
    Sex = Sex_st)

  return(init_out)
}
```

```
###Specify zero-inflated Poisson distribution
##nimbleFunction adopted from https://r-nimble.org/nimbleExamples/zero_inflated_poisson.html
dZIP <- nimbleFunction(
  run = function(x = integer(), lambda = double(),
                zeroProb = double(), log = logical(0, default = 0)) {
    returnType(double())

## First handle non-zero data
    if (x != 0) {
      ## return the log probability if log = TRUE
      if (log) return(dpois(x, lambda, log = TRUE) + log(1 - zeroProb))
      ## or the probability if log = FALSE
      else return((1 - zeroProb) * dpois(x, lambda, log = FALSE))
    }
    totalProbZero <- zeroProb + (1 - zeroProb) * dpois(0, lambda, log = FALSE)
    if (log) return(log(totalProbZero))
    return(totalProbZero)
  })

rZIP <- nimbleFunction(
  run = function(n = integer(), lambda = double(), zeroProb = double()) {
    returnType(integer())
    isStructuralZero <- rbinom(1, prob = zeroProb, size = 1)
    if (isStructuralZero) return(0)
    return(rpois(1, lambda))
  })
```

```
#register custom distribution with nimble
registerDistributions(list(
  dZIP = list(
    BUGSdist = "dZIP(lambda, zeroProb)",
    discrete = TRUE,
    range = c(0, Inf),
    types = c('value = integer()', 'lambda = double()', 'zeroProb = double()')
  )))
```

```
###Specify model code
##Priors
mod_code <- nimbleCode({
  beta0 ~ dunif(bmin, bmax)
  beta1 ~ dnorm(0,1)
  psi.sex ~ dunif(0,1)
  psi <- sum(lambda[1:nt])/bigM

  for(sx in 1:2){
    alpha0[sx] ~ dnorm(0, .01)
    log(lam0[sx]) <- alpha0[sx]
    alpha1[sx] <- 1/(2*sigma[sx]*sigma[sx]) #half normal rate of decay
    sigma[sx] ~ dunif(0,12) #spatial decay parameter measured in kilometers
  }

  ##State process
  for(t in 1:nt){#nt is the number of sessions
    for(i in 1:bigM){
      ingroup[i,t] <- yrid[i] == t
      ingroup2[i,t] <- z[i]*ingroup[i,t] #whether each individual in ingroup[ ,t] was in the actual
                                                      #population at time t (i.e., N[t])
    }
    N[t] <- sum(ingroup2[1:bigM,t])
    D[t] <- (N[t]/A) * 100 #report density in per 100 km sq
    pi[t] <- lambda[t]/sum(lambda[1:nt])
  }
```

```
  for(t in 1:nt){
    log(lambda[t]) <- beta0 + beta1*(Time[t])
  }

  for(i in 1:bigM){
    Sex[i] ~ dbern(psi.sex)
    Sex2[i] <- Sex[i] + 1 #convert to categorical classes

    z[i] ~ dbern(psi) #probability that individual in augmented population is in true population
    yrid[i] ~ dcat(pi[1:nt]) #multinomial process determining when (i.e., which session) an
                                  #individual is in the population

    #Estimated activity centers
    S[i, 1] ~ dunif(xmin, xmax)
    S[i, 2] ~ dunif(ymin, ymax)

##Observation process
    for(j in 1:ntraps){
      d2[i,j] <- pow(pow(S[i,1] - X[j,1], 2) + pow(S[i,2] - X[j,2], 2), 1)
      pzero[i, j] <- 1 - (z[i] * Kmat[j, yrid[i]])
      lam[i, j] <- K[j] * lam0[Sex2[i]] * exp(-d2[i,j]*alpha1[Sex2[i]])
      y[i,j] ~ dZIP(lambda = lam[i,j], zeroProb = pzero[i,j])
    }
  }
})
```

Appendix 4.4 Supplementary tables and figures

Table S4.4.1 *Model state spaces and proportion habitat. Non-habitat was defined as areas classified as water or urban land uses (Plummer 2017; see Chapter 2 for details).*

Site	Buffer (km)	Area (km^2)	Habitat (km^2)	% Habitat
Atherstone	16	2510	2510	100.00%
HiP	12	2889	2883	99.78%
Ithala	12	1775	1775	99.99%
Makalali	12	1735	1734	99.94%
Timbavati	12	1706	1706	100.00%
uMkhuze	12	1487	1478	99.40%
Welgevonden	16	2619	2619	99.99%

Table S4.4.2*: Posterior diagnostic checks. "MPSRF" is the multivariate potential scale reduction factor (Brooks and Gelman 1998). "N_{max}" is the maximum cumulative number of individuals estimated to be in the "true" population across all sessions (i.e., $Z_i = 1$) and M is the augmented population size.*

Site	MPSRF	N_{max}	M	N_{max}:M (%)
Atherstone	1.003	844	1800	47%
HiP	1.005	989	2100	47%
Ithala	1.002	970	1680	58%
Makalali	1.002	795	1400	57%
Timbavati	1.002	1252	2040	61%
uMkhuze	1.006	803	1440	56%
Welgevonden	1.006	758	1860	41%

Table S4.4.3*: Effective sampling sizes of monitored parameters in the state model.*

Site	D_1	D_2	D_3	D_4	D_5	D_6	B_0	B1
Atherstone	3076	3963	5091	4922	3875	3096	3599	1948
HiP	3894	5609	7133	6277	4941	3869	3973	2538
Ithala	6344	7852	8757	8068	6467	6083	4780	4333
Makalali	5064	6637	7751	6688	5451	NA	4653	3701
Timbavati	4680	5853	6887	6942	5954	4818	3869	3734
uMkhuze	5934	6710	8835	8784	7190	5655	5009	3904
Welgevonden	3618	5021	6515	6812	4973	3979	4211	2265

***Table S4.4.4**: Effective sampling sizes of monitored parameters in the detection model.*

Site	**α_0 Female**	**α_0 Male**	**ψ_{sex}**	**σ Female**	**σ Male**
Atherstone	11916	12342	1534	8219	4774
HiP	13001	17969	2515	8028	9086
Ithala	16851	20901	4465	11443	10020
Makalali	13412	18656	2940	9032	8043
Timbavati	11854	14942	3425	8780	8352
uMkhuze	15341	18501	3459	10472	3799
Welgevonden	14135	18036	1950	6936	5531

Appendix 4.5: Trace plots

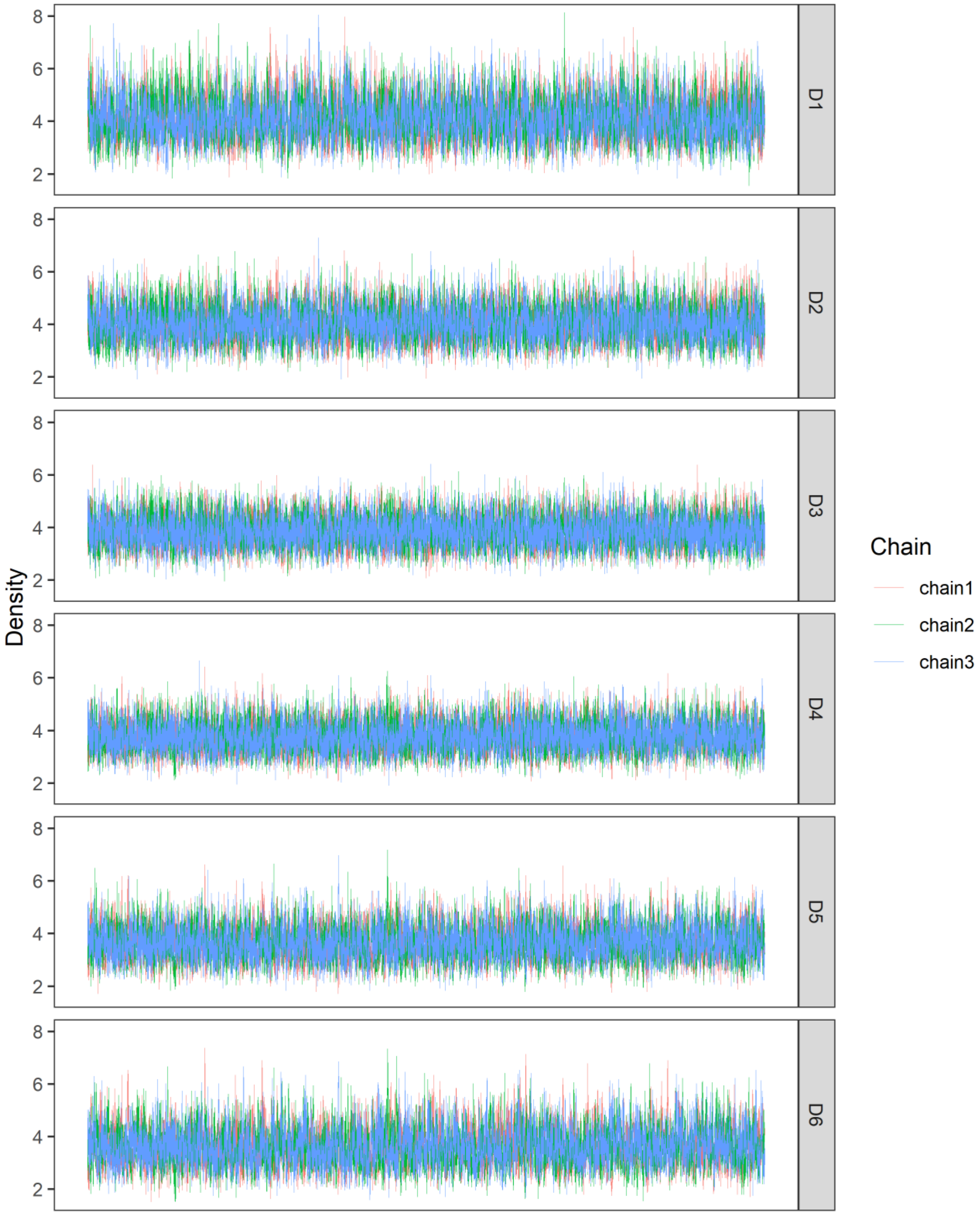

Figure S4.5.1*: Posterior trace plots of density (leopards per 100 km^2) estimated for six sessions at Atherstone Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

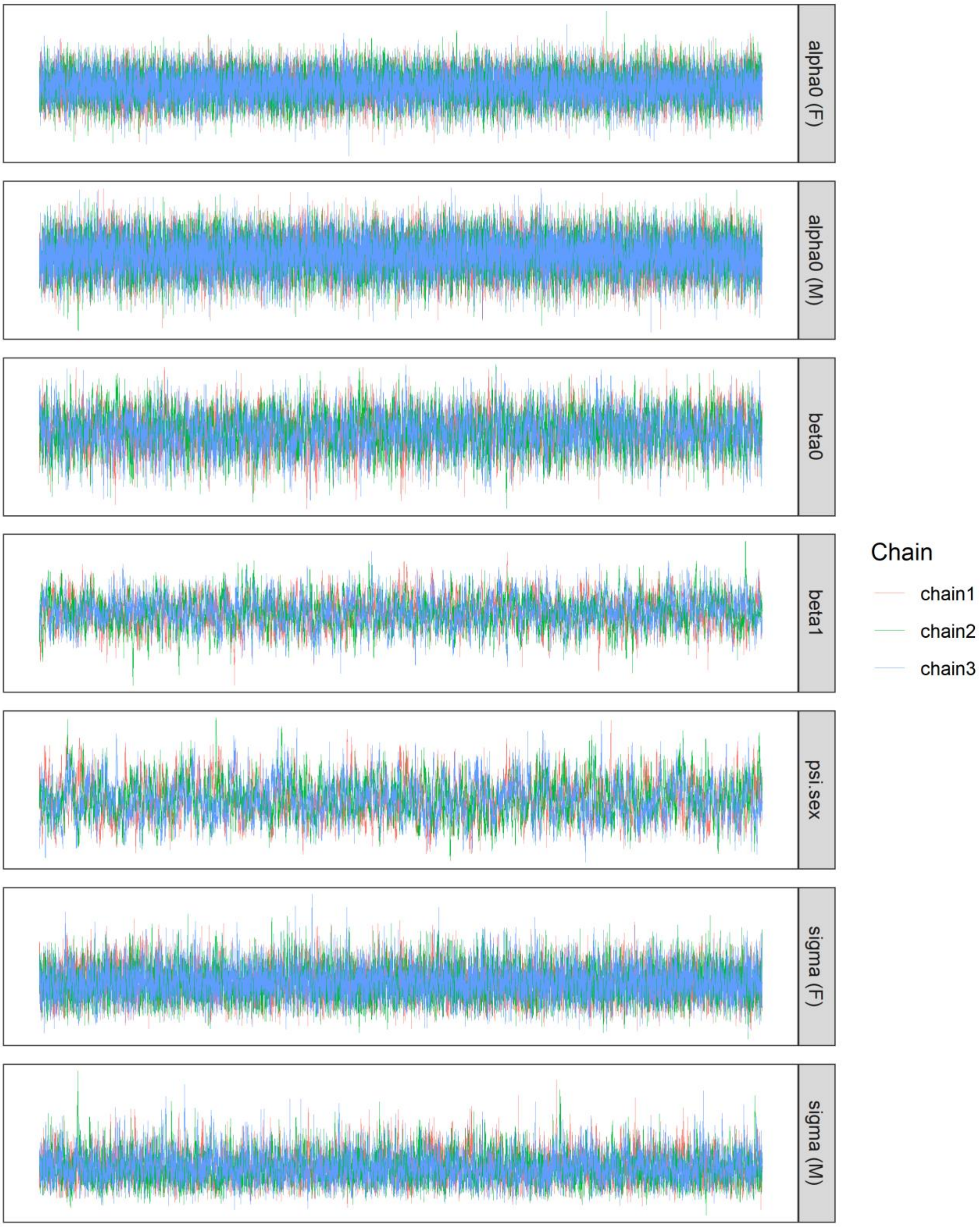

***Figure S4.5.2**: Posterior trace plots of selected model parameters estimated for Atherstone Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

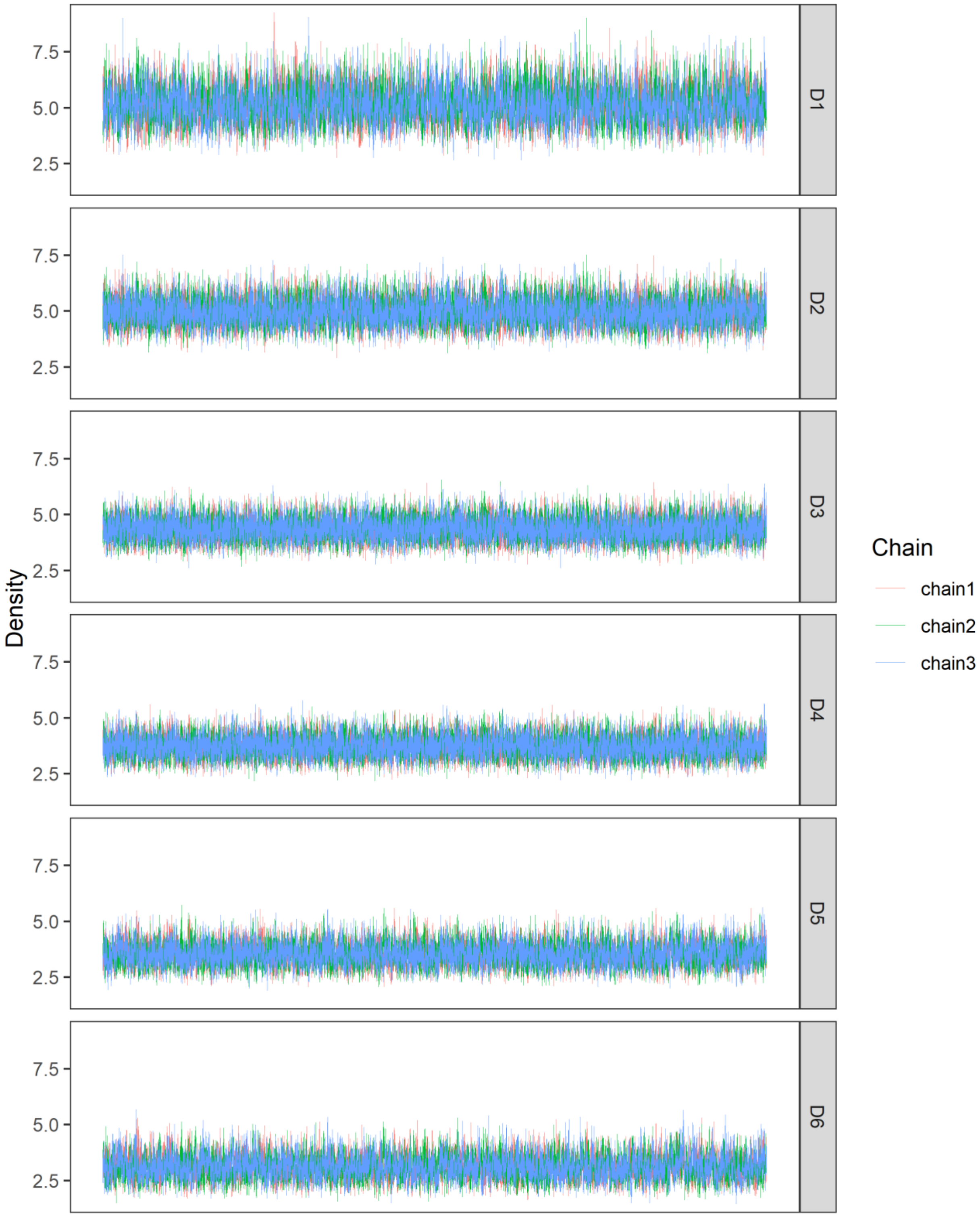

Figure S4.5.3: *Posterior trace plots of density (leopards per 100 km^2) estimated for six sessions at Hluhluwe-iMfolozi Park, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

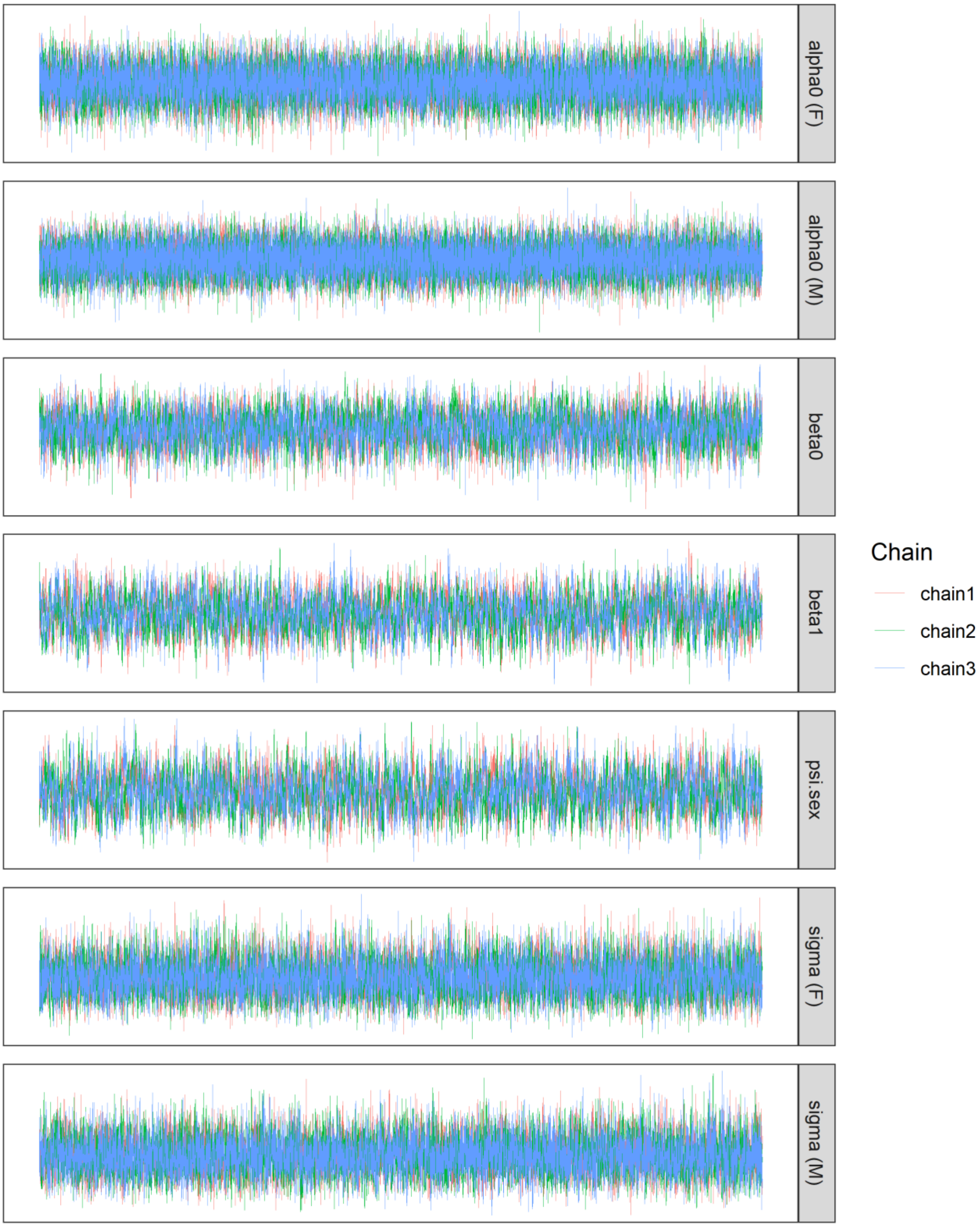

***Figure S4.5.4**: Posterior trace plots of selected model parameters estimated for Hluhluwe-iMfolozi Park, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

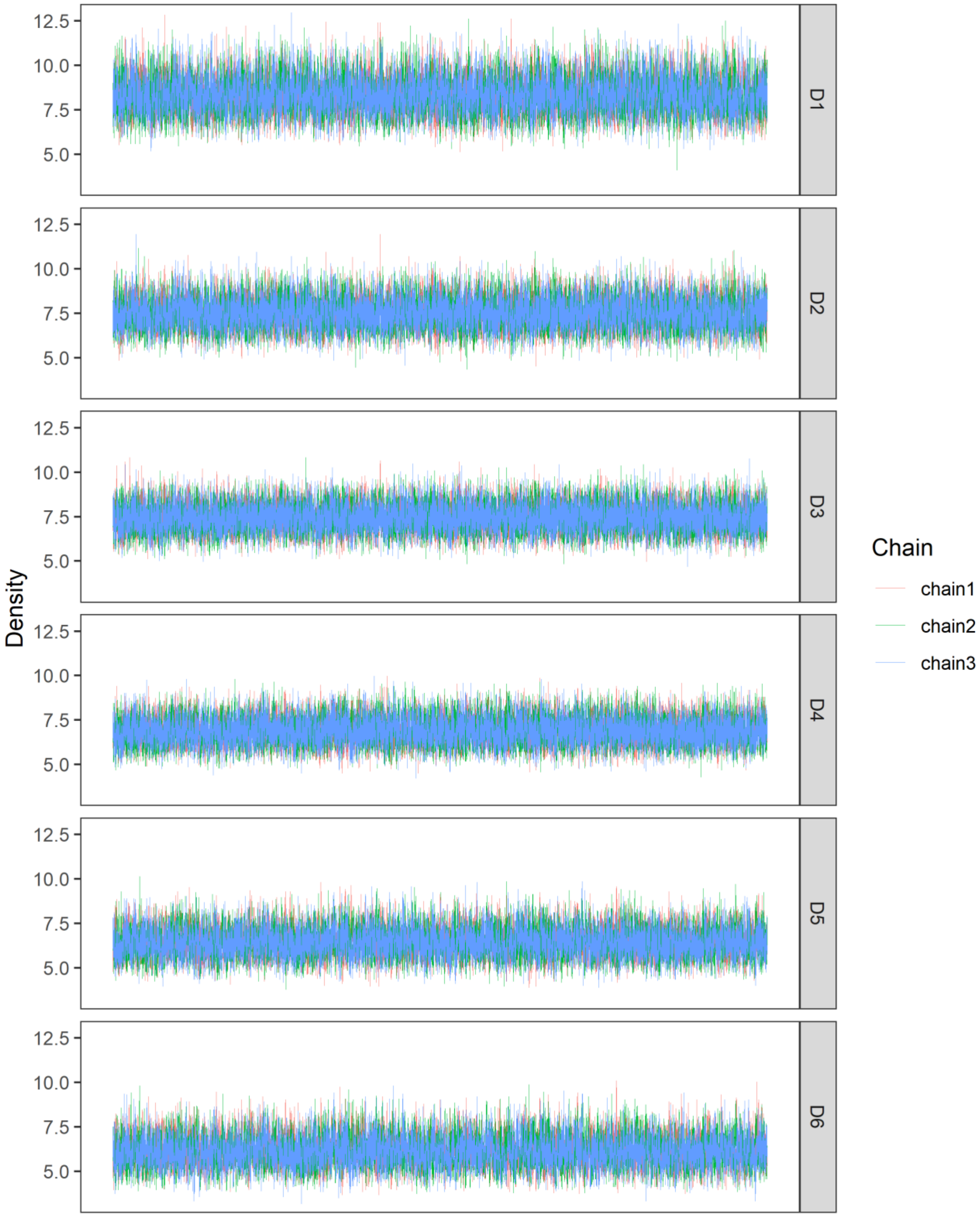

Figure S4.5.5*: Posterior trace plots of density (leopards per 100 km^2) estimated for six sessions at Ithala Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

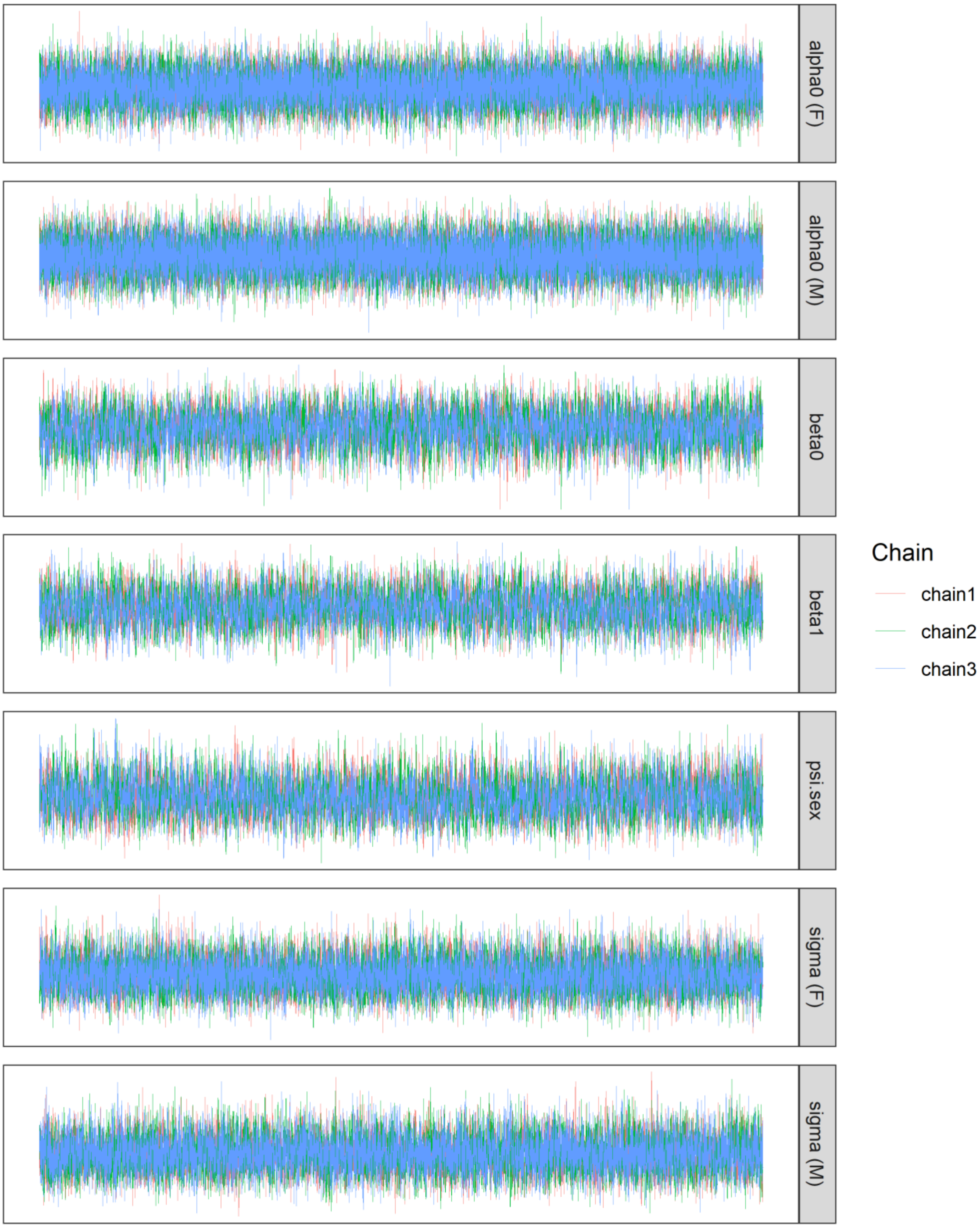

Figure S4.5.6*: Posterior trace plots of selected model parameters estimated for Ithala Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

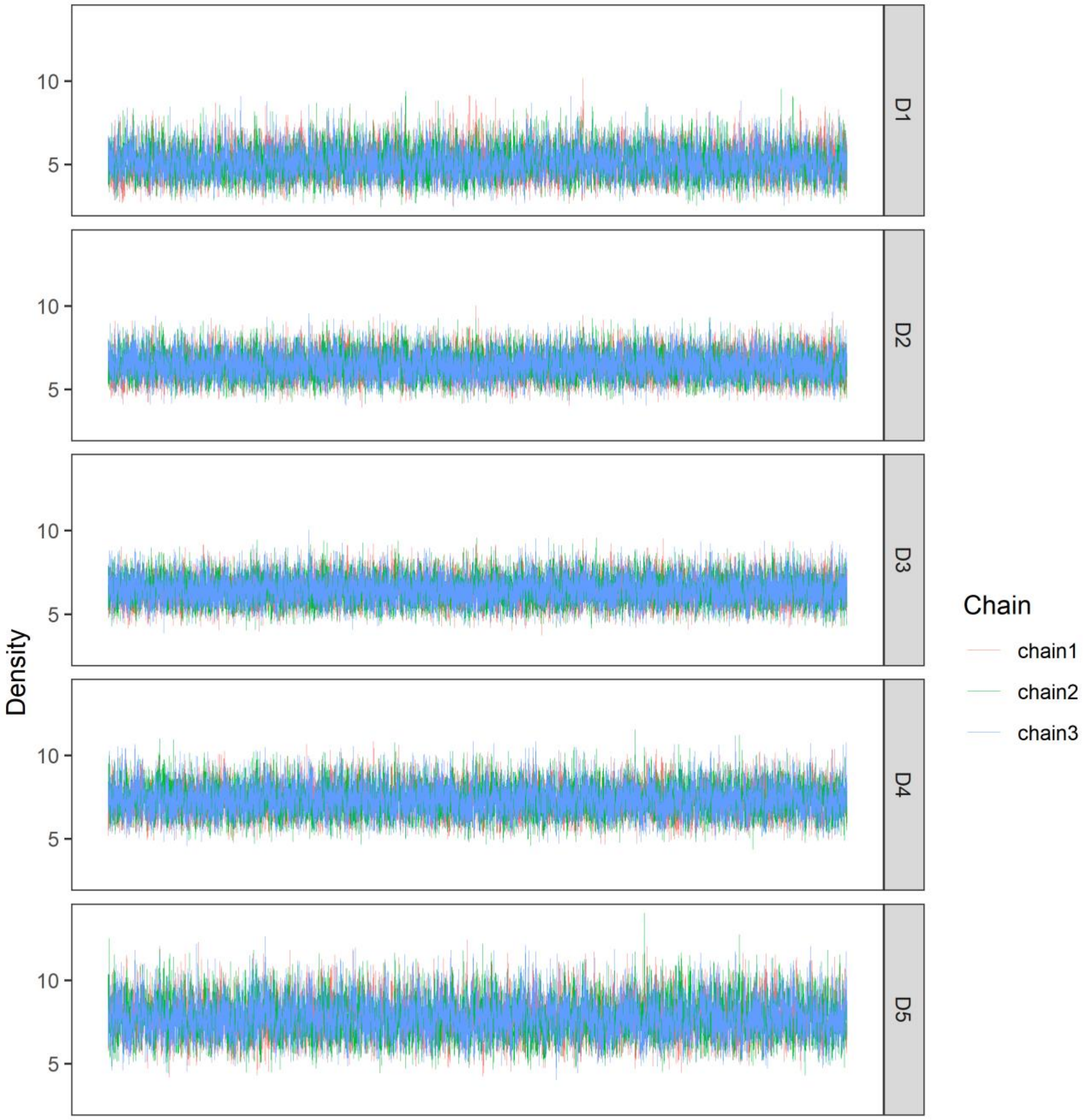

Figure S4.5.7*: Posterior trace plots of density (leopards per 100 km^2) estimated for five sessions at Makalali Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

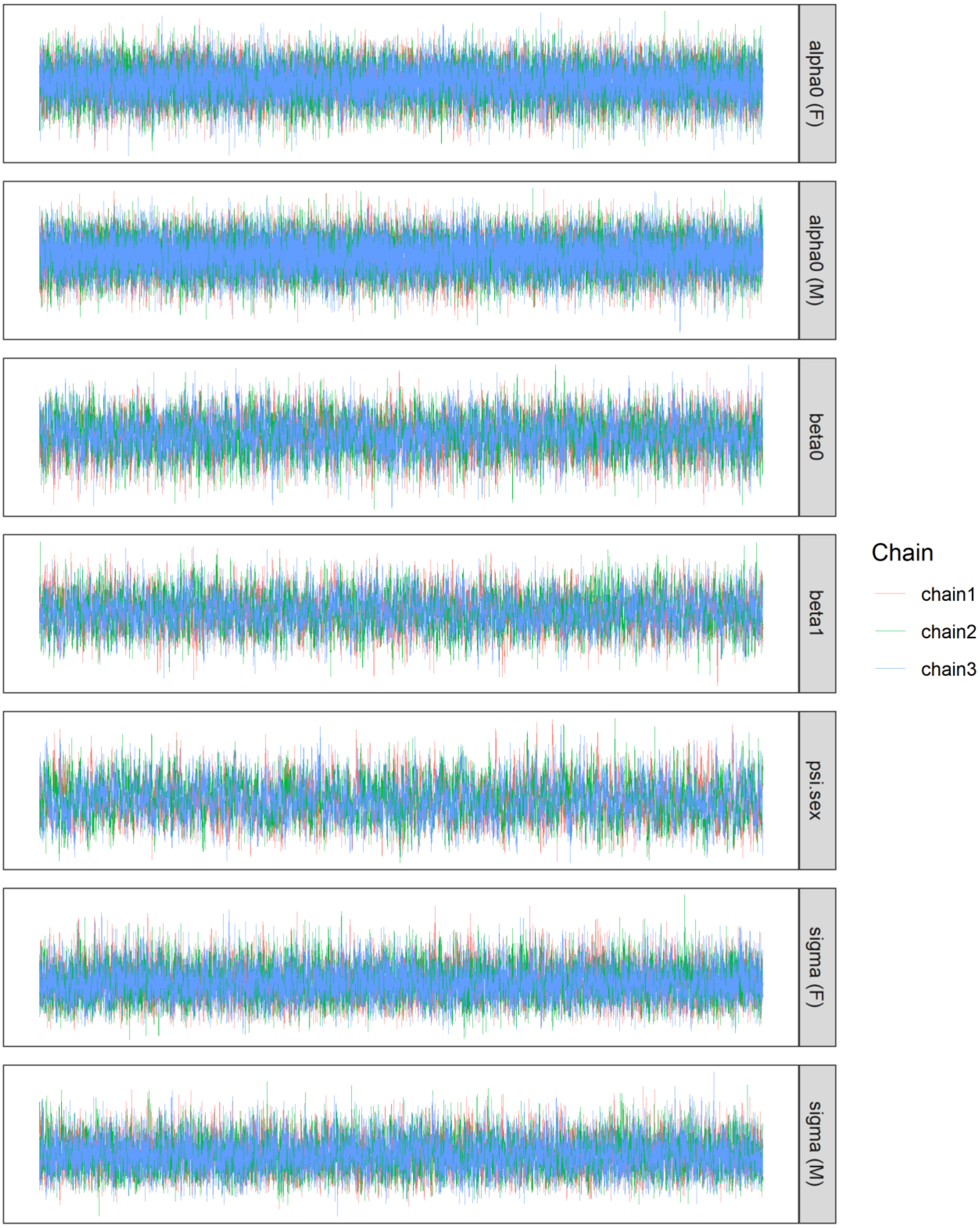

Figure S4.5.8*: Posterior trace plots of selected model parameters estimated for Makalali Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

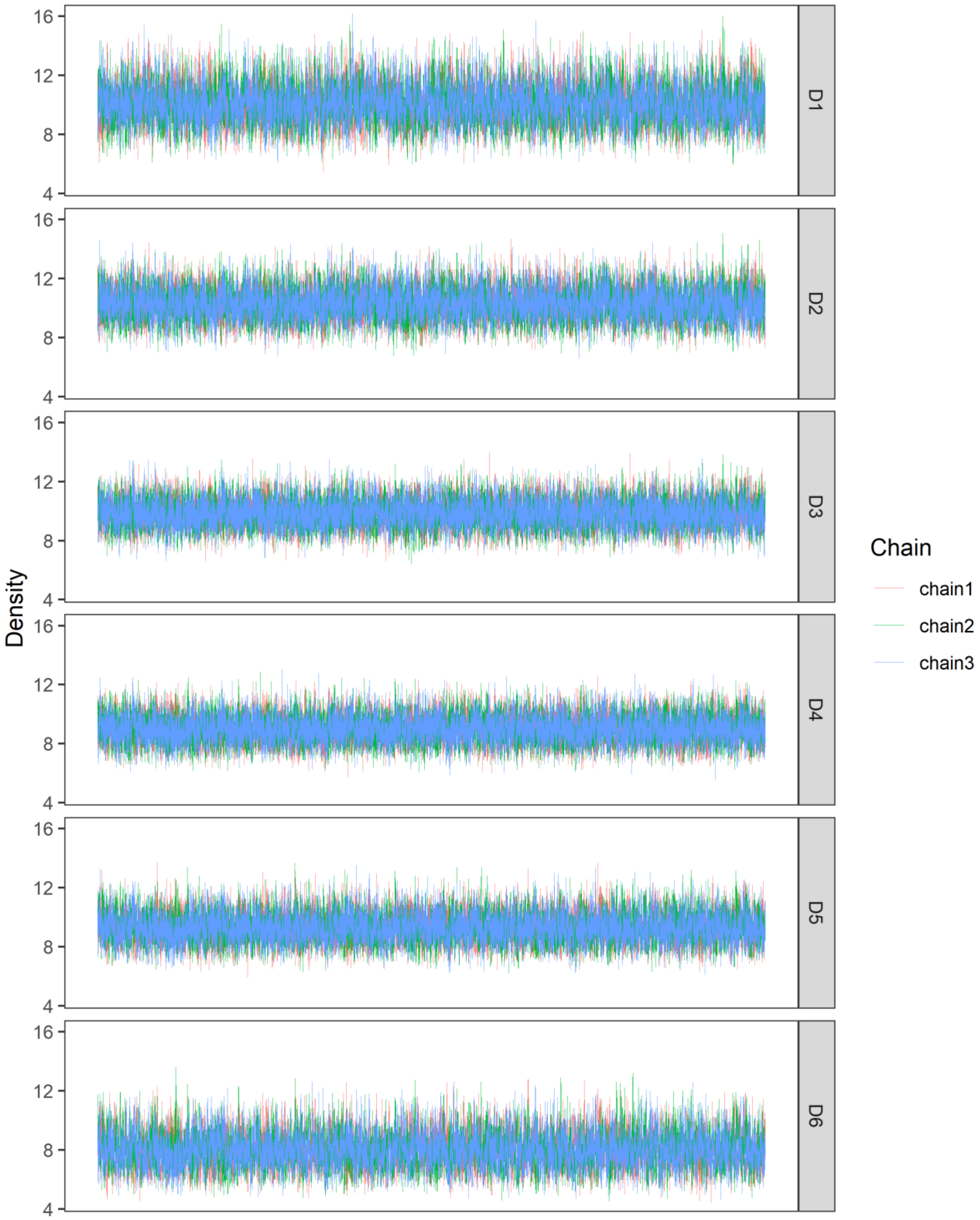

Figure S4.5.9*: Posterior trace plots of density (leopards per 100 km^2) estimated for six sessions at Timbavati Private Nature Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

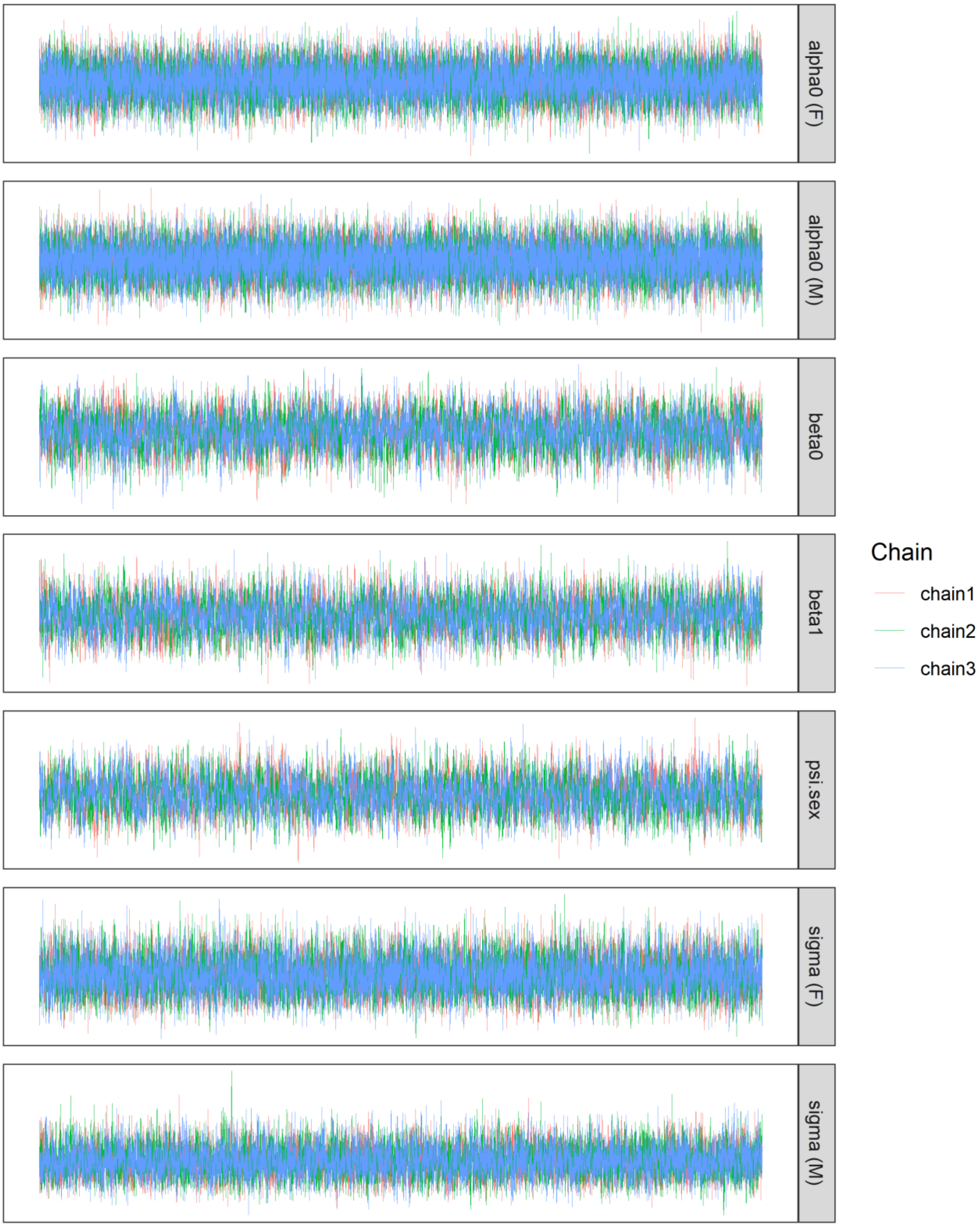

Figure S4.5.10*: Posterior trace plots of selected model parameters estimated for Timbavati Private Nature Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

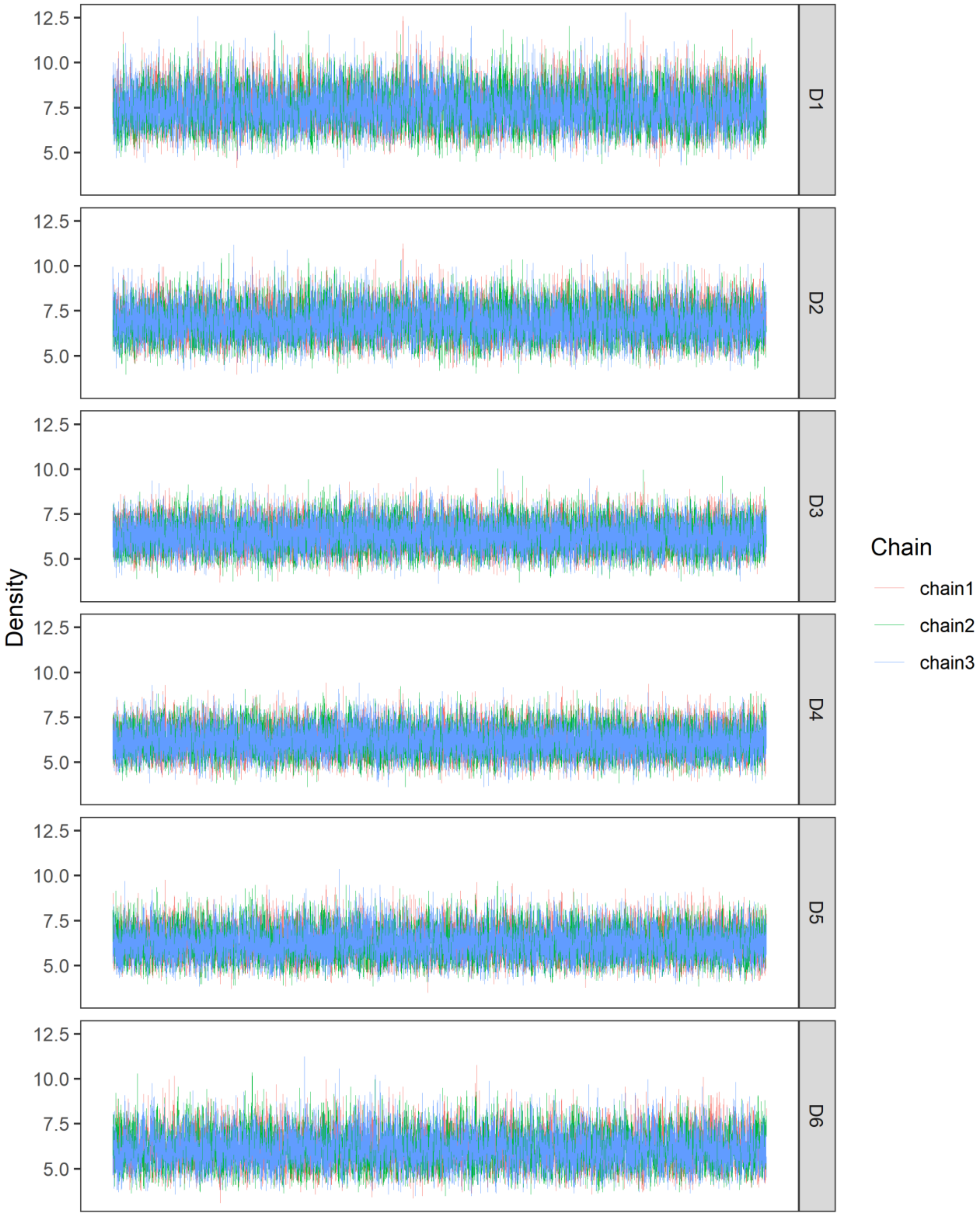

***Figure S4.5.11**: Posterior trace plots of density (leopards per 100 km^2) estimated for six sessions at uMkhuze Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

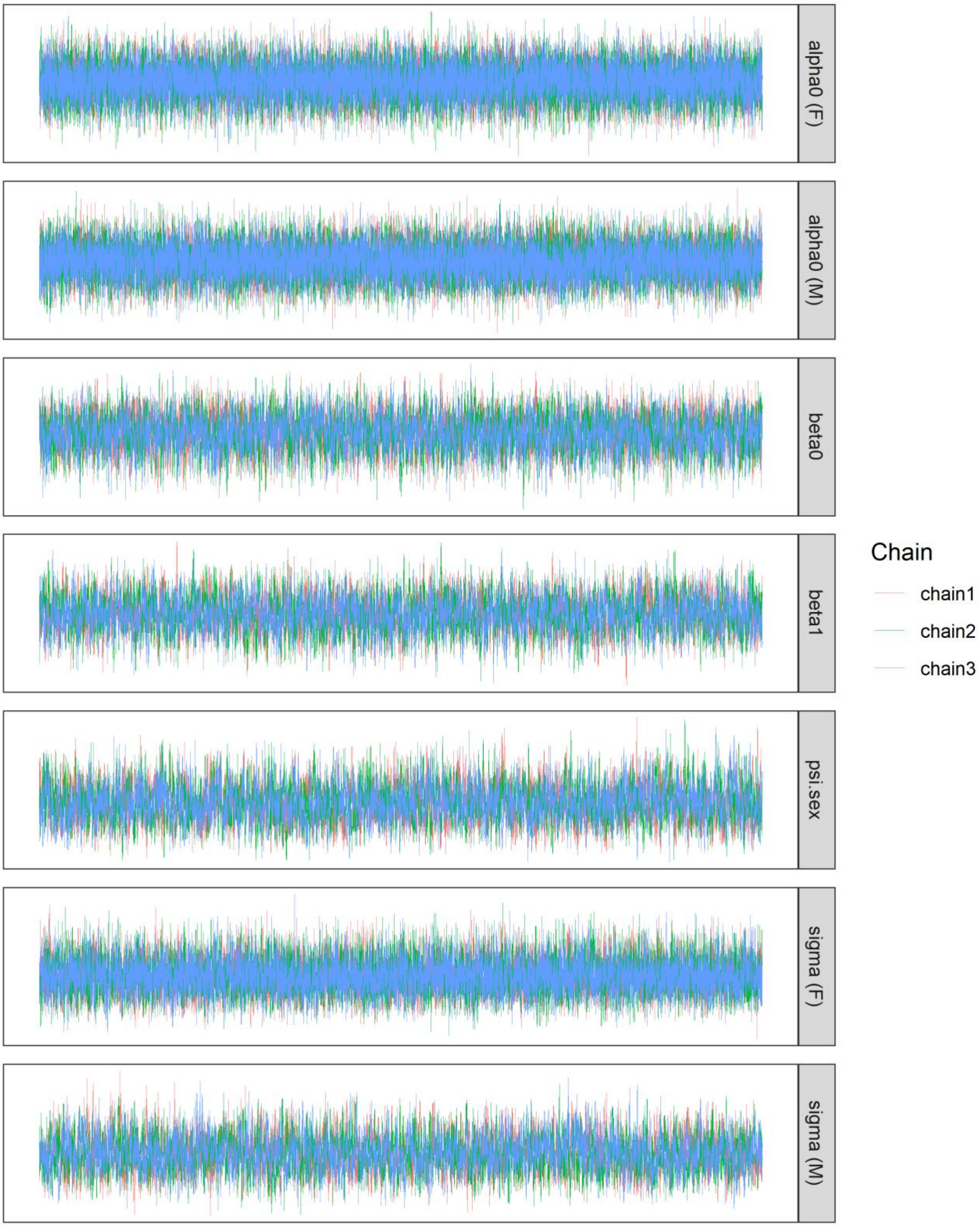

***Figure S4.5.12**: Posterior trace plots of selected model parameters estimated for uMkhuze Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

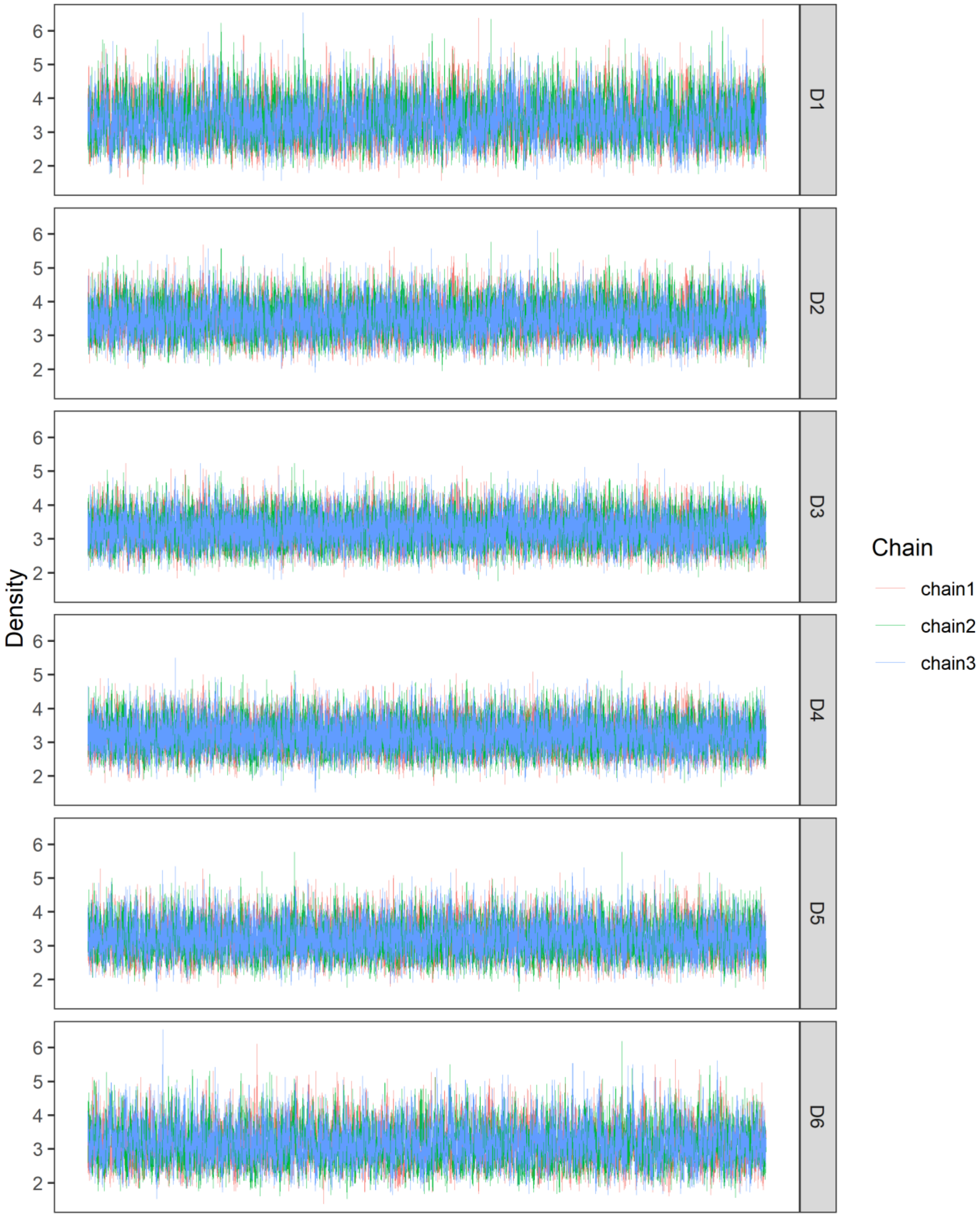

***Figure S4.5.13**: Posterior trace plots of density (leopards per 100 km^2) estimated for six sessions at Welgevonden Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

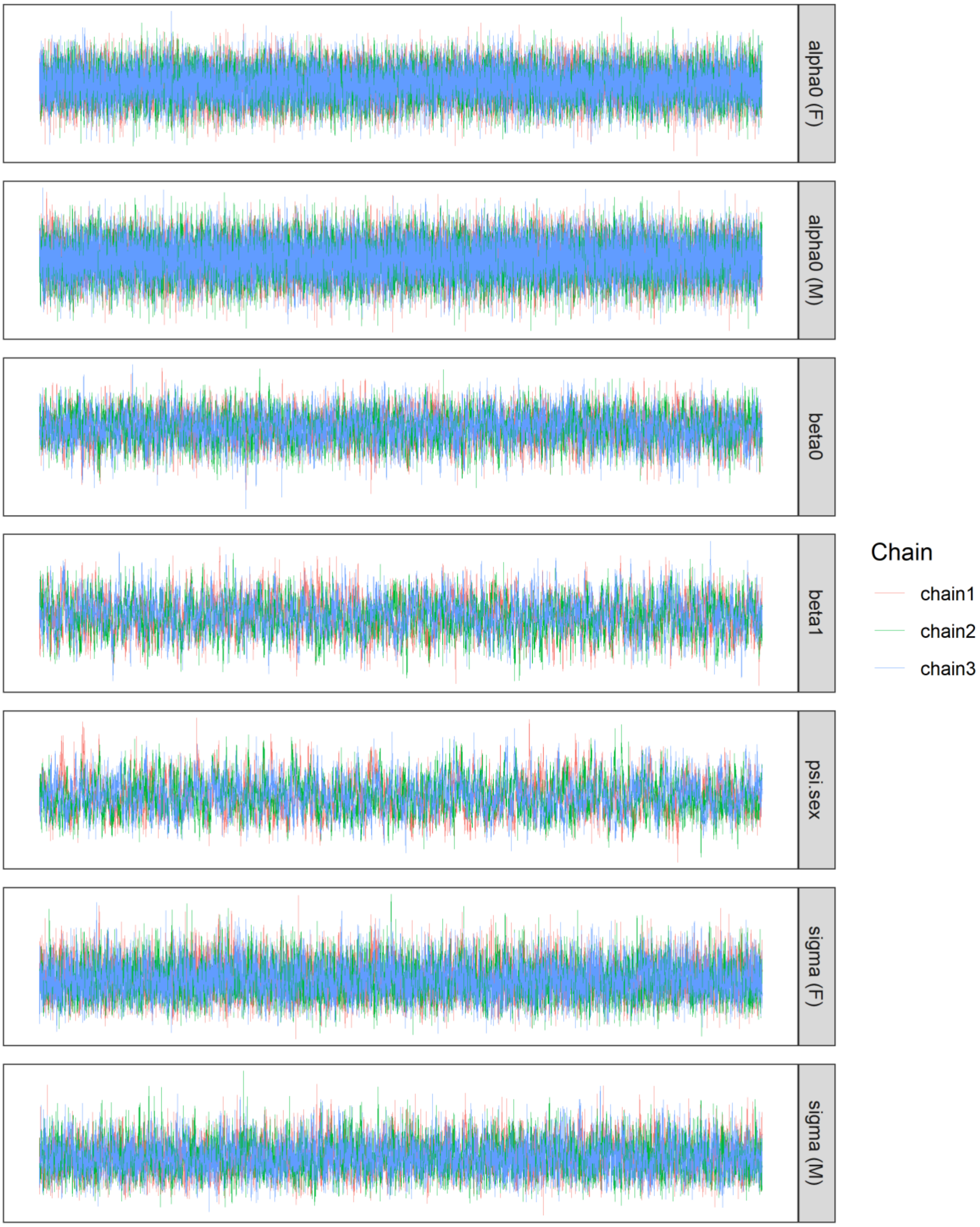

Figure S4.5.14*: Posterior trace plots of selected model parameters estimated for Welgevonden Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

Appendix 4.6: Posterior distributions

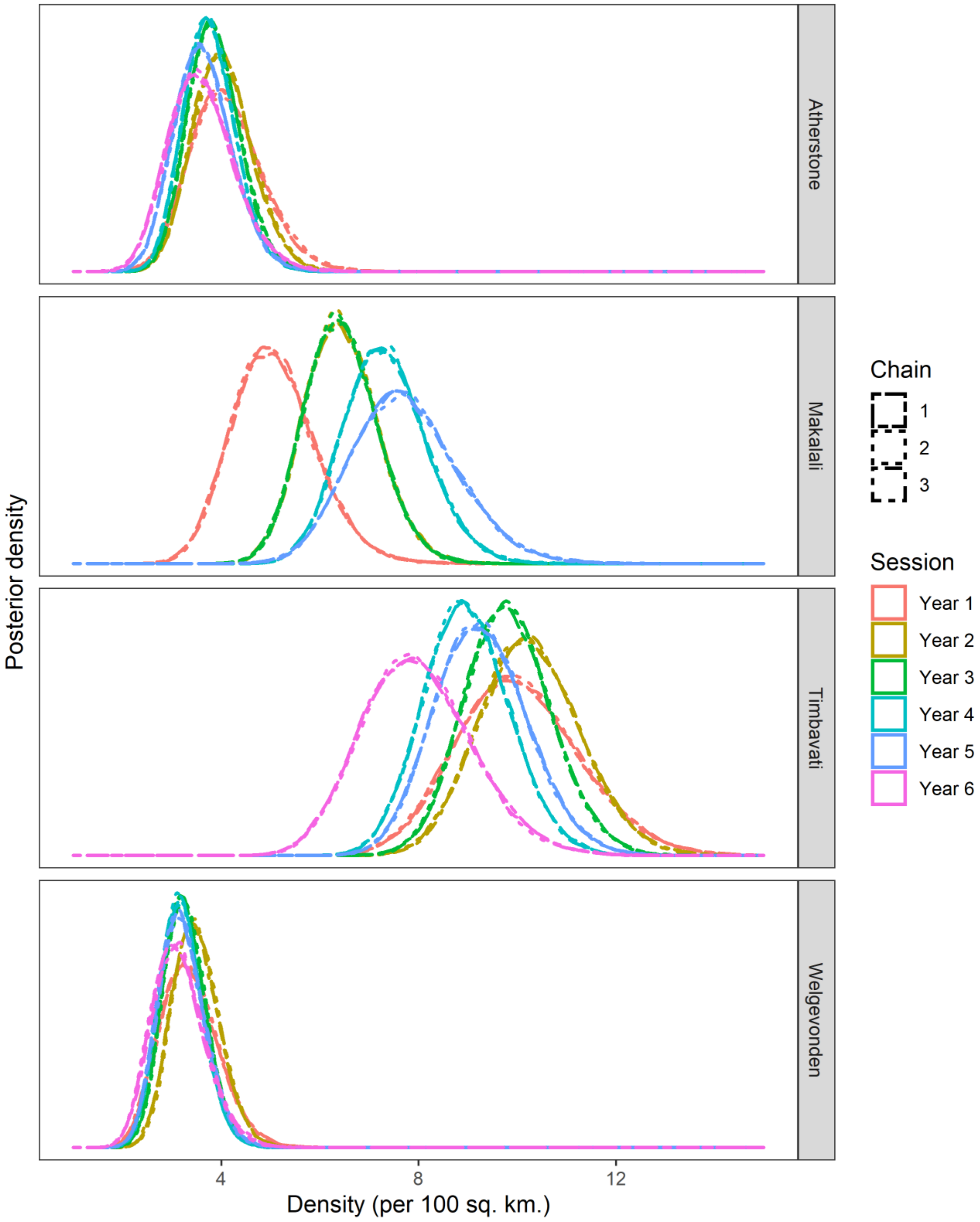

***Figure S4.6.1**: Posterior distributions of leopard density for four study sites in Limpopo Province, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

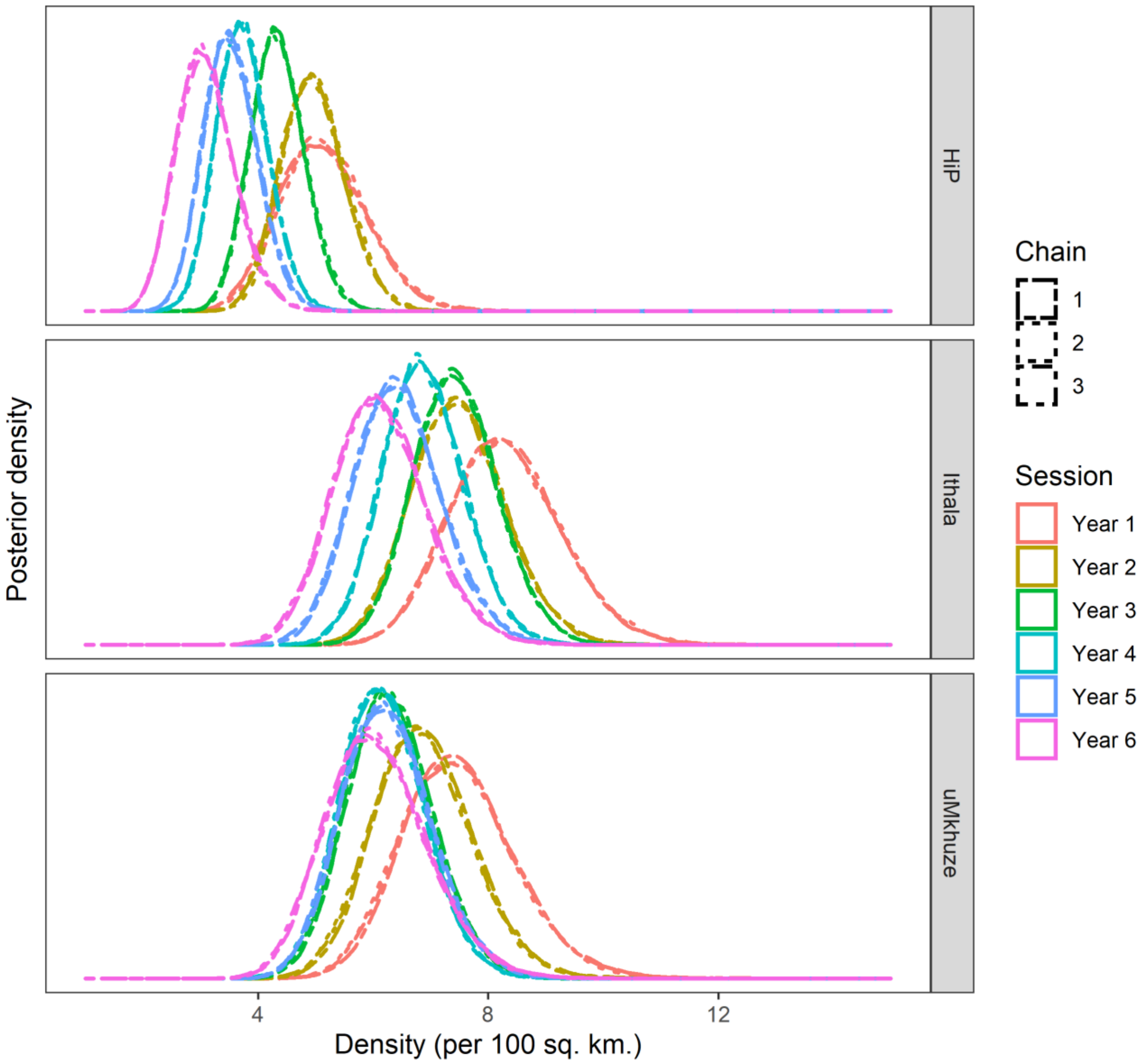

***Figure S4.6.2**: Posterior distributions of leopard density for three study sites in KwaZulu-Natal Province, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

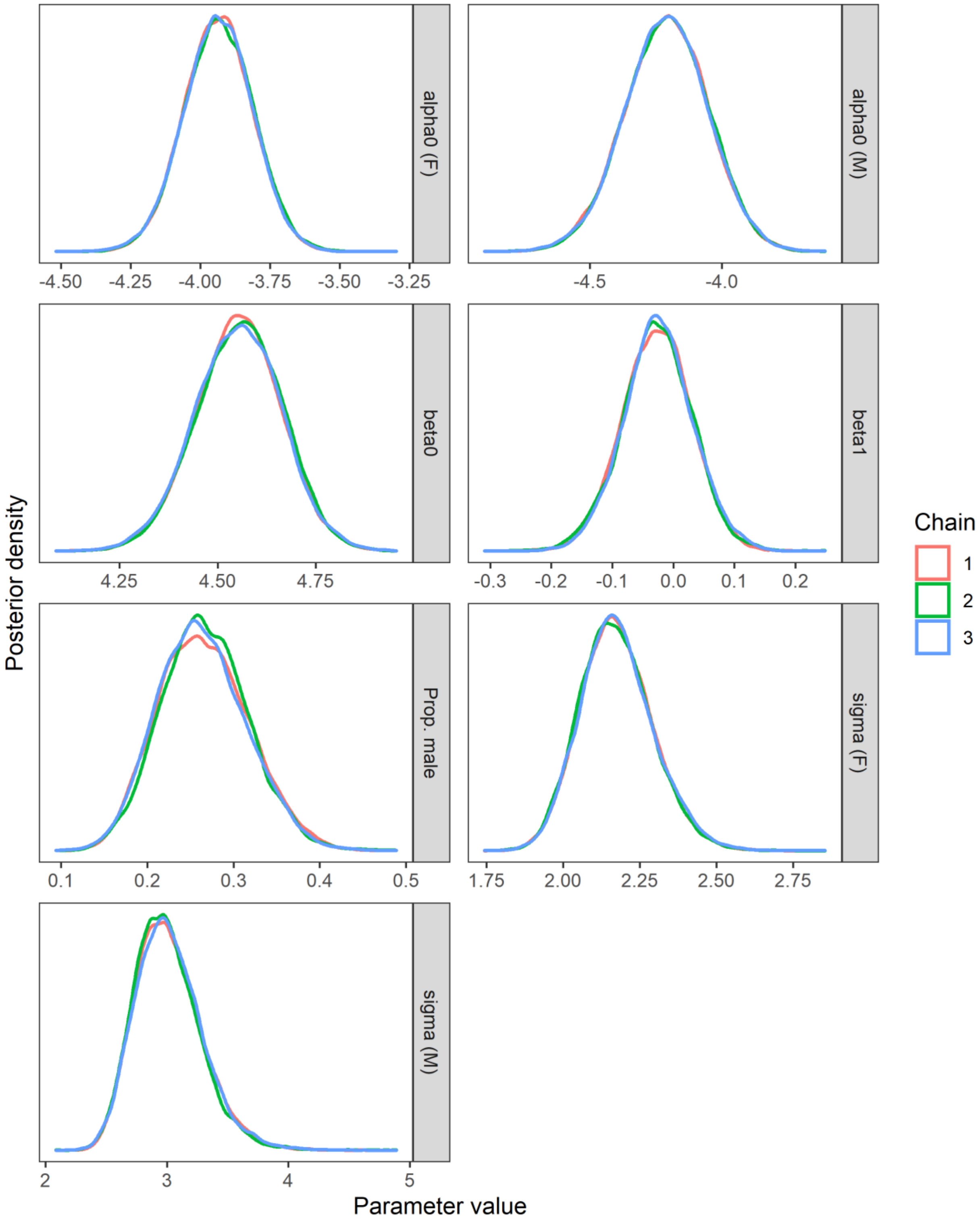

***Figure S4.6.3**: Posterior distributions of selected model parameters estimated for Atherstone Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

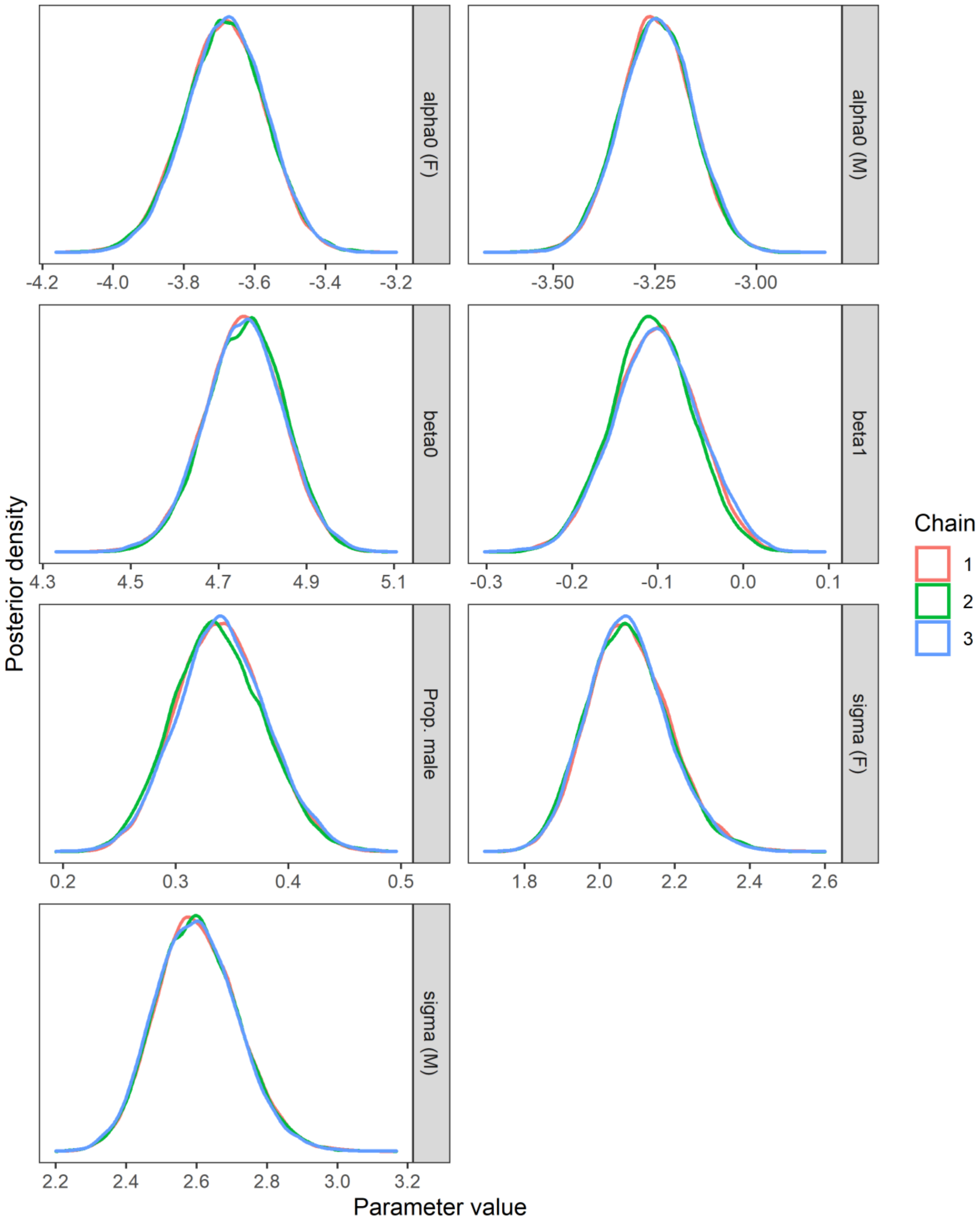

Figure S4.6.4: *Posterior distributions of selected model parameters estimated for Hluhluwe-iMfolozi Park, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

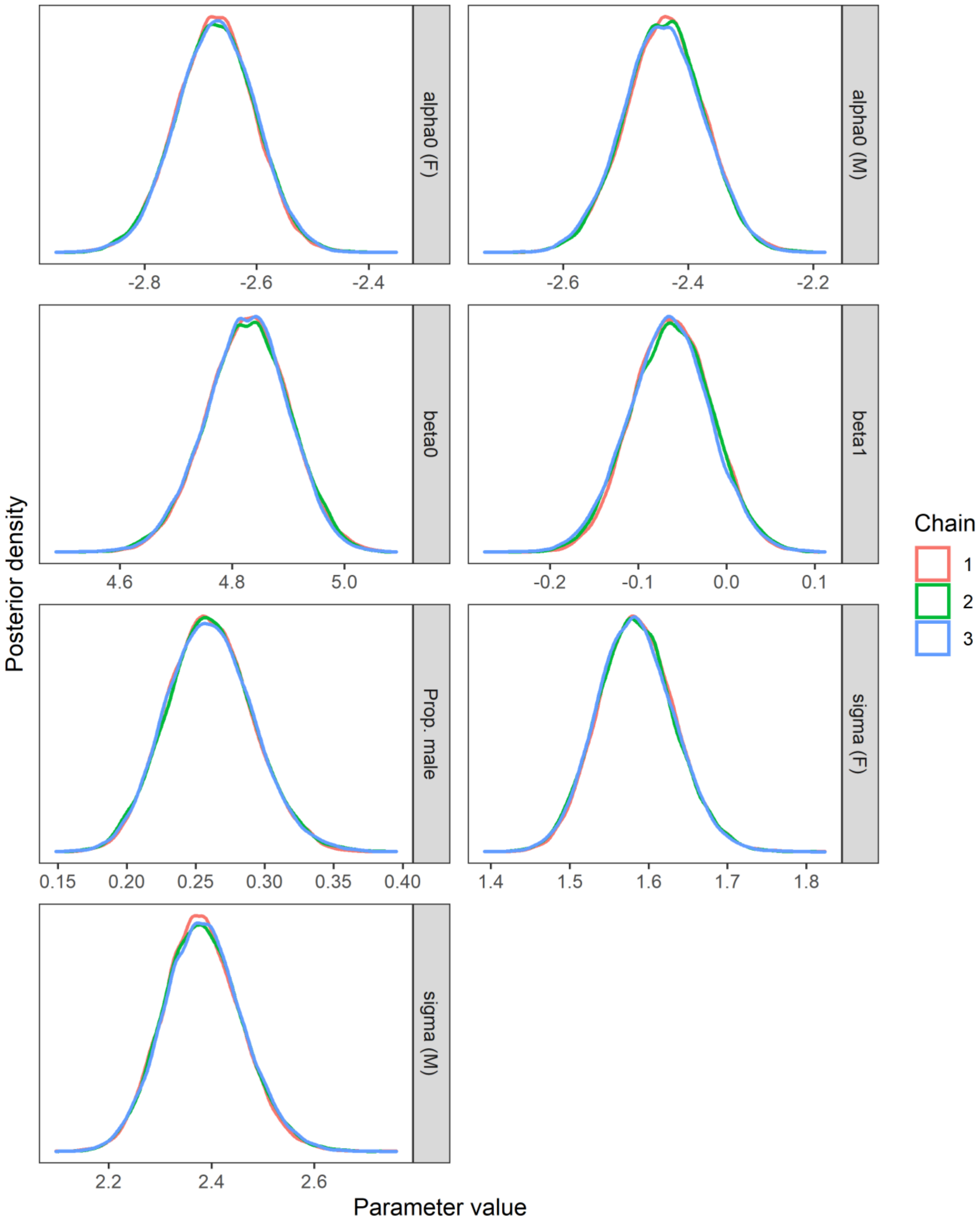

Figure S4.6.5*: Posterior distributions of selected model parameters estimated for Ithala Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

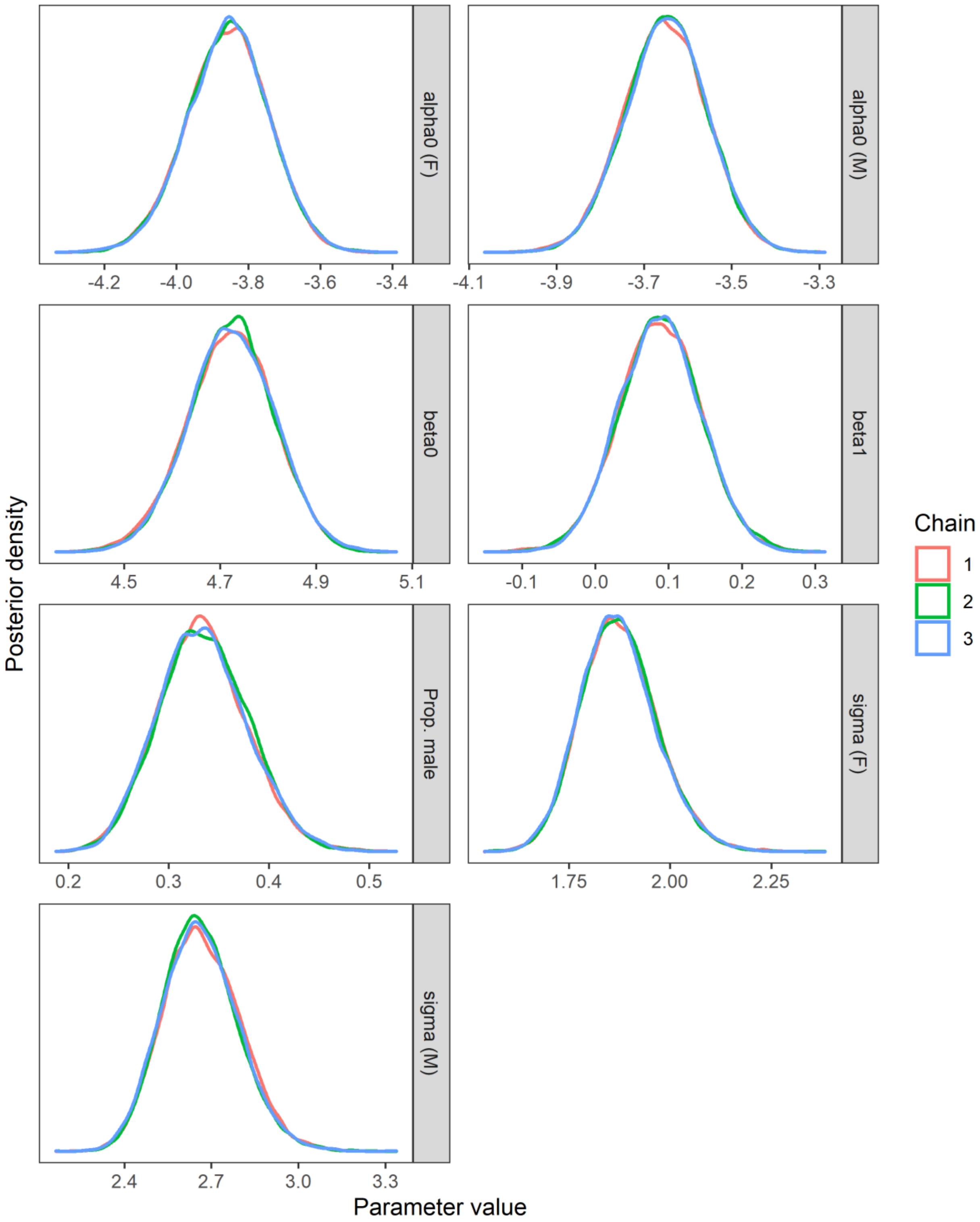

Figure S4.6.6*: Posterior distributions of selected model parameters estimated for Makalali Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

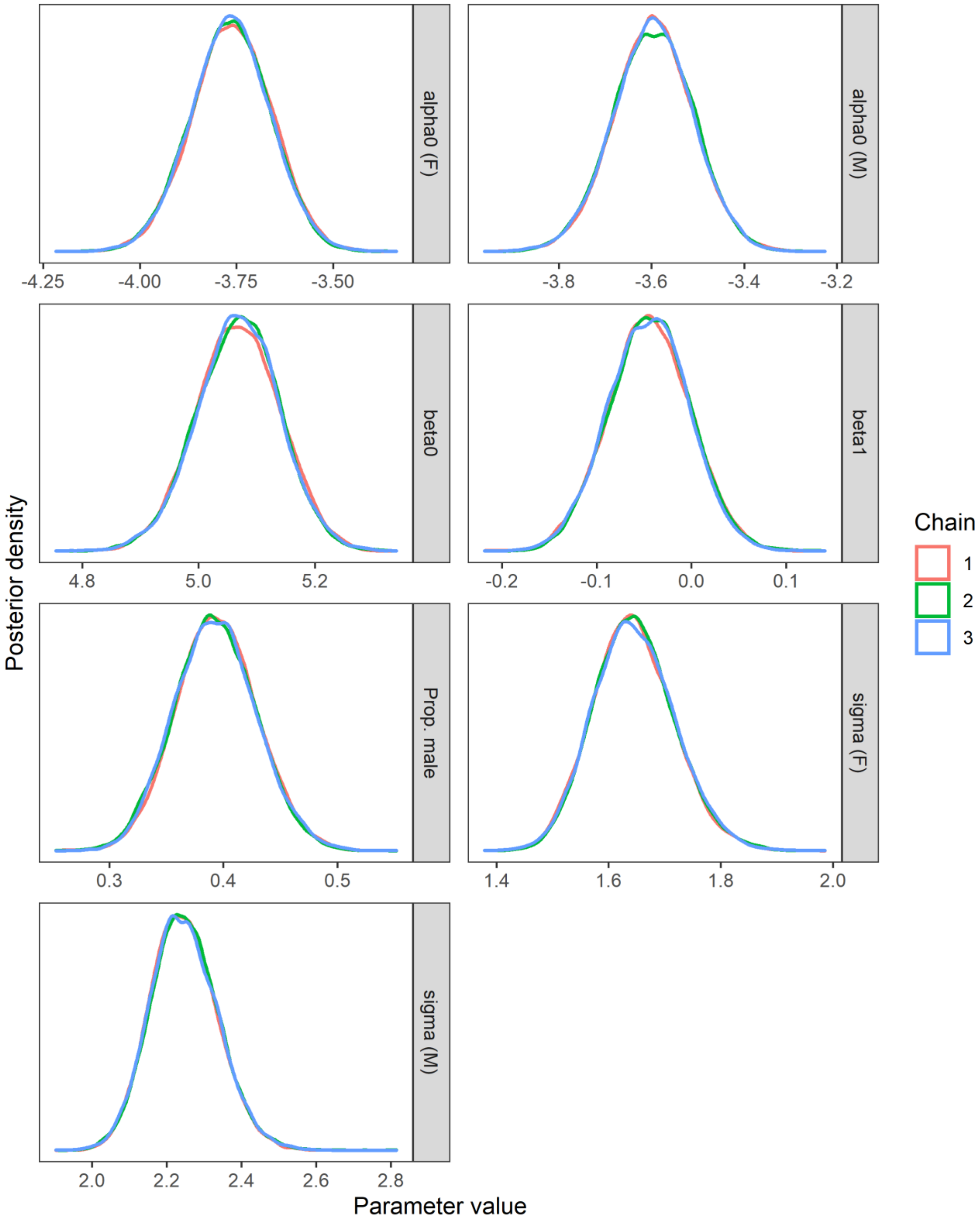

***Figure S4.6.7**: Posterior distributions of selected model parameters estimated for Timbavati Private Nature Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

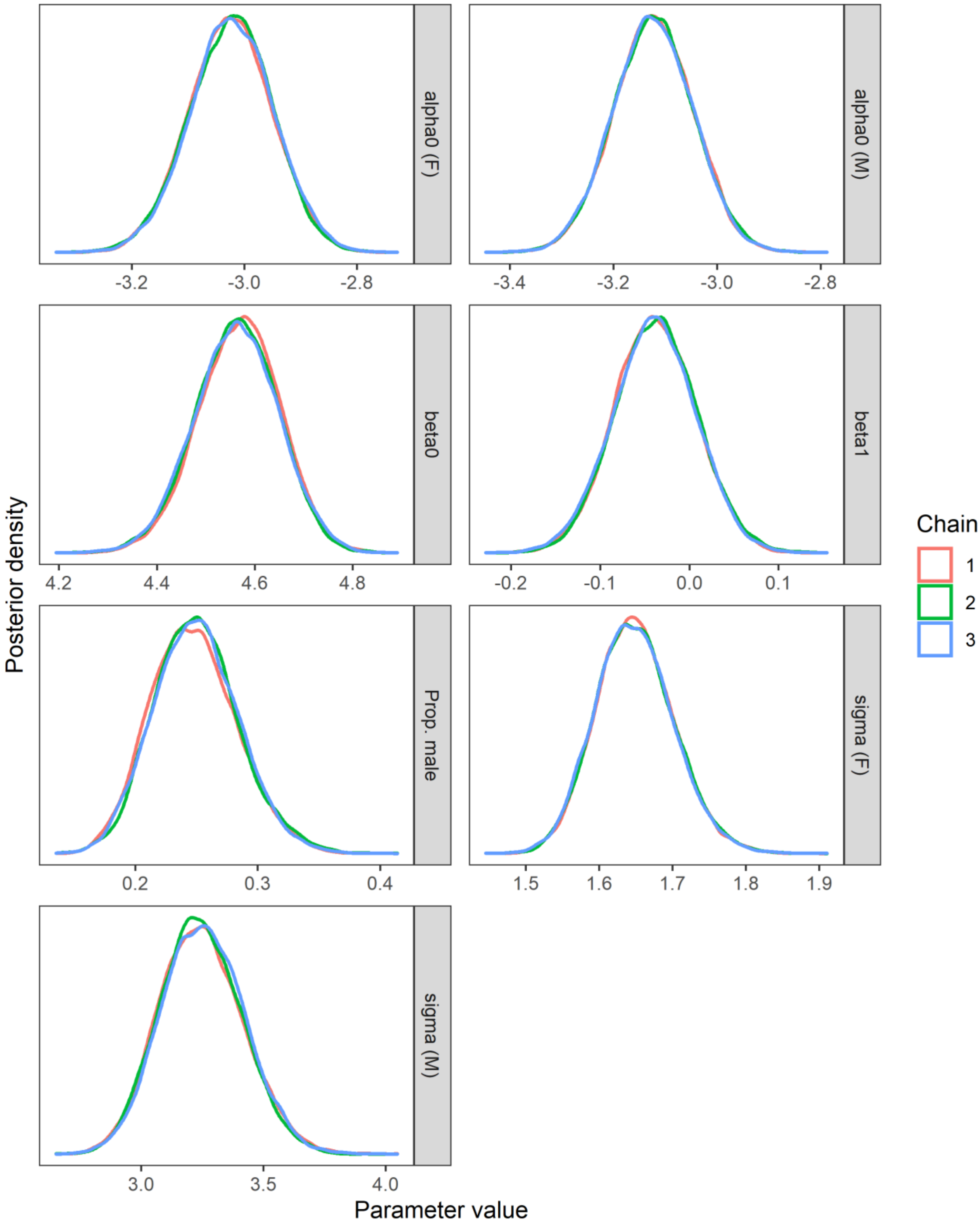

Figure S4.6.8*: Posterior distributions of selected model parameters estimated for uMkhuze Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

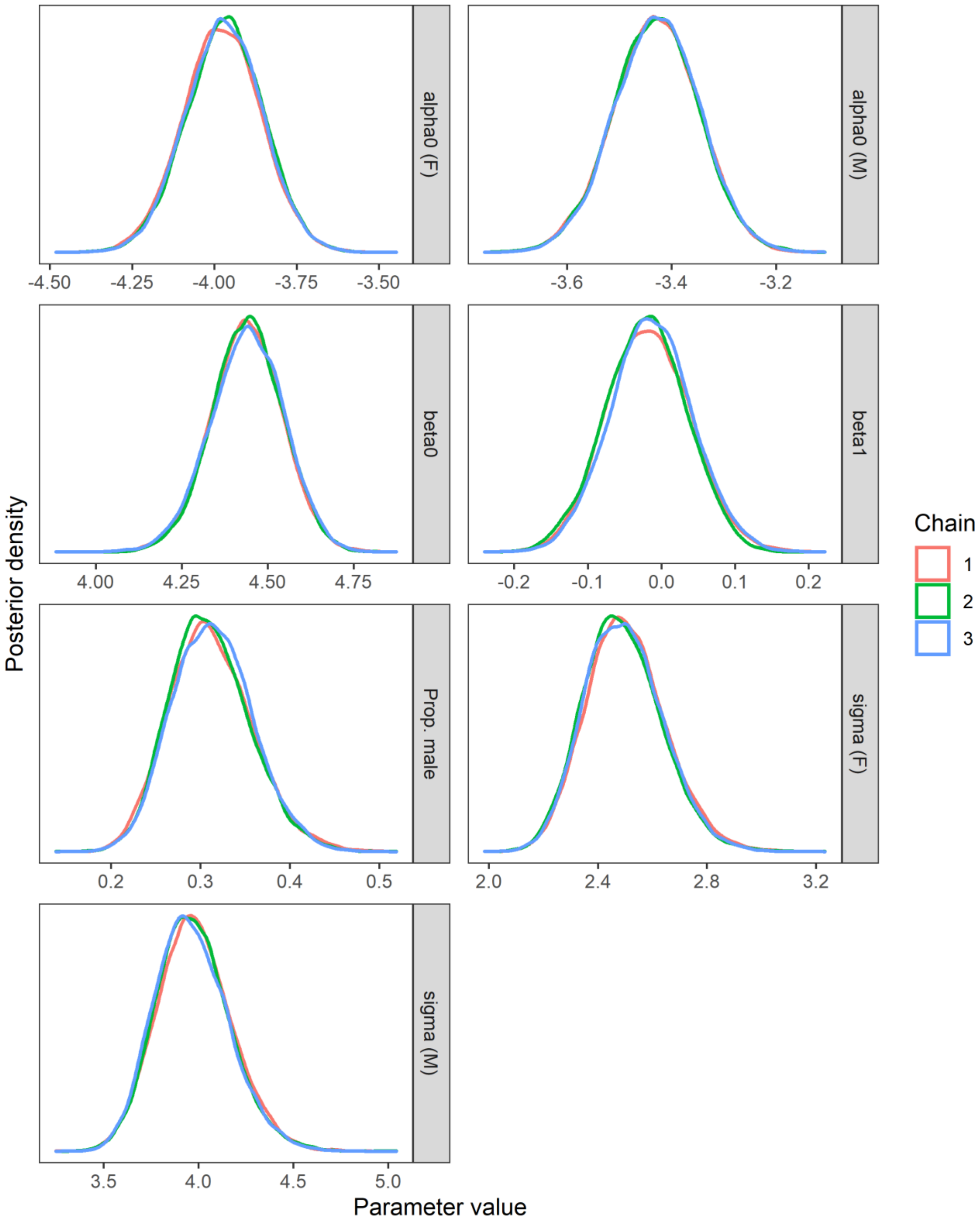

***Figure S4.6.9**: Posterior distributions of selected model parameters estimated for Welgevonden Game Reserve, South Africa. Plots represent three chains of 25000 posterior samples after a burn-in of 5000 samples.*

CHAPTER 5

THE DRIVERS OF LEOPARD DENSITY IN NORTHEASTERN SOUTH AFRICA

Abstract

Conservation aims to influence outcomes for populations and ecosystems but doing so requires understanding the processes that determine those outcomes. In this chapter, I investigate the drivers of leopard density within protected areas (PAs) in northeastern South Africa to understand what conditions are most conducive to abundant populations. I tested multiple working hypotheses that considered the relative influence of bottom-up biological factors and top-down anthropogenic factors on leopard density and evaluated support for each hypothesis using an information theoretic approach. I formulated a model of leopard density at 27 study sites in response to each hypothesis using multi-session spatial capture-recapture models with density represented as an inhomogeneous point process. Four of the ten hypotheses exhibited some support (i.e., ΔAICc < 7), two of which exhibited strong support with ΔAICc < 1. Together, the four supported hypotheses indicate that leopard density is primarily limited by human impacts, but that habitat suitability and management conditions play a role in moderating these effects. The proportion of camera stations that recorded domestic animals, a proxy for the extent of human impacts and effectiveness of protected areas, was the only variable present in all four supported models. Protected areas are the cornerstone of large felid conservation, but only when the human-wildlife interface is well-managed and wildlife populations are sheltered from anthropogenic impacts. To ensure the long-term viability of leopard populations, wildlife managers should devote greater resources to reducing unlawful incursions into PAs while promoting contiguous networks of protected areas which offer leopard and other large mammal populations improved connectivity.

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Rogan et al. in press. Troubled spots: Human impacts constrain the density of an apex predator inside protected areas. Ecological Applications.

5.1 Introduction

Conservation science aims to prevent extinctions, maintain stable and resilient populations, promote ecosystem function, and foster benefits for local communities (Kareiva and Marvier 2012). Throughout this thesis, I have emphasized the importance of monitoring for informing management and improving conservation efforts. To this point, I have examined how to assess leopard population status and measure past trends in populations. Ultimately, however, conservation demands securing biodiversity in the future and ensuring long-term viability of populations (Soulé 1985). Thus, it is not enough merely to measure the contemporary status of populations. We must understand the threats species face across their range and then promote more positive outcomes.

Achieving these long-term goals for leopards requires an understanding of carnivore ecology in the Anthropocene. Where prey and space are plentiful and human interference is minimal, carnivores generally thrive (Fuller and Sievert 2001, Carbone and Gittleman 2002, Karanth et al. 2004), but seldom exceed the capacity of the ecosystem to support them in the long term (Hayward et al. 2007, Farhadinia et al. 2015). Leopards, being such versatile hunters, may be more resilient to changes in the prey base than other large carnivores (e.g., Athreya et al., 2016; Kafley et al., 2019; Mann et al., 2019) and hence less sensitive to prey loss and more likely to persist in human impacted landscapes.

While we have surprisingly little data on what habitat characteristics are associated with leopard density specifically (with some notable exceptions such as Bailey 1993, Ramesh et al. 2017, Havmøller et al. 2019, Searle et al. 2020), studies consistently show that leopard occurrence and habitat selection are associated with prey abundance, vegetation structure, topography, and proximity to riverine habitat (Gavashelishvili and Lukarevskiy 2008, Hebblewhite et al. 2011, Burton et al. 2012, Swanepoel et al. 2013, Mondal et al. 2013, Abade et al. 2014b, Fattebert et al. 2015b, Pitman et al. 2017a, Ramesh et al. 2017, Searle et al. 2020, Chaudhary et al. 2020, Puri et al. 2020). In extreme conditions, even bioclimatic variables such as snowfall can influence or limit leopard occurrence (Gavashelishvili and Lukarevskiy 2008).

The Anthropocene, however, is defined by the ubiquity of human interference and leopards, while resilient, are vulnerable to the cumulative impacts. Large carnivores face human pressure in the form of restricted space and vagility, loss of prey, conflict with farmers, snaring, targeted poaching, and disease transmission (Gittleman et al. 2001, Ray et al. 2005, Loveridge et al. 2010, Winterbach et al. 2013). Unquestionably, human-induced mortality reduces leopard density and threatens populations (Balme and Hunter 2004, Balme et al. 2009b, 2010b, Packer et al. 2009, Williams et al. 2017a, Naude et al. 2020a), while overwhelming evidence demonstrates that diverse human factors undermine large carnivore populations more generally including human population density, infrastructure, land use, livestock farming, and hunting (Wolf and Ripple 2016, Jędrzejewski et al. 2017, Everatt et al. 2019, Thatte et al. 2019, Aebischer et al. 2020, Nickel et al. 2020, Searle et al. 2020).

How these factors impact populations depends on species' biological traits (Cardillo et al. 2004). Leopards have demonstrated an ability to persist, though perhaps not thrive, in human dominated landscapes (Athreya et al. 2013, Kafley et al. 2019, Lamichhane et al. 2019, Kshettry et al. 2020, Devens et al. 2021). Burton et al. (2012) unexpectedly found that leopard occurrence within a Ghanaian protected area was more likely in areas where illegal hunting was more common, further evidence that human presence does not preclude leopards. Behavioral adaptations may allow large felid populations to withstand human impacts, even in the case of lions (Schuette et al. 2013) despite their sensitivity to human presence (Riggio et al. 2013). Generally, however, studies have drawn direct negative associations between leopard ecology and human activities such as poaching, retaliatory killing for livestock losses and trophy hunting (Balme et al. 2009b, Henschel et al. 2011, Rosenblatt et al. 2016, Ramesh et al. 2017, Abade et al. 2018, Puri et al. 2020).

Protected areas (PAs) with effective fences and adequate management resources, or that otherwise constitute effective refugia, may facilitate abundant leopard populations (Balme et al. 2019, Farhadinia et al. 2019, Noack et al. 2019). Leopard populations within PAs also appear to fare better in the core than on the periphery (Balme et al. 2010b, Thapa and Kelly 2017). Together, these findings suggest that land sparing is a more effective approach for conserving leopard *abundance* (Di Minin et al. 2013b, Gilroy et al. 2015, Stephens 2015, Jiang et al. 2017), even if land sharing and coexistence are necessary to preserve leopards' range (Crespin and García-Villalta 2014, Carter and Linnell 2016).

Protected areas are the cornerstone for conserving most large predator species (Watson et al. 2016) but “protectedness” for species within PAs is not uniform and differs among and within sites (Packer et al. 2013, Lindsey et al. 2014, 2017, 2018, Swanepoel et al. 2015b, Abade et al. 2018, Pekor et al. 2019). A third of global protected areas are under intense human pressure, with higher rates within extant leopard range and among small reserves (Jones et al. 2018). Declines in mammal populations within PAs are especially common in Africa (Craigie et al. 2010, Rija et al. 2020). Nominally protected areas with scarce resources and few mechanisms to enforce restrictions on human behavior, so called “paper parks” (Bruner et al. 2001), may not offer any protection to populations. Often, anthropogenic influences within PAs depend less on the PA’s nominal status than on edge effects and the integrity of the PA (i.e., whether management effectively enforces restrictions on human activities) (Woodroffe and Ginsberg 1998, Balme et al. 2010b, Packer et al. 2013, Rosenblatt et al. 2016, Veldhuis et al. 2019, Loveridge et al. 2020). In theory, larger PAs should offer greater protection because of their capacity to buffer core areas of the reserve (Harcourt et al. 2001, Newmark 2008). PA effectiveness, however, may depend more on human factors around the PA than on size alone (Parks and Harcourt 2002). Disentangling levels of protectedness, PA integrity, size, and *de facto* protectedness is difficult. To do so while also accounting for localized variation in resources and imperfect detection is exceptionally challenging for data scarce species (but see Jędrzejewski et al. 2017; Mills et al. 2020).

Spatial capture-recapture models offer enormous potential to confront these challenges relative to classical modeling techniques. While some studies have relied on post-hoc analyses of variation in carnivore density estimated using SCR models (Thornton & Pekins 2015; Ramesh et al. 2017; Williams et al. 2017), SCR models that explicitly incorporate heterogeneous density offer the best approach for disentangling differences in population density and detection. Such models have proven effective for investigating range expansion (Sun et al. 2017), effects of land use and habitat fragmentation (Murphy et al. 2017), habitat quality and management (Lamb et al. 2018), and protectedness (Bahaa-el-din et al. 2016, Havmøller et al. 2019) on population density for myriad carnivores.

In this chapter, I harnessed the potential of multi-session SCR models with inhomogeneous density to investigate drivers of leopard density in and around PAs in South Africa. I considered multiple working hypotheses coupled with an information theoretic approach to determine which hypotheses the data best support (Burnham and Anderson 2002, Elliott and Brook 2007, Garamszegi 2011, Havmøller et al. 2019). In the broadest sense, I investigated whether leopard density is driven more by “bottom-up” biological factors that determine prey availability and the carrying capacity of a landscape (e.g., Carbone and Gittleman 2002, Hayward et al. 2007, Kiffner et al. 2009) or “top-down” anthropogenic factors that either protect or impede abundant populations (e.g., Dorresteijn et al., 2015; Everatt et al., 2014; Kiffner et al., 2009; Kissui & Packer, 2004). I also draw conclusions about the effectiveness of South Africa’s network of protected areas for conserving leopards. To my knowledge, this analysis constitutes the most data-rich analysis of the drivers of leopard density ever produced.

5.2 Methods

5.2.1 Data processing

Details on data collection and image classification are available in Chapter 2. Both density and predictor variables for any given habitat cell are likely to be temporally correlated (or certain to be in the case of static predictor variables). Including multiple surveys from any given area thus results in repeat sampling of nearly identical density-covariate relationships. Because of this temporal dependence, we can expect the models to underestimate the variance in the underlying density-predictor relationships. In addition, repeatedly sampling some sites but not others leads to overweighting areas sampled frequently relative to those that were sampled once. Therefore, to avoid pseudo-replication (Arnqvist 2020), I included a single survey from each site, resulting in a dataset of 27 surveys from North West, Gauteng, Limpopo, Mpumalanga, and KwaZulu-Natal provinces. In addition to surveys from sites analyzed in Chapter 3, the dataset included surveys from four study sites that recorded too few leopard captures to permit single-session SCR model fitting, but which could be included within multi-site models with shared detection functions among sites (Mohamed et al. 2013). I excluded two study sites, Khamab Kalahari GR and Ukhahlamba Drakensberg Park because they recorded few or zero captures and have no biological analog among other study sites; Khamab was the only study site in the desert biome and the Drakensberg mountains host a high-altitude montane grassland system that is unique within southern Africa. I used 2016 surveys whenever they were available (n = 23), as that was the year when the maximum number of sites were surveyed. For sites that were not surveyed in 2016, I used the survey nearest in time to 2016 (See Table 5.1 for details).

***Table 5.1**: Summary of the surveys at each ste included in the heterogeneous density analysis.*

Site name	Year	Biome	Stations	Effort*	Individuals	Captures	Spatial Recaptures	Males#	Females#
Atherstone	2016	Savanna	40	1852	16	32	13	4	10
Barberton	2016	Savanna	33	984	0	0	0	0	0
Blyde	2016	Savanna	31	1316	6	20	5	3	2
Dinokeng	2016	Savanna	36	1604	0	0	0	0	0
E. Shores	2016	Forest	41	1810	23	146	54	8	14
HiP	2016	Grassland	46	2031	19	58	19	7	12
Ithala	2016	Grassland	30	1345	30	134	38	9	19
KZNPRs	2015	Grassland	62	2644	30	156	48	9	21
Lajuma	2016	Grassland	40	1883	24	146	47	7	14
Lapalala	2016	Savanna	40	1991	14	59	17	7	6
Loskop	2016	Savanna	34	1897	16	77	23	9	6
Madikwe	2016	Savanna	40	1854	4	7	2	4	0
Makalali	2016	Savanna	40	1982	23	89	26	11	10
Manyoni	2015	Grassland	40	1793	7	69	22	6	1
Mapesu	2018	Savanna	35	1558	10	50	15	5	1
Munyawana	2016	Forest	42	2283	31	189	62	9	17
Ophate	2014	Grassland	36	1855	3	20	6	2	1
Pilanesberg	2016	Savanna	40	1784	27	64	16	14	11
Somkhanda	2016	Grassland	29	1246	7	42	18	4	3
Songimvelo	2016	Grassland	27	1151	1	1	0	0	1
Tembe	2016	Forest	32	1427	22	123	36	8	12
Timbavati	2016	Savanna	40	1935	29	106	40	15	10
uMkhuze	2016	Grassland	40	1784	21	94	36	9	11
Venetia	2016	Savanna	40	1897	20	76	18	10	10
Welgevonden	2016	Savanna	40	1292	15	57	22	8	7
Wonderkop	2015	Savanna	37	1600	10	27	12	4	5
Zingela	2016	Savanna	40	1716	16	46	13	8	6

* The cumulative number of days during which camera stations were operational. # The difference between the total number of individuals and the cumulative number of males and females is the number of unsexed individuals.

I formulated capture histories using the same methods as described in Chapter 4. Each survey was treated as a unique session, with each site thus represented by one session. To avoid duplicating individuals for which left and right flanks could not be identified, I included only individuals with a known left flank. I recorded the number of captures of each individual at each station using a "count" trap formulation based on an 8-hour test of independence between captures. Trapping effort was calculated as the number of days at least one camera at each station was operational.

5.2.2 Hypotheses and predictor variables

Testing multiple working hypotheses is an inductive approach to understanding complex systems. It involves formulating a set of competing hypotheses *a priori* that might plausibly predict an ecological response. I developed hypotheses based on previous research on the ecology, management, and demographics of leopard populations and other large carnivores (Dochtermann and Jenkins 2011) while making sure to generate hypotheses with varying complexity to avoid the pitfalls of underfitting or overfitting models (Garamszegi 2011). I then translated each hypothesis into a set of relevant predictor variables that I selected based on their prior use for investigating leopard density and distribution, my knowledge of study sites and study populations, and the commonality of predictors' measurability and reliability across all sites and surveys. I modeled each hypothesis using a single model specification, which I incorporated into SCR models by representing the state process as an inhomogenous point process (Havmøller et al. 2019).

I formulated hypotheses on the existing evidence that 1) leopard density depends on the availability of resources within ecosystems, 2) that humans can have negative impacts on leopard populations, and 3) that effective management of protected areas can mitigate these human impacts. All hypotheses investigated some combination of these three premises and each predictor variable was intended to measure a specific aspect of one of these premises. Though no predictor variable perfectly represents a given premise, the assumption is that the set of predictors together are meaningfully representative of the overall hypothesis. I developed ten working hypotheses, each with a density model specifying between one and seven parameters (Table 5.2).

I measured each predictor variable at either of two spatial scales. I included predictors that were constant within study sites as session-level covariates in the models. Predictors that varied within sites I measured at the scale of each habitat cell in the state space. To account for the fact that activity centers represent the center of each leopard's area of use (AoUs) during the sampling period (i.e., second-order selection; Johnson 1980), I measured spatially continuous variables (i.e., those represented as rasters) at the second-order scale around each habitat cell using an inverse-distance weighted mean (Chandler and Hepinstall-Cymerman 2016). These covariate values were calculated as the mean of all raster pixels within the modeled AoU – defined as a circle with radius r_{AU} – of the habitat cell with weights assigned using a half-normal function with spatial decay parameter, $\hat{\sigma}$, derived from the $D_{session}$ model (see Model Fitting and Evaluation below). For a leopard with activity center s_i, the relative weight of each surrounding raster pixel thus reflected the relative probability of the leopard being detected at that pixel's location. The farther from the activity center, the more raster cells occur. Thus, an unweighted mean threatens to swamp local conditions in the immediate vicinity of the activity center with covariate observations comparatively far away. Distance-weighted means address this imbalance and further offer the advantage of being empirically derived rather than subjective. The derived scale was broadly consistent with other measures of leopard second-order selection (e.g., Pitman et al. 2017a).

After sampling predictor variables, I standardized continuous variables by pooling across sites and rescaling to have a mean of 0 and a standard deviation of 1 (Schielzeth 2010). For distance and area variables that differed by several orders of magnitude, I log-transformed values prior to standardizing based on an assumption of diminishing marginal returns in those variables' effects. Rescaling variables using the distribution across all sites emphasizes broad-scale general responses to predictor variables rather than within-site response to local factors. I confirmed that no two predictor variables had a pairwise correlation greater than 0.7.

5.2.2.1 Biological variables

I selected predictor variables that reflect prey resources and habitat suitability to provide a measure of the availability of biological resources. While humans also influence bottom-up processes for large carnivores (Dorresteijn et al. 2015, Mills et al. 2020) and do so at many of the study sites (e.g., stocking, supplementary feeding, and culling of herbivores), I considered these as indirect effects on the overall availability of prey. I estimated relative prey abundance for each site as the mean capture rate across all stations in each survey for prey species in leopards' preferred weight range. Although relative abundance indices ("RAIs"; O'Brien et al. 2003) are not always reliable when comparing across species and ecosystems (Sollmann et al. 2013), research shows that camera-trap surveys of non-migratory African herbivores are sufficiently accurate to draw broad inferences about populations (Palmer et al. 2018). Based on reports of leopard prey preference in Hayward et al. (2006), Schwarz and Fischer (2006), and Pitman et al. (2014), I defined prey species as herbivores with a weight between 10 and 70 kgs, which encompassed 15 recorded species. Prey captures were considered independent capture events if at least 0.5 hour passed between consecutive observations of the same species or if observations of the same species less than 0.5 hour apart were non-consecutive (c.f., O'Brien et al., 2003).

Carnivore predation is often less a matter of prey abundance than prey vulnerability (Hopcraft et al. 2005, Coon et al. 2020). Leopard hunts are most successful in moderately dense vegetation (Balme et al. 2007). Furthermore, prey may be especially vulnerable in riparian zones, especially for water dependent species. I therefore included two measures of prey vulnerability: normalized difference vegetation index ('NDVI'; Pettorelli et al. 2011) as a measure of vegetation density and the log-transformed Euclidean distance from the centroid of each habitat cell in the state space to the nearest major river (Silberbauer 2012). I acquired NDVI values from MODIS MOD13A1 ~500 m vegetation indices data set recorded at 16-day intervals (Huete et al. 2002) and sampled at the temporal midpoint of each survey. I included NDVI in the models as an additive linear and quadratic effect to account for optimal hunting in moderately dense habitat (Balme et al. 2007) as well as positive selection of moderate and dense vegetation for movement and resting (Naha et al. 2021).

5.2.2.2 Protected areas and anthropogenic variables

I included three predictor variables to account for the extent of protected areas and their management: a binary variable for each habitat cell describing whether the centroid of the cell was located outside (0) or inside (1) a protected area, a binary variable for management type indicating whether reserves were primarily managed by state (0) or private (1) entities, and a continuous measure of PA size. Private PAs in general have greater financial resources and better fences than state reserves for keeping people and domestic animals out (see Packer et al. 2013 for a discussion of the interrelated effects of fences and management budgets on large-carnivore density). I measured PA size as the log-transformed area of each PA and all contiguous PAs. Although some adjacent reserves have fences between them, these are generally not effective barriers to leopard movement. For example, all seven leopards observed within the Amakhosi/Zeekoepan reserve in the KZN network of private reserves (KPGR, Mahlalela, Mkuze Falls, and Amakhosi/Zeekoepan, hereafter simplified to "KZNPRs") were also recorded on adjacent reserves despite the presence of fences. Terrestrial PA boundaries were acquired from the World Database on Protected Areas (IUCN & UNEP-WCMC, 2016) and from PA managers. I subset WDPA protected areas to those designated as conserved areas, national parks, nature reserves, provincial nature reserves, or Ramsar sites. I also considered a third variable, perimeter-to-area ratio, but excluded it because it was strongly correlated with log-transformed PA size ($r > 0.8$) and the latter variable was more interpretable.

I measured human pressure around and within protected areas based on the intensity of human activity and infrastructure, human encroachment into protected areas, and potential edge effects. I estimated human activity and infrastructure via the Human Footprint Index ('HFI'; Venter et al. 2016b, 2016a), which integrates data on human population density, infrastructure, and land use into an index with values from 0 (no footprint) to 50 (maximum footprint) measured at 1 km resolution, and which correlates with large mammal mortality (Hill et al. 2020), large-felid occurrence and population fragmentation (Jędrzejewski et al. 2018, Thatte et al. 2019), reduced mammalian mobility (Tucker et al. 2018), and extinction risk (Di Marco et al. 2018). I measured human encroachment as the proportion of camera stations in each survey that recorded domestic animals. Most observations of humans are from the research team, tourists, or rangers and people engaging in prohibited activities cannot reliably be identified.

Domestic animals, on the other hand, are prohibited within the study site PAs except for rare instances of canine anti-poaching units (which are themselves indicators of potential poaching activity). Most photos of domestic animals recorded livestock, but many also recorded dogs, a common means of bushmeat hunting in southern Africa. However, as livestock farming is often associated with, and even facilitates bushmeat hunting (Rogan et al. 2018), it was not possible to tease apart the relative influence of those two types of disturbance. The extent of domestic animals thus represents a composite measure of human interference and exploitative competition with wildlife (Everatt et al. 2019). I elected to measure the proportion of stations that detected domestic animals to reflect the geographic extent of this disturbance and because large herds of livestock often result in frequent detections even if livestock are confined to a small portion of the reserve. By contrast, a RAI might have overstated the impact of localized domestic animal activity. I also integrated the proportional extent of domestic animals with PA size to create a log-transformed “effective PA-size” predictor variable intended to represent the extent of space where human impacts are actually mitigated. I defined “effective size” as the log-transformed size of the protected area reduced by the proportion of stations that detected domestic animals. The predictor variable was thus calculated using the expression

$\ln(Size \times (1 - Domestic))$ where “*Size*” is the area of the PA and all contiguous protected areas in square kilometers and “*Domestic*” is the proportion of stations that recorded domestic animals.

I measured potential edge effects (Balme et al. 2010b) as the log-transformed distance from the centroid of each habitat cell within a PA to the nearest protected-area boundary. In the case of the Eastern Shores section of iSimangaliso Wetland Park, however, which is sandwiched between the ocean and a lagoon, I excluded the shoreline as edge and only included terrestrial boundaries. For every reserve, the state space extended beyond protected areas and for some small reserves, habitat cells were predominantly located outside PAs. I assumed a uniform effect for cells outside PAs: all cells had a distance of 0 from the edge. The distribution of distances to PA boundaries was thus heavily zero-inflated and created a false equivalency between habitat cells immediately within a PA boundary and those far outside it. I therefore isolated the effect of distance to edge to only habitat cells located inside PAs by including this variable in models as an interaction with the binary protectedness variable: for habitat cells outside PAs (protectedness = 0) the interaction term would automatically take a value of zero, and inside protected areas (protectedness = 1) the interaction term would take the value of the log-transformed distance-to-edge predictor value.

I considered the hypothesis that private management would not influence leopard density directly but would influence the response of leopard density to human impacts. I therefore included a hypothesis (Hyp. 9) that investigated leopard density in response to human impacts (proportional extent of domestic animals, HFI, and edge effects) as main effects and as interactions with management, while controlling for different levels of baseline protection between state and private reserves.

5.2.3 Model fitting and evaluation

The purpose of this analysis was not to generate the most precise or accurate estimates of leopard density but rather to test hypotheses regarding the drivers of leopard density using the most interpretable models possible. To this end, I fit a single multi-session SCR model for each working hypothesis to all 27 surveys (i.e., sessions) with the state process, density, modeled using an inhomogeneous Poisson point process (see Table 5.2 for density predictor variables). I used a spatially coarse parameterization of the detection process by keeping the parameters in the detection model constant within biomes. Sharing detection parameters across sites both allowed inclusion of surveys from sites with too few captures to fit unique detection functions and smoothed the stochasticity in the detection process that I discussed in Chapter 3.

Table 5.2*: Working hypotheses and associated density models for investigating the drivers of leopard density in and around 27 protected areas in northeastern South Africa. "Prey" is a relative abundance index of leopards' preferred prey species. "NDVI" is the normalized difference vegetation index, a measure of vegetation density. "Distance-to-river" is the log-transformed distance of each habit cell centroid to the nearest major river. "Protected" and "Management" are binary variables indicating whether habitat cells are located outside or within PAs and whether study sites are primarily managed by state or private entities, respectively. "HFI" is the Human Footprint Index. "PA size" is the log-transformed size of study PAs and all contiguous protected areas. "Domestic" is the proportion of camera stations at each study site that recorded domestic animals and "effective PA-size" is the log-transformed size of protected areas reduced by the proportion of stations with domestic animals. "Edge-distance" is the log-transformed distance of each habitat cell centroid to the nearest PA boundary.*

ID	Hypothesis	Density model	No. of parameters
Hyp. 1	Leopard density increases with prey abundance and vulnerability.	D ~ Prey + NDVI + NDVI^2 + ln(Distance-to-river)	5
Hyp. 2	Leopard density increases in habitat where prey is most vulnerable.	D ~ NDVI + NDVI^2 + ln(Distance-to-river)	4
Hyp. 3	Leopard density is greater within PAs than in adjacent unprotected areas	D ~ Protected	2
Hyp. 4	Leopard density is greater in PAs with better management characteristics	D ~ ln(PA-size) + Management + Protected	4
Hyp. 5	Abundant large-carnivore populations require large habitat patches.	D ~ ln(PA-size)	2
Hyp. 6	Leopard density is limited by human impacts on PAs.	D ~ HFI + Domestic + Protected + Protected:ln(Edge-distance)	5
Hyp. 7	Leopard density increases with the effective size of a PA, defined as the area in which domestic animal incursions are absent.	D ~ ln(effective PA-size)	2
Hyp. 8	Leopard density is greater in PAs with greater management resources but is limited by human impacts.	D ~ ln(PA-size) + Management + Domestic + HFI + Protected + Protected:ln(Edge-distance)	7
Hyp. 9	Leopard density is limited by human impacts, but greater management resources mitigate some of these effects.	D ~ Domestic + HFI + Protected + Protected:ln(Edge-distance) + Management:HFI + Management:Protected + Management:Protected:ln(Edge-distance)	8
Hyp. 10	Leopard density is determined by broad scale (i.e., site-level) anthropogenic factors and localized habitat suitability.	D ~ ln(PA-size) + Management + Domestic + NDVI + NDVI^2 + ln(Distance-to-river)	7

To ensure that habitat covariates were representative of the effective sampling area of the camera array, I restricted the state space to include only habitat cells for which an individual's expected area of use would encompass at least one station. While artificially constricting the state space would be expected to inflate estimates of density, it excludes distant land uses for which I have no meaningful data and any effect should be limited to the intercept in the density model rather than predictor effects of interest. I estimated the radius of an expected circular home-range size (r_{AU}) from an initial SCR model with density varying by session (i.e., site) and detection parameters λ_0 and σ varying by biome (hereafter "$D_{session}$ model") that I fit to a state space defined as a 15-km buffer around camera stations (i.e., replicating the approach in Chapter 3). I discretized all state spaces into 500 m X 500 m (0.25 km^2) habitat cells and excluded cells with centroids located in pixels classified as "water" or "urban" land uses (Plummer et al. 2017). I mapped biome boundaries from Olson et al. (2001) and assigned sites to the biome in which the majority of their camera stations were situated (see Appendix 5.1).

Using the estimates of σ from the $D_{session}$ model, I calculated the expected AoU radius using the formula $r_{AU} = 2.447\sigma$ (Royle et al. 2013b). Although I initially intended to estimate AoU radii for each biome, estimates of σ for each biome were nearly identical and varied by less than 100m. I therefore used a single σ estimate for all biomes based on the geometric mean, $\hat{\sigma}$, and for all subsequent models, I defined the state space for each session to be only habitat pixels less than $2.447\hat{\sigma}$ from the nearest station. I ensured that constraining the state space would not introduce undue bias by also fitting the $D_{session}$ model to the $\hat{\sigma}$-defined state space and comparing parameter estimates (see Appendix 5.2 for details).

I then fit models to test each of the ten hypotheses in R package "secr" v. 4.1.0 (Efford 2019) by maximizing the full likelihood, optimized using the Nelder-Mead estimator. I modeled predictor variables that were constant across sites as session-level effects and localized predictor variables at the level of each habitat cell. I maintained a constant parameterization of the detection model for all hypotheses (Havmøller et al. 2019). I modeled the detection process using a hazard half-normal decay function with parameters λ_0 and σ. I accounted for variation in λ_0 using an interaction between biome and sex. In the case of σ, however, I only modeled variation in response to sex, and not biome, as I had already found no variation among biomes. I included sex in the models as a two-class partially observed finite mixture.

Preliminary model fitting revealed that naïve starting values for the optimization process (i.e., intercepts for D, λ_0, and σ derived from the first session and all other parameter estimates

Table 5.3*: Site-level characteristics of protected areas (PAs) included in the study. PA size includes each site and adjacent PAs. Prey relative abundance index ("RAI") is derived from capture rates of preferred prey species. Extent of domestic animals is measured as a proportion of camera stations that recorded domestic animals. Proportion protected is the proportion of habitat cells in each state space that lie within PAs.*

Site	Biome	Management type	PA size (km^2)	Prey RAI	Extent of domestic animals	Proportion protected
Atherstone	Savannas	State	287	1.28	0.38	0.43
Barbeton	Savannas	Private	271	1.23	0.64	0.43
Blyde	Savannas	State	304	0.37	0.23	0.31
Dinokeng	Savannas	Private	211	0.78	0.25	0.34
EShores	Forest	State	1430	0.74	0.07	0.97
HiP	Grasslands	State	932	0.44	0.07	0.69
Ithala	Grasslands	State	294	0.83	0.10	0.43
KZNPRs	Grasslands	Private	624	2.15	0.02	0.46
Lajuma	Grasslands	Private	336	0.45	0.42	0.49
Lapalala	Savannas	Private	492	0.45	0.25	0.55
Loskop	Savannas	State	253	0.78	0.03	0.39
Madikwe	Savannas	State	620	0.40	0.05	0.68
Makalali	Savannas	Private	233	0.42	0.22	0.37
Manyoni	Grasslands	Private	225	1.58	0.12	0.37
Mapesu	Savannas	Private	602	0.64	0.29	0.27
Munyawana	Forest	Private	1430	1.12	0.05	0.57
Ophate	Grasslands	State	299	1.04	0.86	0.36
Pilanesberg	Savannas	State	589	0.33	0.12	0.70
Somkhanda	Grasslands	Private	624	1.40	0.28	0.58
Songimvelo	Grasslands	State	420	0.96	0.70	0.74
Tembe	Forest	State	299	1.06	0	0.54
Timbavati	Savannas	Private	21416	0.49	0.07	0.93
uMkhuze	Grasslands	State	1430	0.76	0.10	0.59
Venetia	Savannas	Private	602	0.37	0	0.49
Welgevonden	Savannas	Private	1000	0.33	0	0.56
Wonderkop	Savannas	State	158	0.37	0.41	0.24
Zingela	Savannas	Private	220	1.52	0.07	0.32

starting at 0), hampered model fit and resulted in models being prone to converging at local maxima. I therefore derived initial values for the D_{session} model from estimates of density, g_0, and σ reported for the inhomogenous density models in Chapter 3 (with λ_0 nearly equivalent to g_0 at the small magnitudes reported; Noss et al. 2012). When fitting models representing hypotheses, I derived optimizer starting values for predictor variables from univariate models for each predictor except NDVI, for which I derived starting values from a bivariate density model with NDVI included as a linear and quadratic effect. I set the starting value for the probability of unsexed individuals being male at 0.4 (-0.4 on the logit-link scale). I set the initial value for male σ to be 1.5 times female σ (0.4 on the log scale) but set male and female λ_0 to be equivalent.

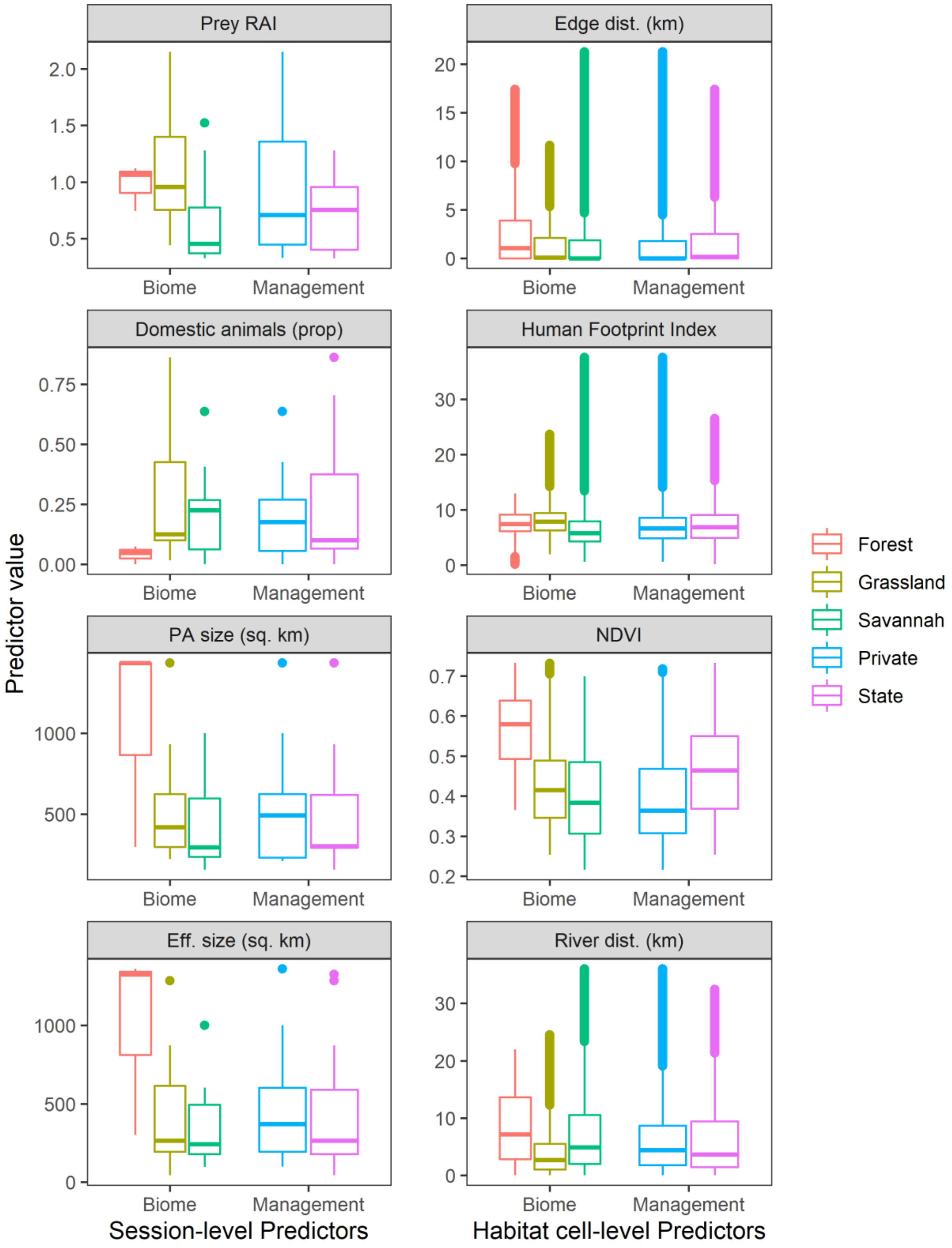

***Figure 5.1**: Distributions of session-level and habitat-cell-level predictor variables among management types (State or Private) and biomes (Forest, Grassland, or Savanna).*

I quantified the relative statistical support for each model and associated hypothesis using a quantitative information theoretic, Akaike's Information Criterion corrected for small sample sizes ("AICc"; Akaike 1981; Hurvich & Tsai 1989). I accepted as having some support any model with a ΔAICc < 7 relative to the best-performing model and compared support between pairs of models using evidence ratios (Burnham et al. 2011). I qualitatively evaluated relative effect sizes based on coefficient estimates of all β parameters in supported models.

5.3 Results

5.3.1 Data summary

5.3.1.1 Capture histories

The 27 surveys recorded 1891 independent observations of 427 individual leopards. The number of individuals observed during each survey ranged from 0 at Dinokeng GR and Barberton NR to 31 at Munyawana PGR (median = 16; IQR = 7 – 23) while the total number of independent captures ranged from 0 to 189 (median = 59; IQR = 30 – 100). Surveys recorded between 0 and 62 spatial recaptures (median = 18, IQR = 12.5 – 36; Table 5.1).

5.3.1.2 Predictor variables

No pairwise correlation among predictor variables exceeded 0.4 in magnitude (Appendix 5.3). Contiguous protected areas ranged in size from 158 km^2 at Wonderkop to more than 21000 km^2 at Timbavati and the adjacent greater Kruger ecosystem (see Table 5.3 for details). Three surveys recorded no domestic animals, while two recorded domestic animals at more than half of all camera stations. Relative prey abundance varied by a factor greater than 6, from 0.33 photos per trap day at Pilanesberg GR and Welgevonden GR to 2.15 at the KZNPRs. NDVI values across the state spaces were mostly between 0.25 and 0.5 but ranged between 0.216 and 0.732 (Table 5.4). The mean distance to the nearest major river within each study site varied substantially, from less than 2000 m to more than 17000 m, with a maximum distance for a single habitat cell greater than 36 km. With the exceptions of the Eastern Shores section and Timbavati, more than a quarter of habitat cells at each site were in unprotected areas, and for fifteen sites, more than half were. The maximum observed distance of a habitat cell from the unprotected edge was more than 21 km. Mean Human Footprint Index ('HFI') values differed only slightly outside protected areas (7.9) compared to inside (6.4) but varied considerably among sites from 3.9 at Lapalala and Welgevonden to more than 13 at Dinokeng. HFI values for some habitat cells exceeded 25 (i.e., half the maximum potential) at three sites: Barberton, Dinokeng, and Pilanesberg. On the other hand, five sites in Limpopo Province had no habitat cells within their state spaces that recorded HFI values above ten. The maximum observed value for any individual habitat cell was 37.6.

Overall, the distributions of variables were similar between state and privately managed reserves, but they differed in skewness (Fig. 5.1). Median standardized values of the prey RAI were similar between the two management types, but privately managed reserves had a much heavier and longer right skew, whereas state reserves exhibited a longer right skew in the proportional extent of domestic animals. Relative prey abundance was similar among the forest and grassland biomes, but lower in the savanna biome. The forest biome hosted larger protected areas and fewer stations recording domestic animals than the other two biomes.

5.3.2 Supported hypotheses

Four of the ten hypotheses exhibited some support with a ΔAICc < 7 (Table 5.5). Supported models included diverse variables covering biological factors, PA management, and human impacts, but only variables representing the latter were included in all four supported models. The proportion of stations that recorded domestic animals was the only predictor variable included in all four models and every model that included it as a predictor showed support. The best performing model (Hyp. 10), which accounted for nearly 50% of the weighting, included broadscale protected-area and anthropogenic factors relating to PA management and human impacts (size, management type, and domestic animals), and localized biological factors (NDVI and distance-to-river). Hyp. 9, which stated that leopard density is limited by anthropogenic impacts but management conditions can mitigate these effects, was two-thirds as likely as the best performing model (ΔAICc = 0.8, wt = 0.35). Models of predictor variables representing only human impacts (Hyp. 6) and human impacts in conjunction with management characteristics (Hyp. 8) exhibited ΔAICc values of nearly 3, indicating these models were a quarter as likely as the top performing model and a third as likely as Hyp. 9. No other model exhibited a ΔAICc vales below 24, indicating that the least supported model that included domestic animals was nevertheless more than ten-thousand times as likely as the best model without it (Hyp. 7).

***Table 5.4**: Summary (mean, standard deviation, minimum, and maximum) of cell-level predictor variables for each study site. "NDVI" is the normalized difference vegetation index and has a maximum value of 1. "HFI" is the Human Footprint Index with values between 0 and 50. "Edge distance" is the distance from each habitat cell to the nearest PA boundary and is limited to only habitat cells located within PAs. "River distance" is the distance from each habitat cell to the nearest major river.*

Site	NDVI			HFI			River distance (m)			Edge distance (m)		
	mean (sd)	min	max	mean (sd)	min	max	mean (sd)	min	max	mean (sd)	min	max
Atherstone	0.45 (0.05)	0.34	0.53	4 (2)	1	8	15807 (8035)	1	32460	2143 (1585)	6	6402
Barbeton	0.43 (0.06)	0.35	0.59	9 (4)	4	29	2583 (1780)	2	7795	1317 (1003)	0	4600
Blyde	0.47 (0.12)	0.26	0.7	7 (3)	2	14	2256 (1805)	1	9018	1125 (850)	1	3815
Dinokeng	0.33 (0.02)	0.26	0.4	13 (7)	5	38	2271 (1632)	0	6426	1002 (785)	2	3623
EShores	0.61 (0.05)	0.44	0.72	5 (3)	0	11	10148 (3987)	20	17563	9433 (4810)	8	17402
HiP	0.47 (0.05)	0.35	0.65	7 (3)	2	14	1797 (1428)	0	7778	4329 (2829)	6	11622
Ithala	0.35 (0.04)	0.27	0.45	7 (2)	4	12	1910 (1367)	1	6002	1982 (1373)	1	5798
KZNPRs	0.38 (0.04)	0.29	0.49	8 (2)	4	11	3409 (2600)	2	11660	1402 (1128)	1	5082
Lajuma	0.56 (0.09)	0.39	0.72	6 (2)	2	16	9610 (6446)	6	24517	2708 (1910)	6	7587
Lapalala	0.44 (0.07)	0.27	0.56	4 (1)	1	7	5045 (3982)	2	17083	2801 (1983)	3	8307
Loskop	0.53 (0.05)	0.43	0.64	8 (2)	4	15	4401 (3113)	2	11278	1755 (1316)	2	4945
Madikwe	0.34 (0.05)	0.26	0.49	5 (2)	1	10	13656 (7888)	1	28768	3736 (2679)	7	10716
Makalali	0.28 (0.02)	0.24	0.35	4 (2)	1	11	7644 (4297)	0	16552	1678 (1218)	1	5099
Manyoni	0.35 (0.03)	0.29	0.45	10 (2)	5	16	4404 (2925)	3	11014	1815 (1341)	1	5456
Mapesu	0.3 (0.03)	0.26	0.39	6 (3)	1	11	11824 (6481)	11	25982	1446 (1047)	7	5065
Munyawana	0.47 (0.05)	0.36	0.57	8 (1)	5	11	2924 (2260)	2	9419	2244 (1608)	4	6863
Ophate	0.31 (0.06)	0.25	0.57	9 (3)	4	24	2099 (1620)	0	7273	1189 (854)	2	4034
Pilanesberg	0.5 (0.06)	0.35	0.58	13 (7)	3	27	5137 (3356)	0	14476	3728 (2612)	2	10726
Somkhanda	0.44 (0.07)	0.25	0.56	8 (2)	4	13	4935 (3152)	4	11181	2142 (1641)	3	6825
Songimvelo	0.67 (0.03)	0.57	0.73	7 (3)	3	13	2088 (1581)	3	6770	2962 (1833)	1	7328
Tembe	0.64 (0.04)	0.53	0.73	8 (2)	5	13	13270 (5137)	1270	21969	2433 (1723)	4	6760
Timbavati	0.25 (0.02)	0.22	0.28	6 (1)	3	9	3929 (2699)	1	12041	8712 (5245)	35	21254
uMkhuze	0.49 (0.06)	0.38	0.64	9 (2)	6	12	8252 (4823)	4	17992	2840 (1879)	3	6894
Venetia	0.29 (0.02)	0.23	0.34	6 (1)	2	12	17652 (8455)	1170	36016	2464 (2048)	0	8237
Welgevonden	0.49 (0.02)	0.46	0.53	4 (1)	1	7	2909 (2187)	2	9421	2387 (1591)	1	6651
Wonderkop	0.48 (0.04)	0.41	0.58	6 (2)	2	11	5004 (3810)	1	15450	1072 (729)	1	3194
Zingela	0.34 (0.03)	0.29	0.4	7 (1)	3	11	10373 (5564)	0	21203	1814 (1248)	1	4754

5.3.3 Predictor effects

Among the four supported models, the extent of domestic animals consistently exhibited a strong negative effect, with β estimates ranging from -0.46 ± 0.07 to -0.37 ± 0.07 (Table 5.6). Back-transforming the effect of domestic animals in the top ranked model indicates that sites with no incursions by domestic animals would be expected to host a population that is a quarter denser than a site with the median proportion (12.5%) and two-thirds denser than a site at the third quartile (28.1%), all other variables being equal.

The binary protectedness variable also exhibited a large magnitude effect, albeit with far less certainty or consistency than for the effect of domestic animals (see Appendix 5.4 for details). In the model for Hyp. 3, which stipulated that protectedness determines leopard density, cells inside protected areas were expected to be twice as densely populated as areas immediately outside PAs (β = 0.71 ± 0.17). The large standard error for this effect across all five models that included protectedness as a predictor variable indicates that most likely this effect was not constant across all sites. The variation explained by this variable also appears to be partially explained by other factors including HFI and extent of domestic animals, as evidenced by the reduced magnitude of the effect when included with a variety of other predictors. There was no indication of greater protectedness in reserve cores compared to the edge as the effect size for distance to edge was less than one standard error in all supported models. On the other hand, leopard density was positively associated with PA size. PAs that spanned 1000 km^2 were associated with a leopard density 11% greater than PAs half that size. A PA that was an order of magnitude greater (i.e., 10000 km^2) would be expected to have a leopard density 42% greater, all other variables being equal.

Leopard density increased linearly with NDVI. One standard deviation in a habitat cell's NDVI value relative to the mean was associate with a nearly 20% increase in leopard density. The magnitude of the effect was greater when accounting for anthropogenic variables than in models that only included biological predictors (see Appendix 5.4). β coefficients provided no indication that the relationship between leopard density and NDVI was unimodal. Although the effect was not distinguishable from zero, the coefficient was positive in all three models. The β coefficient for log-transformed distance to river exhibited a maximum magnitude of 0.02, which was much less than the magnitude of the standard error.

***Table 5.5**: Relative support and weights for the ten working hypotheses quantified using Akaike's information theoretic corrected for small sample sizes (ΔAICc). The number of parameters includes those in both the density and detection models. "NDVI" is the normalized difference vegetation index; "HFI" is the human footprint index; "management" refers to whether a protected area is predominantly managed by state or private entities; "Protected" describes whether a habitat cell is within a protected area; and "domestic" refers to the proportion of stations that recorded domestic animals.*

Hyp.	Predictor variables	No. of parameters	ΔAICc	Weight
10	ln(PA-size) + Management + Domestic + NDVI + NDVI^2 + ln(Distance-to-river)	17	0	0.46
9	Domestic + HFI + Protected + Protected:ln(Edge-distance) + Management:HFI + Management:Protected + Management:Protected:ln(Edge-distance)	18	0.8	0.31
8	ln(PA-size) + Management + Domestic + HFI + Protected + Protected:ln(Edge-distance)	17	2.8	0.12
6	HFI + Domestic + Protected + Protected:ln(Edge-distance)	15	2.9	0.11
7	ln(effective PA-size)	12	24.3	0
4	ln(PA-size) + Management + Protected	14	38.9	0
5	ln(PA-size)	12	43.9	0
3	Protected	12	50.5	0
2	NDVI + NDVI2 + ln(Distance-to-river)	14	65.5	0
1	Prey + NDVI + NDVI^2 + ln(Distance-to-river)	15	68.1	0

***Table 5.6**: Estimated effects (and std. errors) of predictor variables in the four supported models of leopard density. "D_0" is the intercept term, "Domestic animals" is the proportion of stations that recorded domestic animals, "HFI" is the Human Footprint Index, "PA size" is the log-transformed size of a PA and other contiguous PAs, "Protected" indicates habitat cells within PAs, "Edge distance" is the log-transformed distance to the nearest PA boundary, "NDVI" is the normalized difference vegetation index, "River distance" is the log-transformed distance to the nearest major river and "Management interactions" refer to distinct effects for predictor variables at sites that are privately managed as opposed to state managed.*

											Management Interactions		
Hyp.	D_0	Domestic animals	HFI	PA size	Pvt. Mgmt.	Protected	Edge dist.	NDVI	NDVI^2	River dist.	HFI	Protected	Edge
10	-8.05 (0.08)	-0.42 (0.07)		0.15 (0.05)	0.06 (0.06)			0.17 (0.06)	0.05 (0.05)	0.02 (0.06)			
9	-8.24 (0.14)	-0.46 (0.07)	-0.16 (0.07)			0.33 (0.18)	0.02 (0.10)				-0.19 (0.07)	-0.06 (0.07)	0.04 (0.09)
8	-8.21 (0.15)	-0.37 (0.07)	-0.12 (0.07)	0.14 (0.05)	-0.02 (0.05)	0.35 (0.18)	-0.06 (0.10)						
6	-8.35 (0.16)	-0.42 (0.07)	-0.10 (0.07)			0.53 (0.20)	0.04 (0.10)						

5.3.4 Detection parameters

Detection parameters among all ten models were highly consistent. Among the four supported models, female σ ranged from 1769 m to 1790 m, while male σ was considerably greater, with values between 2861 m and 2899 m. Baseline detection was also greater for males than for females but was as or more variable among biomes than between sexes; baseline detection was greatest in the forest biome and lowest in the savanna biome (Table 5.7). Males were estimated to account for 43-44% of the total population.

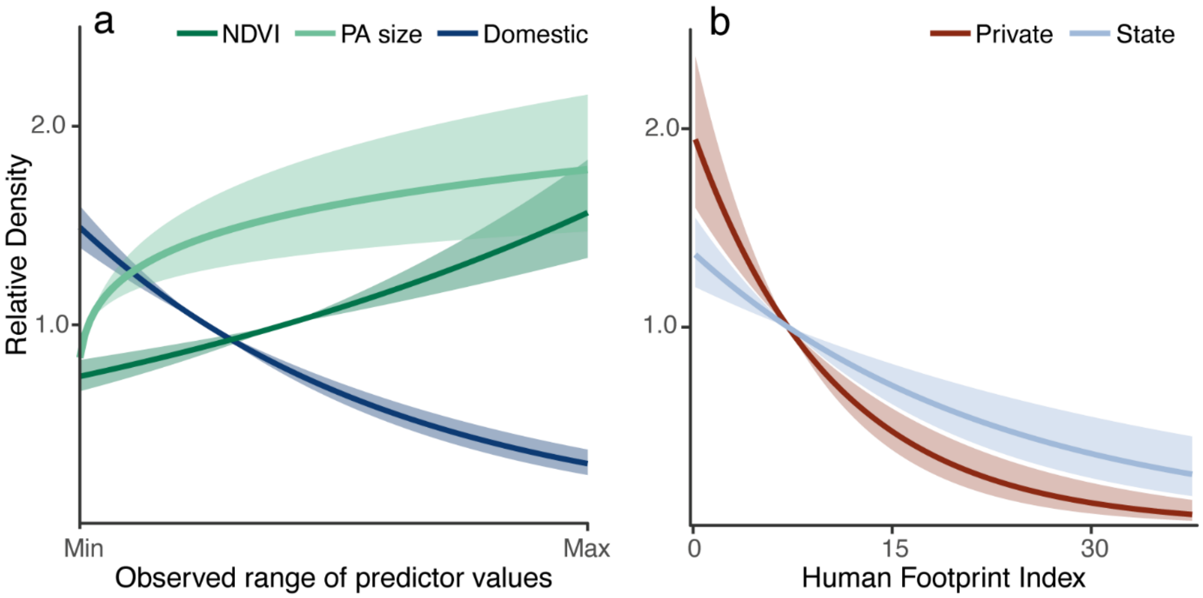

Figure 5.2: *Multiplicative effect ($e^{\beta x}$; lines) plus or minus one std. error (shaded regions) of selected predictors on leopard density based on the two strongly supported hypotheses, Hyp. 10 (a) and Hyp. 9 (b). The observed range of predictor values for (a) are 0.216 – 0.732 for inverse-distance weighted means of the Normalized Difference Vegetation Index ("NDVI"), 158 – 21416 km^2 for the log-transformed size of protected areas and all contiguous PAs ("PA size"), and 0 – 0.861 for proportional extent of domestic animals ("Domestic").*

5.4 Discussion

Humans and their activities have decimated large carnivore populations worldwide (Loveridge et al. 2010, Di Marco et al. 2014, Ripple et al. 2014), but these population-level effects are not inevitable (Linnell et al. 2001, Schuette et al. 2013, Chapron et al. 2014). Large, strictly protected areas offer refuge and are thus the cornerstone of large carnivore conservation globally even though these species often receive the least protection from gazettement (Ashrafzadeh et al. 2020, Ferreira et al. 2020). Despite their importance, conservationists have very little information on which specific characteristics of protected areas are most conducive to conserving large carnivore populations.

Table 5.7 *Detection parameter estimates for male and female leopards.* p_{male} *is the estimated probability of an unsexed or unobserved individual being male.* λ_0 *is the baseline detection rate in the hazard half-normal detection model and* σ *is the spatial decay parameter in meters. See Appendix 5.5 for std. errors.*

	Grasslands λ_0		**Forest λ_0**		**Savannas λ_0**		**σ**		
Hyp.	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	p_{male}
m10	0.035	0.043	0.042	0.044	0.020	0.026	1776	2899	0.43
m9	0.034	0.041	0.043	0.049	0.020	0.024	1769	2873	0.44
m8	0.035	0.043	0.041	0.049	0.019	0.026	1775	2878	0.44
m6	0.034	0.043	0.041	0.048	0.019	0.025	1790	2861	0.43
m7	0.035	0.043	0.043	0.049	0.018	0.026	1786	2876	0.44
m4	0.035	0.043	0.044	0.048	0.020	0.026	1773	2842	0.43
m5	0.035	0.043	0.043	0.048	0.019	0.026	1782	2872	0.43
m3	0.034	0.043	0.042	0.048	0.019	0.025	1771	2864	0.43
m2	0.035	0.043	0.043	0.049	0.019	0.026	1775	2880	0.43
m1	0.035	0.043	0.043	0.047	0.020	0.026	1782	2886	0.43

5.4.1 Drivers of leopard density

Leopards, being widespread and conflict-prone, are illustrative of how different characteristics of PAs may drive differences in population-level parameters of a large carnivore. I analyzed data from 27 study PAs in northeastern South Africa to investigate how leopard density varies in relation to select bottom-up biological processes and top-down anthropogenic factors (Kiffner et al. 2009, Dorresteijn et al. 2015, Everatt et al. 2019). The results were unequivocal: human impacts in and around protected areas are limiting South Africa’s leopard populations. Biological factors such as vegetation density matter too, but only when accounting for the broad-scale pressure humans put on large carnivores and the ecosystems in which they live.

The primacy of anthropogenic factors is consistent with the bulk of research that documents the harmful effects humans exert on large carnivores. Unquestionably, people kill leopards in and around these study sites (Balme et al. 2010b, Swanepoel et al. 2014, 2015c, Pitman et al. 2017b). However, we cannot say with confidence the degree to which most killings result from leopards being targeted specifically, for example to provide skins for the Shembe Church followers (Naude et al. 2020b), or as a result of by-catch when targeting wildlife for food. What is clear is that where indices of human presence are greatest, leopard density is lowest.

Fortunately, effective PA management can mitigate the harm people do. The mere presence of humans is not inherently detrimental to wildlife (Bruskotter et al. 2017) but it is well established that people kill carnivores worldwide for a variety of reasons and otherwise interfere with ecological processes. Even large carnivores' fear of human voices can influence their behavior and space use (Suraci et al. 2019). In this study, I found that leopard density was negatively associated with a measure of the intensity of the human footprint. In addition, land sparing – designating land as protected areas – had a positive influence on leopard density and larger PAs yielded greater densities. A call to set aside land for large carnivores is nothing new (e.g., Di Minin et al. 2013b, Stephens 2015), but here I show that it applies even in the case of a species often lauded for its ability to coexist with humans. Large reserves offer clear benefits to biological diversity generally and African carnivore populations specifically (Harcourt et al. 2001, Brugière et al. 2015), but only if their integrity is maintained (Midlane et al. 2014, Di Minin and Toivonen 2015).

PAs that failed to limit incursions from domestic animals, and by extension the prohibited human activities that often accompany domestic animal presence, hosted markedly sparser leopard populations. Proportional extent of domestic animals within a PA seemed to best explain variation in leopard density among study sites; all models that included it, and no models that excluded it, showed statistical support. Its strong effect mirrors other recent findings that where livestock and pastoralists tread, carnivores usually fare poorly (Brugière et al. 2015, Abade et al. 2018, Aebischer et al. 2020). The effects of pastoralism on large carnivore occurrence, abundance, and persistence may be worse than the effects of bushmeat hunting (Everatt et al. 2019, Aebischer et al. 2020), but pastoralism and bushmeat hunting often go together (Everatt et al. 2015, Rogan et al. 2018). The strength of the relationship between leopard density and domestic animals is especially telling given that observations of domestic animals are a coarse approximation of the intensity of prohibited human activities within PAs. Furthermore, though proportional extent of domestic animals is fundamentally a spatial variable, the weaker effect of the effective PA size predictor indicates that domestic animal presence should not be interpreted purely in a spatial sense. In other words, a PA in which domestic animals roam across half the area is likely to host a lower density of leopards than another PA that is half the size but with no domestic animal presence. This suggests that domestic animal presence is either an indicator of generalized management failures or that the harmful effects I associate with domestic animals (e.g., poaching and conflict) extend beyond the areas in which domestic animals forage. These conclusions mirror a number of studies that found effects from human interference permeating throughout entire PAs (Kiffner et al. 2013, Midlane et al. 2014, Veldhuis et al. 2019).

Contrary to expectations, PAs that are privately managed did not mitigate the negative relationship between leopard density and the human footprint; they intensified it. Private reserves with a low human footprint maximized leopard density but those with a substantial human footprint hosted sparse populations. While the absence of a main effect for management type and a positive interaction with HFI are somewhat surprising, the reasons become clear when considering the specific context of these study sites. Two privately managed PAs were outliers in that the state spaces for those leopard populations encompassed areas of unusually high human footprint relative to other sites. Dinokeng Nature Reserve is situated on the edge of one of the largest metropoles (Johannesburg-Pretoria) on the continent. Barberton Nature Reserve is a state reserve but most of the land has been granted to private entities for management. Furthermore, much of the reserve was actively mined until recently (illegal mining continues) and much of the natural habitat was severely degraded (*pers. obs.*). Neither of the surveys at these sites recorded leopards. The observed interaction between human footprint and private management may thus reflect a positive feedback loop. Private PAs far from urban centers with lots of large carnivores such as leopards are the most profitable and thus have the most management resources, whereas private PAs without large carnivores struggle to earn revenue and consequently cannot fund management interventions (Clements et al. 2016, Clements and Cumming 2018).

Also contrary to my stated hypotheses, the β coefficient for a log-linear edge effect was indistinguishable from 0 (see Appendix 5.6). Importantly, the lack of a clear edge effect does not contradict past research that did find such effects (e.g., Balme et al. 2010b). Sparser activity centers immediately outside PAs relative to inside them translate into a gradient of leopard activity within a home-range radius of the boundary. Two other factors likely play a role in the absence of an observed effect of distance-to-edge, one related to leopard biology and the other to characteristics of these sites. Though this study did not investigate leopard mortality directly, it has consistently proven greater on the edge of PAs than in the core (e.g., Balme et al. 2010b; Pitman et al. 2015; Swanepoel et al. 2015a). Leopards may shift home ranges or disperse into “gaps” left by dead leopards (Naude et al. 2020a) effectively smoothing density within PAs. A key site characteristic that may influence the absence of a distance-to-edge effect is the influence of PA size. Areas far from boundaries are necessarily within large reserves (Laurance and Yensen 1991). Although even a large PA could theoretically be of a shape such that most of the reserve is close to a boundary, that was not the case across these study sites as evidenced by the high correlation between size and area-to-perimeter ratio. Scale also matters. Jacobson et al. (2016) defined edge areas for leopards as anywhere within 10 km of a boundary; here 95% of habitat pixels met that criterion.

Hypotheses positing that leopard density was only associated with bottom-up biological resources showed the weakest support of all ten hypotheses. The only biological variable that exhibited a β coefficient of greater magnitude than its standard error was the linear effect of NDVI. Its effect in the best supported model was approximately equivalent to the effects of PA size and HFI. Furthermore, the effect of NDVI was one standard deviation greater in the top model than in the models with only biological effects, which suggests that the relationship is more evident when controlling for anthropogenic factors.

5.4.2 Detection and movement

Estimates of the detection parameters raise some questions for future research. While estimates of most model parameters were sensitive to starting values, σ estimates, which theoretically relate to the mean size of individuals' home ranges, were noticeably insensitive to both starting values and specification of the density model (Table 5.7). The similarity in σ among PAs in different biomes is remarkable and contradicts my original hypothesis that σ would vary among biomes. It also suggests that broadscale environmental factors are weak drivers of variation in leopard home-range size.

While stochasticity, individual variation, and high sampling error would in part explain the high temporal variation in σ discussed in Chapter 3, research from northeastern South Africa has found strong signals of density-dependence in leopard dispersal and second-order selection (Fattebert et al. 2015a, Naude et al. 2020a). This density-dependence may influence home-range size (Efford et al. 2016, Kumar et al. 2019), at least in suitable habitat where leopards do not need uncharacteristically large areas to meet their resource requirements. Rather than shift the extent of space use in response to available resources, leopards may instead vary the intensity of space use, as indicated by the measurable differences in λ_0 among biomes. Although differences in λ_0 may reflect variability in detection rather than intensity of space use (e.g., relative use of roads or drainages), they may also indicate variation in how rapidly leopards traverse their home ranges in the respective biomes (Efford 2014). Further investigation of leopard space use among populations and over time could yield more reliable parameterizations of multi-session SCR models.

5.4.3 Limitations

While this study found compelling and consistent evidence that top-down anthropogenic factors are the primary determinant of leopard density among these study sites, several limitations emerged. The measures of bottom-up biological resources used here are coarse and, in the case of the prey RAI and distance to major rivers, simplistic. For example, Burton et al. (2012) found a strong influence of prey abundance on leopard distribution, but their index of prey was recorded at a much higher resolution and thus with more variability (a factor of 41 versus a factor of 6 here) than the coarse session-level covariate considered here.

The biological predictors I used do not fully disentangle key biological processes among these study sites. They encompass a wide range of habitats (ranging from grassy mountains to forested coastal plains), which allows us to draw broad inferences about leopard ecology. However, all study sites fall within regions that Swanepoel et al. (2013) predicted to be “suitable” leopard habitat and thus this analysis may not reflect factors influencing leopard density at the extremes of their range (e.g., tropical rainforest or desert). Additionally, my hypotheses assume that predictor effects are constant across all sites, but effects may vary depending on habitat type. For example, the effect of rivers may be different in the relative aridity of Madikwe compared to the denser, wetter vegetation of Munyawana. Perhaps the greatest limit to investigating the effect of biological resources however is the difficulty of reliably measuring those resources across dozens of study sites. Because of those challenges and the need for consistent predictors across all study sites, this study made no attempt to quantify important variables such as year effects (Werner et al. 2020) or fine-scale variation in resources such as ephemeral water sources (Naidoo et al. 2020, Messager et al. 2021) that play important roles in ecosystem processes.

The challenges of reliably measuring variables at the appropriate scale extends to anthropogenic factors. This analysis would undoubtedly improve with an explicit measure of conflict (e.g., problem animal permits; Pitman et al. 2015), but such statistics are not consistently available across all study sites as they fall under different jurisdictions. Similarly, these models do not consider the historical legacies of each study population nor any differences in wildlife management in areas outside PAs. Without understanding the dynamics of leopard density outside PAs, we cannot fully understand how effective PAs are at conserving leopard abundance relative to adjacent unprotected areas. Camera-trapping outside protected areas, and especially on public or communal lands, can be impractical due to safety risks and camera theft. However, future research should integrate camera-trap sampling with alternative sampling methods (e.g., spoor surveys or citizen science; see Chapter 3) to generate data that are more representative of areas inside and outside PAs (Sun et al. 2019).

Just as predictor variables cannot possibly account for every relevant factor, the working hypotheses are a subjective subset of potential relationships, and the predictor variables do not perfectly represent each hypothesis. Reflecting on the model results, the four supported hypotheses are over-fitted in that they each include variables with no measurable effect, nor do they include all meaningful predictors. As a result, these models are not optimized for estimating leopard density nor for predicting density across landscapes. This issue is evident in a comparison of the top two models (see Appendix 5.6). Although the two models provide similar estimates of leopard density for most sites, some sites such as the Eastern Shores section of iSimangaliso Wetland Park show widely divergent expected densities. This does not mean either model is uninformative or biased but rather that neither perfectly accounts for all the factors that determine density within the study area. Specifically, the differences in these two models result from the inclusion of PA size, NDVI, and HFI in one model but not the other. Generating an accurate prediction surface would require an alternative modeling framework beyond the scope of this analysis.

5.4.4 Lessons for conserving leopards in South Africa

Despite these limitations, this study nevertheless paints a clear picture of leopard density within protected areas of South Africa during the Anthropocene. Leopard and other large carnivore populations across the continent (Newmark 2008) and globally (Jędrzejewski et al. 2017) need large spaces that shelter them from human impacts. In a country where most protected areas are relatively small and isolated, reserves which are part of a larger connected network such as the transfrontier conservation areas and the iSimangaliso-uMkhuze-Munyawana complex are boons for leopard conservation (Curveira-Santos et al. 2021). Although some studies have celebrated the capacity of small isolated reserves to host abundant large carnivore populations (Packer et al. 2013, Noack et al. 2019), this and other studies offer substantial evidence that as a general rule bigger is better (Crooks 2002, Newmark 2008). Conservationists should thus prioritise efforts to convert rangelands around protected areas to expand existing private reserves (Clements et al. 2019) rather than seek to promulgate more small and isolated reserves. However, PA size alone is not enough. The lesser magnitude of the effective PA size coefficient relative to the additive effects of PA size and domestic animals shows that increasing the size of protected areas is only effective when those areas are well-managed. We must do more to ensure that PAs have the resources needed to be effective (Lindsey et al. 2018, Pekor et al. 2019). Even for a protected area the size of greater Kruger NP (~21500 km^2), with recent evidence of concerted leopard poaching (Panthera unpublished data), maintaining the integrity of the PA is likely critical for maintaining an abundant leopard population.

South Africa is a long way from the favorable policy framework that has coincided with large carnivore recovery in the northern hemisphere (Linnell et al. 2001, Chapron et al. 2014). Laws meant to prevent the illegal trade in leopard products are seldom enforced (Naude et al. 2020b) and many of the study sites have hosted legal leopard hunts within the last leopard generation. Most of all, the prevalence of domestic animals across as much as three-quarters of select reserves speaks to the nominal status of many of the “protected” sites in this study. Unquestionably, sites such as Barberton Nature Reserve are currently just “paper parks”, at least in terms of large carnivore management. The existing network of protected areas in northeastern South Africa can ensure the viability of its leopard populations, but only if the policy framework is revised and wildlife authorities treat gazettement as a cornerstone of conservation rather than a comprehensive solution.

Appendix 5.1: Chapter 5 study sites in relation to ecological biomes.

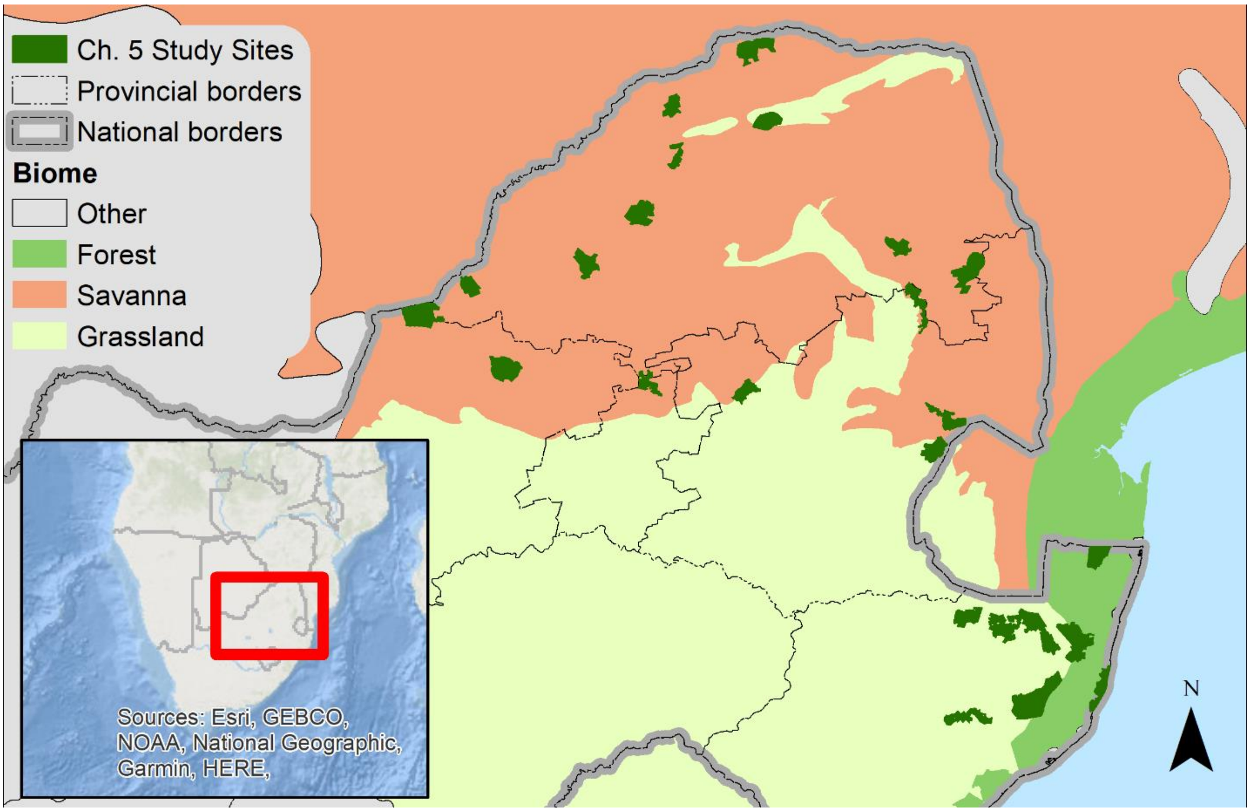

Figure S5.1*: 27 study sites in northeastern South Africa in relation to major ecological biomes* (Olson et al. 2001).

Appendix 5.2: Comparison of $D_{session}$ model for full (15 km buffer) and constrained (6.4 km buffer) state spaces.

Parameter	**Full habitat mask**	**$\hat{\sigma}$ habitat mask**	**Proportional Difference**
Density intercept (Atherstone)	-7.99 (0.25)	-7.98 (0.25)	0
Density - Barberton	-2.58 (1.03)	-2.50 (0.99)	-0.03
Density - Blyde	-1.04 (0.47)	-1.03 (0.48)	-0.01
Density - Dinokeng	-2.60 (1.02)	-2.52 (0.99)	-0.03
Density - Eastern Shores	0.93 (0.33)	0.94 (0.33)	0.01
Density - HiP	-0.20 (0.34)	-0.20 (0.34)	0
Density - Ithala	0.58 (0.31)	0.58 (0.31)	0
Density - KZNPRs	0.33 (0.31)	0.31 (0.31)	-0.06
Density - Lajuma	0.31 (0.33)	0.32 (0.33)	0.03
Density - Lapalala	-0.37 (0.37)	-0.36 (0.37)	-0.03
Density - Loskop	0.13 (0.35)	0.14 (0.36)	0.08
Density - Madikwe	-1.61 (0.56)	-1.58 (0.56)	-0.02
Density - Makalali	0.37 (0.33)	0.39 (0.33)	0.05
Density - Manyoni	-0.24 (0.40)	-0.23 (0.40)	-0.04
Density - Mapesu	-2.01 (0.64)	-1.93 (0.63)	-0.04
Density - Munyawana	0.49 (0.32)	0.47 (0.32)	-0.04
Density - Ophate	0.53 (0.31)	0.53 (0.31)	0
Density - Pilanesberg	-0.65 (0.45)	-0.63 (0.45)	-0.03
Density - Somkhanda	-2.58 (1.09)	-2.43 (1.02)	-0.06
Density - Songimvelo	0.32 (0.33)	0.33 (0.33)	0.03
Density - Tembe	0.63 (0.31)	0.63 (0.31)	0
Density - Timbavati	0.37 (0.34)	0.39 (0.34)	0.05
Density - uMkhuze	0.18 (0.33)	0.16 (0.34)	-0.11
Density - Venetia	0.07 (0.36)	0.08 (0.36)	0.14
Density - Welgevonden	-0.36 (0.40)	-0.34 (0.40)	-0.06
Density - Wonderkop	0.04 (0.35)	0.04 (0.36)	0
Density - Zingela	-0.85 (0.45)	-0.85 (0.45)	0
lambda0 intercept (Forests)	-3.28 (0.08)	-3.28 (0.08)	0
lambda0 - Grasslands	-0.05 (0.10)	-0.04 (0.10)	-0.20
lambda0 - Savannas	-0.5 (0.10)	-0.51 (0.10)	0.02
sigma intercept (Forests)	7.87 (0.04)	7.87 (0.04)	0
sigma - Grasslands	-0.03 (0.05)	-0.04 (0.05)	0.33
sigma - Savannas	-0.03 (0.05)	-0.04 (0.05)	0.33

Appendix 5.3: Predictor variable correlation table.

	Prey	**Domestic**	**ln(PA size)**	**Management**	**NDVI**	**HFI**	**ln(River)**
Domestic	0.07						
ln(PA size)	-0.18	-0.35					
Management	0.25	-0.11	0.15				
NDVI	-0.06	0.05	-0.12	-0.35			
HFI	0.18	0.09	-0.09	-0.04	-0.08		
ln(River)	-0.04	-0.16	-0.02	0.04	-0.05	-0.18	
ln(Edge)	0	0	0	0	0.01	-0.23	-0.02

Appendix 5.4: Estimated effect sizes for all ten fitted models

Hyp.	**D**	**Domestic**	**Eff. size**	**HFI**	**HFI: Mgmt**	**NDVI^2**	**PA size**	**Mgmt**	**NDVI**	**Prey**	**Prtcd**	**Prtcd: Edge**	**Prtcd: Edge: Mgmt**	**Prtcd: Mgmt**	**River**	**ΔAICc**
10	-8.05 (0.08)	-0.42 (0.07)				0.05 (0.05)	0.15 (0.05)	0.06 (0.06)	0.17 (0.06)						0.02 (0.06)	0
9	-8.24 (0.14)	-0.46 (0.07)		-0.16 (0.07)	-0.19 (0.07)						0.33 (0.18)	0.02 (0.1)	0.04 (0.09)	-0.06 (0.07)		0.79
8	-8.21 (0.15)	-0.37 (0.07)		-0.12 (0.07)			0.14 (0.05)	-0.02 (0.05)			0.35 (0.18)	-0.06 (0.10)				2.76
6	-8.35 (0.16)	-0.42 (0.07)		-0.1 (0.07)							0.53 (0.2)	0.04 (0.1)				2.94
7	-7.91 (0.05)		0.3 (0.04)													24.34
4	-8.29 (0.15)						0.18 (0.04)	-0.01 (0.05)			0.58 (0.18)					38.91
5	-7.89 (0.05)						0.22 (0.04)									43.93
3	-8.37 (0.15)										0.71 (0.17)					50.46
2	-7.9 (0.07)					0.02 (0.04)			0.12 (0.05)						0.1 (0.06)	65.48
1	-7.93 (0.07)					0.03 (0.04)			0.11 (0.05)	0 (0.05)					0.1 (0.06)	68.06

Appendix 5.5: Detection parameter estimates with standard errors for all ten fitted models.

	Female λ_0			**Male λ_0**			**σ (m)**				
Hyp.	**Forest**	**Savanna**	**Grassland**	**Forest**	**Savanna**	**Grassland**	**Female**	**Male**	**p_{male}**	**ΔAICc**	**Weight**
10	0.0422 (0.0039)	0.0198 (0.002)	0.0351 (0.0029)	0.0442 (0.0043)	0.0256 (0.0018)	0.0429 (0.003)	1780 (50)	2900 (70)	0.43 (0.03)	0	0.46
9	0.0427 (0.0039)	0.0202 (0.002)	0.0343 (0.0028)	0.0489 (0.0047)	0.0242 (0.0017)	0.0415 (0.0029)	1770 (50)	2870 (60)	0.44 (0.03)	0.79	0.31
8	0.0427 (0.0039)	0.019 (0.0019)	0.0348 (0.0029)	0.0486 (0.0047)	0.0257 (0.0018)	0.0427 (0.003)	1770 (50)	2880 (70)	0.44 (0.03)	2.76	0.12
6	0.0414 (0.0038)	0.0186 (0.0019)	0.0338 (0.0028)	0.0478 (0.0046)	0.025 (0.0017)	0.0426 (0.0029)	1790 (50)	2860 (60)	0.43 (0.03)	2.94	0.11
7	0.0429 (0.0039)	0.0185 (0.0019)	0.0345 (0.0028)	0.049 (0.0047)	0.0258 (0.0018)	0.0434 (0.003)	1790 (50)	2880 (70)	0.44 (0.03)	24.34	0
4	0.0436 (0.0039)	0.0196 (0.0019)	0.0351 (0.0029)	0.0483 (0.0047)	0.0255 (0.0018)	0.0433 (0.003)	1770 (50)	2840 (60)	0.43 (0.03)	38.91	0
5	0.0428 (0.0039)	0.0188 (0.0019)	0.0346 (0.0029)	0.0484 (0.0047)	0.0258 (0.0018)	0.0433 (0.003)	1780 (50)	2870 (70)	0.43 (0.03)	43.93	0
3	0.0422 (0.0038)	0.0185 (0.0019)	0.0342 (0.0028)	0.048 (0.0046)	0.0253 (0.0017)	0.0425 (0.0029)	1770 (50)	2860 (60)	0.43 (0.02)	50.46	0
2	0.0427 (0.0039)	0.0192 (0.0019)	0.0345 (0.0028)	0.0489 (0.0047)	0.0256 (0.0018)	0.0429 (0.003)	1770 (50)	2880 (70)	0.43 (0.03)	65.48	0
1	0.0427 (0.0039)	0.0198 (0.002)	0.0351 (0.0029)	0.0466 (0.0045)	0.0257 (0.0018)	0.0429 (0.003)	1780 (50)	2890 (70)	0.43 (0.03)	68.06	0

Appendix 5.6 Illustration of spatial variation in relative predicted leopard density.

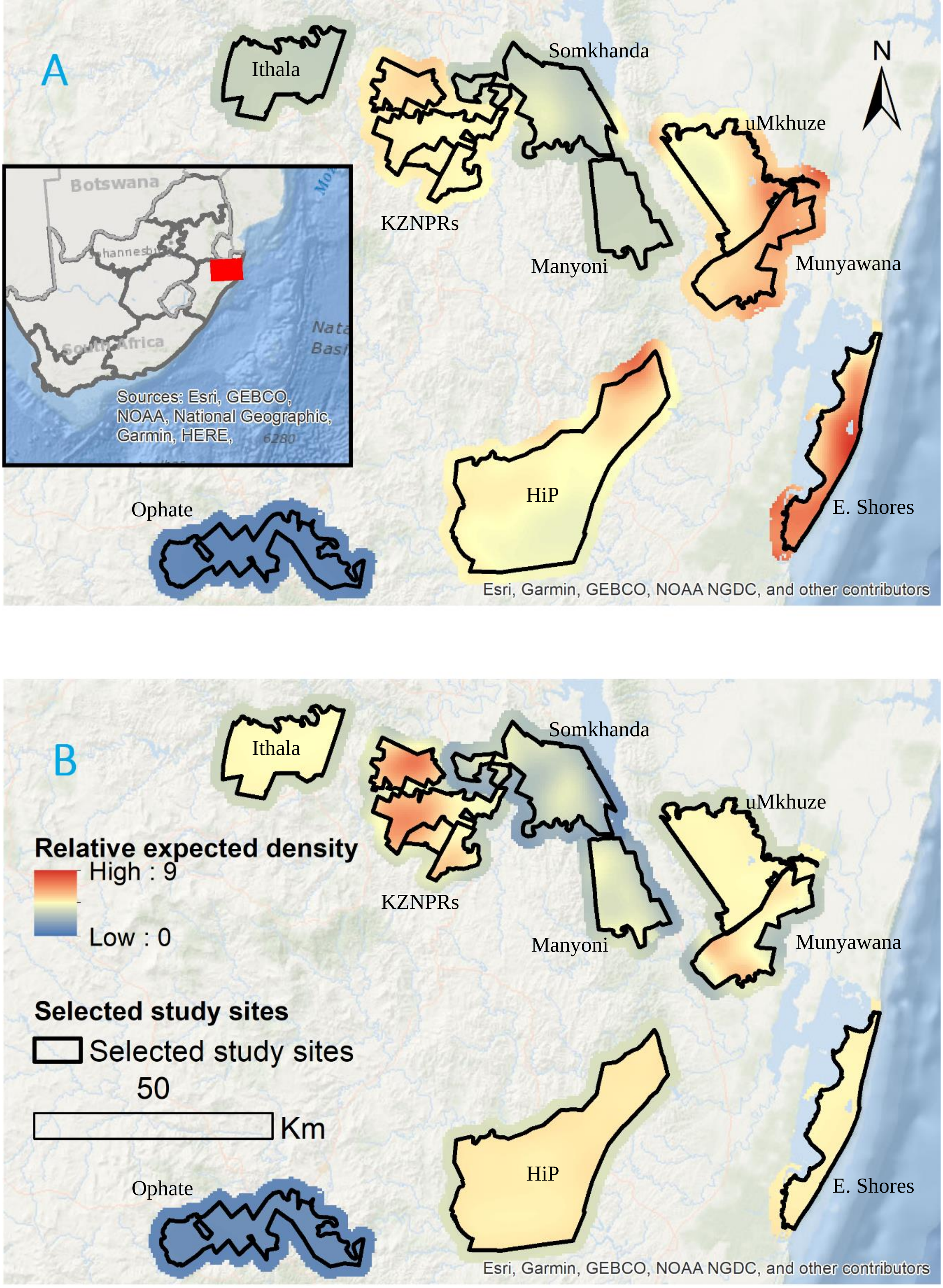

***Figure S5.6**: Relative expected density for leopards at study sites in northern KwaZulu-Natal Province, South Africa based on the models for the top two supported hypotheses: 9 (A) and 10 (B).*

CHAPTER 6

SYNTHESIS

Wild felids, like many other taxa, face a precarious existence in the Anthropocene. More than 80% of the 38 wild felid species are either threatened or have decreasing population sizes (IUCN 2020), while their propensity for coming into conflict with humans necessitates active management. Yet they are also iconic species that fill critical ecological niches and, in some areas, are cornerstones of lucrative tourism industries. Conserving these species is therefore essential. Doing so effectively depends on robust monitoring to identify threatened populations, inform management, and evaluate interventions.

In this thesis, I used spatial capture-recapture (SCR) models to analyze one of the largest camera-trap survey datasets ever compiled for a wild felid species to investigate population status of an elusive and wide-ranging apex predator, African leopards (*Panthera pardus*). Although they are among the most widespread felid species, leopards are perhaps the most data scarce species in the *Panthera* genus in terms of population dynamics. We have estimates of population density or abundance for relatively few subpopulations relative to most other large felids and, alarmingly, only a handful of estimates of population growth rates. However, leopards are among the species to benefit most from the widespread adoption of SCR modeling for camera-trap surveys (Green et al. 2021).

This general paucity of longitudinal data is concerning given leopards' range and habitat are greatly diminished and the species is widely persecuted for predating livestock (Jacobson et al. 2016). Since I embarked on this PhD five years ago, our cognizance of the plight of African leopards has grown markedly. Jacobson et al. (2016) mapped the severe loss of leopard habitat and Williams et al. (2017) showed how quickly a population can diminish. More encouragingly, Balme et al. (2019) and Noack et al. (2017) provided evidence of high-density populations free from anthropogenic mortality, but these populations stand in contrast to the sparser populations reported here and elsewhere. Loveridge et al. (2020) and Naude et al. (2020) described the impact of wire snaring and the illegal skin trade, respectively, on leopard populations, two emergent threats that compound prey loss, habitat loss, and fragmentation

(Jacobson et al. 2016). Faced with immense, widespread threats and a dearth of population-level assessments, efforts to conserve most leopard populations are faltering (Stein et al. 2016).

Clearly, conservationists must do more. We must reckon with the international trade in illegal leopard furs and work to eliminate the unsustainable and illegal demand (Naude et al. 2020b). We must improve management of protected areas including reducing the ingress of domestic animals and their human herders, addressing the targeted poaching of leopards, and mitigating the effects of trophy hunting (Loveridge et al. 2020, Searle et al. 2020). Achieving these objectives almost certainly requires increasing funding for PA management (Lindsey et al. 2018) and providing decision makers with robust data on leopard populations over time.

In order to address the lack of robust population data and better guide leopard conservation, I fit SCR models to data from Panthera's leopard monitoring program for Southern Africa (LMP) to 1) test the efficacy of using proxies for density to efficiently monitor leopard populations, 2) assess the conservation status of monitored populations based on the probability that those populations are declining, and 3) investigate the landscape and management characteristics most conducive to conserving leopard density. By fitting SCR models to data from more than 80 camera-trap surveys conducted within 28 protected areas, I drew lessons on best practices for monitoring leopard density. I also provide wildlife managers with critical information on the conservation needs of study populations and an understanding of the regional factors that determine leopard density that would not be evident in smaller-scale studies.

6.1 Summary of findings

6.1.1 Proportion of area used as a proxy for leopard density

Despite the usefulness of SCR, it poses substantial field challenges. For cryptic, far-ranging species such as leopards, sampling must be both intensive (i.e., at fine scales) to generate recaptures of individuals and extensive to sufficiently cover the spatial extent of the far-roaming target population. In other words, it is resource intensive and mandates high-quality data from which individuals can be recognized. SCR modeling is therefore difficult to implement when monitoring at a regional level or over long timeframes. By contrast occupancy modeling, which estimates species' occurrence from presence/non-detection data, is more suitable for regional monitoring because sampling can be coarser than for SCR analyses and individual identification is unnecessary. Data for occupancy models can be processed efficiently using machine learning image classification (Norouzzadeh et al. 2018, Tabak et al. 2019) without the comparative rigor needed to reliably identify individuals (Johansson et al. 2020). Occupancy is also related to abundance and density, although this relationship is highly variable and sensitive to sampling methods (Blackburn et al. 2006, Wilson 2008). I therefore tested whether occupancy (interpreted here as proportion of area used) and Royle-Nichols abundance were reliable proxies for density among leopard populations at 24 independent study sites on the basis that these parameters can be obtained more efficiently than directly estimating density through SCR.

I showed how populations that exhibit greater movement of individuals will appear to be more abundant, regardless of population density. Furthermore, I found that leopard space use was saturated for many of the study PAs (i.e., $\Psi = 1$) but density varied greatly among these populations. Relativizing occupancy and RN abundance accounted for the effect of saturation, but the relationship with density remained weak and too imprecise to inform management. Thus, occupancy and Royle-Nichols abundance cannot be relied on to either compare density among populations or to approximate density with a meaningful level of precision. However, it may be useful in some circumstances for tracking variation in density *within* a population. Secondarily, these findings serve to reinforce how critical the spatially explicit detection model is to robust density estimation.

6.1.2 Temporal trends in leopard population density

While estimates of density and occurrence are useful, often conservationists are more interested in population trends than snapshot estimates. Trends are typically non-linear and muddled by the noise of stochastic population processes. These complications, coupled with high sampling variance when monitoring rare, cryptic species, mean monitoring usually must continue for ten years or more to estimate population trends with confidence (White 2019). Such long timeframes, however, are at odds with conservation’s crisis ethos. When waiting ten years to detect trends with certainty would be irresponsible, an alternative approach is to use a Bayesian framework to estimate the posterior probability of declines and inform management based on the relative likelihood of various outcomes.

I thus applied multi-session closed-population SCR models to camera-trap datasets from seven study sites that were monitored for at least 5 years. Keeping detection parameters constant across sessions to smooth noise and increase the ratio of observations to estimated parameters, I modeled density at each site as a stochastic realization of a log-linear trend in expected abundance. I found that four of the seven populations were more likely than not to have declined at rates exceeding a halving of population density over three leopard generations. Worse, I found with high confidence that the leopard population at Hluhluwe-iMfolozi Park declined during the study period, with a three-in-four chance that this rate of decline would lead to a loss of more than 80% of the population over three generations. Only one of the seven sites exhibited evidence of population growth. Collectively, these findings indicate that South African protected areas in general are not imparting sufficient protection on leopard populations.

6.1.3 Anthropogenic and ecological drivers of leopard density

To understand why leopard populations are mostly faring poorly, I applied multi-session SCR models with inhomogenous density to survey data from 27 study sites to investigate the relative effects of bottom-up ecological processes and top-down anthropogenic factors on leopard density. I used an information theoretic approach to weigh statistical support for ten hypotheses of how leopard density responds to human impacts, PA management, and ecological factors. I found unequivocal evidence that leopard density largely responds to the level of human impacts within PAs, best approximated by the proportional extent of the PA occupied by domestic animals. Leopard density also exhibited a strong positive association with vegetation greenness (NDVI) and PA size but decreased where the human footprint was more prevalent. These results show that PA managers must take additional steps to protect leopards and minimize unlawful human disturbance within PAs lest these reserves become nothing more than “paper parks.”

6.2 Improving leopard monitoring

This study highlights SCR models as a powerful tool for monitoring and understanding populations of rare and cryptic species such as wild felids. While the SCR framework requires more intensive data collection than occupancy analyses, its capacity for modeling the effect of space use on detectability yields more dynamic insights than measures such as the proportion of area occupied. I have demonstrated the potential of long-term monitoring programs and SCR analyses to provide unique insights to guide conservation efforts. However, SCR is not a panacea for scarce data and presents considerable challenges. Estimating complex processes from few observations will always result in high uncertainty. Field methods need to continue evolving to efficiently gather the data necessary for robust statistical modeling. Recent advances in survey design (Dupont et al. 2021, Durbach et al. 2021), the relative tradeoff between sampling duration and the assumption of population closure (Dupont et al. 2019), and determinants of precision (Efford and Boulanger 2019) can guide more effective and precise surveys. The LMP can draw on these studies to improve its monitoring protocols within an SCR framework.

Efford and Boulanger (2019) showed that in most cases model precision is largely determined by the inverse of the square root of the lesser of two survey parameters: 1) the number of individuals observed and 2) the number of cumulative spatial recaptures among individuals. In the most simplistic sense, this heuristic dictates observing as many individuals as possible while observing individuals at an average of two stations each. We can infer, therefore, that any survey that does not detect individuals at two stations or more on average is underperforming and that surveys of small populations will always be imprecise regardless of the number of detections. To achieve a target coefficient of variation of 20%, a survey must be designed such that it is expected to detect 25 individuals at least 50 times (more than 50 captures will virtually always be necessary because of repeat observations of individuals at the same trap). Any survey with fewer individuals or fewer detections has limited statistical power. Sparse and threatened populations thus require the greatest sampling effort. Unfortunately, only a fifth of studies that use SCR meet the 20% coefficient of variation target (Green et al. 2021).

Efford and Boulanger (2019) further describe “pathological designs” of surveys analyzed using SCR as those that are inherently destined to yield insufficient data for unbiased and reasonably precise inference. The authors highlight two primary sources of pathology: trap arrays that do not exceed the movement of an individual, and those that result in insufficient spatial recaptures (which they define as fewer than five spatial recaptures) because of excessive spacing between traps or because sampling periods are too brief. Though LMP surveys generally surpass the threshold of “pathological” with ease, they do not always meet the emergent consensus of the gold standard in survey design as indicated by Clark (2019), Dupont et al. (2019, 2021), Efford and Boulanger (2019), and Durbach et al. (2021). Fewer than half of the 88 surveys I reported in Chapter 3 cleared the 25/50 hurdle. As a result, single-session models applied to the LMP dataset are plagued with imprecision and vulnerable to excessive bias (Dupont et al. 2021).

Although practitioners may be quick to point the finger at trap spacing when faced with insufficient data, precision and bias depend on several factors. Trap spacing for the LMP is typically less than the recommended 2σ (Efford and Fewster 2013, Dupont et al. 2021) but other aspects of LMP sampling design are suboptimal. Both precision – measured as the coefficient of variation on density (i.e., “relative standard error”), determined by the number of individuals observed and the number of spatial recaptures of each individual (Efford and Boulanger 2019) – and bias – usually measured as relative root mean square error of model estimates fit to simulated data – are sensitive to five factors: the number of individuals available for capture, the number of detectors, trap spacing relative to the scale of individual movement, baseline detection, and sampling duration (usually discretized into a number of sampling occasions).

Prescribing rules to address these factors is nigh impossible because all these elements are inter-related, and surveys can make use of tradeoffs among the different elements to compensate when one of them is suboptimal. General data standards can be inferred, however, from simulations that test the sensitivity of SCR model precision and relative bias to variations in survey design and population parameters. For example, Clark (2019) established a baseline scenario for simulating survey data of black bears based on a density of 15 bears per 100 km^2, g_0 of 0.1, traps spaced at 2σ, with 324 detectors grouped in 36 clusters of 9 that were active for 6 occasions. Sun et al. (2014), also simulating data informed by black bears, used scenarios of 500 individuals and 128 detectors active for 10 occasions with g_0 equal to 0.05, 0.1, or 0.2 and trap spacing ranging from ~0.5σ – ~9σ. Dupont et al. (2021) considered a baseline scenario derived from snow leopards of 300 individuals sampled using a grid spaced at 2σ with g_0 of 0.2 over five occasions for 49, 100, or 144 detectors. Royle et al. (2009) simulated data informed by tigers based on a scenario of 120 individuals sampled using 100 detectors operating for six occasions at 1σ spacing with g_0 of 0.5. All these studies have substantial differences, but collectively they differ from typical LMP surveys in several crucial ways. They all assume more stations and more abundant populations than most LMP surveys. Thus, LMP surveys suffer from few observed individuals, one of the two pillars that determine precision. Dupont et al. (2021) found that even with 49 detectors, the coefficient of variation for density was at least 0.2; few LMP surveys exceed 40 stations. This effect is exacerbated for sparse populations of only a few leopards per 100 km^2; in such cases detector arrays must span ~1000 km^2 to encompass the area of use of at least 25 individuals.

LMP surveys are not only constrained by the number of individuals observed; they also tend to record relatively few observations of each individual, largely because of low baseline detection. That LMP surveys suffer from low detection is not immediately apparent given that in this thesis I have measured it based on one-day occasions (Chapter 3) or daily detection rates (Chapters 4 & 5). However, we can standardize scenarios using cumulative non-detection probabilities. In the four simulation scenarios described above, cumulative baseline non-detection probability ranged from 0.15 to 0.6 in Sun et al.'s (2014) low detectability scenario. By comparison, the median non-detection probability from the 88 surveys described in Chapter 3 ($g_0 = 0.01$) over a standard 45-day LMP survey yields a cumulative baseline non-detection probability of 0.64. Even a 60-day LMP survey would still yield a cumulative baseline non-detection probability of 0.55, greater than that considered by all of the simulation scenarios except Sun et al.'s worst-case example.

Capture-recapture model performance is most sensitive to detection probability (Ivan et al. 2013) and when cumulative detection rates across all occasions are too low, it has cascading effects on other aspects of survey design. Whereas detector spacing of 2σ is optimal when individuals are highly detectable (e.g., cumulative non-detection of 0.33), when individuals are extremely undetectable (e.g., cumulative non-detection of 0.77), the optimal spacing shrinks to 1σ and bias remains high even when operating with 100 detectors (see Fig. 2B in Efford and Boulanger, 2019). In short, LMP surveys are imprecise (and potentially biased) not because the station spacing is excessive but because they sample too few individuals at too few locations for too short a time.

Fortunately, these factors are relatively straightforward to rectify for future surveys. The standard 45-day survey is based on a conservative approach to meeting the assumption of population closure. Dupont et al. (2019) showed that relaxing the standard for population closure greatly increases precision while only creating undue bias in the case of exceptionally long sampling periods. In their example of a species with a moderately slow life-history, red foxes, precision improved substantially for survey periods up to five months, after which gains were marginal. Bias, however, was lowest for sampling periods of 2.5 – 5 months, after which it increased slowly. Based on these results, surveys of approximately 3 months represent the best tradeoff between bias, precision, and wasted field resources; 45 days is unjustifiable.

Another approach is to conduct fewer larger surveys by consolidating surveys among adjacent or highly connected sites. Harihar et al. (2021) combined large trap arrays (118 – 236 stations) with moderate sampling durations (60 days) to achieve highly precise estimates from single-session models with coefficients of variation of 10% – 15% for density despite relatively sparse populations below 5 leopards per 100 km^2.

A similar approach can be taken for Panthera's LMP. For example, the Munyawana-uMkhuze complex should be modeled as a single population in line with other studies of those sites (e.g., Balme et al. 2010b, Fattebert et al. 2015, Naude et al. 2020a), while many of the private reserves in KwaZulu-Natal might similarly be consolidated as was done in the case of the 2015 survey of KPGR, Amakhosi/Zeekoepan, Mahlalela, and Mkhuze Falls reserves. Because the LMP operates in predominantly small reserves, the size of its surveys and the number of individuals available for detection will always be constrained. Nor can research teams control how frequently leopards pass cameras. Therefore, in the case of surveys in small, isolated reserves, the LMP should compensate with longer sampling durations and camera spacing of 1σ rather than 2σ. A similar effect can also be achieved either by using temporally replicated surveys modeled with constant parameters (as was done in Chapter 4 and by Kumar et al. 2019), or by using informed priors in Bayesian models to constrain the excessive uncertainty in the detection parameters of some surveys.

In general, while the number of surveys conducted under the auspices of the LMP is impressive, more rigorous sampling would yield clearer insights into study populations. Sub-optimal survey design, insufficient statistical power, and poor data quality are the most common issues that plague monitoring programs and impede their effectiveness (Legg and Nagy 2006). There is clear evidence that these factors undermine the LMP and ought to be addressed. The monitoring program would see a greater return on its investment with fewer, more extensive (more stations cover the area of use of more individuals) and intensive (longer sampling duration) surveys, even at the cost of reducing the number of sites surveyed each year. It would further benefit from more rigorous identification of individuals using a more robust processing stream and multiple observers (Choo et al. 2020, Johansson et al. 2020).

6.3 Conclusions

Given the scope for improvement, the LMP to date should be viewed as a baseline rather than a target. That the discussion on effective monitoring has even reached the point of emphasizing precision and survey design represents an immense achievement relative to the alarming dearth of population data when the LMP began. To complement the documented loss of leopard range, I provide evidence that even flagship leopard populations are declining. We can see the effect that poor PA management has on leopard density and that PAs are not capable of conserving leopards if they do not spare leopards from the harm humans pose. While it would be informative to have more precise estimates of population survival, recruitment, and immigration, it is unquestionably time to turn our attention to interventions in addition to routine passive monitoring. I urge wildlife management authorities in South Africa to develop conservation initiatives more directly targeted at conserving leopards.

More generally, this study validates the capacity of large-scale multi-year monitoring programs to inform conservation beyond what is feasible with small-scale studies. Though the resources needed to monitor populations on the scale of the LMP are substantial, the rewards are too. Inter-organizational collaborations that share resources, standardize methods, and expand the geographic scope of monitoring programs offer enormous potential for more representative and informative monitoring (e.g., Ahumada et al. 2020). We cannot rely on piecemeal approaches to conserving leopards but must find collective, far-reaching solutions commensurate with the scale of the challenges leopards face.

LIST OF ABBREVIATIONS

AIC	Akaike’s Information Criterion
AICc	AIC corrected for small sample sizes
AKDE	Autocorrelated kernel density estimate
AoU	Area of use
CI	Confidence interval
Cr	Critically endangered
CR	Capture-recapture
En	Endangered
EP	Elephant Park
ESA	Effective Sampling Area
GOF	Goodness-of-fit
GR	Game Reserve
HFI	Human Footprint Index
HiP	Hluhluwe-iMfolozi Park
HPD	Highest posterior density
HR	Home range
Hyp.	Hypothesis
IQR	Interquartile range
IUCN	International Union for Conservation of Nature
KDE	Kernel density estimate
km	Kilometres
KPGR	KwaZulu Private Game Reserve

KZN	KwaZulu-Natal Province
KZNPRs	KwaZulu-Natal private reserves
Lc	Least Concern
LMP	Panthera's leopard monitoring program for Southern Africa
m	Meters
MCMC	Markov-chain Monte Carlo
MCP	Minimum convex polygon
MLE	Maximum likelihood estimation
MODIS	Moderate Resolution Imaging Spectrometer
MPSRF	Multivariate potential scale reduction factor
NDVI	Normalized Difference Vegetation Index
NP	National Park
NR	Nature Reserve
PA	Protected area
PAU	Proportion of area used
PGNR	Private Game and Nature Reserve
PGR	Private Game Reserve
Pvt.	private
RAI	Relative abundance index
RC	Research Center
RCNR	River Canyon Nature Reserve

RN	Royle-Nichols
SCR	Spatial capture-recapture
SE	Standard error
St.	State
UNEP-WCMC	United Nations Environment Programme – World Conservation Monitoring Centre
UNESCO	United Nations Educational, Scientific and Cultural Organization
Vu	Vulnerable
WDPA	World Database of Protected Areas
Wld.	Wilderness
Wt.	Weight

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Vegetation Index ("NDVI"), 158 – 21416 km^2 for the log-transformed size of protected areas and all contiguous PAs ("PA size"), and 0 – 0.861 for proportional extent of domestic animals ("Domestic").