Using spatial explicit capture-recapture model to investigate the demography and spatial dynamics of lion prides in Pilanesberg National Park

By

Isabella Aletta Bettings

Submitted in fulfilment of the requirements for the degree of Master of Science,
Nature Conservation to be awarded at the Nelson Mandela University

December 2022

Supervisor: Prof Jan. A. Venter,
Co-supervisors: Prof Hervé. Fritz, Dr David G. Marneweck

DECLARATION

I, Isabella Aletta Bettings (220134316), hereby declare that the dissertation for Master of Science is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

IA Bettings 08 March 2022

ISABELLA ALETTA BETTINGS DATE

Official use:

In accordance with Rule G5.11.4,

5.11.4 I hereby declare that the above-mentioned dissertation is my own work and that is has not previously been submitted for assessment to another university or for another qualification. However, material from publications by the candidate may be embodied in a treatise/dissertation/thesis.

PREFACE

The work described in this dissertation was conducted in the Department of Conservation Management, on Nelson Mandela University, George Campus, George, South Africa. This study took place from January 2020 until March 2022 under the supervision of Prof Jan A. Venter (Department of Conservation Management, Nelson Mandela University), Dr David G. Marneweck (*Endangered Wildlife Trust, Johannesburg, South Africa*) and Prof Hervé. Fritz (*Department of Conservation Management, Faculty of Science, George Campus, Nelson Mandela University and REHABS International Research Laboratory, CNRS-Université Lyon 1-Nelson Mandela University, George Campus, Madiba drive 6531 George, South Africa*). Further statistical technical and training support was provided by Dr Nicholas B. Elliot (Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire, OX13 5QL, UK) and Dr Arjun M. Gopalaswamy (*Carnassials Global, 44/1, Regus Supreme, K. R. Road, 7th Block, Jayanagar, Bengaluru, 560070, India and Wildlife Conservation Society, Global Conservation Programs, 2300, Southern Boulevard, Bronx, New York, 10460, USA*),

The following study represents the original work conducted by the author and has not yet been submitted for any qualification to any tertiary institution. Where use has been made of the work of others, it is acknowledged in the text.

IA Bettings

ISABELLA A. BETTINGS

ABSTRACT

Lions are apex predators that play a vital role in the ecosystem. They regulate prey species through predation and other non-consumptive means. Factors that have influenced the decline of lion populations across Africa in the last half century, are loss of habitat, human wildlife conflict and the depletion of prey species. Extensive reintroductions of lions have been conducted across South Africa in order to restore their numbers in protected areas.

The Pilanesberg National Park (PNP) was one of many protected areas that reintroduced lions. Their numbers were well documented by management until 2005 where they lost track of the population numbers. During this unfortunate period, there was an observed decline in prey numbers. The aim of this dissertation was to estimate the abundance, movement, and sex ratio of lions, in PNP.

Abundance, movement, and sex ratio were determined by a three-month intensive lion survey. The location of each lion encounter was recorded on a mobile device which had an application installed called Cybertracker (v3). Photographs were taken of each Lion to build identification kits. For the data analysis, I used the Bayesian spatial explicit capture-recapture (SECR) model. This model takes time, space, and the robustness of an individual lion into account. Robustness is the measure of how well a lion maintains their functionality, when various stressors are applied (Harmsen, Foster, & Quigley, 2020).

The estimated lion population in PNP was 44 lions (>1 year) with a density of 8.8 lions per 100 km^2. The estimated mean home range size of male lions was 279 km^2 with a highest probability density (HPD) range of 179 – 385 km^2. The estimated mean home range of female lions was 191 km^2 with a HPD range of 135 – 262 km^2. The larger home range size for male lions and smaller home range size for females is found throughout the African continent in protected areas. The estimated sex ratio was 0.9♀:1♂, which is unexpected as PNP sex ratios between male and female lions is usually 2♀:1♂.

A future sampling design for PNP was produced from the completed lion survey dataset. I drove a total of 7350 km and evaluated the influence of varied sampling efforts (i.e., kms driven) on precision estimates and relative bias for abundance, movement, and sex ratio. I found that a minimum of 4 000 km was needed to adequately estimate the lion abundance, movement, and sex ratio in this small fenced protected area. These findings can be used to help guide management to the most cost-effective sampling method and still obtain accurate estimates for monitoring lions. By showing management what is required for appropriate lion surveys this might help improve future monitoring.

TABLE OF CONTENTS

DISSERTATION LAYOUT

This study focuses on the determination of the abundance, movement, and sex ratios of lions in PNP. Chapter 3 and 4 were written as independent papers for different journals, dictating some replications and non-uniform formatting. Each chapter relates to the central theme of the dissertation.

Chapter 1 *Introduction*. Provides general background and literature review for the study.

Chapter 2 *Study area and study species*. This chapter describes the study area and the study species.

Chapter 3 *The population demography of African lions (Panthera leo) in Pilanesberg National Park, South Africa.* This chapter provides an estimate of the population, sex ratios and ranging behaviour of lion in Pilanesberg using the SECR method.

Chapter 4 *How much sampling effort is required when using Bayesian spatial explicit capture-recapture models to estimate African lion populations in small fenced protected areas?* This chapter provides an estimate on how much effort is needed to conduct an accurate lion SECR survey in a fenced park like in Pilanesberg National Park.

Chapter 5 *Synthesis.* This chapter provides a synthesis of the results, highlights caveats, provides recommendations and provides suggestions for future research.

AUTHOR CONTRIBUTION STATEMENT

I, Isabella Bettings conceptualised the research, collected, processed, analysed the data, and wrote the manuscripts. Conceived and designed the research: Prof J.A. Venter (JAV), Dr D.G. Marneweck (DGM), Dr N.B. Elliot (NBE), Dr A.M. Gopalaswamy (AMG), and Prof H. Fritz (HF). Analysed and interpreted the data: NBE and AMG. Contributed reagents/materials/analysis tools: NBE, AMG, DGM, HF. Wrote the manuscripts: JAV, DGM, NBE, and AMG. Critical revision: JAV.

IA Bettings	08 March 2022
ISABELLA A. BETTINGS	DATE

LIST OF FIGURES

Chapter 2

Chapter 3

consumption by lions for a year was calculated in the following way. Male lions roughly consume 10 kg and female 7 kg of meat per day (Fritz, Loreau, Chamaillé-Jammes, Valeix, & Clobert, 2011). The mean average body mass of a blue wildebeest is 125 kg, for which we used 70%, e.g. 93.75 kg, of the carcasses that is consumed by lions (Fritz et al., 2011). To calculate the number of wildebeest W that could be consumed per year for male (L_{Male}) and female (L_{Female}) lions, we used the formula, $W = \frac{(L_{Male}*10\ kg)*365}{93.75} + \frac{(L_{Female}*7\ kg)*365}{93.75}$ (see Carbone, Teacher, & Rowcliffe, 2007). Therefore, per capita consumption of wildebeest is 30.76 in 2001 as compared to 33.36 in 2020, as per our study, indicating an 8.4% increase in per capita wildebeest consumption but could lead to even larger kill rates owing to disturbance caused by males.

Chapter 4

LIST OF TABLES

Chapter 3

LIST OF APPENDICES

Chapter 3

Supplementary Figures:

Supplementary Figure S.1: Encounter history plots displaying the locations (dark grey squares) where each of the 37 observed individuals were sighted in Pilanesberg National Park, South Africa. Light grey cells correspond to pixels that were sampled during the survey.

Supplementary Figure S.2: Model 1-5. Gelman plot. This plot shows the evolution of Gelman and Rubin's shrink factor as the number of iterations increases. Look at where the estimates level off to assess post-hoc burn. A potential problem with Gelman diagnostics is that it may mis-diagnose convergence if the shrink factor happens to be close to 1 by chance. By calculating the shrink factor at several points in time, Gelman plot shows if the shrink factor has really converged, or whether it is still fluctuating.

Supplementary Figure S.3: Model 1-5. Trace plots. To assess the mixing of a chain. In the trace plots, we want to try to avoid flat bits (where the chain stays in the same state for too long) or too many consecutive steps in one direction.

Supplementary Figure S.4: Model 1-5. Autocorrelation plot. The lag-*k* autocorrelation is the correlation between every sample and the sample k steps before. This autocorrelation should become smaller as *k* increases, i.e., samples can be considered as independent. If, on the other hand, autocorrelation remains high for higher values of k, this indicates a high degree of correlation between our samples and slow mixing.

Supplementary Figure S.5: Model 1-5. Pairwise plots between estimated parameters from the posterior MCMC draws. We used these to visually assess covariance and parameter redundancy (or identifiability) issues as a result of model overfitting relative to sample size. Since abundance (N_{super}) and density (*D.adj*) were the parameters of primary interest to our study, we were particularly concerned to assess whether there were correlations between these parameters and any other parameter.

Supplementary Tables:

Supplementary Table S.1: Model 1-5. For Gelman-Rubin the potential shrink reduction factor should be less than 1.1 for each parameter.

Supplementary Table S.2: Posterior estimates of parameters for Models 1-5. Model 1 was selected for reporting due to (a) Bayesian *p* value lying within the extremities (0.15-0.85), (b) minimal pairwise correlations and (c) the highest marginal likelihood value.

Supplementary Table S.3: Model 1-5 Parameter estimates. Look for how different median is to the mean. This indicates nature of the posterior distribution. Ideally, we would like them to be nearly the same.

Supplementary Table S.4: 41 protected areas (small, medium, and large) where the light grey colour is fenced protected areas. The figure describes lion densities per km^2 throughout Africa's continent which was assessed in different years (Elliot et al., 2020; Packer, Loveridge, et al., 2013).

Chapter 4

Supplementary Figures:

Supplementary Figure S.2.1: The coefficient of variance from increment 1 000 – 7 000 km. The results indicate that increment 1 000 to 3 000 have a great level of dispersion around the mean, while increments 4 000 to 7 000 km are lower which indicates precision as it gets closer to the mean (Kazemi & Jafari, 2020).

Supplementary Figure S.2.2: The relative bias of the posterior estimate. The true value of the posterior mean estimate is the full set of increment 7 000 km.

Supplementary Tables:

Supplementary Table S.2.2: The specification and diagnostics of increment 1, which include models 1, 2, and 3.

Supplementary Table S.2.3: The specification and diagnostics of increment 2 000 km and 3 000 km, which includes models 1, 2, and 3.

Supplementary Table S.2.4: The specification and diagnostics of increment 4 and 5, which includes models 1 and 2.

ACKNOWLEDGMENTS

During the writing of this dissertation, I received considerable amount of assistance and support from various people.

I would first like to thank my supervisor, Professor Jan Venter, for making this dissertation possible. A great deal of time and organising could not have been possible without you. Your knowledge, insight, and feedback pushed me to look at the bigger picture to produce high level of work.

I would like to thank my co-authors Dr. Nicholas Elliot and Dr. Arjun Gopalaswamy for all their time and a great deal of effort they have put in to help me with Cybertracker, and data analysis. I hope you get more opportunities in South Africa to use SECR and change the future of lion conservation. It was an honour working with you.

I would like to thank my co-supervisor Dr. David Marneweck for assisting and motivating me throughout the whole dissertation process. Thank you for putting in so much time and effort to help me verify the identity of all the lions.

I would like to thank my co-supervisor Prof Hervé Fritz for support and knowledge.

I also want to thank Steve Dell and Charlotte Marias for guidance during my data collection period. Thank for trusting me to be part of various projects in Pilanesberg National Park. Your hard work and dedication inspired me.

I also want to thank Northwest Parks Board for the accommodation and all the kindness during my data collection. I would also like to thank John Power that assisted me with maps.

Thank you to my family that supported me during these two years. The support, love, and prayer helped me through these incredible two years.

The Copen Hagen Zoo is thanked for the financial assistance for this study.

The Ernest and Ethel Ericksen Trust bursary is thanked for their financial assistance in this study.

CHAPTER 1
INTRODUCTION

Introduction

Carnivores are one of the most widely distributed groups of large mammals (Briers-Louw, 2017). The majority of large terrestrial carnivores have a wide range but are rare because of their position at the top of their respective food webs (Ripple et al., 2014; Winterbach, Winterbach, Somers, & Hayward, 2013). Carnivores are considered iconic species but in many cases are the most vulnerable (Ripple et al., 2014; Sobratee, & Slotow, 2019; Van de Kerk, de Kroon, Conde, & Jongejans, 2013). The majority of large carnivores have experienced substantial population decline and range constriction during the past two centuries (Packer, Loveridge, et al., 2013; Ripple et al., 2014). Because large carnivores naturally range over large areas it is difficult to maintain viable populations. Some individuals come into close contact with humans resulting in conflict (Packer, Swanson, et al., 2013). Few species encapsulate these problems more dramatically than the African lion (*Panthera leo*) (Packer et al., 2013a; Packer et al., b).

A large proportion of published work, since lions are the most extensively studied species, indicates drastic lion declines in its range states, but rarely mentions the stability of lion populations in countries such as South Africa, Zimbabwe, Botswana, and Namibia (Bauer et al., 2015; Sobratee, & Slotow, 2019). The International Union for Conservation of Nature (IUCN) has categorised lions in South Africa as “least concern” after the implementation of efficient conservation practices (Hutchinson, & Roberts, 2020), however, lion populations in the east, west, and central parts of Africa are declining and are subsequently categorised as “critically endangered” (Bauer et al., 2015; Hutchinson, & Roberts, 2020).

In unfenced protected areas, such as in Kenya and Tanzania, humans are killing free roaming lions mainly due to human wildlife conflict (Dolrenry et al., 2014). The increase of human encroachment and decline in prey species has also had a negative impact on lions in these areas (Dolrenry, Stenglein, Hazzah, Lutz, & Frank, 2014; Winterbach et al., 2013). South African, national parks, nature reserves, and privately owned game reserves are required to have adequate predator proof fencing when containing large carnivores (Hayward et al., 2009). Fencing limits human wildlife conflict, especially when it borders on communal or commercial livestock areas (Lindsey et al., 2012).

Fencing is not cost-free as multiple ecological and behavioural processes could be limited (Hayward, Hayward, Druce, & Kerley, 2009). Such limitations include a decreased range (limiting emigration and migration), impacts on social structure, increased intra- and inter-specific competition, and effects on prey availability (Hayward et al., 2009; Kowalczyk et al., 2012). Managing lions in small protected areas is often challenging as lions produce offspring with low mortality rates resulting in rapid population growth (Mcevoy, Ferreira, & Parker, 2021; Miller & Funston, 2014). Therefore an essential part of effective management is proper monitoring (Miller et al., 2013)

Methods to count lion populations

African lions are one of the most extensively studied large species in the world (Packer, Loveridge, et al., 2013). However, there are numerous ecological models that are inaccurate and lack precision when trying to estimate population sizes (Balme, Hunter, & Slotow, 2009; Funston et al., 2010; Midlane, O'Riain, Balme, Robinson, & Hunter, 2014; Midlane, O'Riaain, Balme, & Hunter, 2015). To evaluate a species abundance, two types of estimates are generally used, relative and absolute abundance (Gese, 2001). Relative abundance does not physically count the animals where absolute abundance does. Most methods that make use of relative abundance are tracking spoor, faecal DNA samples and call up stations, where as absolute abundance involves physically counting the animal to estimate the density of the population using direct observations (Gese, 2001). The relationship between absolute abundance and relative abundance should be measured with independent data where the sampled parameter needs to be in a limited range (Gopalaswamy, Delampady, Karanth, Kumar, & Macdonald, 2015; Hayward et al., 2015). Factors such as observers, animal movement, and environmental factors can influence these relationships. It is important to repeat data collection in the limited range to ensure the temporal and spatial factors are taken into inconsideration. Therefore, studies that use estimate abundance and direct observation should be preferred over relative abundance methods (Hayward et al., 2015).

Further, monitoring carnivore populations can be divided into two categories namely direct and indirect methods (Alibhai, Jewell, & Evans, 2017; Gese, 2001; Jewell, 2013). The direct methods comprise of a) direct observation and driving effort, which involves close-up photographs to build identification kits, measuring the distance of animal from the road and trap camera locations to help calculate movement patterns and b) the physical markings of animals by clipping digits, barcode implants, dying, notching of ears and branding through chemical immobilisation or physical capture (Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Elliot & Gopalaswamy, 2017; Jewell, 2013; Lindner & Fuelling, 2002; Pennycuick & Rudnai, 1970). Indirect methods include a) camera traps for capture-recapture purposes, b) spoor identification of a species, c) vocalisation identification, and d) genetic sampling, by gathering scat, dung or hair samples (Alibhai et al., 2017; Jewell, 2013; Kiffner, Meyer, Mühlenberg, & Waltert, 2009; Midlane et al., 2015; Tende, Ottosson, Hansson, & Bensch, 2008; Wijers et al., 2021).

The use of call up stations is a method which is not expensive or labour intensive (Midlane et al., 2015). For this method, a few sites throughout the park are plotted using a Global Positioning System (GPS) (Brink, Smith, & Skinner, 2012; Ferreira & Funston, 2010). After which a team will go out late at night, preferably with a 4x4 vehicle and speaker to play distress calls of a buffalo or pig to attract individual predators (Brink et al., 2012; Groom, Funston, & Mandisodza, 2014). The ideal weather is cooler and windless nights. The individual or group of predators will then be identified through photographs when they approach the call up location (Brink et al., 2012). In many cases, monitoring staff will only count the number of individuals that approached the vehicle as each animal can be identified through the photographs for which the capture recapture model can be applied. However, by only counting individuals with no identification, this method is therefore classified as relative abundance. The limitation of this method is that it ignores possible inaccuracies such as the overestimation of the population size or the possibility of counting the same predator twice (Elliot & Gopalaswamy, 2017; Midlane et al., 2015). Another limitation of the method is predators becoming habituated to the call up stations which can cause an underestimation of the population size (Groom et al., 2014).

Spoor tracking is an indirect method that is cost effective and repeatable, however it can be time consuming (Gese, 2001; Spong, 2002). All tracks are counted in a transect to estimate the specific predator population size (Gusset & Burgener, 2005; Midlane et al., 2014). The tracks should be clear, and only personal with experience should assists with the project (Midlane et al., 2015). Spoor tracking predators with low densities are more accurate compared to predators with larger populations (Funston et al., 2010). A limitation to this method is that not all predators use the roads to travel from one place to another (Belant et al., 2019). Another limitation of indices is that they very rarely include measures of variability, to show the assumed relationship between index and actual population size (Hayward et al., 2015). The population therefore can either be over or underestimated (Elliot & Gopalaswamy, 2017). Another restriction to spoor tracking is the terrain as different soil types affect track identification (Balme et al., 2009).

The collecting of faecal samples is usually used for cryptic predators to analyse their DNA and diet (Mondol et al., 2009). This method is labour intensive and expensive as the researcher needs to identify each faecal sample (López-Bao et al., 2018). Fresh faecal samples require DNA analysis (Mondol et al., 2009), so they will be sent to a lab for DNA extraction in order to create profiles of each individual. The capture recapture model can also be incorporated into this process (López-Bao et al., 2018).

Over the last decade, new models were developed to accurately estimate lion abundance across an array of ecological conditions (Braczkowski, Gopalaswamy, Elliot, et al., 2020; Elliot & Gopalaswamy, 2017; Forsyth, Ramsey, & Woodford, 2019; Milleret et al., 2020). This made it possible to estimate the effectiveness of lion conservation in specific reserves by measuring how thoroughly the population density is observed when compared to the expected density (Packer, Loveridge, et al., 2013). Camera trapping and direct observation are more recently developed methods which have improved over the years to help estimate predator population size and density. Both these methods often use the Bayesian spatial explicit capture recapture model to estimate the population size. Both methods apply variables such as space, time, effort, set survey periods, age and sex classification, and the capture and recapture possibility of an individual (Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Elliot & Gopalaswamy, 2017; Kane, Morin, & Kelly, 2015).

The setting up of camera traps has many variables that should be considered these include location, flash settings, the height of camera and whether baiting the trap will be effective (Edwards et al., 2018; Tarugara, Clegg, Gandiwa, & Muposhi, 2019). This method is costly in the beginning, but it can be repeated multiple times. Camera trapping can also be labour intensive since the researcher needs to constantly change both the batteries and memory cards. Cameras are placed either in grids or in strategic places where a specific predator may walk past (Borchers, Distiller, Foster, Harmsen, & Milazzo, 2014; Edwards et al., 2018). Identifying individuals through distinctive patterns on their bodies such as stripes and spots can be captured through camera traps and later incorporated into capture recapture models (Noack, Heyns, Rodenwoldt, & Edwards, 2019). Camera traps are an indirect method but do produce quality data, however, it can be used for continuous data collection and behavioural analysis (Caravaggi et al., 2017). The more camera traps in the study area, the more accurate and precise the estimation of the population size becomes (Kane et al., 2015).

Direct observation is one of the few methods that can define an animal's behavioural characteristics (Goodall, Ferreira, Funston, & Maruping-Mzileni, 2019). Collecting data remotely allows for the direct judgement of quantitative large scale patterns as they transpire (Goodall et al., 2019). To start the process, a 4x4 vehicle with observers is used. The lion search occurs daily, although twice a day will increase the success rate (Braczkowski, Gopalaswamy, Mustafa, et al., 2020). The observers use a handheld GPS device or mobile phone to locate the pride or an individual lion. The GPS coordinates, along with previously identified lions are then used for the Bayesian spatial explicit capture recapture model (Elliot et al., 2020). The shortcomings of this method is cost and time (Braczkowski, Gopalaswamy, Elliot, et al., 2020; Elliot & Gopalaswamy, 2017).

The selected monitoring method does require consistency in order to determine changes in the populations by being accurate and precise. Having said that, indirect methods may be lacking in accuracy and precision due to their indices (Balme et al., 2009; Witmer, 2005). For example, the indices of indirect methods are easier to obtain, however, many factors (observers, environment, animal status and movement) can influence the indices since it does not possess a stable linear relationship with true abundance, which often gives an unclear population size (Balme et al., 2009; Hayward et al., 2015; Witmer, 2005).

Estimating population sizes requires consistency, repetition, and time (Boitani et al., 2012; Gese, 2001), therefore it is vital that the appropriate management plan is chosen in order to develop and maintain sound conservation strategies (Milleret et al., 2020), with minimal loss to time and financial restraints (Braczkowski, Gopalaswamy, Elliot, et al., 2020; Milleret et al., 2020).

Aims and objectives

The lion population monitoring in The Pilanesberg National Park has been facing a number of challenges over the years. Larger lion populations have in the past (see Tambling and du Toit (2005)) and receintly potentially played a role in the decline of prey species since 2014 (North-West Parks and tourism Board, unpublished data). For this study, we used search-encounter based sampling procedures over a 90-day monitoring period to record individual lions across the park. Using the lion and prey numbers we can assist park management by helping them make healthy in the future.

The overall aim of this study was to determine the abundance, sex ratio, and movement of lions. To achieve this, the following objectives were set:

I. To determine the abundance, sex ratio, and movement of lions in Pilanesberg National Park.
II. To determine how much lion survey effort is needed for efficient long-term monitoring of lions in Pilanesberg National Park.

References

Alibhai, S., Jewell, Z., & Evans, J. (2017). The challenge of monitoring elusive large carnivores: An accurate and cost-effective tool to identify and sex pumas (Puma concolor) from footprints. *PloS one*, *12*(3), e0172065. https://doi.org/10.1371/journal.pone.0172065

Arnholt, A. T., & Herbert, J. (1995). Estimating the mean with known coefficient of variation. *The American Statistician*, *49*(4), 367–369.

Auffray, J.-C., Renaud, S., & Claude, J. (2009). Rodent Biodiversity in Changing Environments. *Kasetsart Journal, Natural Science*, *43*(1), 83–93. Retrieved from https://www.researchgate.net/publication/228350392

Balme, G. A., Hunter, L. T. B., & Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, *73*(3), 433–441. https://doi.org/10.2193/2007-368

Barthold, J. A., Loveridge, A. J., Macdonald, D. W., Packer, C., & Colchero, F. (2016). Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, *53*(2), 295–304.

https://doi.org/10.1111/1365-2664.12594

Bauer, H., & Van Der Merwe, S. (2004). Inventory of free-ranging lions Panthera leo in Africa. *Oryx*, *38*(1), 26–31. https://doi.org/10.1017/S0030605304000055

Bauer, Hans., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., … Packer, C. (2015). Lion (Panthera leo) populations are declining rapidly across Africa, except in intensively managed areas. *PNAS*, *112*(48), 14894–14899. https://doi.org/10.1073/pnas.1500664112

Belant, J. L., Bled, F., Mkasanga, I. J., Wilton, C. M., Mwampeta, S. B., Beyer, D. E., … Fyumagwa, R. (2019). Track surveys do not provide accurate or precise lion density estimates in Serengeti. *Global Ecology and Conservation*, *19*, e00651. https://doi.org/10.1016/j.gecco.2019.e00651

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, *90*, 171–180. https://doi.org/10.1016/j.anbehav.2014.01.030

Boitani, L., Ciucci, P., & Mortelliti, A. (2012). Designing carnivore surveys. In *Carnivore ecology and management: a handbook of techniques* (pp. 8–29). Oxford University Press. https://doi.org/10.1093/acprof

Borchers, D. (2012). A non-technical overview of spatially explicit capture-recapture models. *Journal of Ornithology*, *152*(2), 435–444. https://doi.org/10.1007/s10336-010-0583-z

Borchers, D., Distiller, G., Foster, R., Harmsen, B., & Milazzo, L. (2014). Continuous-time spatially explicit capture-recapture models, with an application to a jaguar camera-trap survey. *Methods in Ecology and Evolution*, *5*(7), 656–665. https://doi.org/10.1111/2041-210X.12196

Botai, C. M., Botai, J. O., Dlamini, L. C., Zwane, N. S., & Phaduli, E. (2016). Characteristics of droughts in South Africa: A case study of Free State and North West provinces. *Water*, *8*(10), 439. https://doi.org/10.3390/w8100439

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., … Allan, J. R. (2020). Restoring Africa's lions: Start with good counts. *Frontiers in Ecology and Evolution*, *8*, 138. https://doi.org/10.3389/fevo.2020.00138

Braczkowski, A., Gopalaswamy, A. M., Mustafa, N., Allan, J., Biggs, D., & Maron, M. (2020). Detecting early warnings of pressure on an African lion (Panthera leo) population in the Queen Elizabeth Conservation Area, Uganda. *Ecological Solution Evidence*, *1*, e12015. https://doi.org/10.1002/2688-8319.12015

Briers-Louw, W. D. (2017). Ecology of three apex predators in Majete Wildlife Reserve, Malawi (Doctoral dissertation). Stellenbosch University, Stellenbosch.

Brink, H., Smith, R. J., & Skinner, K. (2012). Methods for lion monitoring: A comparison from the Selous Game Reserve, Tanzania. *African Journal of Ecology*, *51*(2), 366–375. https://doi.org/10.1111/aje.12051

Broekhuis, F., Elliot, N. B., Keiwua, K., Koinet, K., Macdonald, D. W., Mogensen, N., … Gopalaswamy, A. M. (2021). Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography*, *44*(3), 358–369.

https://doi.org/10.1111/ecog.05154

Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PloS one*, *11*(5), 1–15. https://doi.org/10.1371/journal.pone.0153875

Caravaggi, A., Banks, P. B., Burton, C. A., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., … Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109–122. https://doi.org/10.1002/rse2.48

Carbone, C., Teacher, A., & Rowcliffe, M. J. (2007). The costs of carnivory. *PLoS Biology*, *5*(2), 0363–0368. https://doi.org/10.1371/journal.pbio.0050022

Carruthers, J. (2011). Pilanesberg National Park, North West Province, South Africa: Uniting economic development with ecological design – A history, 1960s to 1984. *Koedoe*, *53*(1), 1–10. https://doi.org/10.4102/koedoe.v53i1.1028

Clark, T. J., Horne, J. S., Hebblewhite, M., & Luis, A. D. (2021). Stochastic predation exposes prey to predator pits and local extinction. *Oikos*, *130*(2), 300–309. https://doi.org/10.1111/oik.07381

Comley, J., Joubert, C. J., Mgqatsa, N., & Parker, D. M. (2020). Battle of the Large Carnivores: Spatial Partitioning in a Small, Enclosed Reserve? *African Journal of Wildlife Research*, *50*(1), 176–189. https://doi.org/10.3957/056.050.0176

Cooper, D. M., Dugmore, A. J., Kitchener, A. C., Metzger, M. J., & Trabucco, A. (2021). A kingdom in decline: Holocene range contraction of the lion (Panthera leo) modelled with global environmental stratification. *Pee*r reviewed journal, *9*, e10504. https://doi.org/10.7717/peerj.10504

Creel, S., Becker, M. S., Durant, S. M., M'Soka, J., Matandiko, W., Dickman, A. J., … Zimmermann, A. (2013). Conserving large populations of lions - the argument for fences has holes. *Ecology Letters*, *16*(11), 1413-e3. https://doi.org/10.1111/ele.12145

Creel, Scott., & Creel, N. M. (1997). Lion density and population structure in the Selous Game Reserve: Evaluation of hunting quotas and offtake. *African Journal of Ecology*, *35*(2), 83–93. https://doi.org/10.1111/j.1365-2028.1997.062-89062.x

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., … Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS one*, *13*(7), e0196213. https://doi.org/10.1371/journal.pone.0196213

De Boer, W. F., Vis, M. J. P., De Knegt, H. J., Rowles, C., Kohi, E. M., van Langevelde, F., … Prins, H. H. T. (2010). Spatial distribution of lion kills determined by water dependency of prey species. *Journal of Mammalogy*, *91*(5), 1280–1286. https://doi.org/10.1644/09-MAMM-A-392.1

de Manuel, M., Barnett, R., Sandoval-Velasco, M., Yamaguchi, N., Vieira, F. G., Mendoza, L. Z. M., … Gilbert, T. M. (2020). The evolutionary history of extinct and living lions. PNAS, *117*(20), 10927–10934. https://doi.org/10.1073/pnas.1919423117

Dey, S., Delampady, M., & Gopalaswamy, A. M. (2019). Bayesian model selection for spatial capture–recapture models. *Ecology and Evolution*, *9*(20), 11569–11583. https://doi.org/10.1002/ece3.5551

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, S. R., & Frank, L. (2014). A metapopulation approach to African lion (*Panthera leo*) conservation. *PloS one*, *9*(2). https://doi.org/10.1371/journal.pone.0088081

Dröge, E., Creel, S., Becker, M. S., Loveridge, A. J., Sousa, L. L., & Macdonald, D. W. (2020). Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecology and Evolution*, *10*(7), 3276–3292. https://doi.org/10.1002/ece3.6065

Durant, S. M., Craft, M. E., Hilborn, R., Bashir, S., Hando, J., & Thomas, L. (2011). Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *Journal of Applied Ecology*, *48*(6), 1490–1500. https://doi.org/10.1111/j.1365-2664.2011.02042.x

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion - conservation stronghold. *Density and Distribution*, *25*, 870–879. https://doi.org/10.1111/ddi.12905

Edwards, S., Cooper, S., Uiseb, K., Hayward, M., Wachter, B., & Melzheimer, J. (2018). Making the most of by-catch data: Assessing the feasibility of utilising non-target camera trap data for occupancy modelling of a large felid. *African Journal of Ecology*, *56*(4), 885–894. https://doi.org/10.1111/aje.12511

Elliot, N. B., Bett, A., Chege, M., Sankan, K., de Souza, N., Kariuki, L., … Gopalaswamy, A. M. (2020). The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice*, 1–11. https://doi.org/10.1111/csp2.217

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., & Macdonald, D. W. (2014). Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, *95*(10), 2860–2869. https://doi.org/10.1890/13-1793.1

Elliot, N. B., & Gopalaswamy, A. M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, *31*(4), 934–943. https://doi.org/10.1111/cobi.12878

Elliot, N. B., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos*, *123*(9), 1049–1056. https://doi.org/10.1111/oik.01266

Estes, R. D. (2012). Lion (*Panthera leo*). In *The behaviour guide to African mammals* (pp. 369–377). London and Los Angeles and Berkeley: The University of California Press.

Everatt, K. T., Kokes, R., & Pereira, C. L. (2019). Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation*, *28*(14), 4099–4114. https://doi.org/10.1007/s10531-019-01866-w

Ferreira, S. M., Beukes, O. B., Haas, T. C., & Radloff, F. G. T. (2020). Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park. *African*

Journal of Ecology, *58*(3), 348–360. https://doi.org/10.1111/aje.12728

Ferreira, S. M., & Funston, P. J. (2010). Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, *37*(3), 194–206. https://doi.org/10.1071/WR09030

Ferreira, S. M., & Hofmeyr, M. (2014). Managing charismatic carnivores in small areas: Large felids in South Africa. *South African Journal of Wildlife Research*, *44*(1), 32–42.

Forsyth, D. M., Ramsey, D. S. L., & Woodford, L. P. (2019). Estimating abundances, densities, and interspecific associations in a carnivore community. *The Journal of Wildlife Management*, *83*(5), 1090–1102. https://doi.org/10.1002/jwmg.21675

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M., & Clobert, J. (2011). A food web perspective on large herbivore community limitation. *Ecography*, *34*(2), 196–202. https://doi.org/10.1111/j.1600-0587.2010.06537.x

Funston, P J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., … Ferreira, S. M. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, *281*(1), 56–65. https://doi.org/10.1111/j.1469-7998.2009.00682.x

Funston, P J., & Levendal, M. (2015). *Biodiversity management plan for the lion (Panthera leo) in South Africa. Government Gazette, 2*. Retrieved from www.gpwonline.co.za

Funston, P J., & Mills, M. G. L. (2006). The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *African Journal of Wildlife Research*, *36*(1), 9–22.

Funston, P J., Mills, M. G. L., & Biggs, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, *253*(4), 419–431.

Funston, Paul J. (2011). Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, *41*(1), 1–10.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–511.

Gese, E. M. (2001). Monitoring of terrestrial carnivore populations. *Conservation Biology Series- Cambridge-*, 372–396.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, *10*(1), 57–63. https://doi.org/10.1007/BF00296396

Gomez, D., Sommaro, L., Steinmann, A., Chiappero, M., & Priotto, J. (2011). Movement distances of two species of sympatric rodents in linear habitats of Central Argentine agro-ecosystems. *Mammalian Biology*, *76*, 58–63. https://doi.org/10.1016/j.mambio.2010.02.001

Goodall, V. L., Ferreira, S. M., Funston, P. J., & Maruping-Mzileni, N. (2019). Uncovering hidden states in African lion movement data using hidden Markov models. *Wildlife Research*, *46*(4), 296–303. https://doi.org/10.1071/WR18004

Gopalaswamy, A. M., Delampady, M., Karanth, U. K., Kumar, S. N., & Macdonald, D. W. (2015). An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods in Ecology and Evolution*, *6*(9), 1055–1066. https://doi.org/10.1111/2041-210X.12351

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program SPACECAP: Software for estimating animal density using spatially explicit capture-recapture models. *Methods in Ecology and Evolution*, *3*(6), 1067–1072. https://doi.org/10.1111/j.2041-210X.2012.00241.x

Groom, R. J., Funston, P. J., & Mandisodza, R. (2014). Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: What is driving the population collapse? *Oryx*, *48*(3), 385–393. https://doi.org/10.1017/S0030605312001457

Gusset, M., & Burgener, N. (2005). Estimating larger carnivore numbers from track counts and measurement. *African Journal of Ecology*, *43*, 320–324.

Harmsen, B. J., Foster, R. J., & Quigley, H. (2020). Spatially explicit capture recapture density estimates: Robustness, accuracy and precision in a long-term study of jaguars (Panthera onca). *PloS one*, *15*(6), e0227468. https://doi.org/10.1371/journal.pone.0227468

Hatfield, R. (2014). Population dynamics of the African lion (*Panthera leo*) within the Maasai Mara region of southern Kenya. *Kaleidoscope*, *11*(1), 70.

Hayward, M. W., Adendorff, J., O'Brien, J., Sholto-douglas, A., Bissett, C., Moolman, L. C., … Kerley, G. I. H. (2007). Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eatern Cape Province. *The Open Conservation Biology Journal*, *1*(1), 1–11.

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, Ullas K., Mackenzie, D. I., … Yarnell, R. W. (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, *52*(2), 286–290. https://doi.org/10.1111/1365-2664.12408

Hayward, M. W., Hayward, G. J., Druce, D. J., & Kerley, G. I. H. (2009). Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity Conservation*, *18*, 887–904. https://doi.org/10.1007/s10531-008-9452-y

Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, *267*, 309–322. https://doi.org/10.1017/S0952836905007508

Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, *139*(1–2), 219–229. https://doi.org/10.1016/j.biocon.2007.06.018

Holekamp, K. E., & Sawdy, M. A. (2019). The evolution of matrilineal social systems in fissiped carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1780), 20180065. https://doi.org/10.1098/rstb.2018.0065

Hrabar, H., & du Toit, J. T. (2005). Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conservation*, *8*(3), 259–267. https://doi.org/10.1017/S1367943005002234

Jewell, Z. (2013). Effect of monitoring technique on quality of conservation science. *Conservation Biology*, *27*(3), 501–508. https://doi.org/10.1111/cobi.12066

Jiménez, J., Nuñez-Arjona, J. C., Rueda, C., González, L. M., Garciá-Domínguez, F., Munõz-Igualada, J., & López-Bao, J. V. (2017). Estimating carnivore community structures. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/srep41036

Kane, M. D., Morin, D. J., & Kelly, M. J. (2015). Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodiversity and Conservation*, *24*(14), 3527–3541. https://doi.org/10.1007/s10531-015-1012-7

Karanth, U. K., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, *79*(8), 2852–2862. https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2

Kazemi, M. R., & Jafari, A. A. (2020). Small sample inference for the common coefficient of variation. *Communications in Statistics: Simulation and Computation*, *49*(1), 226–243. https://doi.org/10.1080/03610918.2018.1484474

Keet, D. F. (2010). Lions. In *Game Ranch Management* (Fith Editi, pp. 295–312). Van Schaik Publication.

Kettles, R., & Slotow, R. (2009). Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research*, *39*(1), 23–33. Retrieved from https://journals.co.za/docserver/fulltext/wild/39/1/wild_v39_n1_a3.pdf?expires=1560189647&id=id&accname=guest&checksum=514349490088AEF9B952A9F9167F8569

Kidwai, Z., Jimenez, J., Louw, C. J., Nel, H. P., & Marshal, J. P. (2019). Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (*Diceros bicornis*) populations from aerial counts. *Global Ecology and Conservation*, *19*, e00687. https://doi.org/10.1016/j.gecco.2019.e00687

Kiffner, C., Meyer, B., Mühlenberg, M., & Waltert, M. (2009). Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania? *Oryx*, *43*(1), 52–59. https://doi.org/10.1017/S0030605307002335

Kissui, B. M., & Packer, C. (2004). Top-down population regulation of a top predator: Lions in the Ngorongoro Crater. Proceedings of *the Royal Society of London*, *271*, 1867–1874. https://doi.org/10.1098/rspb.2004.2797

la Grange, M., Kellner, K., Cilliers, S. S., & Götze, A. R. (2009). Vegetation classification of the proposed Heritage Park, North-West Province, South Africa (North-West University; Vol. 75). https://doi.org/10.1016/j.sajb.2009.02.149

Lahoz-Monfort, J. J., Harris, M. P., Morgan, B. J. T., Freeman, S. N., & Wanless, S. (2014). Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. *Journal of Applied Ecology*, *51*(2), 534–543. https://doi.org/10.1111/1365-2664.12214 le Roux, E., Marneweck, D. G., Clinning, G., Druce, D. J., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2019). Top–down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography*, *42*(6), 1115–1123. https://doi.org/10.1111/ecog.03791

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008a). Feeding behaviour of lions (*Panthera leo*) on a small reserve. *African Journal of Wildlife Research*, *38*(1), 66–78.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008b). Home range utilisation and territorial behavior of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PloS one*, *3*(12), e3998. https://doi.org/10.1371/journal.pone.0003998

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008c). Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. *African Zoology*, *43*(2), 230–236. https://doi.org/10.3377/1562-7020-43.2.230

Lesilau, F., Verschueren, S., van't Zelfde, M., Musters, K. C. J. M., de Snoo, G. R., & de Iongh, H. H. (2021). Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: The case study of Nairobi National Park, Kenya. *Mammalia*, *85*(3), 198–207. https://doi.org/10.1515/mammalia-2020-0116

Lindner, E., & Fuelling, O. (2002). Marking methods in small mammals: ear-tattoo as an alternative to toe-clipping. *The Zoological Society of London*, *256*, 159–163.

Lindsey, P. A., Petracca, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., … Hunter, L. T. B. (2017). The performance of African protected areas for lions and their prey. *Biological Conservation*, *209*, 137–149. https://doi.org/10.1016/j.biocon.2017.01.011

López-Bao, J. V., Godinho, R., Pacheco, C., Lema, F. J., García, E., Llaneza, L., … Jiménez, J. (2018). Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. *Scientific Reports*, *8*(1), 1–8. https://doi.org/10.1038/s41598-018-20675-9

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, *54*(3), 815–825. https://doi.org/10.1111/1365-2664.12794

Macdonald, D. W., Loveridge, A. J., & Nowell, K. (2010). Dramatis personae: an introduction to the wild felids. In *The biology and conservation of wild felids* (First Edit, pp. 3–59). Oxford University Press (OUP).

Magome, H., Cain, J. W., Owen-Smith, N., & Henley, S. R. (2008). Forage selection of sable antelope in Pilanesberg Game Reserve, South Africa. *African Journal of Wildlife Research*, *38*(1), 35–41. https://doi.org/10.3957/0379-4369-38.1.35

Mari, L., Gatto, M., & Casagrandi, R. (2008). Local resource competition and the skewness of the sex ratio: A demographic model. *Mathematical Biosciences and Engineering*, *5*(4), 813–830. https://doi.org/10.3934/mbe.2008.5.813

Massey, A. L., King, A. A., & Foufopoulos, J. (2014). Fencing protected areas: A long-term assessment of the effects of reserve establishment and fencing on African mammalian diversity. *Biological Conservation*, *176*, 162–171. https://doi.org/10.1016/j.biocon.2014.05.023

Mbizah, M. M., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2019). Applying the resource dispersion hypothesis to a fission–fusion society: A case study of the African lion (*Panthera leo*). *Ecology and Evolution*, *9*(16), 9111–9119. https://doi.org/10.1002/ece3.5456

Mcevoy, O. K. (2019). *The management of lions (Panthera leo) in small, fenced wildlife reserves*. (Doctoral dissertation) Grahamstown, South Africa: Rhodes University.

Mcevoy, O. K., Ferreira, S. M., & Parker, D. M. (2021). The influence of population demographics on lion (*Panthera leo*) growth rates in small, fenced wildlife reserves. *African Journal of Wildlife Research*, *51*(1), 75–89.

Midlane, N., O'Riain, M. J., Balme, G. A., Robinson, H. S., & Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, *172*, 101–108. https://doi.org/10.1016/j.biocon.2014.02.006

Midlane, Niel., O'Riaain, J. M., Balme, G. A., & Hunter, L. T. B. (2015). To track or to call: comparing methods for estimating population abundance of African lions *Panthera leo* in Kafue National Park. *Biodiversity and Conservation*, *24*(6), 1311–1327. https://doi.org/10.1007/s10531-015-0858-z

Miller, S. M., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D. J., … Zimmermann, D. (2013). Management of reintroduced lions in small, fenced reseved in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research*, *43*(2), 138–154.

Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: A management dilemma. *South African Journal of Wildlife Research*, *44*(1), 43–55.

Miller, S. M., Riggio, J., Funston, P. J., Power, R. J., Williams, V., & Child, M. F. (2016). A conservation assessment of *Panthera leo*. In *The red list of mammals of South Africa*. Swaziland and Lesotho.

Milleret, C., Dupont, P., Chipperfield, J., Turek, D., Brøseth, H., Gimenez, O., … Bischof, R. (2020). Estimating abundance with interruptions in data collection using open population spatial capture–recapture models. *Ecosphere*, *11*(7), 1–14. https://doi.org/10.1002/ecs2.3172

Mondol, S., Karanth, U. K., Kumar, S. N., Gopalaswamy, A. M., Andheria, A., & Ramakrishnan, U. (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation*, *142*(10), 2350–2360. https://doi.org/10.1016/j.biocon.2009.05.014

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, *78*(2), 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024

Mucina, L., Rutherford, M. C., & Powrie, W. (2006). Vegetation atlas of South Africa, Lesotho and Swaziland. In L. Mucina & M. C. Rutherford (Eds.), *Vegetation Map* *of Southern Africa, Lesotho and Swaziland* (pp. 750–760). Pretoria: South Africa National Biodiversity Institute.

Noack, J., Heyns, L., Rodenwoldt, D., & Edwards, S. (2019). Leopard density estimation within an enclosed reserve, namibia using spatially explicit capture-recapture models. *Animals*, *9*(10), 724. https://doi.org/10.3390/ani9100724

Packer, C., Herbst, L., Pusey, A., Bygott, A., Hanby, J. P., Cairns, S. J., & Borgerhoff-Mulder, M. (1988). *Reproduction success of lions: studies of individual variation in contrasting breeding systems* (T. Clutton-Brock, Ed.). Chicago: University of Chicago Press.

Packer, C., Loveridge, A. J., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., … Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology Letters*, *16*(5), 635–641. https://doi.org/10.1111/ele.12091

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups : Food is not enough. *The American Naturalist*, *136*(1), 1–19.

Packer, C., Swanson, A., Canney, S., Loveridge, A., Garnett, S., Pfeifer, M., … Macnulty, D. (2013). The case for fencing remains intact. *Ecology Letters*, *16*(11), 7–8. https://doi.org/10.1111/ele.12171

Packer, Craig. (2019). The African lion: A long history of interdisciplinary research. *Frontiers in Ecology and Evolution*, *7*(259), 1–6. https://doi.org/10.3389/fevo.2019.00259

Pekor, A., Miller, J. R. B., Flyman, M. V., Kasiki, S., Kesch, M. K., Miller, S. M., … Lindsey, P. A. (2019). Fencing Africa’s protected areas: Costs, benefits, and management issues. *Biological Conservation*, *229*, 67–75. https://doi.org/10.1016/j.biocon.2018.10.030

Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, *160*(4), 497–508. https://doi.org/10.1111/j.1469-7998.1970.tb03093.x

Périquet, S., Fritz, H., & Revilla, E. (2015). The lion king and the hyaena queen: Large carnivore interactions and coexistence. *Biological Reviews*, *90*(4), 1197–1214. https://doi.org/10.1111/brv.12152

Pfeffer, S. E. (2016). *Comparison of three different indirect methods to evaluate ungulate population densities*. Swedish university of africultural science.

Power, R. J. (2002). Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe*, *45*(2), 67–75. https://doi.org/10.4102/koedoe.v45i2.32

Prox, L., & Farine, D. (2020). A framework for conceptualizing dimensions of social organization in mammals. *Ecology and Evolution*, *10*(2), 791–807. https://doi.org/10.1002/ece3.5936

Pusey, A. E., & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, *101*(4), 275–310.

Rafiq, K., Bryce, C. M., Rich, L. N., Coco, C., Miller, D. A. W., Meloro, C., … Hayward,

M. W. (2019). Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Current Biology*, *29*(14), R681–R682. https://doi.org/10.1016/j.cub.2019.05.056

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., … Pimm, S. (2013). The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation*, *22*(1), 17–35. https://doi.org/10.1007/s10531-012-0381-4

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Royle, A. J., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture-recapture*. Academic Press.

Royle, A. J., & Converse, S. J. (2014). Hierarchical spatial capture-recapture models: Modelling population density in stratified populations. *Methods in Ecology and Evolution*, *5*(1), 37–43. https://doi.org/10.1111/2041-210X.12135

Royle, A. J., Fuller, A. K., & Sutherland, C. (2018). Unifying population and landscape ecology with spatial capture–recapture. *Ecography*, *41*(3), 444–456. https://doi.org/10.1111/ecog.03170

Royle, A. J., Karanth, U. K., Gopalaswamy, A. M., & Kumar, S. N. (2009). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, *90*(11), 3233–3244. https://doi.org/10.1890/08-1481.1

Royle, A. J., Sutherland, C., Fuller, A. K., & Sun, C. C. (2015). Likelihood analysis of spatial capture-recapture models for stratified or class structured populations. *Ecosphere*, *6*(2), 1–11. https://doi.org/10.1890/ES14-00148.1

Rutherford, M. C., Mucina, L., Lötter, C., Bredenkamp, G. J., Jacobus, H. L., Scott-shaw, C. R., … Hurter, P. J. H. (2006). Savanna Biome. In *The vegetation of South Africa, Lesotho and Swaziland.* (pp. 440–529). Pretoria: South Africa National Biodiversity Institute.

Schaller, G. B. (1972). The Serengeti Lion. Chicago: Univeristy of Chicago Press. https://doi.org/10.1017/CBO9781107415324.004

Silk, J. B. (1984). Local resource competition and the evolution of male-biased sex ratio. *Journal of Theoretical Biology*, *108*(2), 203–213.

Skinner, J. D., & Chimimba, C. T. (2005). Lion. In *The mammals of the Southern African sub-region* (Third Edit, pp. 390–396). Cambridge University Press.

Slotow, R., & Hunter, L. T. B. (2009). Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: The African lion in South Africa. In *Reintroduction of Top-Order Predators, (5), 43*. https://doi.org/10.1002/9781444312034.ch3

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), 20142711. https://doi.org/10.1098/rspb.2014.2711

Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., & Harwood, J. (2010). The functional response of a generalist predator. *PloS one*, *5*(5). https://doi.org/10.1371/journal.pone.0010761

Snyman, A., Jackson, C. R., & Funston, P. J. (2015). The effect of alternative forms of hunting on the social organization of two small populations of lions *Panthera leo* in Southern Africa. *Oryx*, *49*(4), 604–610. https://doi.org/10.1017/S0030605313001336

Sobratee, N., & Slotow, R. (2019). A critical review of lion research in South Africa: The impact of researcher perspective, research mode, and power structures on outcome bias and implementation gaps. *Frontiers in Ecology and Evolution*, *7*(81), 1–17. https://doi.org/10.3389/fevo.2019.00081

Spong, G. (2002). Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology*, *52*(4), 303–307. https://doi.org/10.1007/s00265-002-0515-x

Stander, P. E. (2019). Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia. *Namibian Journal of Environment*, *3*, 1–10.

Stoffelen, A., Adiyia, B., Vanneste, D., & Kotze, N. (2020). Post-apartheid local sustainable development through tourism: an analysis of policy perceptions among “responsible” tourism stakeholders around Pilanesberg National Park, South Africa. *Journal of Sustainable Tourism*, *28*(3), 414–432. https://doi.org/10.1080/09669582.2019.1679821

Tambling, C. J., & du Toit, J. T. (2005). Modelling wildebeest population dynamics: Implications of predation and harvesting in a closed system. *Journal of Applied Ecology*, *42*, 431–441. https://doi.org/10.1111/j.1365-2664.2005.01039.x

Tarugara, A., Clegg, B. W., Gandiwa, E., & Muposhi, V. K. (2019). Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population. *Global Ecology and Conservation*, *18*, e00627. https://doi.org/10.1016/j.gecco.2019.e00627

Tende, T., Ottosson, U., Hansson, B., & Bensch, S. (2008). Population density and abundance of Lions in Yankari Game Reserve, 2008. Unpublish report, Lund University, Sweden.

Trinkel, M., Fleischmann, P. H., & Slotow, R. (2017). Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population. *Journal of Zoology*, *301*(1), 41–50. https://doi.org/10.1111/jzo.12387

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation*, *13*(4), 374–382. https://doi.org/10.1111/j.1469-1795.2009.00344.x

Trinkel, Martina., & Angelici, F. M. (2016). The decline in the Lion population in Africa and possible mitigation measures. In F. M. Angelici (Ed.), *Problematic Wildlife* (Edition 1, pp. 45–68). https://doi.org/10.1007/978-3-319-22246-2

Tumenta, P. N., van't Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., Udo de Haes, H. A., & De Iongh, H. H. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology*, *78*(6), 461–469. https://doi.org/10.1016/j.mambio.2013.08.006

Van de Kerk, M., de Kroon, H., Conde, D. A., & Jongejans, E. (2013). Carnivora population dynamics are as slow and as fast as those of other mammals: Implications for their conservation. *PloS one*, *8*(8), e70354. https://doi.org/10.1371/journal.pone.0070354

Van Dyk, G., & Slotow, R. (2003). The effects of fences and lions on the ecology of African wild dogs reintroduced to Pilanesberg National Park, South Africa. *African Zoology*, *38*(1), 79–94. https://doi.org/10.1080/15627020.2003.11657196

Van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (Panthers, leo). *Journal of Zoology*, *206*(1), 97–112. https://doi.org/10.1111/j.1469-7998.1985.tb05639.x

Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, *143*(11), 2631–2637. https://doi.org/10.1016/j.biocon.2010.07.005

VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, *77*(4), 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028

Vega Yon, G. G., & Marjoram, P. (2019). fmcmc: A friendly MCMC framework. *The Journal of Open Source Software*, *4*(39), 1427. https://doi.org/10.2307/2334940

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science*, *297*(5585), 1339–1343. https://doi.org/10.1126/science.1073257

Wijers, M., Trethowan, P., Du Preez, B., Chamaillé-Jammes, S., Loveridge, A. J., Macdonald, D. W., & Markham, A. (2021). Vocal discrimination of African lions and its potential for collar-free tracking. *Bioacoustics*, *30*(5), 575–593. https://doi.org/10.1080/09524622.2020.1829050

Wild, G., & West, S. A. W. (2009). Genomic imprinting and sex allocation. *American Naturalist*, *173*(1), 1–14. https://doi.org/10.1086/593305

Winterbach, H. E. K., Winterbach, C. W., Somers, M. J., & Hayward, M. W. (2013). Key factors and related principles in the conservation of large African carnivores. *Mammal Review*, *43*(2), 89–110. https://doi.org/10.1111/j.1365-2907.2011.00209.x

Witmer, G. W. (2005). Wildlife population monitoring: some practical considerations. *Wildlife Research*, *32*, 259–263.

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation*, *3*(2), 165–173. https://doi.org/10.1017/S136794300000086X

Woolley, L. A., Page, B., & Slotow, R. (2011). Foraging strategy within African elephant family units: Why body size matters. *Biotropica*, *43*(4), 489–495. https://doi.org/10.1111/j.1744-7429.2010.00733.x

CHAPTER 2
STUDY AREA AND SPECIES

Introduction

This chapter includes a detailed description of The Pilanesberg National Park. I also provide a comprehensive overview of the focal species The African lion (*Panthera leo*).

Study area

The Pilanesberg National Park (PNP) is located in the North West province which was previously known as Bophuthatswana “Tswana Homeland” (Carruthers, 2011; Stoffelen, Adiyia, Vanneste, & Kotze, 2020). Before PNP was governmentally declared and redesigned as a natural area in the 1970’s, it was pastoral farming lands of three communities known as Bafokeng, Bakgatla, and Bakubung (Stoffelen et al., 2020). After PNP were declared a protected area, management started to reintroduce animals that occurred in that area (Hrabar & du Toit, 2005). PNP (25°08’ to 25°22’S; 26°57’ to 27°13’E) opened as a protected area in 1977 (Carruthers, 2011; Stoffelen et al., 2020), (Figure 1). Presently, PNP covers approximately 55 000 ha which is fenced off and electrified to keep megaherbivores and large carnivores in the park (Tambling & du Toit, 2005; Vanak, Thaker, & Slotow, 2010). Approximability 6000 different types of animals were reintroduced to serve as a tourist attraction (Van Dyk, & Slotow, 2003), as PNP is situated next to the world-famous Sun City (Kidwai et al., 2019; Stoffelen et al., 2020; Van Dyk, & Slotow, 2003). PNP is visited by international as well as local tourists every day (Stoffelen et al., 2020). PNP is open to the public 7 days a week with seasonal open and close times (Magome, Cain, Owen-Smith, & Henley, 2008). Three main gates are available for tourists to enter namely, Manyane gate, Bakubung gate, and Bakgatla gate, requiring an entrance fee before access is allowed (Carruthers, 2011; Magome et al., 2008). The entrance payments as well as concession fees helps generate an income for PNP (Carruthers, 2011). High-end lodges are situated throughout PNP, which offer drives for private guests, which generates further income for PNP (Stoffelen et al., 2020).

PNP has geological importance as it is found in the relic of a quondam alkaline volcano (Kidwai et al., 2019; la Grange, Kellner, Cilliers, & Götze, 2009; Rutherford et al., 2006). PNP is one of the few places in the world that consist of a composite alkaline rich ring (Rutherford et al., 2006). Most of the caldera of the volcano is eroded and has left a broken ring of low mountains and hills (Rutherford et al., 2006). The width of the floor valleys surrounded by mountains and hills stretches as far as 1-2 kilometres (Rutherford et al., 2006). in the alkaline composite, various types of rocks can be found such as, silica-poor, sodium- and potassium-rich rocks. The most dominant rock found will be foyaite, tuff with lava which is mixed with syenite (Rutherford et al., 2006).

According to Mucina et al., (2006), the park falls in the Savanna biome and consists of Pilanesberg Mountain Bushveld. It has a unique ecotone of wetter Bushveld vegetation and Kalahari Thornveld known as Sour Bushveld (Kidwai et al., 2019; Vanak et al., 2010; Woolley, Page, & Slotow, 2011). The remaining vegetation types in the park consists mainly of broad leaf bushveld, mixed Senegalia, and patches of open grasslands and thickets due to past mining operations and agricultural practises (Rutherford et al., 2006; Van Dyk & Slotow, 2003). Although the predominant vegetation types comprise of *Senegalia caffra* woodlands, *Vachellia karroo* woodlands, *Senegalia mellifera*, *Combretum* woodlands, Mixed *Senegalia* woodland, Grassland (Vanak et al., 2010).

Due to past agricultural and prominent geological activities the vegetation in PNP can be subdivided into eight categories, 1) Mesocline savanna, 2) Xerocline savanna, 3) pediment- and secondary grassland, 4) Savanna valleys, 5) summit, 6) secondary grasslands, 7) Senegalia thorn thickets, and 8) riverine (Magome et al., 2008). In the western and southern side of the slopes, mesocline savanna occur with tree species, *Faurea saligna*, *Senegalia caffra*, and *Setaria lindenbergiana* with two common grass layers, *Trachypogon spicatus* and *Themeda triandra* (Magome et al., 2008). On the north, northwest, and east slopes Xerocline savanna is found, with a predominant tree species *Combretum apiculatum* with two common grass layers namely, *Heteropogon contortus* and *Chrysopogon serrulatus* (Magome et al., 2008). In the pediment grasslands common grasses such as *Diheteropogon amplectens*, Elionurus muticus, *Heteropogon contortus* occur with secondary grassland, *Eragrotis superba*, *Themeda triandra*, *Cymbopogon excavatus*, *Elionurus muticus* (Magome et al., 2008). Tree species *Senegalia karroo*, *Combretum imberbe*, *Senegalia tortilis* with grass species *Panicum maximum* and *Heteropogon contortus* are found in a savanna valley. The vegetation in thorn thicket and riverine are dominated by *Senegalia karroo*, *Senegalia tortilis* with common tree species, *Protea caffra*, *Faurea saligna*, *Lannea discolor*, together with grass species, *Heteropogon contortus*, *Diheteropogon amplectens*, *Themeda triandra* (Magome et al., 2008).

PNP falls in the summer rainfall region with an average rainfall of 632 mm, although regular droughts do occur (Carruthers, 2011; la Grange et al., 2009; Van Dyk & Slotow, 2003). The last drought PNP experience was in 2015/2016 (Botai, Botai, Dlamini, Zwane, & Phaduli, 2016). The mean temperature during the summer varies between (19°C and 31°C) and winter between (3°C and 21°C) (la Grange et al., 2009). PNP consists of several saline springs, one perennial river and a large man-made dam roughly 2 km^2, situated in the middle of the park, called Mankwe dam. There are other smaller man-made dams throughout PNP (Carruthers, 2011).

PNP does have other large, medium, and small carnivores such as leopard, cheetah, brown hyena (*Parahyaena brunnea*), caracal (*Caracal caracal*), black backed jackal (*Canis mesomelas*), civet (*Civettictis civetta*), and serval (*Leptailurus serval*). They also have very large dangerous, and protected mammals that attracts a great deal of tourism such as African buffalo (*Syncerus caffer*), African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), and hippopotamus (*Hippopotamus amphibius*). Other mammalian species includes, blue wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), impala (*Aepyceros melampus*), giraffe (*Giraffa cameopardalis*) hartebeest (*Alcelaphus buselaphus*), tsessebe (*Damaliscus lunatus*), kudu (*Tragelaphus strepsiceros*), and eland (*Tragelaphus oryx*), klipspringer (*Oreotragus oreotragus*), mountain reedbuck (*Redunca fulvorufula*) steenbok (*Raphicerus campestris*), and common duiker (*Sylvicapra grimmia*).

At present, the apex predator in the park is the African lion. Lions were introduced into the park in 1993 (Van Dyk & Slotow, 2003). These newly introduced lions were translocated from Etosha National Park with their offspring being distributed to other reintroduction programmes across South Africa (Funston & Levendal, 2015).

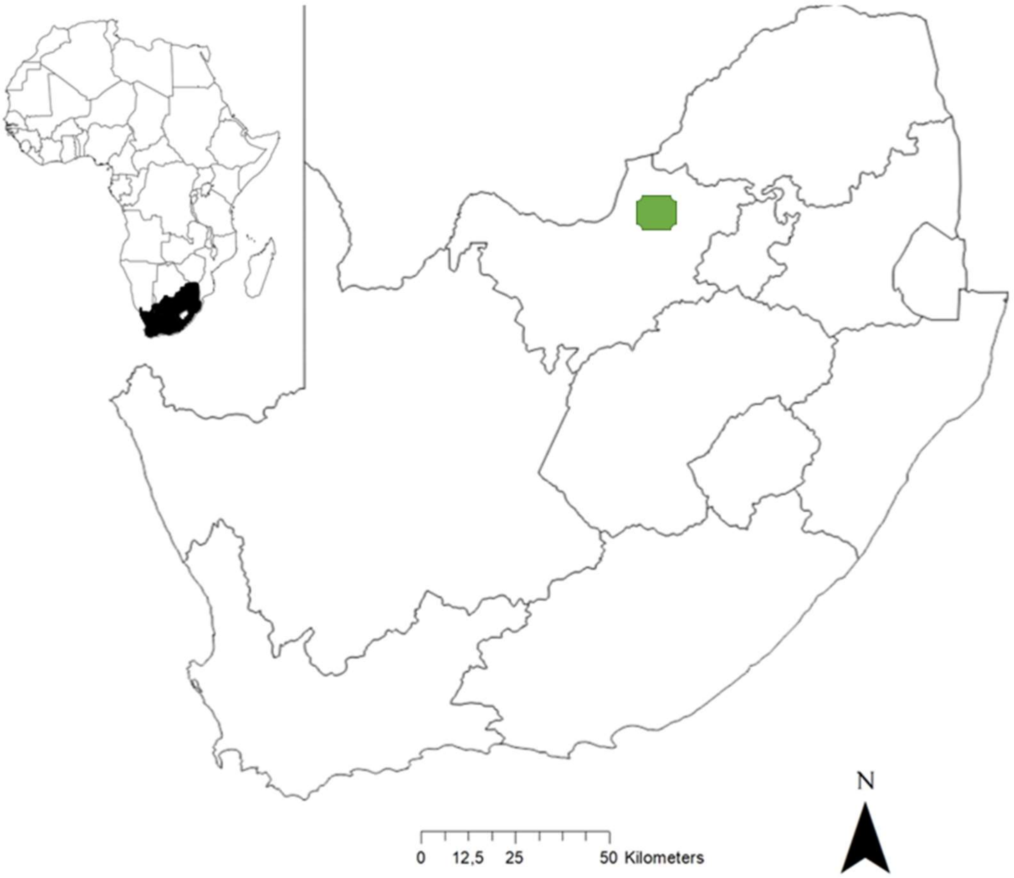


Figure 1: Location of Pilanesberg National Park in Southern Africa indicated in green.

Study species

The lion (*Panthera leo*) was named by Linnaeus in 1758 (Funston & Levendal, 2015). The African lion is the largest terrestrial carnivore in the southern hemisphere which belongs to the cat family Felidae (Macdonald, Loveridge, & Nowell, 2010). Lions ranged across continents such as Africa, North America, and Eurasia during the late Pleistocene Epoch (Cooper, Dugmore, Kitchener, Metzger, & Trabucco, 2021; de Manuel et al., 2020; Trinkel & Angelici, 2016). Lions that occurred throughout these continents were known as the cave lion (*Panthera leo spelaea*) discovered in Alaska, Eurasia, and Yukon, modern lion (*Panthera leo leo*) in Eurasia, and lastly American lion (*Panthera leo atrox*) in North America (de Manuel et al., 2020). Nearly 14000 years ago, the cave and American lion populations rapidly disappeared and became extinct. As the extinction of lion populations progressed in the last sesquicentennial years, the middle Eastern populations, and Barbary lion (*Panther leo leo*) followed the same pattern (de Manuel et al., 2020). In due course the modern lion vanished from

Southwestern Eurasia and North Africa during the 19th and 20th centuries (de Manuel et al., 2020). At this time, the presence of lions is restricted to two regions such as Sub-Saharan Africa and Kathiawar Peninsula of west central of India (Cooper et al., 2021; de Manuel et al., 2020). The Kathiawar Peninsula lion population are known as Asiatic lions (*Panthera leo persica*) which are restricted and isolated (de Manuel et al., 2020). In the last half-century lions experienced a 50% decline in abundance and 75% loss of range due to poaching, unwarranted trophy hunting, development of communities and agricultural landscapes, and loss of prey species due to fragmentation, and environmental changes (Cushman et al., 2018; Dures et al., 2019; Everatt, Kokes, & Pereira, 2019; Loveridge, Valeix, Elliot, & Macdonald, 2017; Pekor et al., 2019). Although lions have declined rapidly in the last half century, historically they also declined due to environmental factors such as prey extinction and reduction of habitat (Cooper et al., 2021).

The life history of species differ from one another, especially carnivores, as interlinked factors influence their food intake, social structure, and environmental conditions (Mcevoy et al., 2021). Life history can be defined as the different life stages that occur between birth and death, for example, cub, sub-adult, adult, sexual maturity, and reproductive state (Van de Kerk et al., 2013). The life span of lions can vary, as males live up to 14 years and females to 18 years (Schaller, 1972). Lions are the largest terrestrial predators in the African continent. The average female weighs 126 kg with males weighing up to 225 kg (Skinner & Chimimba, 2005). Due to the weight difference and the male's distinctive mane, lions can be defined as a sexually dimorphic species (West & Packer, 2002). Lions are predominantly found in the savanna biome, which contains different habitats such as savanna mosaic, thick bushland, open humid woodlands, and arid land ecosystems (Cooper et al., 2021). Lions are not water dependent as they can obtain the majority of their fluid needs from their prey (Briers-Louw, 2017).

Of all the felids, lions are the most social, as they hunt and live in prides (Elliot, Valeix, Macdonald, & Loveridge, 2014; Estes, 2012; Funston, Mills, & Biggs, 2001; Skinner & Chimimba, 2005; Spong, 2002). The pride social structure, can be characterised as females rearing their cubs for, less than 2-years with males that share a home range or territory (Van Orsdol, Hanby, & Bygott, 1985). A pride structure can endure for many generations (Lehmann, Funston, Owen, & Slotow, 2008a). The number of members in a pride can vary from two to 35, where female numbers fluctuate from two to 18 and males one to 17 (Schaller, 1972; Van Orsdol et al., 1985). While a pride is a stable social unit, it often occurs that pride members will subdivide into smaller subgroups but will stay in the home range, known as fission-fusion social group (Mosser, & Packer, 2009; Prox, & Farine, 2020). Female lions are known to be matrilineal, power over pride. However, it does appear that females disperse to form new prides (Dolrenry et al., 2014; Holekamp and Sawdy, 2019; Pusey, & Packer, 1987). Occasionally, females will attempt to join established prides and are usually rejected due to strong matrilineal bonds in the pride (Funston, & Levendal, 2015; Holekamp and Sawdy, 2019). At the age of 40 months sub-adult males are rejected or leave willingly from the pride and form coalitions (Van Orsdol et al., 1985). A coalition consists of two or more related males and every so often an unrelated male joins (Funston & Levendal, 2015; Van Orsdol et al., 1985).

The social system of lions can become complex as a) males in most cases disperse and roam up to three times further, than females, from their birthplace to establish their own territory and defend a female pride and b) females defend their cubs against roaming males and other prides, known as primary social grouping (Dolrenry et al., 2014; Gomez, Sommaro, Steinmann, Chiappero, & Priotto, 2011; Holekamp & Sawdy, 2019). Seeing that female prides are closely related, it depends on unrelated roaming male coalitions to bring in new genes (Holekamp, & Sawdy, 2019). Males are much larger than females and will fight other males in order to prevent the new male taking over the pride and killing his cubs (Pusey, & Packer, 1987). Home ranges can be defended by both male and female lions, although males generally patrol, urinate via spraying, and roar as a deterrent to other males (Spong, 2002; Van Orsdol et al., 1985). males may die much younger than females resulting in a shorter reproduction period (Barthold, Loveridge, Macdonald, Packer, & Colchero, 2016). If a new male takes over a pride he forces out all sub-adult males and usually kills the cubs (Lehmann, Funston, Owen, & Slotow, 2008b; Packer, Scheel, & Pusey, 1990).

Lions are sexual dimorphic and have different sexual maturity stages for males and females (Barthold et al., 2016). The sexual maturity of female lions varies between 24 – 36 months and male lion spermatogenesis starts from 36 – 48 months or later (Lehmann, Funston, Owen, & Slotow, 2008c; Schaller, 1972). A female's gestation period is approximately 110 days (Briers-Louw, 2017). Lions have a polygynandry mating system (Barthold et al., 2016; Dolrenry et al., 2014; Gomez et al., 2011; Pusey, & Packer, 1987). Small fenced protected areas can influence the tenure period males have over a pride (Packer, Loveridge, et al., 2013; Trinkel et al., 2010). For example, in Madikwe game reserve, a male coalition had a tenure period of 9-years over a pride and bred with the same relatives for 5-years (Trinkel et al., 2010). This could potentially decrease the genetic variability. Males normally have a tenure period between 2 to 3-years over a pride (Miller et al., 2013; Trinkel, Fleischmann, & Slotow, 2017).

Lions are nocturnal predators, even though they are active between 3 to 4 hours during the day (Schaller, 1972). Their inactive hours fluctuate between 20 to 21 hours a day, as the heat increases they will look for shaded areas to rest and cool down (Schaller, 1972; Skinner & Chimimba, 2005). Lions hunt mammals from a weight range of 50 to 300 kg (Skinner & Chimimba, 2005). However, their preferred prey species varies from a weight range of 190 to 550 kg which include, African buffalo (*Syncerus caffer*), blue wildebeest, gemsbok (*Oryx gazella*), zebra (*Equus quagga*), and giraffe (*Giraffa camelopardalis*) (Hayward & Kerley, 2005). It is also known that lions are habitat generalists, meaning their dietary and habitat preference can deviate (Dolrenry et al., 2014). Lions occasionally hunt large prey species such as elephants, white rhinoceroses (*Ceratotherium simum*), and hippopotamuses (*Hippopotamus amphibius*) (Hayward & Kerley, 2005; Keet, 2010). Factors that influence hunting success consists of their hunting method, pride size and structure, and vegetation cover (Funston et al., 2001; Hayward & Kerley, 2005; le Roux et al., 2019). Large prides can be beneficial for hunting success being able to protect the carcass from any interspecific competition (Packer et al., 1990; Schaller, 1972; Van Orsdol et al., 1985). Selecting a certain prey body biomass can sometimes be influenced by sex (Funston & Mills, 2006). For example, males tend to hunt large body prey species such as African buffalo or sub-adult giraffes while small to intermediate prey are generally hunted by females such as impala, wildebeest, and zebra (De Boer et al., 2010; Estes, 2012; Funston & Mills, 2006; le Roux et al., 2019).

Species change their evolutionary behavioural patterns to adapt to spatial and temporal scales as it diversifies in each ecosystem (Auffray, Renaud, & Claude, 2009). Prey species availability differs depending on the biome, with some biomes being able to support larger prey densities than others.(Briers-Louw, 2017; Stander, 2019). The home ranges of lions in throughout the African continent differs tremendously for example, in Ngorongoro Crater, Tanzania, the home range is as small as 20 km^2, in Etosha National Park, Namibia, it deviates as far as 2075 km^2, and in the Kgalagadi Transfrontier Park, South Africa, it deviates as far as 4500 km^2 (Funston & Levendal, 2015; Funston, 2011; Stander, 2019). The scarcer the prey the larger the home ranges of lions (Gittleman & Harvey, 1982; Schaller, 1972).

Lions are apex predators (Funston & Levendal, 2015). Therefore, they have a pivotal ecological role in the regulation of prey species. This top-down effect is important when managing lions as they can influence the prey population dynamics (Funston & Levendal, 2015).which makes them an important species to protected areas (Cooper et al., 2021; Lindsey et al., 2017; Ripple et al., 2014).

References

Alibhai, S., Jewell, Z., & Evans, J. (2017). The challenge of monitoring elusive large carnivores: An accurate and cost-effective tool to identify and sex pumas (Puma concolor) from footprints. *PloS one*, *12*(3), e0172065. https://doi.org/10.1371/journal.pone.0172065

Arnholt, A. T., & Herbert, J. (1995). Estimating the mean with known coefficient of variation. *The American Statistician*, *49*(4), 367–369.

Auffray, J.-C., Renaud, S., & Claude, J. (2009). Rodent Biodiversity in Changing Environments. *Kasetsart Journal, Natural Science*, *43*(1), 83–93. Retrieved from https://www.researchgate.net/publication/228350392

Balme, G. A., Hunter, L. T. B., & Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, *73*(3), 433–441. https://doi.org/10.2193/2007-368

Barthold, J. A., Loveridge, A. J., Macdonald, D. W., Packer, C., & Colchero, F. (2016). Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, *53*(2), 295–304. https://doi.org/10.1111/1365-2664.12594

Bauer, H., & Van Der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, *38*(1), 26–31. https://doi.org/10.1017/S0030605304000055

Bauer, Hans., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., … Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *PNAS*, *112*(48), 14894–14899. https://doi.org/10.1073/pnas.1500664112

Belant, J. L., Bled, F., Mkasanga, I. J., Wilton, C. M., Mwampeta, S. B., Beyer, D. E., … Fyumagwa, R. (2019). Track surveys do not provide accurate or precise lion density estimates in Serengeti. *Global Ecology and Conservation*, *19*, e00651. https://doi.org/10.1016/j.gecco.2019.e00651

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, *90*, 171–180. https://doi.org/10.1016/j.anbehav.2014.01.030

Boitani, L., Ciucci, P., & Mortelliti, A. (2012). Designing carnivore surveys. In *Carnivore ecology and management: a handbook of techniques* (pp. 8–29). https://doi.org/10.1093/acprof

Borchers, D. (2012). A non-technical overview of spatially explicit capture-recapture models. *Journal of Ornithology*, *152*(2), 435–444. https://doi.org/10.1007/s10336-010-0583-z

Borchers, D., Distiller, G., Foster, R., Harmsen, B., & Milazzo, L. (2014). Continuous-time spatially explicit capture-recapture models, with an application to a jaguar camera-trap survey. *Methods in Ecology and Evolution*, *5*(7), 656–665. https://doi.org/10.1111/2041-210X.12196

Botai, C. M., Botai, J. O., Dlamini, L. C., Zwane, N. S., & Phaduli, E. (2016). Characteristics of droughts in South Africa: A case study of Free State and North West provinces. *Water*, *8*(10), 439. https://doi.org/10.3390/w8100439

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., … Allan, J. R. (2020). Restoring Africa's lions: Start with good counts. *Frontiers in Ecology and Evolution*, *8*, 138. https://doi.org/10.3389/fevo.2020.00138

Braczkowski, A., Gopalaswamy, A. M., Mustafa, N., Allan, J., Biggs, D., & Maron, M. (2020). Detecting early warnings of pressure on an African lion (*Panthera leo*) population in the Queen Elizabeth Conservation Area , Uganda. *Ecological Solution Eviddence*, *1*, e12015. https://doi.org/10.1002/2688-8319.12015

Briers-Louw, W. D. (2017). Ecology of three apex predators in Majete Wildlife Reserve, Malawi (Doctoral dissertation). Stellenbosch University, Stellenbosch.

Brink, H., Smith, R. J., & Skinner, K. (2012). Methods for lion monitoring: A comparison from the Selous Game Reserve, Tanzania. *African Journal of Ecology*, *51*(2), 366–375. https://doi.org/10.1111/aje.12051

Broekhuis, F., Elliot, N. B., Keiwua, K., Koinet, K., Macdonald, D. W., Mogensen, N., … Gopalaswamy, A. M. (2021). Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography*, *44*(3), 358–369. https://doi.org/10.1111/ecog.05154

Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PloS one*, *11*(5), 1–15. https://doi.org/10.1371/journal.pone.0153875

Caravaggi, A., Banks, P. B., Burton, C. A., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., … Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109–122. https://doi.org/10.1002/rse2.48

Carbone, C., Teacher, A., & Rowcliffe, M. J. (2007). The costs of carnivory. *PLoS Biology*, *5*(2), 0363–0368. https://doi.org/10.1371/journal.pbio.0050022

Carruthers, J. (2011). Pilanesberg National Park, North West Province, South Africa:

Uniting economic development with ecological design – A history, 1960s to 1984. *Koedoe*, *53*(1), 1–10. https://doi.org/10.4102/koedoe.v53i1.1028

Clark, T. J., Horne, J. S., Hebblewhite, M., & Luis, A. D. (2021). Stochastic predation exposes prey to predator pits and local extinction. *Oikos*, *130*(2), 300–309. https://doi.org/10.1111/oik.07381

Comley, J., Joubert, C. J., Mgqatsa, N., & Parker, D. M. (2020). Battle of the Large Carnivores: Spatial Partitioning in a Small, Enclosed Reserve? *African Journal of Wildlife Research*, *50*(1), 176–189. https://doi.org/10.3957/056.050.0176

Cooper, D. M., Dugmore, A. J., Kitchener, A. C., Metzger, M. J., & Trabucco, A. (2021). A kingdom in decline: Holocene range contraction of the lion (*Panthera leo*) modelled with global environmental stratification. *PeerJ*, *9*, e10504. https://doi.org/10.7717/peerj.10504

Creel, S., Becker, M. S., Durant, S. M., M’Soka, J., Matandiko, W., Dickman, A. J., … Zimmermann, A. (2013). Conserving large populations of lions - the argument for fences has holes. *Ecology Letters*, *16*(11), 1413-e3. https://doi.org/10.1111/ele.12145

Creel, Scott., & Creel, N. M. (1997). Lion density and population structure in the Selous Game Reserve: Evaluation of hunting quotas and offtake. *African Journal of Ecology*, *35*(2), 83–93. https://doi.org/10.1111/j.1365-2028.1997.062-89062.x

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., … Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS one*, *13*(7), e0196213. https://doi.org/10.1371/journal.pone.0196213

De Boer, W. F., Vis, M. J. P., De Knegt, H. J., Rowles, C., Kohi, E. M., van Langevelde, F., … Prins, H. H. T. (2010). Spatial distribution of lion kills determined by water dependency of prey species. *Journal of Mammalogy*, *91*(5), 1280–1286. https://doi.org/10.1644/09-MAMM-A-392.1

de Manuel, M., Barnett, R., Sandoval-Velasco, M., Yamaguchi, N., Vieira, F. G., Mendoza, L. Z. M., … Gilbert, T. M. (2020). The evolutionary history of extinct and living lions. PNAS, *117*(20), 10927–10934. https://doi.org/10.1073/pnas.1919423117

Dey, S., Delampady, M., & Gopalaswamy, A. M. (2019). Bayesian model selection for spatial capture–recapture models. *Ecology and Evolution*, *9*(20), 11569–11583. https://doi.org/10.1002/ece3.5551

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, S. R., & Frank, L. (2014). A metapopulation approach to African lion (*Panthera leo*) conservation. *PloS one*, *9*(2). https://doi.org/10.1371/journal.pone.0088081

Dröge, E., Creel, S., Becker, M. S., Loveridge, A. J., Sousa, L. L., & Macdonald, D. W. (2020). Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecology and Evolution*, *10*(7), 3276–3292. https://doi.org/10.1002/ece3.6065

Durant, S. M., Craft, M. E., Hilborn, R., Bashir, S., Hando, J., & Thomas, L. (2011). Long-term trends in carnivore abundance using distance sampling in Serengeti

National Park, Tanzania. *Journal of Applied Ecology*, *48*(6), 1490–1500. https://doi.org/10.1111/j.1365-2664.2011.02042.x

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion - conservation stronghold. *Density and Distribution*, *25*, 870–879. https://doi.org/10.1111/ddi.12905

Edwards, S., Cooper, S., Uiseb, K., Hayward, M., Wachter, B., & Melzheimer, J. (2018). Making the most of by-catch data: Assessing the feasibility of utilising non-target camera trap data for occupancy modelling of a large felid. *African Journal of Ecology*, *56*(4), 885–894. https://doi.org/10.1111/aje.12511

Elliot, N. B., Bett, A., Chege, M., Sankan, K., de Souza, N., Kariuki, L., … Gopalaswamy, A. M. (2020). The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice*, 1–11. https://doi.org/10.1111/csp2.217

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., & Macdonald, D. W. (2014). Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, *95*(10), 2860–2869. https://doi.org/10.1890/13-1793.1

Elliot, N. B., & Gopalaswamy, A. M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, *31*(4), 934–943. https://doi.org/10.1111/cobi.12878

Elliot, N. B., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos*, *123*(9), 1049–1056. https://doi.org/10.1111/oik.01266

Estes, R. D. (2012). Lion (*Panthera leo*). In *The behaviour guide to African mammals* (pp. 369–377). London and Los Angeles and Berkeley: The University of California Press.

Everatt, K. T., Kokes, R., & Pereira, C. L. (2019). Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation*, *28*(14), 4099–4114. https://doi.org/10.1007/s10531-019-01866-w

Ferreira, S. M., Beukes, O. B., Haas, T. C., & Radloff, F. G. T. (2020). Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park. *African Journal of Ecology*, *58*(3), 348–360. https://doi.org/10.1111/aje.12728

Ferreira, S. M., & Funston, P. J. (2010). Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, *37*(3), 194–206. https://doi.org/10.1071/WR09030

Ferreira, S. M., & Hofmeyr, M. (2014). Managing charismatic carnivores in small areas: Large felids in South Africa. *South African Journal of Wildlife Research*, *44*(1), 32–42.

Forsyth, D. M., Ramsey, D. S. L., & Woodford, L. P. (2019). Estimating abundances, densities, and interspecific associations in a carnivore community. *The Journal of Wildlife Management*, *83*(5), 1090–1102. https://doi.org/10.1002/jwmg.21675

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M., & Clobert, J. (2011). A food web perspective on large herbivore community limitation. *Ecography*, *34*(2), 196–202. https://doi.org/10.1111/j.1600-0587.2010.06537.x

Funston, P J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., … Ferreira, S. M. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, *281*(1), 56–65. https://doi.org/10.1111/j.1469-7998.2009.00682.x

Funston, P J., & Levendal, M. (2015). *Biodiversity management plan for the lion (Panthera leo) in South Africa. Government Gazette, 2*. Retrieved from www.gpwonline.co.za

Funston, P J., & Mills, M. G. L. (2006). The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *African Journal of Wildlife Research*, *36*(1), 9–22.

Funston, P J., Mills, M. G. L., & Biggs, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, *253*(4), 419–431.

Funston, Paul J. (2011). Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, *41*(1), 1–10.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–511.

Gese, E. M. (2001). Monitoring of terrestrial carnivore populations. *Conservation Biology Series- Cambridge-*, 372–396.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, *10*(1), 57–63. https://doi.org/10.1007/BF00296396

Gomez, D., Sommaro, L., Steinmann, A., Chiappero, M., & Priotto, J. (2011). Movement distances of two species of sympatric rodents in linear habitats of Central Argentine agro-ecosystems. *Mammalian Biology*, *76*, 58–63. https://doi.org/10.1016/j.mambio.2010.02.001

Goodall, V. L., Ferreira, S. M., Funston, P. J., & Maruping-Mzileni, N. (2019). Uncovering hidden states in African lion movement data using hidden Markov models. *Wildlife Research*, *46*(4), 296–303. https://doi.org/10.1071/WR18004

Gopalaswamy, A. M., Delampady, M., Karanth, U. K., Kumar, S. N., & Macdonald, D. W. (2015). An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods in Ecology and Evolution*, *6*(9), 1055–1066. https://doi.org/10.1111/2041-210X.12351

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program SPACECAP: Software for estimating animal density using spatially explicit capture-recapture models. *Methods in Ecology and Evolution*, *3*(6), 1067–1072. https://doi.org/10.1111/j.2041-210X.2012.00241.x

Groom, R. J., Funston, P. J., & Mandisodza, R. (2014). Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: What is driving the population collapse? *Oryx*, *48*(3), 385–393.

https://doi.org/10.1017/S0030605312001457

Gusset, M., & Burgener, N. (2005). Estimating larger carnivore numbers from track counts and measurement. *African Journal of Ecology*, *43*, 320–324.

Harmsen, B. J., Foster, R. J., & Quigley, H. (2020). Spatially explicit capture recapture density estimates: Robustness, accuracy and precision in a long-term study of jaguars (*Panthera onca*). *PloS one*, *15*(6), e0227468. https://doi.org/10.1371/journal.pone.0227468

Hatfield, R. (2014). Population dynamics of the African lion (*Panthera leo*) within the Maasai Mara region of southern Kenya. *Kaleidoscope*, *11*(1), 70.

Hayward, M. W., Adendorff, J., O'Brien, J., Sholto-douglas, A., Bissett, C., Moolman, L. C., … Kerley, G. I. H. (2007). Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eatern Cape Province. *The Open Conservation Biology Journal*, *1*(1), 1–11.

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, Ullas K., Mackenzie, D. I., … Yarnell, R. W. (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, *52*(2), 286–290. https://doi.org/10.1111/1365-2664.12408

Hayward, M. W., Hayward, G. J., Druce, D. J., & Kerley, G. I. H. (2009). Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity Conservation*, *18*, 887–904. https://doi.org/10.1007/s10531-008-9452-y

Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, *267*, 309–322. https://doi.org/10.1017/S0952836905007508

Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, *139*(1–2), 219–229. https://doi.org/10.1016/j.biocon.2007.06.018

Holekamp, K. E., & Sawdy, M. A. (2019). The evolution of matrilineal social systems in fissiped carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1780), 20180065. https://doi.org/10.1098/rstb.2018.0065

Hrabar, H., & du Toit, J. T. (2005). Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conservation*, *8*(3), 259–267. https://doi.org/10.1017/S1367943005002234

Jewell, Z. (2013). Effect of monitoring technique on quality of conservation science. *Conservation Biology*, *27*(3), 501–508. https://doi.org/10.1111/cobi.12066

Jiménez, J., Nuñez-Arjona, J. C., Rueda, C., González, L. M., Garciá-Domínguez, F., Munõz-Igualada, J., & López-Bao, J. V. (2017). Estimating carnivore community structures. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/srep41036

Kane, M. D., Morin, D. J., & Kelly, M. J. (2015). Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodiversity and Conservation*, *24*(14), 3527–3541. https://doi.org/10.1007/s10531-015-1012-7

Karanth, U. K., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, *79*(8), 2852–2862. https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2

Kazemi, M. R., & Jafari, A. A. (2020). Small sample inference for the common coefficient of variation. *Communications in Statistics: Simulation and Computation*, *49*(1), 226–243. https://doi.org/10.1080/03610918.2018.1484474

Keet, D. F. (2010). Lions. In *Game Ranch Management* (Fith Editi, pp. 295–312). Van Schaik Publication.

Kettles, R., & Slotow, R. (2009). Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research*, *39*(1), 23–33. Retrieved from https://journals.co.za/docserver/fulltext/wild/39/1/wild_v39_n1_a3.pdf?expires=1560189647&id=id&accname=guest&checksum=514349490088AEF9B952A9F9167F8569

Kidwai, Z., Jimenez, J., Louw, C. J., Nel, H. P., & Marshal, J. P. (2019). Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (*Diceros bicornis*) populations from aerial counts. *Global Ecology and Conservation*, *19*, e00687. https://doi.org/10.1016/j.gecco.2019.e00687

Kiffner, C., Meyer, B., Mühlenberg, M., & Waltert, M. (2009). Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania? *Oryx*, *43*(1), 52–59. https://doi.org/10.1017/S0030605307002335

Kissui, B. M., & Packer, C. (2004). Top-down population regulation of a top predator: Lions in the Ngorongoro Crater. Proceedings of *the Royal Society of London*, *271*, 1867–1874. https://doi.org/10.1098/rspb.2004.2797

la Grange, M., Kellner, K., Cilliers, S. S., & Götze, A. R. (2009). Vegetation classification of the proposed Heritage Park, North-West Province, South Africa (North-West University; Vol. 75). https://doi.org/10.1016/j.sajb.2009.02.149

Lahoz-Monfort, J. J., Harris, M. P., Morgan, B. J. T., Freeman, S. N., & Wanless, S. (2014). Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. *Journal of Applied Ecology*, *51*(2), 534–543. https://doi.org/10.1111/1365-2664.12214

le Roux, E., Marneweck, D. G., Clinning, G., Druce, D. J., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2019). Top–down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography*, *42*(6), 1115–1123. https://doi.org/10.1111/ecog.03791

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008a). Feeding behaviour of lions (*Panthera leo*) on a small reserve. *African Journal of Wildlife Research*, *38*(1), 66–78.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008b). Home range utilisation and territorial behavior of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PloS one*, *3*(12), e3998. https://doi.org/10.1371/journal.pone.0003998

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008c). Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. *African Zoology*, *43*(2), 230–236. https://doi.org/10.3377/1562-7020-43.2.230

Lesilau, F., Verschueren, S., van't Zelfde, M., Musters, K. C. J. M., de Snoo, G. R., & de Iongh, H. H. (2021). Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: The case study of Nairobi National Park, Kenya. *Mammalia*, *85*(3), 198–207. https://doi.org/10.1515/mammalia-2020-0116

Lindner, E., & Fuelling, O. (2002). Marking methods in small mammals: ear-tattoo as an alternative to toe-clipping. *The Zoological Society of London*, *256*, 159–163.

Lindsey, P. A., Petracca, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., … Hunter, L. T. B. (2017). The performance of African protected areas for lions and their prey. *Biological Conservation*, *209*, 137–149. https://doi.org/10.1016/j.biocon.2017.01.011

López-Bao, J. V., Godinho, R., Pacheco, C., Lema, F. J., García, E., Llaneza, L., … Jiménez, J. (2018). Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. *Scientific Reports*, *8*(1), 1–8. https://doi.org/10.1038/s41598-018-20675-9

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, *54*(3), 815–825. https://doi.org/10.1111/1365-2664.12794

Macdonald, D. W., Loveridge, A. J., & Nowell, K. (2010). Dramatis personae: an introduction to the wild felids. In *The biology and conservation of wild felids* (First Edit, pp. 3–59). Oxford University Press (OUP).

Magome, H., Cain, J. W., Owen-Smith, N., & Henley, S. R. (2008). Forage selection of sable antelope in Pilanesberg Game Reserve, South Africa. *African Journal of Wildlife Research*, *38*(1), 35–41. https://doi.org/10.3957/0379-4369-38.1.35

Mari, L., Gatto, M., & Casagrandi, R. (2008). Local resource competition and the skewness of the sex ratio: A demographic model. *Mathematical Biosciences and Engineering*, *5*(4), 813–830. https://doi.org/10.3934/mbe.2008.5.813

Massey, A. L., King, A. A., & Foufopoulos, J. (2014). Fencing protected areas: A long-term assessment of the effects of reserve establishment and fencing on African mammalian diversity. *Biological Conservation*, *176*, 162–171. https://doi.org/10.1016/j.biocon.2014.05.023

Mbizah, M. M., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2019). Applying the resource dispersion hypothesis to a fission–fusion society: A case study of the African lion (*Panthera leo*). *Ecology and Evolution*, *9*(16), 9111–9119. https://doi.org/10.1002/ece3.5456

Mcevoy, O. K. (2019). *The management of lions (Panthera leo) in small, fenced wildlife reserves*. (Doctoral dissertation) Grahamstown, South Africa: Rhodes University.

Mcevoy, O. K., Ferreira, S. M., & Parker, D. M. (2021). The influence of population demographics on lion (*Panthera leo*) growth rates in small, fenced wildlife reserves. *African Journal of Wildlife Research*, *51*(1), 75–89.

Midlane, N., O'Riain, M. J., Balme, G. A., Robinson, H. S., & Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, *172*, 101–108. https://doi.org/10.1016/j.biocon.2014.02.006

Midlane, Niel., O'Riaain, J. M., Balme, G. A., & Hunter, L. T. B. (2015). To track or to call: comparing methods for estimating population abundance of African lions *Panthera leo* in Kafue National Park. *Biodiversity and Conservation*, *24*(6), 1311–1327. https://doi.org/10.1007/s10531-015-0858-z

Miller, S. M., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D. J., … Zimmermann, D. (2013). Management of reintroduced lions in small, fenced reseved in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research*, *43*(2), 138–154.

Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: A management dilemma. *South African Journal of Wildlife Research*, *44*(1), 43–55.

Miller, S. M., Riggio, J., Funston, P. J., Power, R. J., Williams, V., & Child, M. F. (2016). A conservation assessment of *Panthera leo*. In *The red list of mammals of South Africa*. Swaziland and Lesotho.

Milleret, C., Dupont, P., Chipperfield, J., Turek, D., Brøseth, H., Gimenez, O., … Bischof, R. (2020). Estimating abundance with interruptions in data collection using open population spatial capture–recapture models. *Ecosphere*, *11*(7), 1–14. https://doi.org/10.1002/ecs2.3172

Mondol, S., Karanth, U. K., Kumar, S. N., Gopalaswamy, A. M., Andheria, A., & Ramakrishnan, U. (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation*, *142*(10), 2350–2360. https://doi.org/10.1016/j.biocon.2009.05.014

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, *78*(2), 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024

Mucina, L., Rutherford, M. C., & Powrie, W. (2006). Vegetation atlas of South Africa, Lesotho and Swaziland. In L. Mucina & M. C. Rutherford (Eds.), *Vegetation Map of Southern Africa, Lesotho and Swaziland* (pp. 750–760). Pretoria: South Africa National Biodiversity Institute.

Noack, J., Heyns, L., Rodenwoldt, D., & Edwards, S. (2019). Leopard density estimation within an enclosed reserve, namibia using spatially explicit capture-recapture models. *Animals*, *9*(10), 724. https://doi.org/10.3390/ani9100724

Packer, C., Herbst, L., Pusey, A., Bygott, A., Hanby, J. P., Cairns, S. J., & Borgerhoff-Mulder, M. (1988). *Reproduction success of lions: studies of individual variation in contrasting breeding systems* (T. Clutton-Brock, Ed.). Chicago: University of Chicago Press.

Packer, C., Loveridge, A. J., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., … Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology*

Letters, *16*(5), 635–641. https://doi.org/10.1111/ele.12091

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups : Food is not enough. *The American Naturalist*, *136*(1), 1–19.

Packer, C., Swanson, A., Canney, S., Loveridge, A., Garnett, S., Pfeifer, M., … Macnulty, D. (2013). The case for fencing remains intact. *Ecology Letters*, *16*(11), 7–8. https://doi.org/10.1111/ele.12171

Packer, Craig. (2019). The African lion: A long history of interdisciplinary research. *Frontiers in Ecology and Evolution*, *7*(259), 1–6. https://doi.org/10.3389/fevo.2019.00259

Pekor, A., Miller, J. R. B., Flyman, M. V., Kasiki, S., Kesch, M. K., Miller, S. M., … Lindsey, P. A. (2019). Fencing Africa's protected areas: Costs, benefits, and management issues. *Biological Conservation*, *229*, 67–75. https://doi.org/10.1016/j.biocon.2018.10.030

Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, *160*(4), 497–508. https://doi.org/10.1111/j.1469-7998.1970.tb03093.x

Périquet, S., Fritz, H., & Revilla, E. (2015). The lion king and the hyaena queen: Large carnivore interactions and coexistence. *Biological Reviews*, *90*(4), 1197–1214. https://doi.org/10.1111/brv.12152

Pfeffer, S. E. (2016). *Comparison of three different indirect methods to evaluate ungulate population densities*. Swedish university of africultural science.

Power, R. J. (2002). Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe*, *45*(2), 67–75. https://doi.org/10.4102/koedoe.v45i2.32

Prox, L., & Farine, D. (2020). A framework for conceptualizing dimensions of social organization in mammals. *Ecology and Evolution*, *10*(2), 791–807. https://doi.org/10.1002/ece3.5936

Pusey, A. E., & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, *101*(4), 275–310.

Rafiq, K., Bryce, C. M., Rich, L. N., Coco, C., Miller, D. A. W., Meloro, C., … Hayward, M. W. (2019). Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Current Biology*, *29*(14), R681–R682. https://doi.org/10.1016/j.cub.2019.05.056

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., … Pimm, S. (2013). The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation*, *22*(1), 17–35. https://doi.org/10.1007/s10531-012-0381-4

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Royle, A. J., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture-recapture*. Academic Press.

Royle, A. J., & Converse, S. J. (2014). Hierarchical spatial capture-recapture models: Modelling population density in stratified populations. *Methods in Ecology and Evolution*, *5*(1), 37–43. https://doi.org/10.1111/2041-210X.12135

Royle, A. J., Fuller, A. K., & Sutherland, C. (2018). Unifying population and landscape ecology with spatial capture–recapture. *Ecography*, *41*(3), 444–456. https://doi.org/10.1111/ecog.03170

Royle, A. J., Karanth, U. K., Gopalaswamy, A. M., & Kumar, S. N. (2009). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, *90*(11), 3233–3244. https://doi.org/10.1890/08-1481.1

Royle, A. J., Sutherland, C., Fuller, A. K., & Sun, C. C. (2015). Likelihood analysis of spatial capture-recapture models for stratified or class structured populations. *Ecosphere*, *6*(2), 1–11. https://doi.org/10.1890/ES14-00148.1

Rutherford, M. C., Mucina, L., Lötter, C., Bredenkamp, G. J., Jacobus, H. L., Scott-shaw, C. R., … Hurter, P. J. H. (2006). Savanna Biome. In *The vegetation of South Africa, Lesotho and Swaziland.* (pp. 440–529). Pretoria: South Africa National Biodiversity Institute.

Schaller, G. B. (1972). The Serengeti Lion. Chicago: Univeristy of Chicago Press. https://doi.org/10.1017/CBO9781107415324.004

Silk, J. B. (1984). Local resource competition and the evolution of male-biased sex ratio. *Journal of Theoretical Biology*, *108*(2), 203–213.

Skinner, J. D., & Chimimba, C. T. (2005). Lion. In *The mammals of the Southern African sub-region* (Third Edit, pp. 390–396). Cambridge University Press.

Slotow, R., & Hunter, L. T. B. (2009). Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: The African lion in South Africa. In *Reintroduction of Top-Order Predators, (5), 43*. https://doi.org/10.1002/9781444312034.ch3

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), 20142711. https://doi.org/10.1098/rspb.2014.2711

Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., & Harwood, J. (2010). The functional response of a generalist predator. *PloS one*, *5*(5). https://doi.org/10.1371/journal.pone.0010761

Snyman, A., Jackson, C. R., & Funston, P. J. (2015). The effect of alternative forms of hunting on the social organization of two small populations of lions *Panthera leo* in Southern Africa. *Oryx*, *49*(4), 604–610. https://doi.org/10.1017/S0030605313001336

Sobratee, N., & Slotow, R. (2019). A critical review of lion research in South Africa: The impact of researcher perspective, research mode, and power structures on outcome bias and implementation gaps. *Frontiers in Ecology and Evolution*, *7*(81), 1–17. https://doi.org/10.3389/fevo.2019.00081

Spong, G. (2002). Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology*, *52*(4), 303–

307. https://doi.org/10.1007/s00265-002-0515-x

Stander, P. E. (2019). Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia. *Namibian Journal of Environment*, *3*, 1–10.

Stoffelen, A., Adiyia, B., Vanneste, D., & Kotze, N. (2020). Post-apartheid local sustainable development through tourism: an analysis of policy perceptions among “responsible” tourism stakeholders around Pilanesberg National Park, South Africa. *Journal of Sustainable Tourism*, *28*(3), 414–432. https://doi.org/10.1080/09669582.2019.1679821

Tambling, C. J., & du Toit, J. T. (2005). Modelling wildebeest population dynamics: Implications of predation and harvesting in a closed system. *Journal of Applied Ecology*, *42*, 431–441. https://doi.org/10.1111/j.1365-2664.2005.01039.x

Tarugara, A., Clegg, B. W., Gandiwa, E., & Muposhi, V. K. (2019). Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population. *Global Ecology and Conservation*, *18*, e00627. https://doi.org/10.1016/j.gecco.2019.e00627

Tende, T., Ottosson, U., Hansson, B., & Bensch, S. (2008). Population density and abundance of Lions in Yankari Game Reserve, 2008. Unpublish report, Lund University, Sweden.

Trinkel, M., Fleischmann, P. H., & Slotow, R. (2017). Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population. *Journal of Zoology*, *301*(1), 41–50. https://doi.org/10.1111/jzo.12387

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation*, *13*(4), 374–382. https://doi.org/10.1111/j.1469-1795.2009.00344.x

Trinkel, Martina., & Angelici, F. M. (2016). The decline in the Lion population in Africa and possible mitigation measures. In F. M. Angelici (Ed.), *Problematic Wildlife* (Edition 1, pp. 45–68). https://doi.org/10.1007/978-3-319-22246-2

Tumenta, P. N., van’t Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., Udo de Haes, H. A., & De Iongh, H. H. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology*, *78*(6), 461–469. https://doi.org/10.1016/j.mambio.2013.08.006

Van de Kerk, M., de Kroon, H., Conde, D. A., & Jongejans, E. (2013). Carnivora population dynamics are as slow and as fast as those of other mammals: Implications for their conservation. *PloS one*, *8*(8), e70354. https://doi.org/10.1371/journal.pone.0070354

Van Dyk, G., & Slotow, R. (2003). The effects of fences and lions on the ecology of African wild dogs reintroduced to Pilanesberg National Park, South Africa. *African Zoology*, *38*(1), 79–94. https://doi.org/10.1080/15627020.2003.11657196

Van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (Panthers, leo). *Journal of Zoology*, *206*(1), 97–112.

https://doi.org/10.1111/j.1469-7998.1985.tb05639.x

Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, *143*(11), 2631–2637. https://doi.org/10.1016/j.biocon.2010.07.005

VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, *77*(4), 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028

Vega Yon, G. G., & Marjoram, P. (2019). fmcmc: A friendly MCMC framework. *The Journal of Open Source Software*, *4*(39), 1427. https://doi.org/10.2307/2334940

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion’s mane. *Science*, *297*(5585), 1339–1343. https://doi.org/10.1126/science.1073257

Wijers, M., Trethowan, P., Du Preez, B., Chamaillé-Jammes, S., Loveridge, A. J., Macdonald, D. W., & Markham, A. (2021). Vocal discrimination of African lions and its potential for collar-free tracking. *Bioacoustics*, *30*(5), 575–593. https://doi.org/10.1080/09524622.2020.1829050

Wild, G., & West, S. A. W. (2009). Genomic imprinting and sex allocation. *American Naturalist*, *173*(1), 1–14. https://doi.org/10.1086/593305

Winterbach, H. E. K., Winterbach, C. W., Somers, M. J., & Hayward, M. W. (2013). Key factors and related principles in the conservation of large African carnivores. *Mammal Review*, *43*(2), 89–110. https://doi.org/10.1111/j.1365-2907.2011.00209.x

Witmer, G. W. (2005). Wildlife population monitoring: some practical considerations. *Wildlife Research*, *32*, 259–263.

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation*, *3*(2), 165–173. https://doi.org/10.1017/S136794300000086X

Woolley, L. A., Page, B., & Slotow, R. (2011). Foraging strategy within African elephant family units: Why body size matters. *Biotropica*, *43*(4), 489–495. https://doi.org/10.1111/j.1744-7429.2010.00733.x

CHAPTER 3

The population demography of African lions (*Panthera leo*) in Pilanesberg National Park, South Africa.

Isabella A Bettings[a], David G Marneweck[a,b], Nicholas B Elliot[c], Arjun M Gopalaswamy[d,e], Herve Fritz[a,f], and Jan A Venter[a,f]

[a]*Department of Conservation Management, Faculty of Science, George Campus, Nelson Mandela University*

[b]*Endangered Wildlife Trust, Johannesburg, South Africa*

[c]*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire, OX13 5QL, UK*

[d]*Carnassials Global, 44/1, Regus Supreme, K. R. Road, 7th Block, Jayanagar, Bengaluru, 560070, India*

[e]*Wildlife Conservation Society, Global Conservation Programs, 2300, Southern Boulevard, Bronx, New York, 10460, USA*

[f]*REHABS International Research Laboratory, CNRS-Université Lyon 1-Nelson Mandela University, George Campus, Madiba drive 6531 George, South Africa*

Abstract

In fenced protected areas, intensive wildlife management is required which is dependent on accurate animal population estimates. This is obtained through monitoring populations to record spatio-temporal fluctuations in population size and structure. The reliability of these estimates affects management decisions and planning with subsequent consequences to ecosystem resilience and health. This is especially the case with large carnivore population management, where obtaining accurate and precise estimates of population size are of critical importance. Counting large carnivores is difficult as they are nocturnal, elusive, live at low ecological densities, and often encounter humans which increases their timidity. We used a search-encounter based Bayesian spatially explicit capture-recapture approach to estimate abundance, density, sex ratio and seasonal home range size of African lions (*Panthera leo*) over the age of one year in Pilanesberg National Park, South Africa. The posterior mean abundance of lions is 44 (posterior SD 3.5). The posterior mean density of PNP lions is 8.8 per 100 km^2 (posterior SD 0.6) in a small fenced protected area, which is generally lower compared to reported estimates in other fenced protected areas. The estimated sex ratio of 0.9♀:1♂ is unusual since most free roaming populations have a sex ratio of 1:2. Lastly, the home range size of males was 279 km^2 and females 191 km^2 which was expected since males commonly have much larger home ranges. We recommend the Bayesian spatial capture-recapture model to be the preferred option for monitoring lions in Pilanesberg and other similar lion habitats.

Key words: Bayesian spatial explicit capture-recapture, fenced protected areas, home range, population density, sex ratio

Introduction

Large African carnivores such as lions (*Panthera leo*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), and cheetahs (*Acinonyx jubatus*) are in decline (Bauer et al., 2015). Factors that caused these declines are habitat transformation, human-wildlife conflict, and prey depletion (Lesilau et al., 2021; Riggio et al., 2013; Trinkel et al., 2017). Wildlife, especially carnivores in unfenced protected areas, are more vulnerable to these factors, which has led to the decline in ranges across Africa (Woodroffe, 2000). Subsequently, fencing of protected areas has, in many cases, become an important conservation tool to protect large predator populations, especially in southern Africa (Hayward, Adendorff, et al., 2007; Packer, Loveridge, et al., 2013). In the early 1990s there was a large number of reintroduction programmes implemented in South Africa when a number of "Big five" reserves were created with adequate fencing so large carnivores could be reintroduced (Ferreira & Hofmeyr, 2014; Hayward, O'Brien, & Kerley, 2007; Miller et al., 2013; Slotow & Hunter, 2009). Numerically, lion populations have thrived in these fenced parks. Today, lions in fenced protected areas make a significant contribution to global lion conservation (Creel et al., 2013; Massey et al., 2014). However, in fenced protected areas, lions came remarkably close to their estimated carrying capacities and are limited by density dependent factors (Packer, Loveridge, et al., 2013).

Managing lion populations in fenced areas is challenging because confinement and limited space inhibit dispersal, affect territorial behaviour, cause genetic isolation, lower disease resistance, and frequently result in overpopulation (Kettles & Slotow, 2009; Miller et al., 2013; Packer, Loveridge, et al., 2013; Slotow & Hunter, 2009; Trinkel et al., 2010). Intensive management therefore becomes the norm when careful consideration of social structure, population genetics, movement behaviour, predator and prey population density, interspecific- and intraspecific-competition are taken into account (Kissui & Packer, 2004; Lehmann et al., 2008c; Miller et al., 2013; Pfeffer, 2016).

Lion populations can be regulated through bottom-up effects (Kissui & Packer, 2004; le Roux et al., 2019), especially in fenced areas where this impact can be more severe as prey populations' ability to spatially avoid predators is inhibited (Clark, Horne, Hebblewhite, & Luis, 2021; Tambling & du Toit, 2005). The 'predator pit' effect (see Clark et al., 2021; Smout et al., 2010) often develops in fenced areas, where predators hunt prey species to a point where they can't recuperate fast enough and therefore cannot sustain their own population. This has happened in Pilanesberg National Park (PNP). Before lions were introduced and in the early years just after their introduction (1984 to 1995) , The wildebeest populations increased by an annual population growth rate of 12% (Tambling & du Toit, 2005) (Figure 1). In 1994, there were a total of 25 lions in the park (six adult males, 12 adult females, and seven cubs) and their annual population growth rate was 10.6% which increased the total population to 59 individuals by 2001 (Tambling & du Toit, 2005). Between 1997 and 2001 the wildebeest population started to collapse and declined by 47% (from pre-1995 population sizes) (Tambling & du Toit, 2005) (Figure 1 (Hayward, O'Brien, et al., 2007; Tambling & du Toit, 2005). Other prey species also started to decline eland (*Tragelaphus oryx*) decreased by 76%, waterbuck (*Kobus ellipsiprymnus*) decreased by 67%, and kudu (*Tragelaphus strepsiceros*) by 65%. Tambling & du Toit (2005) concluded that fenced protected areas with uncontrolled high predator numbers and overharvesting can lead to prey population declines and ecosystem degradation. Once park authorities realised this was an issue, lion numbers were decreased, and wildebeest numbers had to be supplemented (Figure 1).

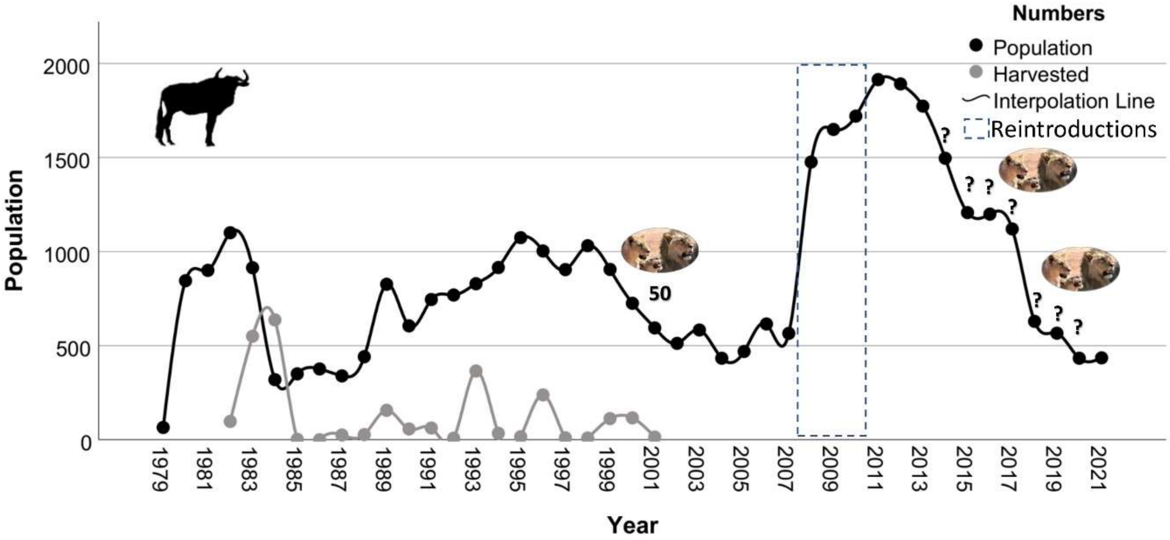


Figure 1. Blue wildebeest population trends over the last 42 years in Pilanesberg National Park (North-West Parks and Tourism Board (NWPTB), unpublished data). The adult lion population at its peak in 2001 consisted of 50 individuals which was considered a contributing factor to the sharp population decline (Tambling & du Toit, 2005). Over the last few years, the wildebeest population started to decline rapidly again but no lion population numbers were available. The monitoring of lions did not actively continue after the blue wildebeest study.

Conservation managers are commonly confronted by four questions when they have to manage lions in small fenced protected areas: 1) how many lions are there, 2) where do they occur, 3) what is the population growth rate, and 4) how many can the park sustain based on the bottom-up regulation factors mentioned earlier (Gese, 2001)? These questions, if left unanswered, can hinder management (Gese, 2001). Estimating population numbers then become critical. However, estimating the population sizes of lions can be challenging since it is time consuming , and requires a great deal of funding (Gese, 2001; Milleret et al., 2020).

In past studies, investigations into the population sizes of lions used two methods, e.g. call-ups and spoor tracking (Everatt, Kokes, & Pereira, 2019; Funston et al., 2010; Midlane, O'Riain, Balme, Robinson, & Hunter, 2014; Midlane, O'Riain, Balme, & Hunter, 2015). Authors specifically found that these type of methods, based on indices, to be problematic due to confounding effects caused by detection probability (Gopalaswamy et al., 2015). For example, carnivores can become habituated and do not respond consistently to call-ups during surveys, and spoor tracking results have been proven to be unreliable (Bauer, & Van Der Merwe, 2004; Belant et al., 2019; Dröge et al., 2020; Elliot & Gopalaswamy, 2017).

The search-encounter based spatial capture-recapture approach (SECR) is an emerging estimation method. It has proven to produce reliable estimates of lion population numbers (Braczkowski, Gopalaswamy, Elliot, et al., 2020; Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Elliot et al., 2020; Elliot, & Gopalaswamy, 2017). The basic concept of SECR was introduced by Efford, (2004) using simulations to develop a buffer from existing 'captures' of individuals at different locations. However, only when explicit likelihood models were constructed (e.g., Borchers, & Efford, Royle et al., 2009) did SECR models gained acceptance (see Royle, Chandler, Sollmann, & Gardner, 2013). In essence, the attention of these models into lion abundance estimation practice was motivated by two important developments, e.g., the availability of good cameras enabling unambiguous identification of lions from photographs taken in the field (e.g., Braczkowski et al., 2020; Elliot, & Gopalaswamy 2017; Elliot et al., 2020), and the adaptation of search-encounter surveys into SECR modelling (Elliot, & Gopalaswamy, 2017; Russell et al., 2012). The Bayesian version of SECR models (Royle et al., 2009), which I have used here for estimating lion densities and other key state variables, is a hierarchical model consisting of a state process (which describes how animals are distributed in an area) and an observation process (which describes the manner in which animals are detected in the survey). The strength of such a hierarchical modelling approach (see Royle et al., 2008) lies in the explicit separation of these two processes allowing us to correct for observation biases. For example, in an area where lions are accustomed to tourists, they may be more detectable compared to areas where tourism is absent despite having the same lion densities.

Over the past few years in PNP, the annual herbivore census has indicated a significant decline in prey species, especially wildebeest (NWPTB, unpublished data) (Figure 1). PNP management concluded that excessive lion numbers in the park resulted in the decline of prey species (Tambling & du Toit, 2005). Due to various reasons, management faced some challenges which hampered effective monitoring of the lion populations. However, in this study, we used a search-encounter based sampling approach over a 109-day monitoring period to record individual lions. We then applied the Bayesian SECR model to accurately estimate the density, sex ratio, and seasonal home range sizes of lions in PNP (Elliot et al., 2020; Elliot & Gopalaswamy, 2017). I hypothesised, that an unmonitored, growing lion population, would be relatively high in PNP, close to that of the large population size recorded in the late 1990s (Tambling & du Toit, 2005) This assumption was based on the evidence that suggested a decreasing prey base (NWPTB, unpublished data). I further hypothesised that the estimated sex ratio would be skewed towards females due to their polygyny mating system and the aggressive behaviour displayed by the territorial males (Dolrenry et al., 2014; Gomez et al., 2011). Lastly, I hypothesised that males would have much larger, overlapping home range sizes with respect to females (Comley, Joubert, Mgqatsa, & Parker, 2020).

Study area

We conducted the study in Pilanesberg National Park (PNP) (25°08' to 25°22'S; 26°57' to 27°13'E, Figure 2), located in the Northwest Province of South Africa. PNP covers approximately 55 000 ha, which is fenced and electrified to confine megaherbivores and large carnivores (Tambling & du Toit, 2005; Vanak et al., 2010). PNP was declared a protected area in 1979, when managers started to reintroduce animals that were known to occur in the area (Van Dyk & Slotow, 2003). Approximately 6000 animals of different types were reintroduced as well as the "big five" to boost tourism (Stoffelen et al., 2020; Van Dyk & Slotow, 2003). Lions were reintroduced in 1993 (Van Dyk & Slotow, 2003). PNP is a popular ecotourism destination which attracts international as well as local tourists (Stoffelen et al., 2020). According to Mucina et al., (2006), PNP falls under the savanna biome and consists mainly of Pilanesberg Mountain Bushveld veld. It has a unique ecotone of wetter Bushveld vegetation and Kalahari Thornveld known as Sour Bushveld (Mucina, Rutherford, & Powrie, 2006; Rutherford et al., 2006). PNP falls under a summer rainfall region with an average rainfall of 632 mm (la Grange et al., 2009; Van Dyk & Slotow 2003). The mean temperature during the summer varies between 19°C and 31°C and winter between 3°C and 21°C (la Grange et al., 2009). There are several natural springs and man-made dams throughout PNP. The big five species which include, African buffalo (*Syncerus caffer*), African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), leopard, and lion are found in PNP. Other herbivore and mammalian species include, blue wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), impala (*Aepyceros melampus*), giraffe (*Giraffa cameopardalis*), hartebeest (*Alcelaphus buselaphus*), tsessebe (*Damaliscus lunatus*), kudu (*Tragelaphus strepsiceros*), and eland (*Tragelaphus oryx*), hippopotamus (*Hippopotamus amphibius*). Other predators in PNP include, brown hyena (*Parahyaena brunnea*), caracal (*Caracal caracal*), black-backed jackal (*Canis mesomelas*), civet (*Civettictis civetta*), serval (*Leptailurus serval*), and cheetah (*Acinonyx jubatus*).

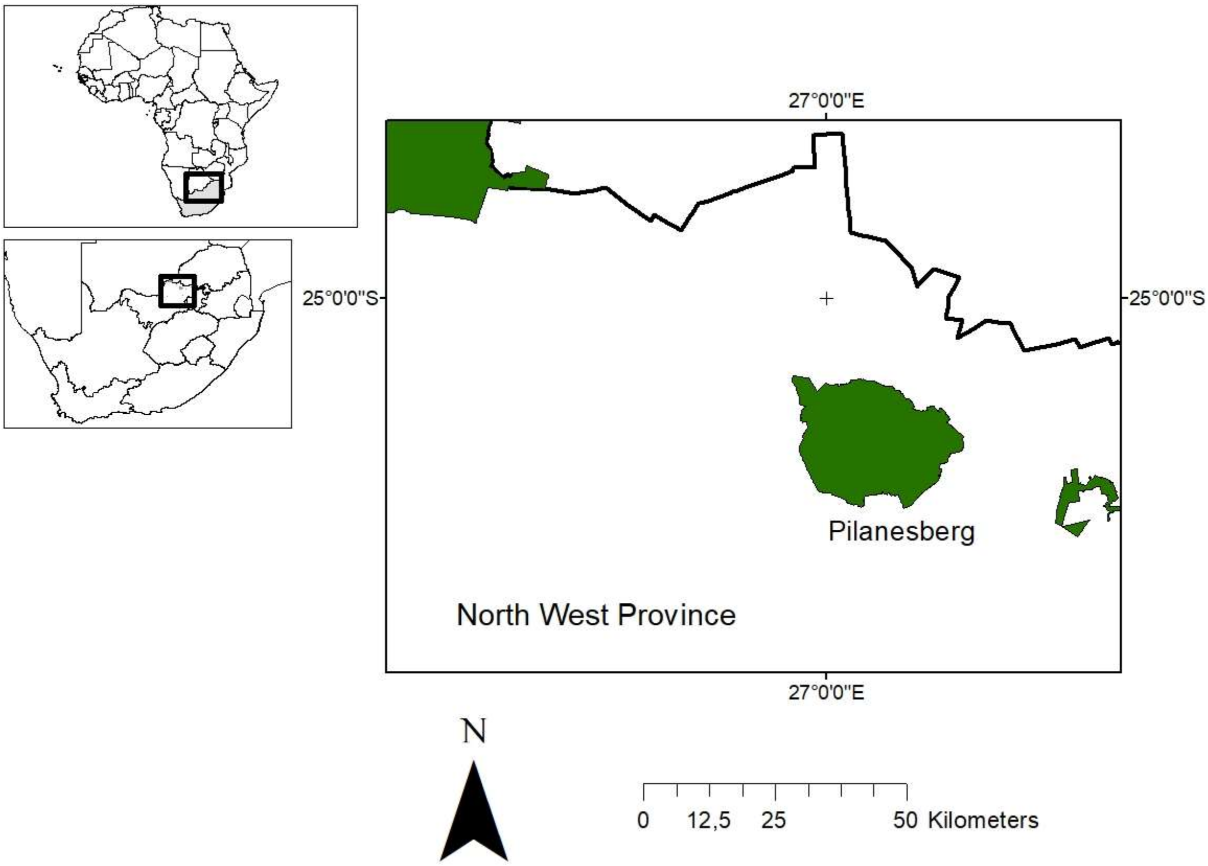


Figure 2. The location of Pilanesberg National Park, a 550 km^2 fully fenced protected area within the North West province of South Africa.

Field methods

We conducted an intensive lion search in the period between 25 August and 10 December 2020 which covered 90 counting days. This timeframe was chosen as a compromise between being long enough to obtain a large dataset, but not long enough that we risked serious violations of the assumptions of closure (Karanth & Nichols, 1998). PNP has an extensive road network, however, the roads do not cover the whole park due to the topography (Figure 3). We drove at an average speed of 15 kph , twice a day, from 05:00-10:30 and late afternoon 16:00-18:30 when the lions were most active (Lehmann, Funston, Owen, & Slotow, 2008a; Lehmann et al., 2008b). We used a Cybertracker (v3) application (www.cybertracker.org), installed on an android smartphone (BlackView) with a built-in Global Positioning System (GPS) to record the observation data. To ensure the fine scale history of my spatial and temporal search effort, the application was set to record my location once every 10 seconds.

We divided PNP into five road sections north, east, south, west, and central segments. Each evening set routes were selected and driven the following morning and afternoon to ensure that the lion encounters were evenly spread (Elliot & Gopalaswamy, 2017). After driving the set routes for the day, we also used citizen science as a guideline, social media and guide call-ins to obtain additional locations for lion sightings (Rafiq et al., 2019). The search/driving effort was recorded throughout the study period. When we used citizen science, we only searched for reported lions after my route was completed. Cybertracker heatmaps were constantly used to review where more/less effort was needed to achieve good coverage (Figure 3).

We created identification (ID) kits for each lion that was encountered (Figure 4). Photographs were taken using a 5D Canon camera and a Sigma 150-600hmm F/5-6,3 DG OS HSM-Canon Sigma lens. Capturing lion photographs at different angles is important to identify and create a profile for each lion (Brink et al., 2012). In essence, each ID kit comprised of, if possible, a) a left and right side of the face, b) a left and right side of the body, c) a front facing picture, and d) scars or unique marks, to create an identification profile for each lion, see (Elliot, et al., 2020; Brink, Smith, & Skinner, 2012; Creel & Creel, 1997; Hatfield, 2014; Kane, Morin, & Kelly, 2015). During a lion encounter we recorded the following data: number of individuals, age class (adult, sub-adult, cub), sex (male, female), activity (sleeping, hunting, moving), habitat (open grasslands, woodlands, riverine), field notes, and precise location. Cubs were counted during the survey but lions <1 year were excluded from the data analysis due to the high mortality rate for lions in that age group (Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Elliot et al., 2020). The photographs were used to determine which individual was observed at each sighting without making assumptions on group composition, since fission-fusion occurs regularly with lions (Mbizah, Valeix, Macdonald, & Loveridge, 2019). Each individual lion had their own ID file, which contained, a left and right side of the face, front of the face, full body both sides (if possible), ears, teeth, and scar photographs. External validation was done on the capture history by one of the authors not involved in the field work. Discrepancies between the original- and validated-data were discussed and produced a final validated capture history.

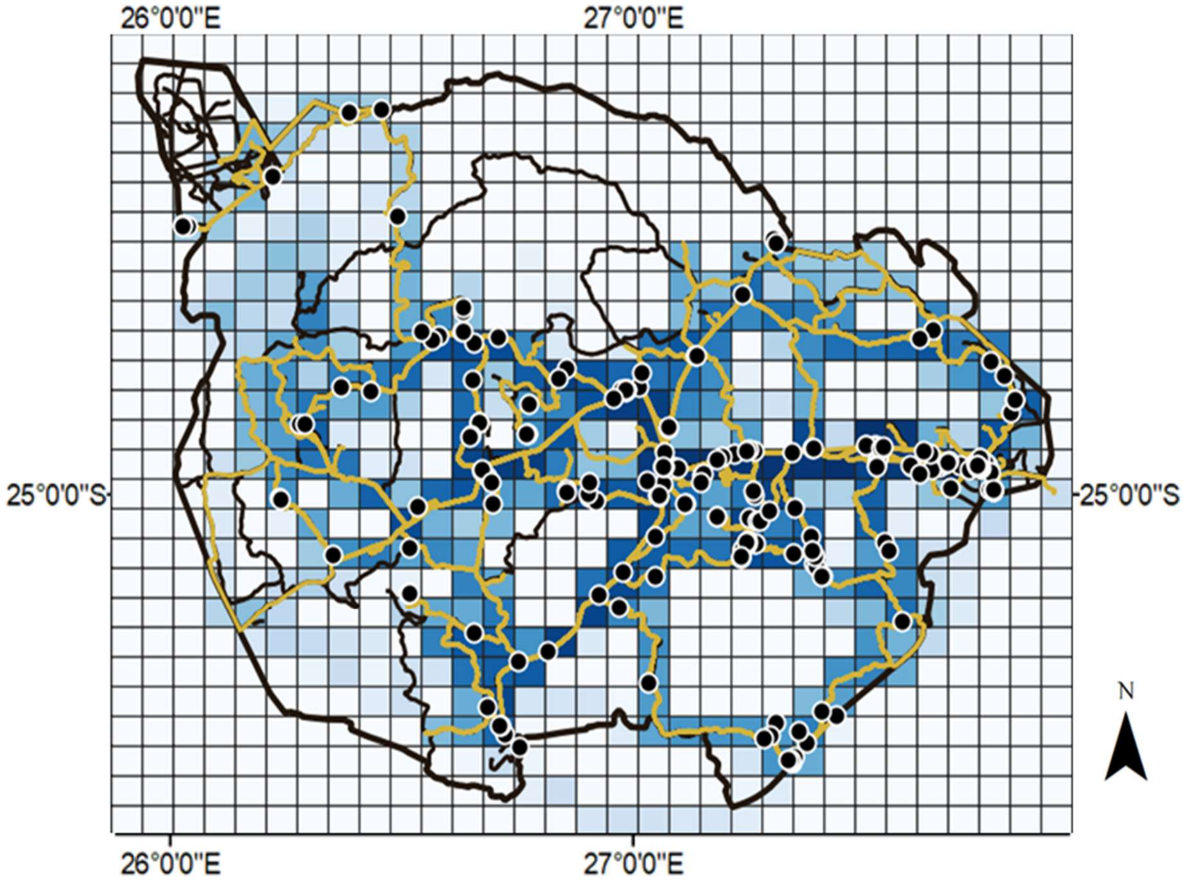


Figure 3. A heatmap that illustrates the driving effort during the lion study in Pilanesberg National Park, South Africa. Light blue shows low effort, whereas the dark blue is high effort. The border of the park is illustrated as a thick black line. The thinner black lines are management roads, and the orange lines are tourist roads. The black dots are lion detections. The size of the grid squares is 1 km x 1 km.

Figure 4: Example of the Pilanesberg National Park lion ID kits created during the lion study, indicating A) one of the adult males and B) one of the adult females recorded during the study.

Analytical framework

For the spatial distribution of lions (state process), we generated a state space that is required to be at least 2.5 times larger than the expected spatial scale parameter sigma (σ) (Royle et al., 2013). We created potential activity centers across the 707 km^2 state space, by presenting it by evenly spaced pixels 0.5 km^2 (Elliot & Gopalaswamy, 2017; Gopalaswamy et al., 2012; Royle & Converse, 2014; Pekor et al., 2019). The activity center is the spatial pattering of which could produce crucial information about interspecific interactions (Forsyth, Ramsey, & Woodford, 2019). Since PNP is fenced off we considered any habitat outside the fenced area as inaccessible habitat (e.g., Elliot et al., 2020) and unlike the approach taken in unfenced protected areas elsewhere in Africa (Elliot & Gopalaswamy, 2017; Gopalaswamy et al., 2012). We set the data augmentation parameter M to a value of 200 in the large state space. M is composed of two values, a) $n = 37$, is the number of individual lions detected and b) $n_z = 163$, the number of individuals augmented for the analysis (Royle et al., 2013; Royle, Karanth, Gopalaswamy, & Kumar, 2009). It represents the maximum amount of lions in the state space (Elliot et al., 2020). Since PNP is a fenced protected area, we set up the study area with the purpose that abundance (N) would be equivalent to (N) estimated that falls in the larger state space, which is frequently called N_{super} in the Bayesian SECR in published work (Elliot et al., 2020). State process involves the estimation of abundance (N) utilising the model, $[N| M, \Psi] \sim$ Binominal (M, Ψ), where Ψ is the probability that an individual animal chosen from M would be a real member of the population. Assuming R was the overall number of pixels defined in the state space, the animals would occupy the pixels based on $(c_1, c_2 \ldots c_R) \mid N, (p_1, p_2 \ldots p_R)$ ~Multinominal $[N, (p_1, p_2 \ldots p_R)]$, where $(c_1, c_2 \ldots c_R)$ represented the number of animals at each pixel and $(p_1, p_2 \ldots p_R)$ represented the pixel occupancy probability of R pixels (Elliot et al., 2020). Before confronting the SECR model with the data, we assume that $(p_1 = p_2 = \ldots = p_R)$ so that the prior probability of an individual animal occurring at a randomly selected pixel, would be $1/R$ (Royle et al., 2013).

In relation to the manner in which individual animals were detected during our survey (observation process), we imitated the measures described by Elliot & Gopalaswamy, (2017). This entailed the compilation of a standard SECR matrix, that consisted of individuals, sampling occasions, and trap locations (0.5 km^2). Since highly sampled traps could possibly increase the number of detections, we included an effort covariate (logarithm of kilometres driven per trap, per day) to model the observation process. The spatial scale parameter (σ) is often used in SECR models to represent the home range or activity range of individuals (Elliot & Gopalaswamy, 2017). Of all the feline species, lions are the most sociable (fission-fusion system) this most likely influences the movement patterns between sexes and will likely influence the spatial scale parameter (Elliot & Gopalaswamy, 2017; VanderWaal, Mosser, & Packer, 2009). Hence, a sex-specific covariate was included since males and females have different home range sizes, which might affect the observation process, and enables the explicit estimation of sex ratio. We calculated the home range size through the formulation bivariate normal kernel estimator: $\pi(\sigma \sqrt{5.99})^2$) (Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Broekhuis et al., 2021).

Candidate models

We defined five priori models and compared their posterior outputs, Table 1. We set the detection function parameter theta (θ) to 1 which implies a fixed, half-normal detection function. The complementary log-log function of covariates described below, illustrates the probability of detecting lion *i* in pixel *j* on sampling occasion *k* (π_{ijk}) (Royle, Chandler, Sollman, Gardner 2013, Elliot and Gopalaswamy, 2017). The function *f* [dist.(*i,j*)| θ, σ_{sex}] defines how the detection rate declines as the distance between the activity centre of individual *i*, and pixel *j* increases, which are conditional on θ and σ_{sex}. Candidate models were constructed (Table 1) and confronted with the data with the aim of selecting the most appropriate model for inference later.

$$cloglog(\pi_{ijk}) = \log\lambda_0 + \beta_{eff}[\log(Effort_{jk})] + \beta_{sex}(\text{sex}_i) - f[dist(i,j)|\,\theta,\sigma_{sex}]$$

Table 1. The five candidate models used to estimate the lion population abundance in PNP, using a Bayesian SECR approach (Elliot et al., 2020).

Model 1 – *N*(.), λ_0(sex + effort), σ(sex): The basal encounter rate and the spatial scale parameter is sex-specific.
Model 2 – *N*(.), λ_0(effort), σ(sex): The spatial scale parameter is sex-specific, but the basal encounter rate is independent of sex.
Model 3 - *N*(.), λ_0(effort), σ(.): The spatial scale parameter and the basal encounter rate are independent of sex.
Model 4 - *N*(.), λ_0(sex + effort), σ(.): The spatial scale parameter is independent of sex, but the basal encounter rate is sex-specific.
Model 5 – N(.) λ_0(effort): This is a conventional non-spatial capture-recapture model, corrected for effort.

We formatted all data to analyse the five models using an adaptation of the SCRbayes package (https://github.com/jaroyle/SCRbayes) in the programming environment R (R Development Core Teams 2021, version 4.1.2) (Elliot & Gopalaswamy, 2017). This package utilises the Metropolis-Hasting algorithm to implement the Bayesian Markov Chain Monte Carlo (MCMC) procedure and generate the posterior distributions of the model parameters (Royle et al. 2009, Elliot et al. 2020). We ran four chains for each model and then set each chain to run with the MCMC sampler for 31000 iterations with an initial burn in of 1000 iterations. We assessed convergence using the Gelman-Rubin diagnostic and defined convergence if the r-hat value was less than 1.1 for each parameter (Gelman & Rubin, 1992; López-Bao et al., 2018; Vega Yon & Marjoram, 2019). If convergence had not been reached, we discarded more initial iterations to achieve convergence (Elliot et al., 2020). To select the appropriate model three criteria were used. First, a goodness-of-fit evaluation (using the

Bayesian *p* value based on individual encounters) was used (Royle et al., 2009, Elliot et al., 2020; López-Bao et al., 2018). The Bayesian *p* value must be within extremities (e.g., between 0.15-0.85) to indicate model adequacy and is used to reject a model rather than to select a model. Second, pair-wise correlation plots from the converged MCMC chains were used to assess parameter redundancy. Third, we used the harmonic mean estimator of the natural logarithm of the marginal likelihood (Dey et al., 2019) to assist with model choice. As such, all three criteria were used during model selection. All model outputs are available in the supplementary information.

Results

The value of the monitoring programme should be determined by the accuracy of the estimates when compared to the effort required by the survey (hence the importance of the next chapter). We conducted counts during 90 of the 108-day survey period and drove 7 350 km in search of lions. We recorded 260 individuals during this period. Due to poor quality of the ID pictures (n = 61 detections) and the exclusion of lions less than a year old (n = 15 detections), we only used 184 detections of the original 260 (Table 2). We identified 37 lions, 17 females and 20 males, with 89 detections being females and 95 being males.

Table 2. African lion detections recorded over our 108-day lion survey in Pilanesberg National Park.

Number of individuals	Number of lion detections	Total detections
1	7	7
2	7	14
3	1	3
4	5	20
5	4	20
7	2	14
8	5	40
10	3	30
11	1	11
12	1	12
13	1	13

Model diagnostic results

Model 1 indicated the least parameter redundancy in the correlation plots. Although Model 2 indicated the best as per the HM estimator of the natural logarithm of the marginal likelihood (Dey et al., 2019). Since Model 1 was most informative and the results, in general, were very consistent across the model sets, we chose to proceed with inference using Model 1 (Table 3 and Appendix 1.

Lion abundance, density, home range size

Based on model 1, the PNP lion population size (as illustrated by the posterior mean abundance) is 44 (mode = 43, posterior *SD* = 3.054, 95% highest posterior density (HPD) interval = 38-49). The mean lion density (individuals >1 year old/100 km^2) is 8.8 (mode = 8.6, posterior *SD* = 0.6%, 95% HPD interval = 7.8-10.1). The estimated sex ratio produced by ψ_{sex} was 0.9♀:1♂. The movement of lions was measured by the σ parameter of model 1. The σ for males and females were 3.854 and 3.189 with a posterior *SD* of 0.332 and 0.273, respectively. Based on this, the average home range estimate of male lions was 279 km^2 with a HPD range of (197 – 385 km^2) and 191 km^2 with a range of (135 – 262 km^2) for female lions.

Model	Model 1		Model 2		Model 3		Model 4		Model 5	
Bayesian P value	0.696		0.686		0.672		0.679		0.999	
Log (Marginal likelihood)	-9342		-7387		-7627		-7910		-8113	
Parameters	Posterior mean (PM)	Posterior Standard Deviation (PSD)	PM	PSD	PM	PSD	PM	PSD	PM	PSD
σ_F - Rate of decline in detection probability (DP) as a female lion's activity center increases as a function of her distance from the centroid of the sample grid cell	3.189	0.273	3.249	0.247						
σ_M - Rate of decrease in DP as a male lion's activity center increases as a function of his distance from the centroid of the sample grid cell	3.854	0.332	3.767	0.303	3.503	0.218	3.513	0.215	NA	NA
β_{sex}- Difference of complementary log-log value of DP between ♂ and ♀	-0.130	0.246	N/A	N/A	N/A	N/A	0.108	0.192	N/A	N/A
β_{eff}- Rate of change in the complementary log-log value of DP as the (log) effort changes by one unit	0.790	0.111	0.786	0.112	0.786	0.111	0.784	0.112	0.769	0.108
λ_0 - Basal encounter rate of an individual (female for sex-specific models) lion whose activity center is located precisely at the centroid of the grid cell	0.005	0.001	0.005	0.001	0.005	0.001	0.004	0.001	0.001	0.000
ψ- Ratio of true number of individuals in the population compared to the data augmented population *M*	0.222	0.033	0.222	0.033	0.220	0.032	0.220	0.033	0.190	0.028
ψ_{sex}- Proportion of lions are male	0.529	0.083	0.529	0.084	0.002	0.007	0.538	0.083	0.003	0.008
N_{super} - Overall number of lions in larger state space	43.854	3.054	43.856	3.078	43.317	2.902	43.451	2.967	37.296	0.558
D Estimated density of adult lion/ 100 km^2	0.088	0.006	0.088	0.006	0.087	0.006	0.087	0.006	0.075	0.001

Table 3. Summary of model diagnostic results for 5 priori candidate models used to evaluate model selection and gave results for 108-day lion survey in PNP using the search-encounter based Bayesian SECR approach (Elliot and Gopalaswamy, 2017).

Discussion

The posterior mean lion abundance of PNP was estimated to be a total of 44, which was lower than expected compared to Tambling & du Toit, (2005) (50 adult lions) in 2001. The lion density in PNP (8.8 individuals per 100 km^2) coincides with the average of 8.8 per 100 km^2 reported by Packer, Loveridge, et al., (2013) (see Table S.4 in the Supplementary information). PNP, compared to 20 other southern African protected areas (excluding the highly productive systems of East Africa) has a slightly higher density compared to an average of 7.8 per 100 km^2 (Figure 5). We must keep in mind that the estimates from the other protected areas are determined using other methods. We noted that despite intensive sampling, our analysis suggests that we detected ~84% of the available individuals, which is still not a 'whole count'. With this caveat in mind, the evidence from this study indicates a mid-level density and not a high density as initially hypothesised.

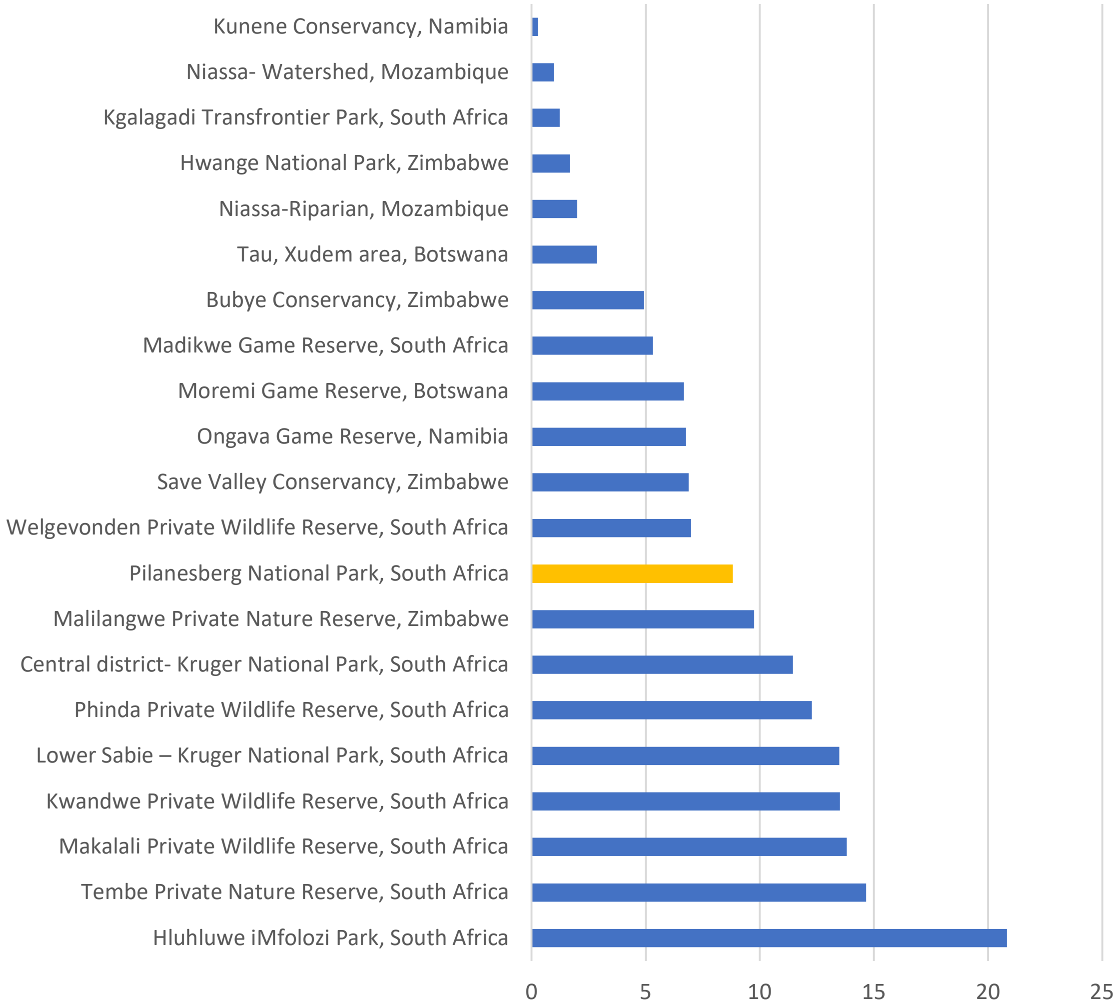


Figure 5: Density of African lions in 21 protected areas across southern Africa showing Pilanesberg National Park (indicated in orange) to be in the mid-range (Packer, Loveridge, et al., 2013).

The estimated sex ratio of PNP (0.9♀:1♂) from this study is not what was generally expected e.g. 2♀:1♂ (Périquet, Fritz, & Revilla, 2015; Schaller, 1972). For example, The Kgalagadi Transfrontier Park (partially fenced) had an estimated sex ratio 1.2♀:0.82♂, Northern Tuli Game Reserve (fenced protected area) sex ratio of 3.9♀:2.3♂, Venetia Limpopo Nature Reserve (fenced protected area) sex ratio of 4.5♀:2.7♂, and Selous Game Reserve (unfenced protected area), sex ratio of 1.78♀:0.65♂ (Creel & Creel, 1997; Ferreira, Beukes, Haas, & Radloff, 2020; Schaller, 1972; Snyman, Jackson, & Funston, 2015). Sex allocation can be determined by two factors namely, environmental determination and chromosome-mediation (Mari, Gatto, & Casagrandi, 2008). Environmental determination could be a) mate competition, b) local resource enhancement, or c) resource competition (Wild & West, 2009). Chromosome-mediated factors occur when either the mother or the offspring controls the sex allocation through the haplodiploids or diploids (Wild & West, 2009). However, additional factors that influence skewed sex ratios towards females are trophy hunting, infanticide, sub-adult males being killed by other males, human-lion conflict, and or nomadic males dying as a result of hunting (Elliot et al., 2020; Elliot, Cushman, Loveridge, Mtare, & Macdonald, 2014; Funston, 2011; Mcevoy, 2019; Miller & Funston, 2014; Mosser & Packer, 2009; Silk, 1984). Only 2 of these factors, e.g. trophy hunting and human-lion conflict, are not present in PNP which could explain the higher number of males in the system, see also Miller & Funston, (2014). We must consider that the estimates of the sex ratios derived in this study on PNP account for the sex-specific differences in detection probability. When comparisons about the sex ratios are made in relation to other study areas, we must be aware of the potential shortcomings of the sex ratio inferences from studies that do not explicitly account for detection probabilities. With that caveat in mind, the sex ratio estimated in PNP raises an important consideration in terms of lion impact on the prey base. Adult male lions (190 kg) weigh on average 35% more compared to females (126 kg), which means males prey biomass intake can be almost twice as much (Fritz et al., 2011; Skinner & Chimimba, 2005). Higher male numbers could have an influence on the prey base in two ways: first through higher consumption rates because of their nutritional requirements (Fritz et al., 2011) and secondly through the increase of female prey kill rates due to more disturbance by roaming males (Smith, Wang, & Wilmers, 2015). Unequal sex ratios in mid-level densities such as PNP can therefore have a greater impact on the prey base, potentially comparable to high-density lion populations. For example, we evaluated the potential impact lions could have on blue wildebeest populations based on the 2001 (50 lions), sex ratio of 2.1♀:1♂ and the 2020 (44 lions),sex ratio of 0.9♀:1♂, using computation (see Appendix S) (Tambling & du Toit, 2005). The consumption potential was very similar. Therefore, sex ratios could potentially have a major influence on the prey base even if lion densities are lower, see Figure 6.

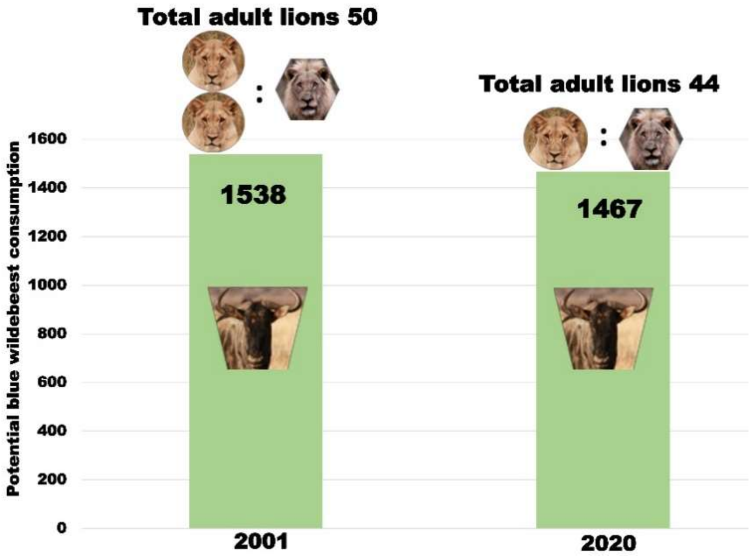


Figure 6: The annual blue wildebeest consumption potential of lions based on the 2001 versus 2020 lion densities and sex ratios in Pilanesberg National Park illustrating the potential effect of sex ratio on prey. Blue wildebeest consumption by lions for a year was calculated in the following way. Male lions roughly consume 10 kg and female 7 kg of meat per day (Fritz et al., 2011). The mean average body mass of a blue wildebeest is 125 kg, for which we used 70%, e.g. 93.75 kg, of the carcasses that is consumed by lions (Fritz et al., 2011). To calculate the number of wildebeest W that could be consumed per year for male (L_{Male}) and female (L_{Female}) lions we used the formula, $W = \frac{(L_{Male} * 10\ kg) * 365}{93.75} + \frac{(L_{Female} * 7\ kg) * 365}{93.75}$, (see Carbone, Teacher, & Rowcliffe, 2007). Therefore, per capita consumption of wildebeest is 30.76 in 2001 as compared to 33.36 in 2020, as per our study, indicating an 8.4% increase in per capita wildebeest consumption but could lead to even larger kill rates owing to disturbance caused by males.

The average range size of male lions (279 km^2) was larger than that of females (191 km^2) which was expected. Males predominantly have larger areas to protect while females stay in smaller ranges to protect their cubs (Lehmann et al., 2008b; Lesilau et al., 2021). Range sizes varies greatly, e.g., a) in Addo National Park, the range of male lions are 124 km^2 and 106 km^2 for female lions, b) in Queen Elizabeth Conservation Area, the ranges of male lions are 204 km^2 and 94 km^2 for female lions, c) in Waza National Park, the ranges of male lions are 1267 km^2 and 764 km^2 for female lions, and d) in Hwange National Park, the ranges of male lions are 524 km^2 and 375 km^2 for female lions (Benhamou, Valeix, Chamaillé-Jammes, Macdonald, & Loveridge, 2014; Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Hayward et al., 2009; Tumenta et al., 2013). We must keep in mind that the range sizes estimated in this study refers to the distance over a shorter, 90-day period compared to that of other estimates which may be referencing to annual home ranges.

Conclusion

Fenced protected areas require intensive management especially when parks have populations of large carnivores (Ferreira & Hofmeyr, 2014; Power, 2002). We have shown that using a monitoring method such as the search-encounter based SECR, we can arrive at accurate and precise numbers and avoid multiple sources of bias (Elliot et al., 2020). Lions not only have economic value as a tourism species (Miller et al., 2013) but also impacts the prey-base. Before the study commenced it was assumed that the lion density in PNP should be high because of the sharp decline in prey species populations. The results showed that the Pilanesberg lion density were, however, calculated to be at a mid-level when compared to other fenced protected areas. The reason for these unexpected results could be linked to the sex ratio driving the prey decline. it is likely not a single factor and other factors such as climate, burning regime, food availability and impact of other predators, see (Botai et al., 2016; Ferreira et al., 2020; Funston, 2011), could be significant contributing factors driving prey decline as well.

A future focus is to determine what the minimum required effort in a fenced park like PNP should be in order to reach an acceptable level of accuracy and precision in abundance and sex ratio estimates when applying Bayesian SECR models. This will help park managers conduct cost-effective lion monitoring while assuring those important ecological parameters are also rigorously estimated.

Acknowledgements

This project was financially supported by Copenhagen Zoo, Nelson Mandela University and Ernest and Ethel Ericksen Trust. We like to thank North West Parks and Tourism Board for allowing us to survey in Pilanesberg National Park. We would like to express our gratefulness to Steve Dell and Charlotte Marais for their assistance throughout the study.

References

Alibhai, S., Jewell, Z., & Evans, J. (2017). The challenge of monitoring elusive large carnivores: An accurate and cost-effective tool to identify and sex pumas (Puma concolor) from footprints. *PloS one*, *12*(3), e0172065. https://doi.org/10.1371/journal.pone.0172065

Arnholt, A. T., & Herbert, J. (1995). Estimating the mean with known coefficient of variation. *The American Statistician*, *49*(4), 367–369.

Auffray, J.-C., Renaud, S., & Claude, J. (2009). Rodent Biodiversity in Changing Environments. *Kasetsart Journal, Natural Science*, *43*(1), 83–93. Retrieved from https://www.researchgate.net/publication/228350392

Balme, G. A., Hunter, L. T. B., & Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, *73*(3), 433–441. https://doi.org/10.2193/2007-368

Barthold, J. A., Loveridge, A. J., Macdonald, D. W., Packer, C., & Colchero, F. (2016). Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, *53*(2), 295–304. https://doi.org/10.1111/1365-2664.12594

Bauer, H., & Van Der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, *38*(1), 26–31. https://doi.org/10.1017/S0030605304000055

Bauer, Hans., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., … Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *PNAS*, *112*(48), 14894–14899. https://doi.org/10.1073/pnas.1500664112

Belant, J. L., Bled, F., Mkasanga, I. J., Wilton, C. M., Mwampeta, S. B., Beyer, D. E., … Fyumagwa, R. (2019). Track surveys do not provide accurate or precise lion density estimates in Serengeti. *Global Ecology and Conservation*, *19*, e00651. https://doi.org/10.1016/j.gecco.2019.e00651

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, *90*, 171–180. https://doi.org/10.1016/j.anbehav.2014.01.030

Boitani, L., Ciucci, P., & Mortelliti, A. (2012). Designing carnivore surveys. In *Carnivore ecology and management: a handbook of techniques* (pp. 8–29). https://doi.org/10.1093/acprof

Borchers, D. (2012). A non-technical overview of spatially explicit capture-recapture models. *Journal of Ornithology*, *152*(2), 435–444. https://doi.org/10.1007/s10336-010-0583-z

Borchers, D., Distiller, G., Foster, R., Harmsen, B., & Milazzo, L. (2014). Continuous-time spatially explicit capture-recapture models, with an application to a jaguar camera-trap survey. *Methods in Ecology and Evolution*, *5*(7), 656–665. https://doi.org/10.1111/2041-210X.12196

Botai, C. M., Botai, J. O., Dlamini, L. C., Zwane, N. S., & Phaduli, E. (2016). Characteristics of droughts in South Africa: A case study of Free State and North West provinces. *Water*, *8*(10), 439. https://doi.org/10.3390/w8100439

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., … Allan, J. R. (2020). Restoring Africa's lions: Start with good counts. *Frontiers in Ecology and Evolution*, *8*, 138. https://doi.org/10.3389/fevo.2020.00138

Braczkowski, A., Gopalaswamy, A. M., Mustafa, N., Allan, J., Biggs, D., & Maron, M. (2020). Detecting early warnings of pressure on an African lion (*Panthera leo*) population in the Queen Elizabeth Conservation Area , Uganda. *Ecological Solution Eviddence*, *1*, e12015. https://doi.org/10.1002/2688-8319.12015

Briers-Louw, W. D. (2017). Ecology of three apex predators in Majete Wildlife Reserve, Malawi (Doctoral dissertation). Stellenbosch University, Stellenbosch.

Brink, H., Smith, R. J., & Skinner, K. (2012). Methods for lion monitoring: A comparison from the Selous Game Reserve, Tanzania. *African Journal of Ecology*, *51*(2), 366–375. https://doi.org/10.1111/aje.12051

Broekhuis, F., Elliot, N. B., Keiwua, K., Koinet, K., Macdonald, D. W., Mogensen, N., … Gopalaswamy, A. M. (2021). Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography*, *44*(3), 358–369. https://doi.org/10.1111/ecog.05154

Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PloS one*, *11*(5), 1–15. https://doi.org/10.1371/journal.pone.0153875

Caravaggi, A., Banks, P. B., Burton, C. A., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., … Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109–122. https://doi.org/10.1002/rse2.48

Carbone, C., Teacher, A., & Rowcliffe, M. J. (2007). The costs of carnivory. *PLoS Biology*, *5*(2), 0363–0368. https://doi.org/10.1371/journal.pbio.0050022

Carruthers, J. (2011). Pilanesberg National Park, North West Province, South Africa: Uniting economic development with ecological design – A history, 1960s to 1984. *Koedoe*, *53*(1), 1–10. https://doi.org/10.4102/koedoe.v53i1.1028

Clark, T. J., Horne, J. S., Hebblewhite, M., & Luis, A. D. (2021). Stochastic predation exposes prey to predator pits and local extinction. *Oikos*, *130*(2), 300–309. https://doi.org/10.1111/oik.07381

Comley, J., Joubert, C. J., Mgqatsa, N., & Parker, D. M. (2020). Battle of the Large Carnivores:

Spatial Partitioning in a Small, Enclosed Reserve? *African Journal of Wildlife Research*, *50*(1), 176–189. https://doi.org/10.3957/056.050.0176

Cooper, D. M., Dugmore, A. J., Kitchener, A. C., Metzger, M. J., & Trabucco, A. (2021). A kingdom in decline: Holocene range contraction of the lion (*Panthera leo*) modelled with global environmental stratification. *PeerJ*, *9*, e10504. https://doi.org/10.7717/peerj.10504

Creel, S., Becker, M. S., Durant, S. M., M'Soka, J., Matandiko, W., Dickman, A. J., … Zimmermann, A. (2013). Conserving large populations of lions - the argument for fences has holes. *Ecology Letters*, *16*(11), 1413-e3. https://doi.org/10.1111/ele.12145

Creel, Scott., & Creel, N. M. (1997). Lion density and population structure in the Selous Game Reserve: Evaluation of hunting quotas and offtake. *African Journal of Ecology*, *35*(2), 83–93. https://doi.org/10.1111/j.1365-2028.1997.062-89062.x

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., … Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS one*, *13*(7), e0196213. https://doi.org/10.1371/journal.pone.0196213

De Boer, W. F., Vis, M. J. P., De Knegt, H. J., Rowles, C., Kohi, E. M., van Langevelde, F., … Prins, H. H. T. (2010). Spatial distribution of lion kills determined by water dependency of prey species. *Journal of Mammalogy*, *91*(5), 1280–1286. https://doi.org/10.1644/09-MAMM-A-392.1

de Manuel, M., Barnett, R., Sandoval-Velasco, M., Yamaguchi, N., Vieira, F. G., Mendoza, L. Z. M., … Gilbert, T. M. (2020). The evolutionary history of extinct and living lions. PNAS, *117*(20), 10927–10934. https://doi.org/10.1073/pnas.1919423117

Dey, S., Delampady, M., & Gopalaswamy, A. M. (2019). Bayesian model selection for spatial capture–recapture models. *Ecology and Evolution*, *9*(20), 11569–11583. https://doi.org/10.1002/ece3.5551

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, S. R., & Frank, L. (2014). A metapopulation approach to African lion (*Panthera leo*) conservation. *PloS one*, *9*(2). https://doi.org/10.1371/journal.pone.0088081

Dröge, E., Creel, S., Becker, M. S., Loveridge, A. J., Sousa, L. L., & Macdonald, D. W. (2020). Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecology and Evolution*, *10*(7), 3276–3292. https://doi.org/10.1002/ece3.6065

Durant, S. M., Craft, M. E., Hilborn, R., Bashir, S., Hando, J., & Thomas, L. (2011). Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *Journal of Applied Ecology*, *48*(6), 1490–1500. https://doi.org/10.1111/j.1365-2664.2011.02042.x

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion - conservation stronghold. *Density and Distribution*, *25*, 870–879. https://doi.org/10.1111/ddi.12905

Edwards, S., Cooper, S., Uiseb, K., Hayward, M., Wachter, B., & Melzheimer, J. (2018). Making the most of by-catch data: Assessing the feasibility of utilising non-target camera trap data for occupancy modelling of a large felid. *African Journal of Ecology*, *56*(4), 885–894. https://doi.org/10.1111/aje.12511

Elliot, N. B., Bett, A., Chege, M., Sankan, K., de Souza, N., Kariuki, L., … Gopalaswamy, A. M. (2020). The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice*, 1–11. https://doi.org/10.1111/csp2.217

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., & Macdonald, D. W. (2014). Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, *95*(10), 2860–2869. https://doi.org/10.1890/13-1793.1

Elliot, N. B., & Gopalaswamy, A. M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, *31*(4), 934–943. https://doi.org/10.1111/cobi.12878

Elliot, N. B., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos*, *123*(9), 1049–1056. https://doi.org/10.1111/oik.01266

Estes, R. D. (2012). Lion (*Panthera leo*). In *The behaviour guide to African mammals* (pp. 369–377). London and Los Angeles and Berkeley: The University of California Press.

Everatt, K. T., Kokes, R., & Pereira, C. L. (2019). Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation*, *28*(14), 4099–4114. https://doi.org/10.1007/s10531-019-01866-w

Ferreira, S. M., Beukes, O. B., Haas, T. C., & Radloff, F. G. T. (2020). Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park. *African Journal of Ecology*, *58*(3), 348–360. https://doi.org/10.1111/aje.12728

Ferreira, S. M., & Funston, P. J. (2010). Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, *37*(3), 194–206. https://doi.org/10.1071/WR09030

Ferreira, S. M., & Hofmeyr, M. (2014). Managing charismatic carnivores in small areas: Large felids in South Africa. *South African Journal of Wildlife Research*, *44*(1), 32–42.

Forsyth, D. M., Ramsey, D. S. L., & Woodford, L. P. (2019). Estimating abundances, densities, and interspecific associations in a carnivore community. *The Journal of Wildlife Management*, *83*(5), 1090–1102. https://doi.org/10.1002/jwmg.21675

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M., & Clobert, J. (2011). A food web perspective on large herbivore community limitation. *Ecography*, *34*(2), 196–202. https://doi.org/10.1111/j.1600-0587.2010.06537.x

Funston, P J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., … Ferreira, S. M. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, *281*(1), 56–65. https://doi.org/10.1111/j.1469-7998.2009.00682.x

Funston, P J., & Levendal, M. (2015). *Biodiversity management plan for the lion (Panthera leo) in South Africa. Government Gazette, 2*. Retrieved from www.gpwonline.co.za

Funston, P J., & Mills, M. G. L. (2006). The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *African Journal of Wildlife Research*, *36*(1), 9–22.

Funston, P J., Mills, M. G. L., & Biggs, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, *253*(4), 419–431.

Funston, Paul J. (2011). Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, *41*(1), 1–10.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–511.

Gese, E. M. (2001). Monitoring of terrestrial carnivore populations. *Conservation Biology Series- Cambridge-*, 372–396.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, *10*(1), 57–63. https://doi.org/10.1007/BF00296396

Gomez, D., Sommaro, L., Steinmann, A., Chiappero, M., & Priotto, J. (2011). Movement distances of two species of sympatric rodents in linear habitats of Central Argentine agro-ecosystems. *Mammalian Biology*, *76*, 58–63. https://doi.org/10.1016/j.mambio.2010.02.001

Goodall, V. L., Ferreira, S. M., Funston, P. J., & Maruping-Mzileni, N. (2019). Uncovering hidden states in African lion movement data using hidden Markov models. *Wildlife Research*, *46*(4), 296–303. https://doi.org/10.1071/WR18004

Gopalaswamy, A. M., Delampady, M., Karanth, U. K., Kumar, S. N., & Macdonald, D. W. (2015). An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods in Ecology and Evolution*, *6*(9), 1055–1066. https://doi.org/10.1111/2041-210X.12351

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program SPACECAP: Software for estimating animal density using spatially explicit capture-recapture models. *Methods in Ecology and Evolution*, *3*(6), 1067–1072. https://doi.org/10.1111/j.2041-210X.2012.00241.x

Groom, R. J., Funston, P. J., & Mandisodza, R. (2014). Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: What is driving the population collapse? *Oryx*, *48*(3), 385–393. https://doi.org/10.1017/S0030605312001457

Gusset, M., & Burgener, N. (2005). Estimating larger carnivore numbers from track counts and measurement. *African Journal of Ecology*, *43*, 320–324.

Harmsen, B. J., Foster, R. J., & Quigley, H. (2020). Spatially explicit capture recapture density estimates: Robustness, accuracy and precision in a long-term study of jaguars (*Panthera onca*). *PloS one*, *15*(6), e0227468. https://doi.org/10.1371/journal.pone.0227468

Hatfield, R. (2014). Population dynamics of the African lion (*Panthera leo*) within the Maasai Mara region of southern Kenya. *Kaleidoscope*, *11*(1), 70.

Hayward, M. W., Adendorff, J., O'Brien, J., Sholto-douglas, A., Bissett, C., Moolman, L. C., … Kerley, G. I. H. (2007). Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eatern Cape Province. *The Open Conservation Biology Journal*, *1*(1), 1–11.

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, Ullas K., Mackenzie, D. I., … Yarnell, R. W. (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, *52*(2), 286–290. https://doi.org/10.1111/1365-2664.12408

Hayward, M. W., Hayward, G. J., Druce, D. J., & Kerley, G. I. H. (2009). Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity Conservation*, *18*, 887–904. https://doi.org/10.1007/s10531-008-9452-y

Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, *267*, 309–322. https://doi.org/10.1017/S0952836905007508

Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, *139*(1–2), 219–229. https://doi.org/10.1016/j.biocon.2007.06.018

Holekamp, K. E., & Sawdy, M. A. (2019). The evolution of matrilineal social systems in fissiped carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1780), 20180065. https://doi.org/10.1098/rstb.2018.0065

Hrabar, H., & du Toit, J. T. (2005). Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conservation*, *8*(3), 259–267. https://doi.org/10.1017/S1367943005002234

Jewell, Z. (2013). Effect of monitoring technique on quality of conservation science. *Conservation Biology*, *27*(3), 501–508. https://doi.org/10.1111/cobi.12066

Jiménez, J., Nuñez-Arjona, J. C., Rueda, C., González, L. M., Garciá-Domínguez, F., Munõz-Igualada, J., & López-Bao, J. V. (2017). Estimating carnivore community structures. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/srep41036

Kane, M. D., Morin, D. J., & Kelly, M. J. (2015). Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodiversity and Conservation*, *24*(14), 3527–3541. https://doi.org/10.1007/s10531-015-1012-7

Karanth, U. K., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, *79*(8), 2852–2862. https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2

Kazemi, M. R., & Jafari, A. A. (2020). Small sample inference for the common coefficient of variation. *Communications in Statistics: Simulation and Computation*, *49*(1), 226–243. https://doi.org/10.1080/03610918.2018.1484474

Keet, D. F. (2010). Lions. In *Game Ranch Management* (Fith Editi, pp. 295–312). Van Schaik Publication.

Kettles, R., & Slotow, R. (2009). Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research*, *39*(1), 23–33. Retrieved from https://journals.co.za/docserver/fulltext/wild/39/1/wild_v39_n1_a3.pdf?expires=1560189647&id=id&accname=guest&checksum=514349490088AEF9B952A9F9167F8569

Kidwai, Z., Jimenez, J., Louw, C. J., Nel, H. P., & Marshal, J. P. (2019). Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (*Diceros bicornis*) populations from aerial counts. *Global Ecology and Conservation*, *19*, e00687. https://doi.org/10.1016/j.gecco.2019.e00687

Kiffner, C., Meyer, B., Mühlenberg, M., & Waltert, M. (2009). Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania? *Oryx*, *43*(1), 52–59. https://doi.org/10.1017/S0030605307002335

Kissui, B. M., & Packer, C. (2004). Top-down population regulation of a top predator: Lions in the Ngorongoro Crater. Proceedings of *the Royal Society of London*, *271*, 1867–1874. https://doi.org/10.1098/rspb.2004.2797

la Grange, M., Kellner, K., Cilliers, S. S., & Götze, A. R. (2009). Vegetation classification of the proposed Heritage Park, North-West Province, South Africa (North-West University; Vol. 75). https://doi.org/10.1016/j.sajb.2009.02.149

Lahoz-Monfort, J. J., Harris, M. P., Morgan, B. J. T., Freeman, S. N., & Wanless, S. (2014). Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. *Journal of Applied Ecology*, *51*(2), 534–543. https://doi.org/10.1111/1365-2664.12214

le Roux, E., Marneweck, D. G., Clinning, G., Druce, D. J., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2019). Top–down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography*, *42*(6), 1115–1123. https://doi.org/10.1111/ecog.03791

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008a). Feeding behaviour of lions (*Panthera leo*) on a small reserve. *African Journal of Wildlife Research*, *38*(1), 66–78.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008b). Home range utilisation and territorial behavior of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PloS one*, *3*(12), e3998. https://doi.org/10.1371/journal.pone.0003998

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008c). Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. *African Zoology*, *43*(2), 230–236. https://doi.org/10.3377/1562-7020-43.2.230

Lesilau, F., Verschueren, S., van't Zelfde, M., Musters, K. C. J. M., de Snoo, G. R., & de Iongh, H. H. (2021). Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: The case study of Nairobi National Park, Kenya. *Mammalia*, *85*(3), 198–207. https://doi.org/10.1515/mammalia-2020-0116

Lindner, E., & Fuelling, O. (2002). Marking methods in small mammals: ear-tattoo as an alternative to toe-clipping. *The Zoological Society of London*, *256*, 159–163.

Lindsey, P. A., Petracca, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., … Hunter, L. T. B. (2017). The performance of African protected areas for lions and their prey. *Biological Conservation*, *209*, 137–149. https://doi.org/10.1016/j.biocon.2017.01.011

López-Bao, J. V., Godinho, R., Pacheco, C., Lema, F. J., García, E., Llaneza, L., … Jiménez, J. (2018). Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. *Scientific Reports*, *8*(1), 1–8. https://doi.org/10.1038/s41598-018-20675-9

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, *54*(3), 815–825. https://doi.org/10.1111/1365-2664.12794

Macdonald, D. W., Loveridge, A. J., & Nowell, K. (2010). Dramatis personae: an introduction to the wild felids. In *The biology and conservation of wild felids* (First Edit, pp. 3–59). Oxford University Press (OUP).

Magome, H., Cain, J. W., Owen-Smith, N., & Henley, S. R. (2008). Forage selection of sable antelope in Pilanesberg Game Reserve, South Africa. *African Journal of Wildlife Research*, *38*(1), 35–41. https://doi.org/10.3957/0379-4369-38.1.35

Mari, L., Gatto, M., & Casagrandi, R. (2008). Local resource competition and the skewness of the sex ratio: A demographic model. *Mathematical Biosciences and Engineering*, *5*(4), 813–830. https://doi.org/10.3934/mbe.2008.5.813

Massey, A. L., King, A. A., & Foufopoulos, J. (2014). Fencing protected areas: A long-term assessment of the effects of reserve establishment and fencing on African mammalian diversity. *Biological Conservation*, *176*, 162–171. https://doi.org/10.1016/j.biocon.2014.05.023

Mbizah, M. M., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2019). Applying the resource dispersion hypothesis to a fission–fusion society: A case study of the African lion (*Panthera leo*). *Ecology and Evolution*, *9*(16), 9111–9119. https://doi.org/10.1002/ece3.5456

Mcevoy, O. K. (2019). *The management of lions (Panthera leo) in small, fenced wildlife reserves*. (Doctoral dissertation) Grahamstown, South Africa: Rhodes University.

Mcevoy, O. K., Ferreira, S. M., & Parker, D. M. (2021). The influence of population demographics on lion (*Panthera leo*) growth rates in small, fenced wildlife reserves. *African Journal of Wildlife Research*, *51*(1), 75–89.

Midlane, N., O'Riain, M. J., Balme, G. A., Robinson, H. S., & Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, *172*, 101–108. https://doi.org/10.1016/j.biocon.2014.02.006

Midlane, Niel., O'Riaain, J. M., Balme, G. A., & Hunter, L. T. B. (2015). To track or to call: comparing methods for estimating population abundance of African lions *Panthera leo* in Kafue National Park. *Biodiversity and Conservation*, *24*(6), 1311–1327. https://doi.org/10.1007/s10531-015-0858-z

Miller, S. M., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D. J., … Zimmermann, D. (2013). Management of reintroduced lions in small, fenced reseved in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research*, *43*(2), 138–154.

Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: A management dilemma. *South African Journal of Wildlife Research*, *44*(1), 43–55.

Miller, S. M., Riggio, J., Funston, P. J., Power, R. J., Williams, V., & Child, M. F. (2016). A conservation assessment of *Panthera leo*. In *The red list of mammals of South Africa*. Swaziland and Lesotho.

Milleret, C., Dupont, P., Chipperfield, J., Turek, D., Brøseth, H., Gimenez, O., … Bischof, R. (2020). Estimating abundance with interruptions in data collection using open population spatial capture–recapture models. *Ecosphere*, *11*(7), 1–14. https://doi.org/10.1002/ecs2.3172

Mondol, S., Karanth, U. K., Kumar, S. N., Gopalaswamy, A. M., Andheria, A., & Ramakrishnan, U. (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation*, *142*(10), 2350–2360. https://doi.org/10.1016/j.biocon.2009.05.014

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, *78*(2), 359–370.

https://doi.org/10.1016/j.anbehav.2009.04.024

Mucina, L., Rutherford, M. C., & Powrie, W. (2006). Vegetation atlas of South Africa, Lesotho and Swaziland. In L. Mucina & M. C. Rutherford (Eds.), *Vegetation Map of Southern Africa, Lesotho and Swaziland* (pp. 750–760). Pretoria: South Africa National Biodiversity Institute.

Noack, J., Heyns, L., Rodenwoldt, D., & Edwards, S. (2019). Leopard density estimation within an enclosed reserve, namibia using spatially explicit capture- recapture models. *Animals*, *9*(10), 724. https://doi.org/10.3390/ani9100724

Packer, C., Herbst, L., Pusey, A., Bygott, A., Hanby, J. P., Cairns, S. J., & Borgerhoff-Mulder, M. (1988). *Reproduction success of lions: studies of individual variation in contrasting breeding systems* (T. Clutton-Brock, Ed.). Chicago: University of Chicago Press.

Packer, C., Loveridge, A. J., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., … Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology Letters*, *16*(5), 635–641. https://doi.org/10.1111/ele.12091

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups : Food is not enough. *The American Naturalist*, *136*(1), 1–19.

Packer, C., Swanson, A., Canney, S., Loveridge, A., Garnett, S., Pfeifer, M., … Macnulty, D. (2013). The case for fencing remains intact. *Ecology Letters*, *16*(11), 7–8. https://doi.org/10.1111/ele.12171

Packer, Craig. (2019). The African lion: A long history of interdisciplinary research. *Frontiers in Ecology and Evolution*, *7*(259), 1–6. https://doi.org/10.3389/fevo.2019.00259

Pekor, A., Miller, J. R. B., Flyman, M. V., Kasiki, S., Kesch, M. K., Miller, S. M., … Lindsey, P. A. (2019). Fencing Africa's protected areas: Costs, benefits, and management issues. *Biological Conservation*, *229*, 67–75. https://doi.org/10.1016/j.biocon.2018.10.030

Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, *160*(4), 497–508. https://doi.org/10.1111/j.1469-7998.1970.tb03093.x

Périquet, S., Fritz, H., & Revilla, E. (2015). The lion king and the hyaena queen: Large carnivore interactions and coexistence. *Biological Reviews*, *90*(4), 1197–1214. https://doi.org/10.1111/brv.12152

Pfeffer, S. E. (2016). *Comparison of three different indirect methods to evaluate ungulate* *population densities*. Swedish university of africultural science.

Power, R. J. (2002). Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe*, *45*(2), 67–75. https://doi.org/10.4102/koedoe.v45i2.32

Prox, L., & Farine, D. (2020). A framework for conceptualizing dimensions of social organization in mammals. *Ecology and Evolution*, *10*(2), 791–807. https://doi.org/10.1002/ece3.5936

Pusey, A. E., & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, *101*(4), 275–310.

Rafiq, K., Bryce, C. M., Rich, L. N., Coco, C., Miller, D. A. W., Meloro, C., … Hayward, M. W. (2019). Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Current Biology*, *29*(14), R681–R682. https://doi.org/10.1016/j.cub.2019.05.056

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., … Pimm, S. (2013). The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation*, *22*(1), 17–35. https://doi.org/10.1007/s10531-012-0381-4

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Royle, A. J., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture-recapture*. Academic Press.

Royle, A. J., & Converse, S. J. (2014). Hierarchical spatial capture-recapture models: Modelling population density in stratified populations. *Methods in Ecology and Evolution*, *5*(1), 37–43. https://doi.org/10.1111/2041-210X.12135

Royle, A. J., Fuller, A. K., & Sutherland, C. (2018). Unifying population and landscape ecology with spatial capture–recapture. *Ecography*, *41*(3), 444–456. https://doi.org/10.1111/ecog.03170

Royle, A. J., Karanth, U. K., Gopalaswamy, A. M., & Kumar, S. N. (2009). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, *90*(11), 3233–3244. https://doi.org/10.1890/08-1481.1

Royle, A. J., Sutherland, C., Fuller, A. K., & Sun, C. C. (2015). Likelihood analysis of spatial capture-recapture models for stratified or class structured populations. *Ecosphere*, *6*(2), 1–11. https://doi.org/10.1890/ES14-00148.1

Rutherford, M. C., Mucina, L., Lötter, C., Bredenkamp, G. J., Jacobus, H. L., Scott-shaw, C.

R., … Hurter, P. J. H. (2006). Savanna Biome. In *The vegetation of South Africa, Lesotho and Swaziland.* (pp. 440–529). Pretoria: South Africa National Biodiversity Institute.

Schaller, G. B. (1972). The Serengeti Lion. Chicago: Univeristy of Chicago Press. https://doi.org/10.1017/CBO9781107415324.004

Silk, J. B. (1984). Local resource competition and the evolution of male-biased sex ratio. *Journal of Theoretical Biology*, *108*(2), 203–213.

Skinner, J. D., & Chimimba, C. T. (2005). Lion. In *The mammals of the Southern African sub-region* (Third Edit, pp. 390–396). Cambridge University Press.

Slotow, R., & Hunter, L. T. B. (2009). Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: The African lion in South Africa. In *Reintroduction of Top-Order Predators, (5), 43*. https://doi.org/10.1002/9781444312034.ch3

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), 20142711. https://doi.org/10.1098/rspb.2014.2711

Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., & Harwood, J. (2010). The functional response of a generalist predator. *PloS one*, *5*(5). https://doi.org/10.1371/journal.pone.0010761

Snyman, A., Jackson, C. R., & Funston, P. J. (2015). The effect of alternative forms of hunting on the social organization of two small populations of lions *Panthera leo* in Southern Africa. *Oryx*, *49*(4), 604–610. https://doi.org/10.1017/S0030605313001336

Sobratee, N., & Slotow, R. (2019). A critical review of lion research in South Africa: The impact of researcher perspective, research mode, and power structures on outcome bias and implementation gaps. *Frontiers in Ecology and Evolution*, *7*(81), 1–17. https://doi.org/10.3389/fevo.2019.00081

Spong, G. (2002). Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology*, *52*(4), 303–307. https://doi.org/10.1007/s00265-002-0515-x

Stander, P. E. (2019). Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia. *Namibian Journal of Environment*, *3*, 1–10.

Stoffelen, A., Adiyia, B., Vanneste, D., & Kotze, N. (2020). Post-apartheid local sustainable development through tourism: an analysis of policy perceptions among “responsible” tourism stakeholders around Pilanesberg National Park, South Africa. *Journal of Sustainable Tourism*, *28*(3), 414–432. https://doi.org/10.1080/09669582.2019.1679821

Tambling, C. J., & du Toit, J. T. (2005). Modelling wildebeest population dynamics: Implications of predation and harvesting in a closed system. *Journal of Applied Ecology*, *42*, 431–441. https://doi.org/10.1111/j.1365-2664.2005.01039.x

Tarugara, A., Clegg, B. W., Gandiwa, E., & Muposhi, V. K. (2019). Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population. *Global Ecology and Conservation*, *18*, e00627. https://doi.org/10.1016/j.gecco.2019.e00627

Tende, T., Ottosson, U., Hansson, B., & Bensch, S. (2008). Population density and abundance of Lions in Yankari Game Reserve, 2008. Unpublish report, Lund University, Sweden.

Trinkel, M., Fleischmann, P. H., & Slotow, R. (2017). Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population. *Journal of Zoology*, *301*(1), 41–50. https://doi.org/10.1111/jzo.12387

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation*, *13*(4), 374–382. https://doi.org/10.1111/j.1469-1795.2009.00344.x

Trinkel, Martina., & Angelici, F. M. (2016). The decline in the Lion population in Africa and possible mitigation measures. In F. M. Angelici (Ed.), *Problematic Wildlife* (Edition 1, pp. 45–68). https://doi.org/10.1007/978-3-319-22246-2

Tumenta, P. N., van't Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., Udo de Haes, H. A., & De Iongh, H. H. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology*, *78*(6), 461–469. https://doi.org/10.1016/j.mambio.2013.08.006

Van de Kerk, M., de Kroon, H., Conde, D. A., & Jongejans, E. (2013). Carnivora population dynamics are as slow and as fast as those of other mammals: Implications for their conservation. *PloS one*, *8*(8), e70354. https://doi.org/10.1371/journal.pone.0070354

Van Dyk, G., & Slotow, R. (2003). The effects of fences and lions on the ecology of African wild dogs reintroduced to Pilanesberg National Park, South Africa. *African Zoology*, *38*(1), 79–94. https://doi.org/10.1080/15627020.2003.11657196

Van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (Panthers, leo). *Journal of Zoology*, *206*(1), 97–112. https://doi.org/10.1111/j.1469-7998.1985.tb05639.x

Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, *143*(11), 2631–2637. https://doi.org/10.1016/j.biocon.2010.07.005

VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, *77*(4), 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028

Vega Yon, G. G., & Marjoram, P. (2019). fmcmc: A friendly MCMC framework. *The Journal of Open Source Software*, *4*(39), 1427. https://doi.org/10.2307/2334940

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science*, *297*(5585), 1339–1343. https://doi.org/10.1126/science.1073257

Wijers, M., Trethowan, P., Du Preez, B., Chamaillé-Jammes, S., Loveridge, A. J., Macdonald, D. W., & Markham, A. (2021). Vocal discrimination of African lions and its potential for collar-free tracking. *Bioacoustics*, *30*(5), 575–593. https://doi.org/10.1080/09524622.2020.1829050

Wild, G., & West, S. A. W. (2009). Genomic imprinting and sex allocation. *American Naturalist*, *173*(1), 1–14. https://doi.org/10.1086/593305

Winterbach, H. E. K., Winterbach, C. W., Somers, M. J., & Hayward, M. W. (2013). Key factors and related principles in the conservation of large African carnivores. *Mammal Review*, *43*(2), 89–110. https://doi.org/10.1111/j.1365-2907.2011.00209.x

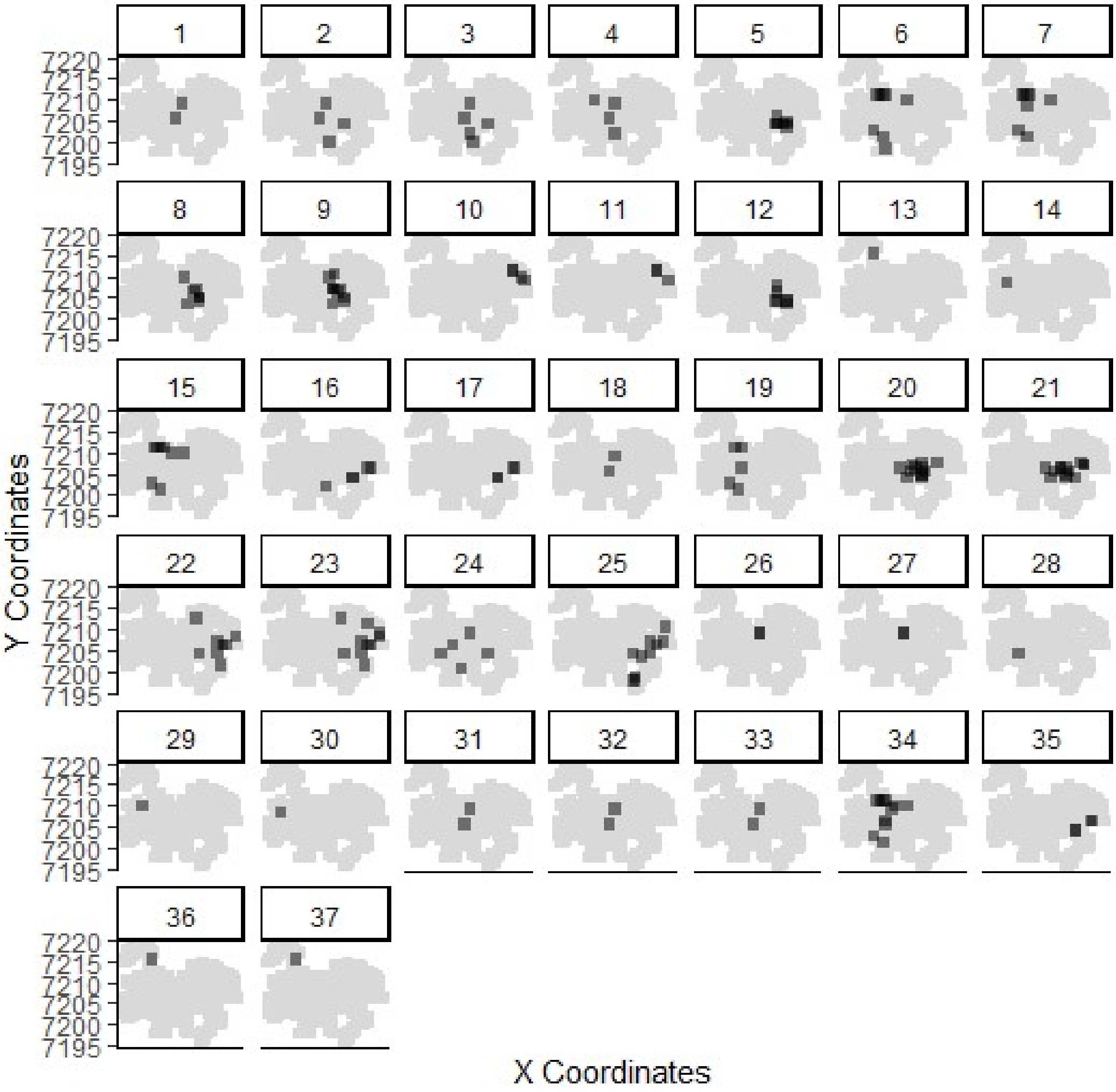
Witmer, G. W. (2005). Wildlife population monitoring: some practical considerations. *Wildlife Research*, *32*, 259–263.

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation*, *3*(2), 165–173. https://doi.org/10.1017/S136794300000086X

Woolley, L. A., Page, B., & Slotow, R. (2011). Foraging strategy within African elephant family units: Why body size matters. *Biotropica*, *43*(4), 489–495. https://doi.org/10.1111/j.1744-7429.2010.00733.x

Appendix

Figure S.1. Encounter history plots displaying the locations (dark grey squares) where each of the 37 observed individuals were sighted in Pilanesberg National Park, South Africa. Light grey cells correspond to pixels that were sampled during the survey.



Gelman-Rubin diagnostic

Table S.1. Model 1-5. For Gelman-Rubin the potential shrink reduction factor should be less than 1.1 for each parameter.

Potential scale reduction factors:

Table S.1. Model 1

	Point estimate	Upper C.I
bsigma	1.00	1.00
Sigma	1.00	1.00
bsigma2	1.00	1.00
Sigma2	1.00	1.00
Lam0	1.00	1.00
Beta.sex	1.00	1.00
Psi	1.00	1.00
Psi.sex	1.00	1.00
Nsuper	1.00	1.00
D.adj	1.00	1.00

Table S.1. Model 2

	Point estimate	Upper C.I
bsigma	1.00	1.00
Sigma	1.00	1.00
bsigma2	1.00	1.00
Sigma2	1.00	1.00
Lam0	1.00	1.00
Beta.sex	1.00	1.00
Psi	1.00	1.00
Psi.sex	1.00	1.00
Nsuper	1.00	1.00
D.adj	1.00	1.00

Table S.1. Model 3

	Point estimate	Upper C.I
bsigma	1.00	1.00
Sigma	1.00	1.00
bsigma2	1.00	1.00
Sigma2	1.00	1.00
Lam0	1.00	1.00
Beta.sex	1.00	1.00
Psi	1.00	1.00
Psi.sex	1.00	1.00
Nsuper	1.00	1.00
D.adj	1.00	1.00

Table S.1. Model 4

	Point estimate	Upper C.I
bsigma	1.00	1.00
Sigma	1.00	1.00
bsigma2	1.00	1.00
Sigma2	1.00	1.00
Lam0	1.00	1.00
Beta.sex	1.00	1.00
Psi	1.00	1.00
Psi.sex	1.00	1.00
Nsuper	1.00	1.00
D.adj	1.00	1.00

Table S.1. Model 5

	Point estimate	Upper C.I
bsigma	1.34	1.35
Sigma	1.44	1.46
bsigma2	1.34	1.35
Sigma2	1.44	1.46
Lam0	1.00	1.00
Beta.sex	1.00	1.00
Psi	1.00	1.00
Psi.sex	1.00	1.00
Nsuper	1.00	1.00
D.adj	1.00	1.00

Figure S.2. Model 1-5. Gelman plot. This plot shows the evolution of Gelman and Rubin's shrink factor as the number of iterations increases. Look at where the estimates level off to assess post-hoc burn. A potential problem with Gelman diagnostics is that it may mis-diagnose convergence if the shrink factor happens to be close to 1 by chance. By calculating the shrink factor at several points in time, Gelman plot shows if the shrink factor has really converged, or whether it is still fluctuating.

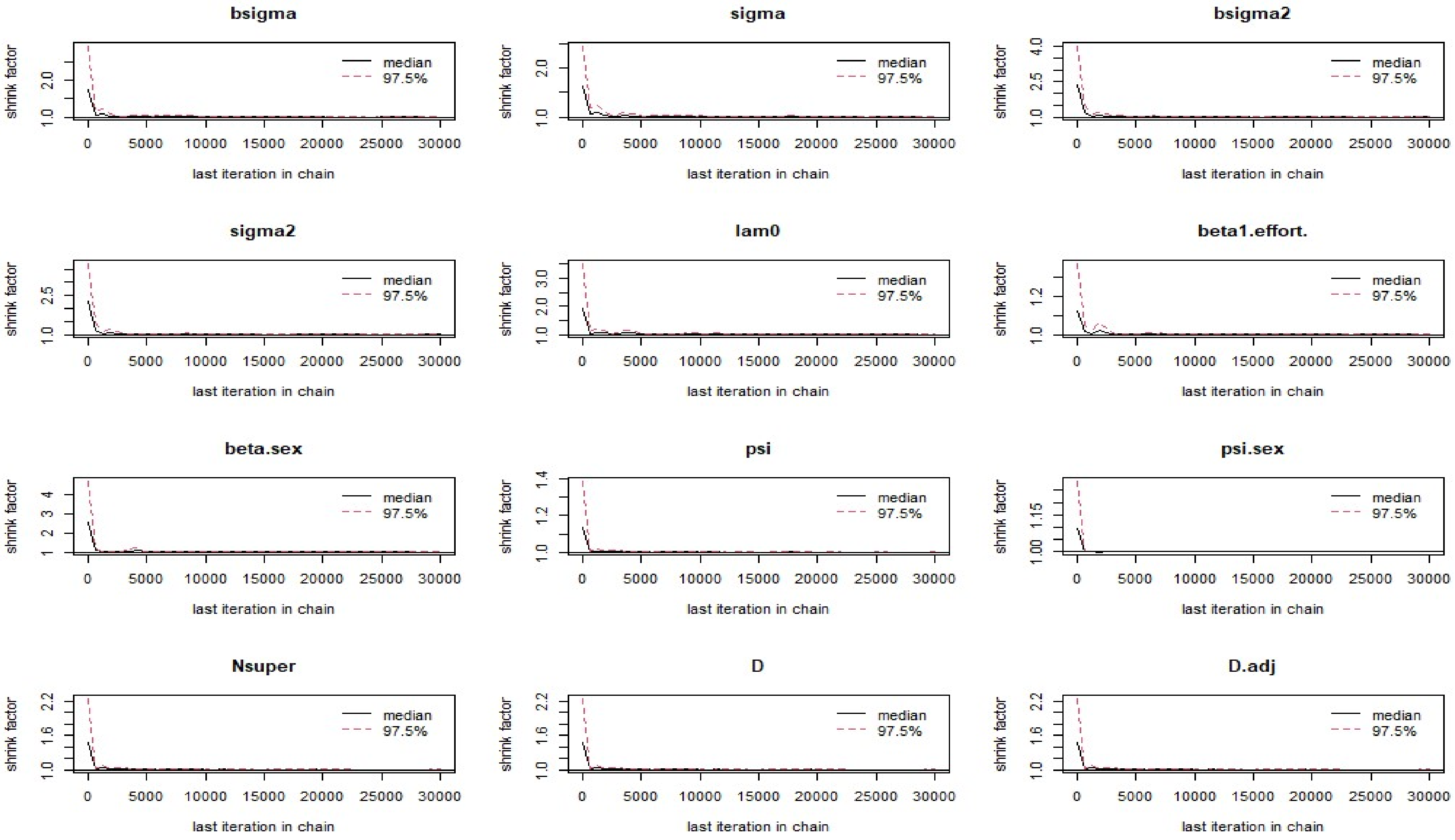


Figure S.2. Model 1

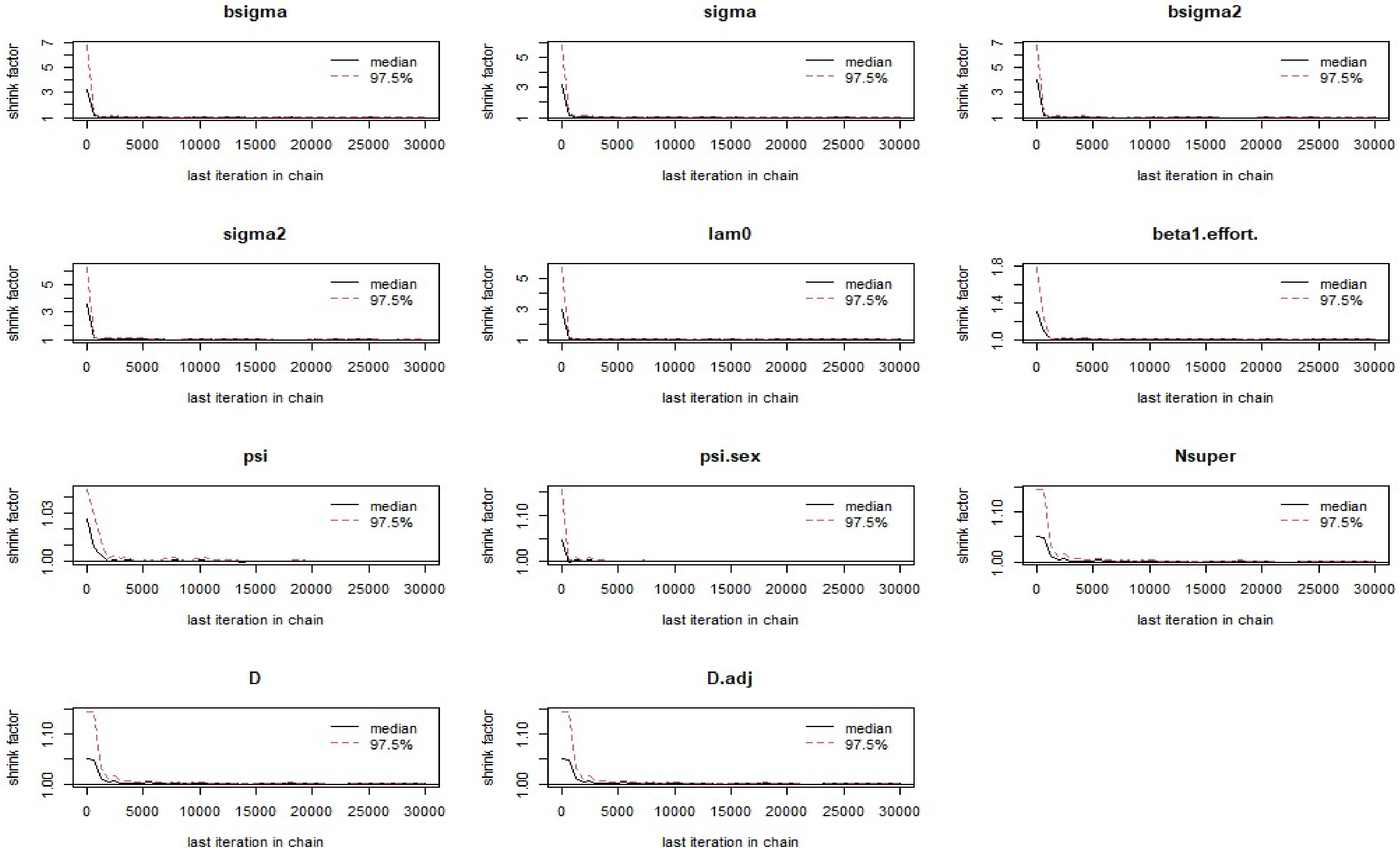


Figure S.2. Model 2

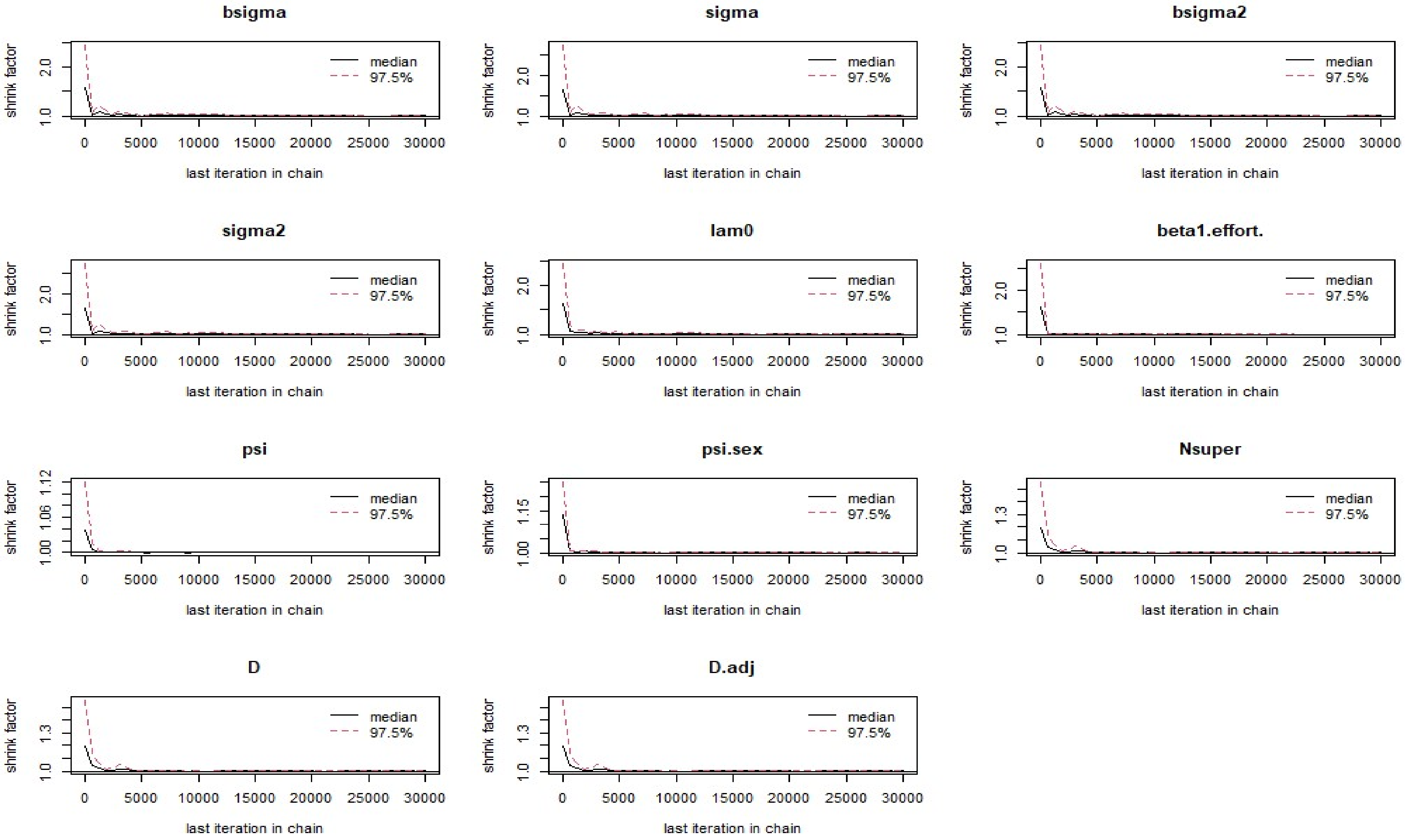


Figure S.2. Model 3

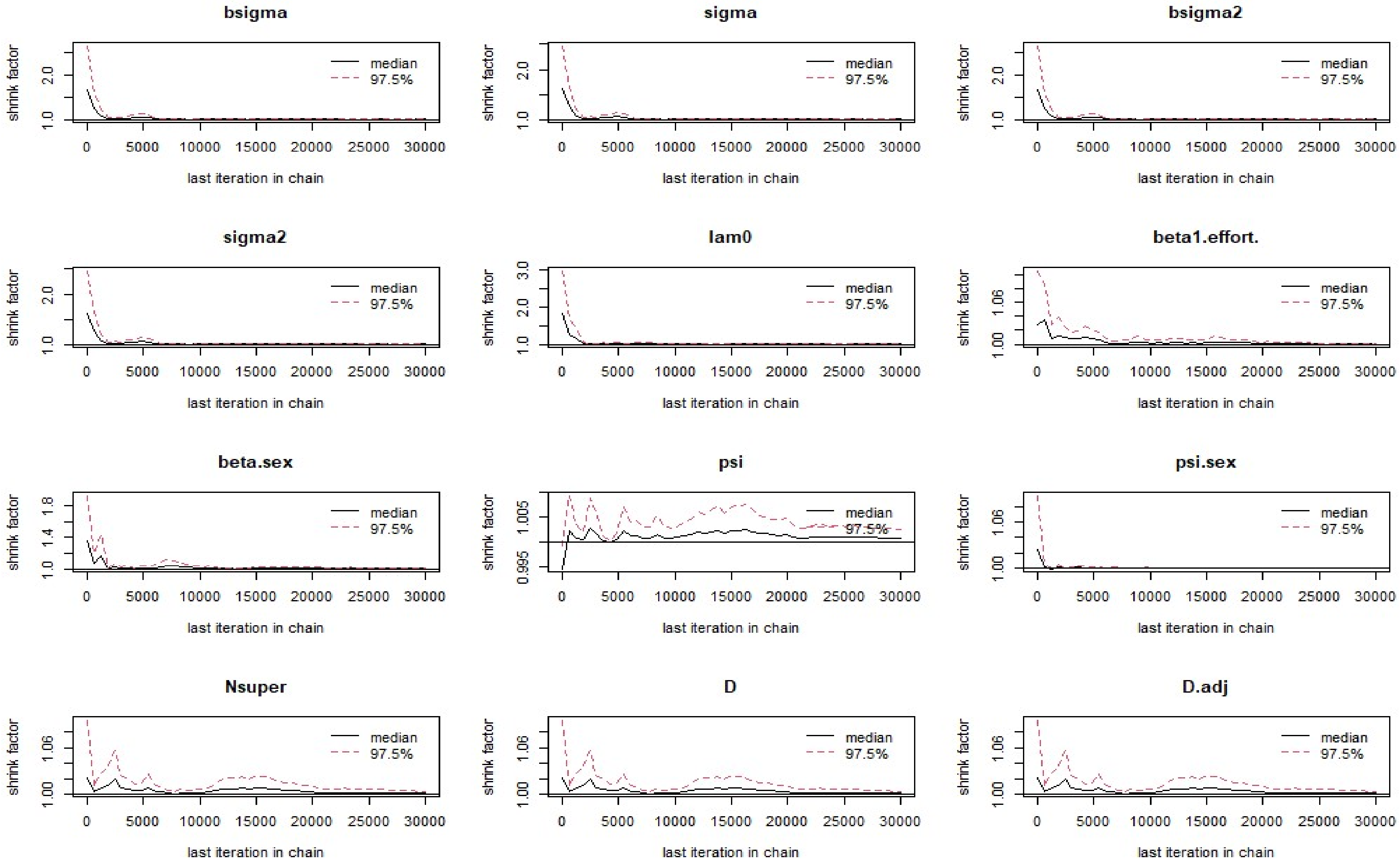


Figure S.2. Model 4

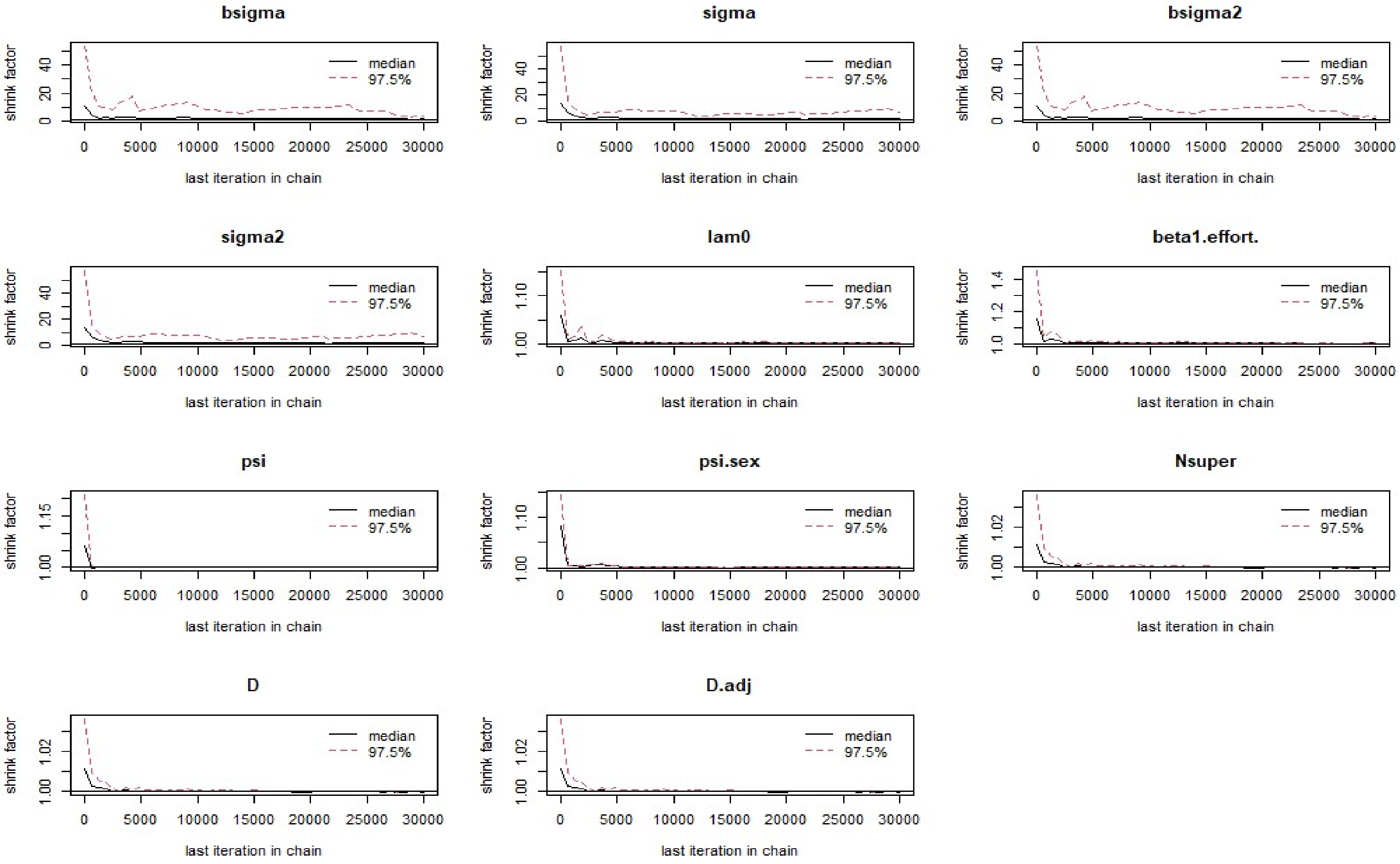


Figure S.2. Model 5

Table S3. Model 1-5. Trace plots. To assess the mixing of a chain. In the trace plots, we want to try to avoid flat bits (where the chain stays in the same state for too long) or too many consecutive steps in one direction.

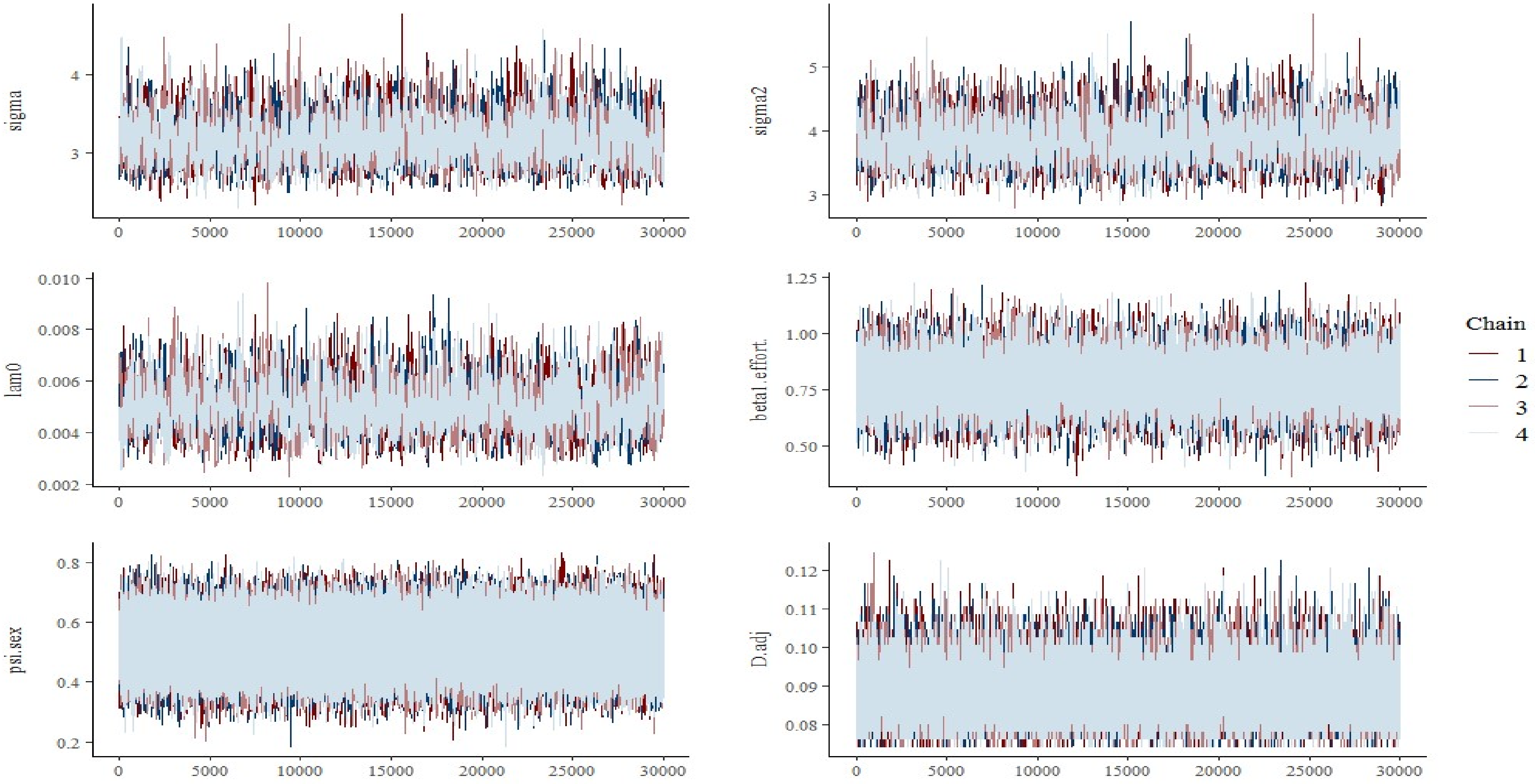


Figure S.3. Model 1

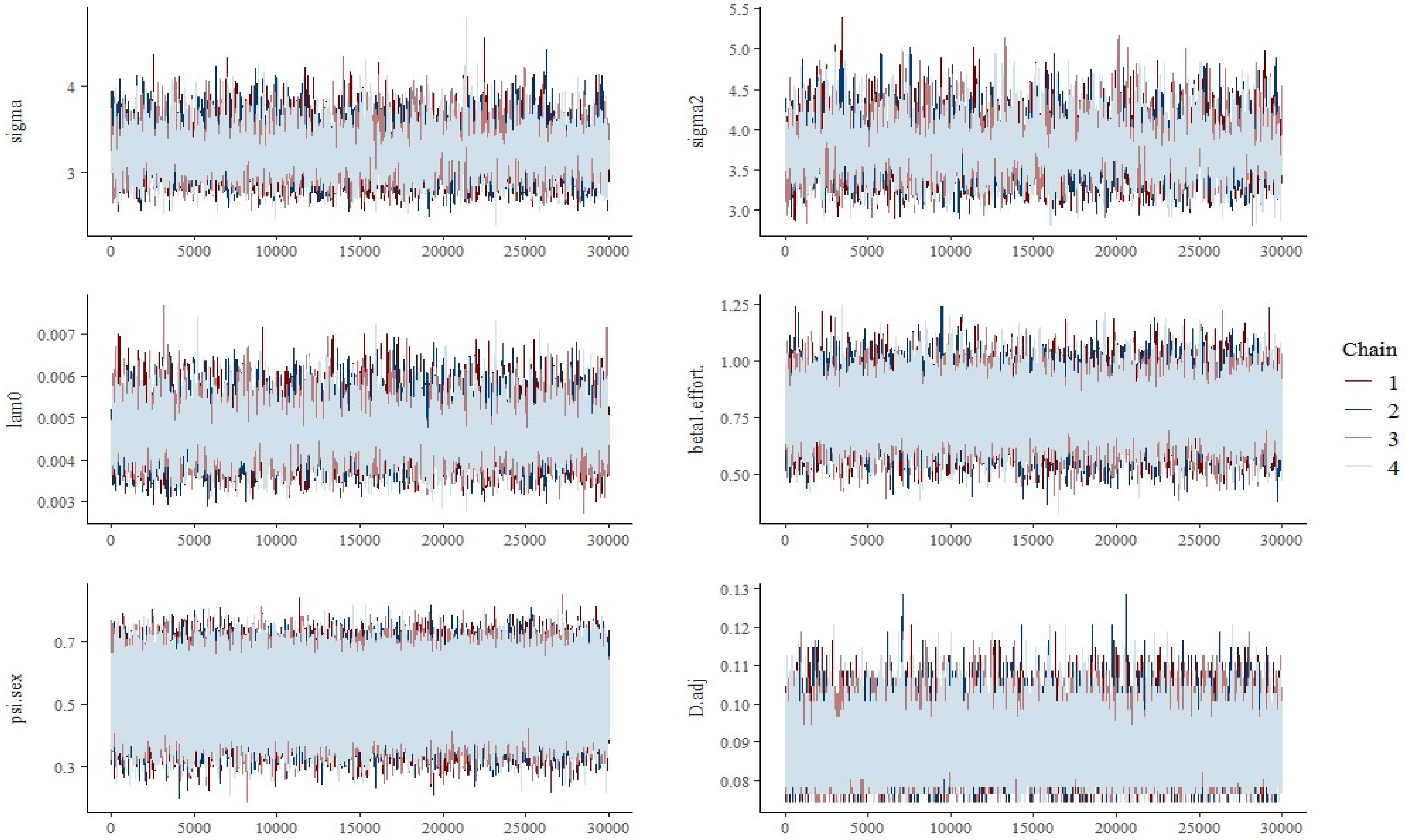


Figure S.3. Model 2

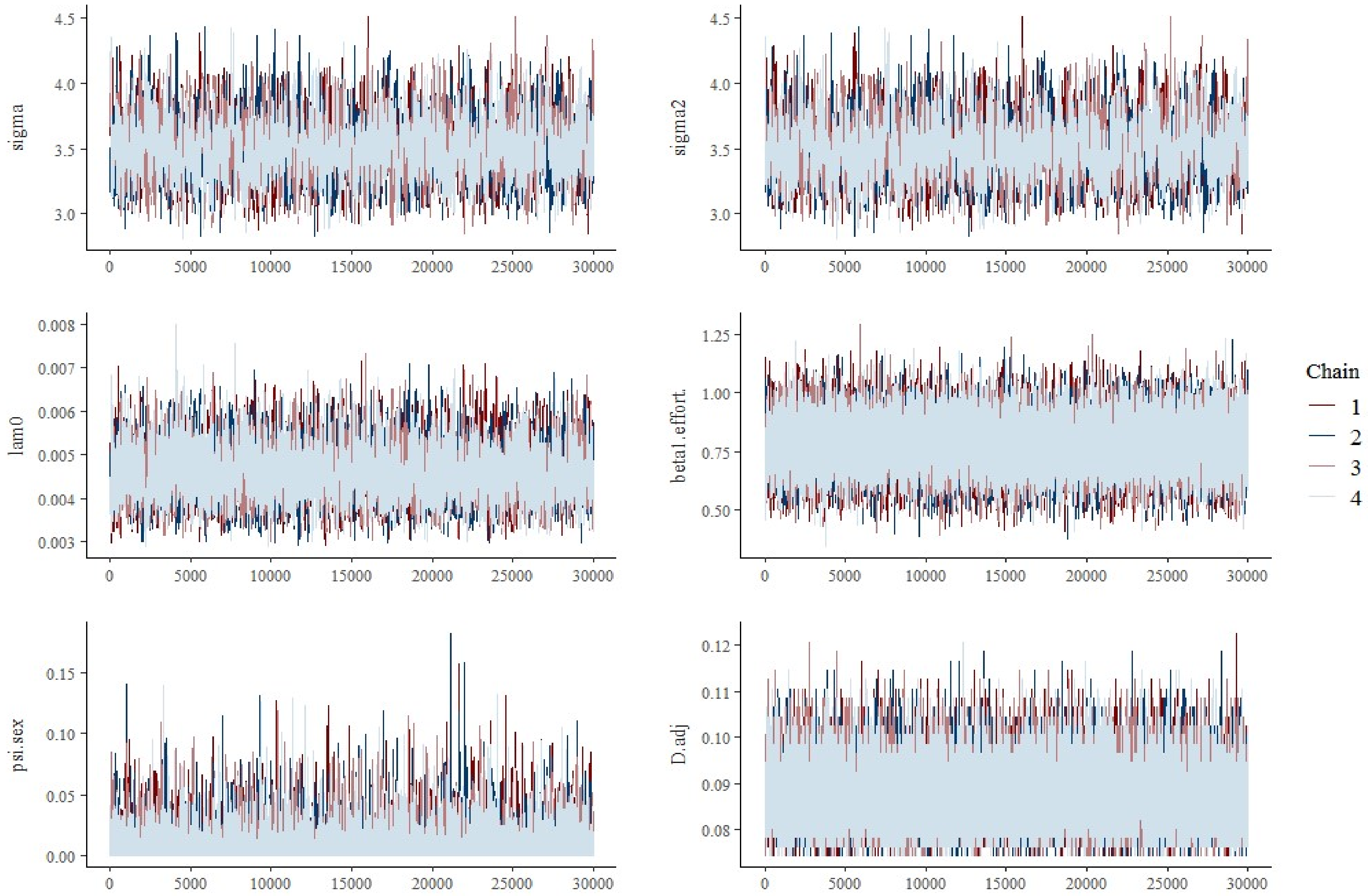


Figure S.3. Model 3

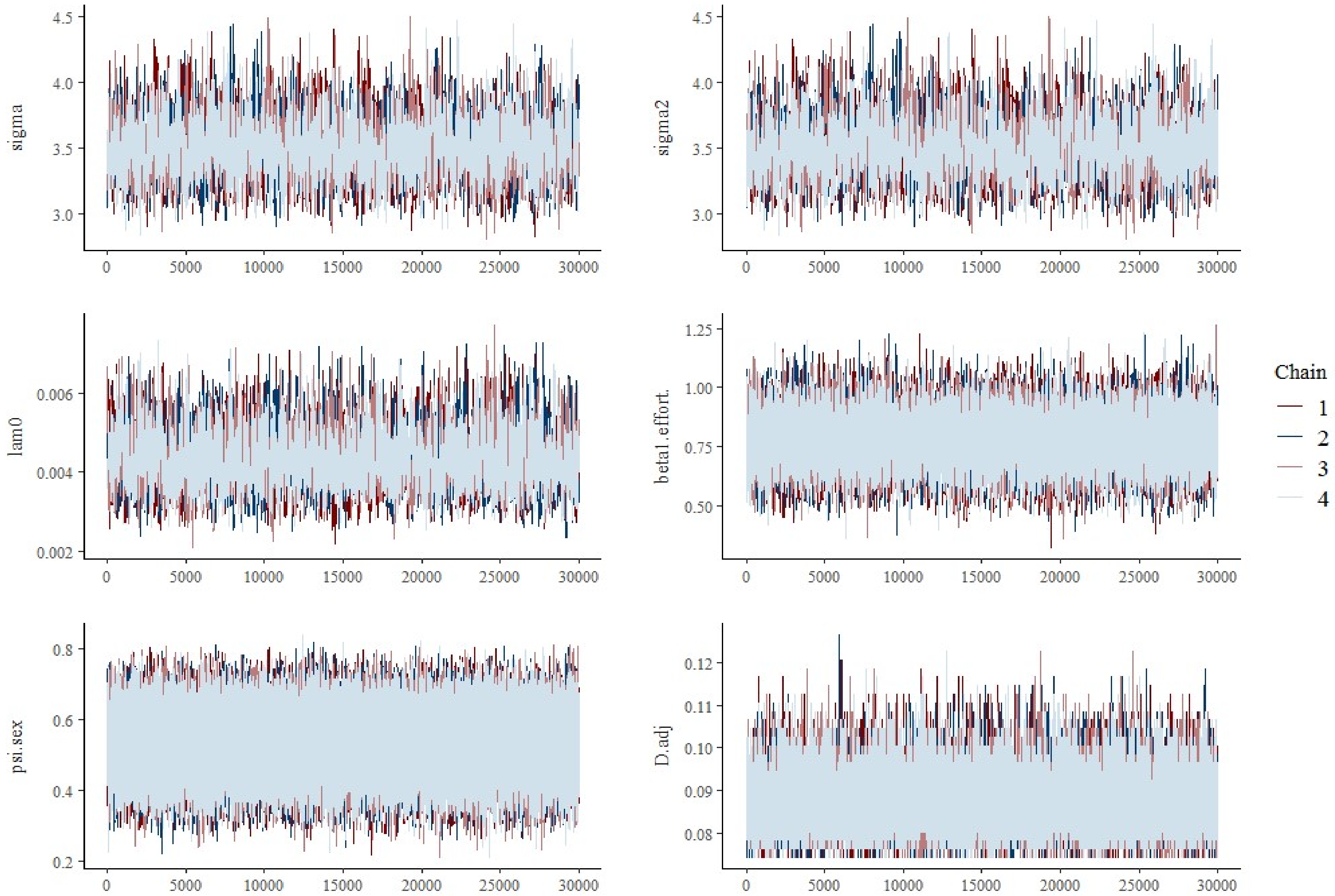


Figure S.3. Model 4

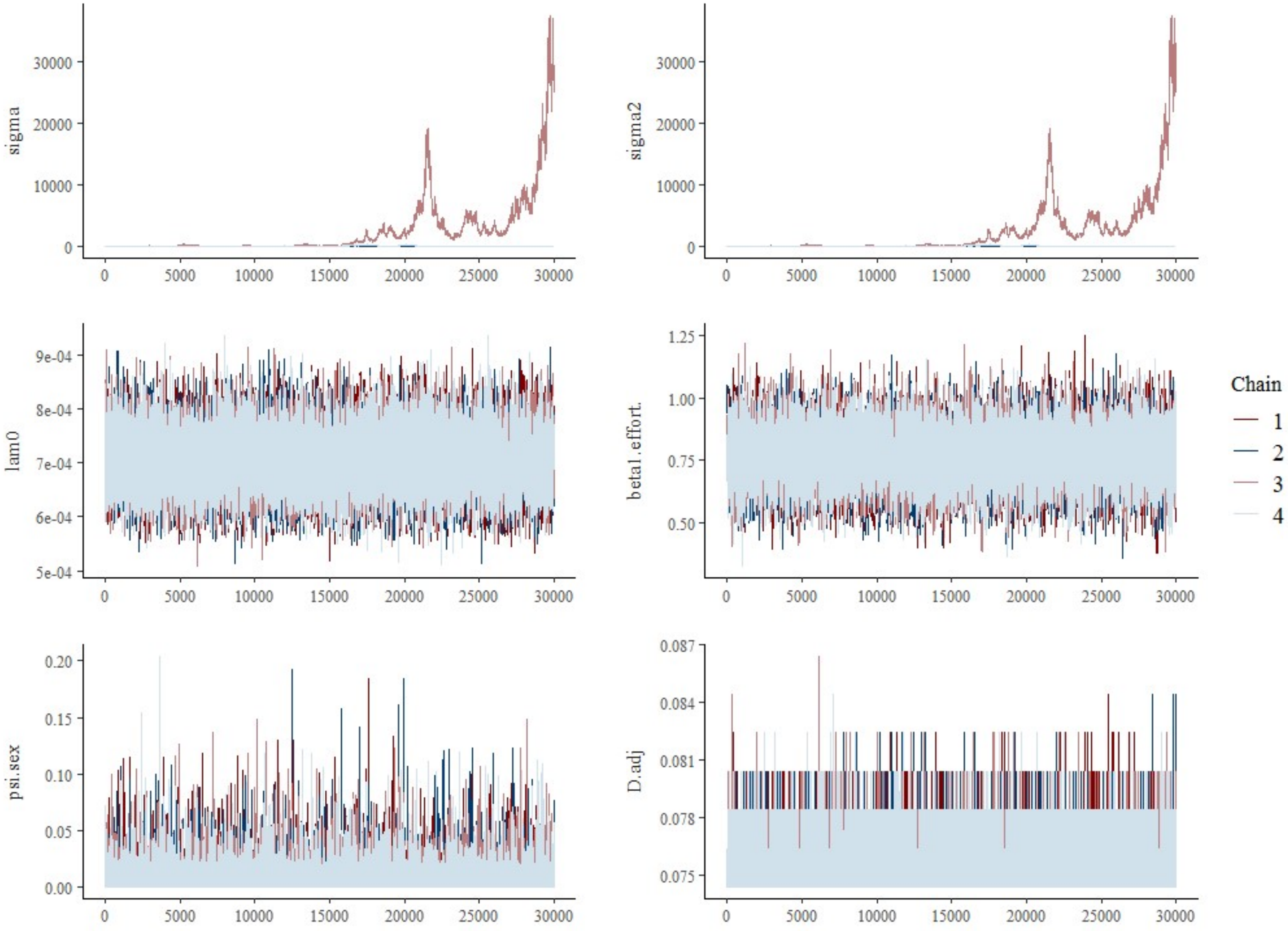


Figure S.3. Model 5

Table S4. Model 1-5. Autocorrelation plot. The lag-*k* autocorrelation is the correlation between every sample and the sample k steps before. This autocorrelation should become smaller as *k* increases, i.e., samples can be considered as independent. If, on the other hand, autocorrelation remains high for higher values of k, this indicates a high degree of correlation between our samples and slow mixing.

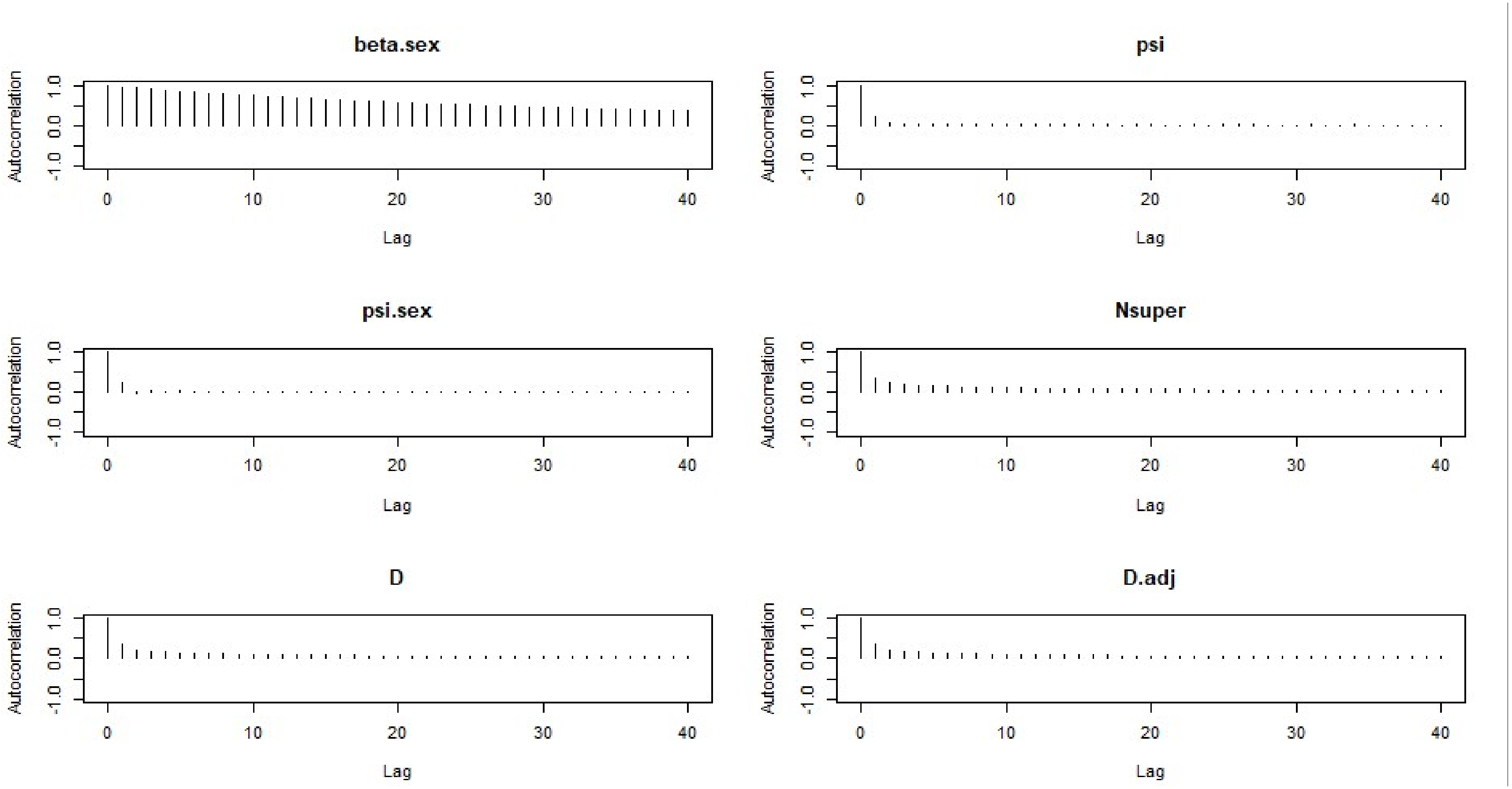
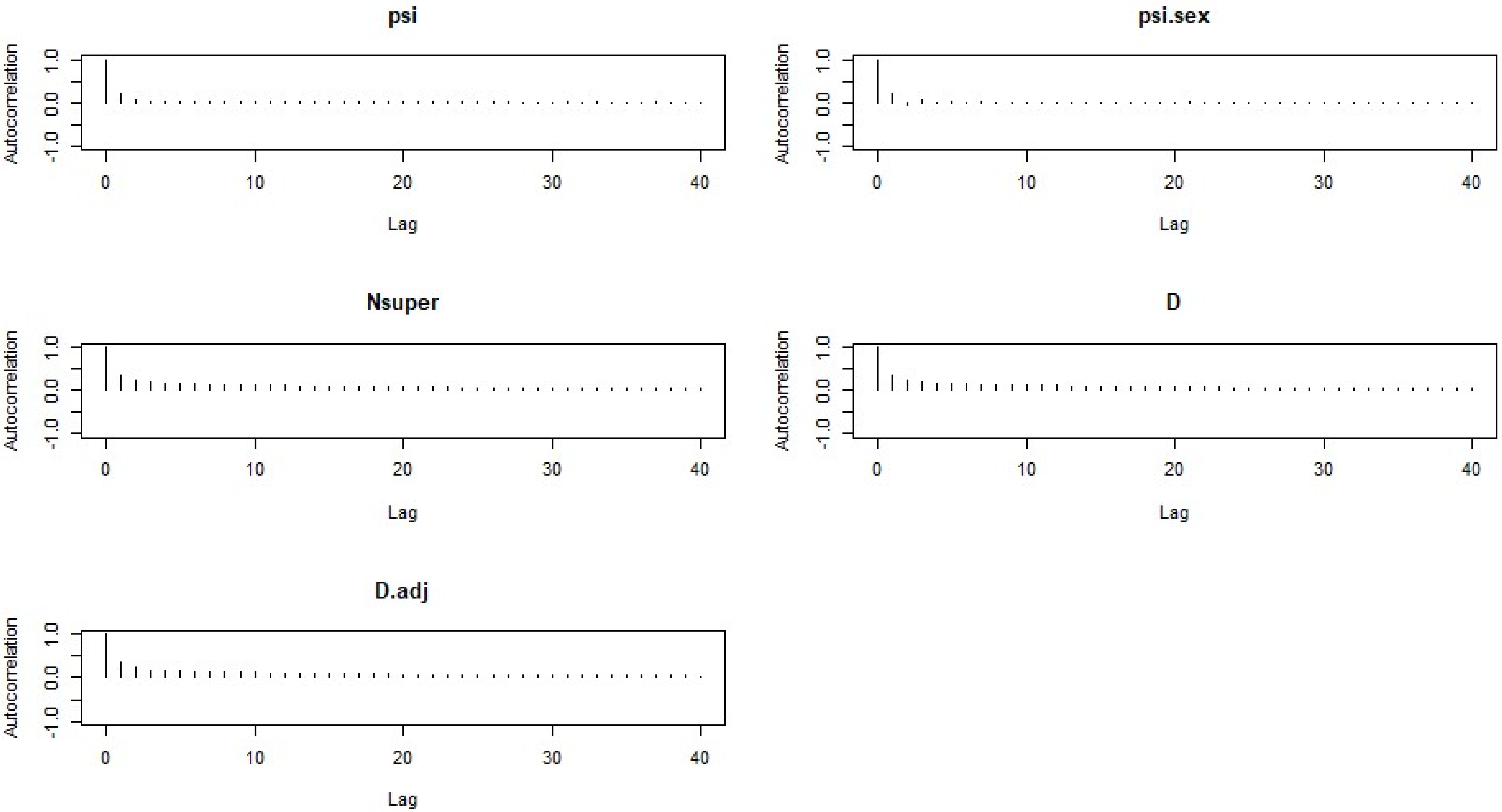


Figure S.4. Model 1


psi

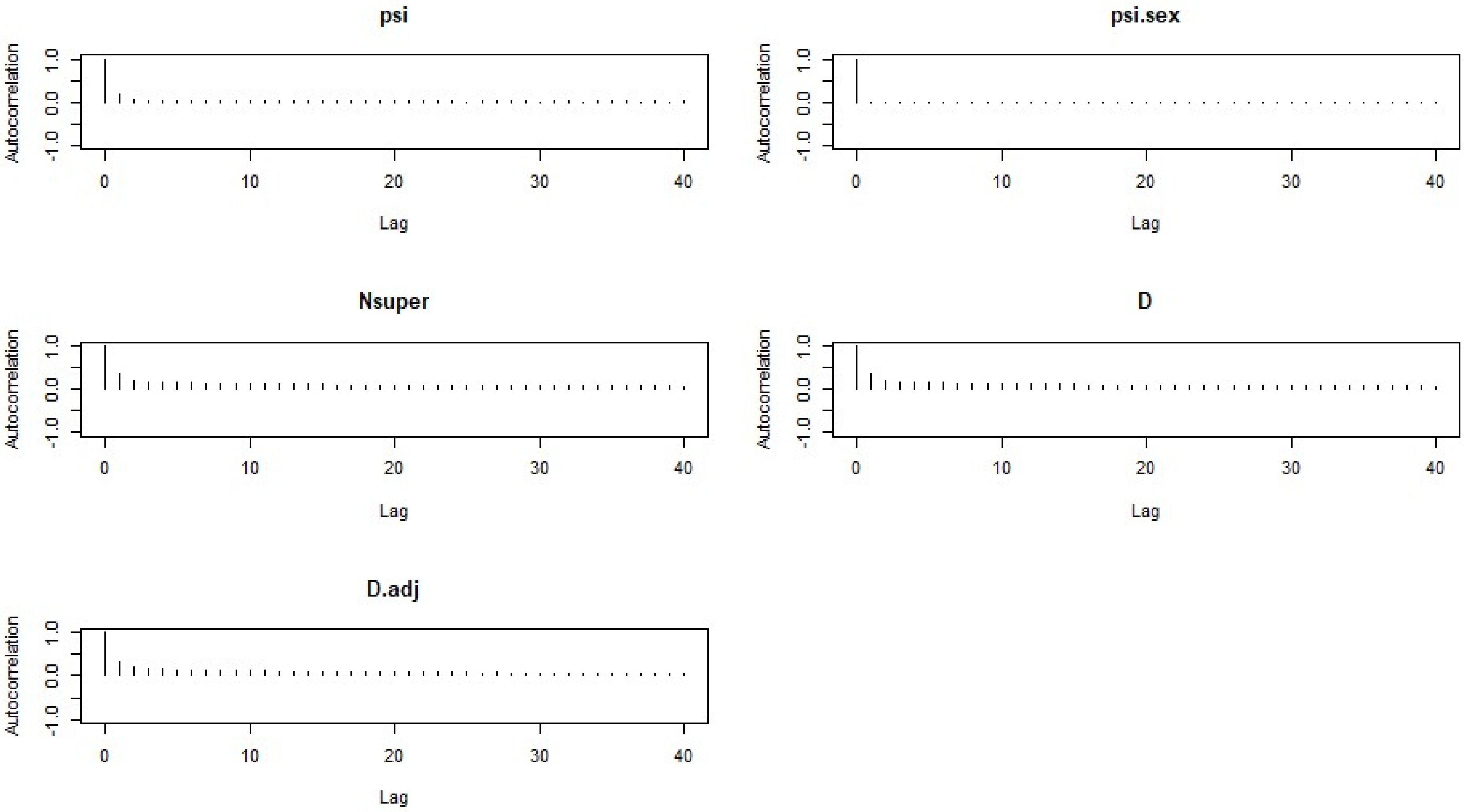
psi.sex

Nsuper

D

D.adj

Figure S.4. Model 2


psi

psi.sex

Nsuper

D

D.adj

Figure S.4. Model 3

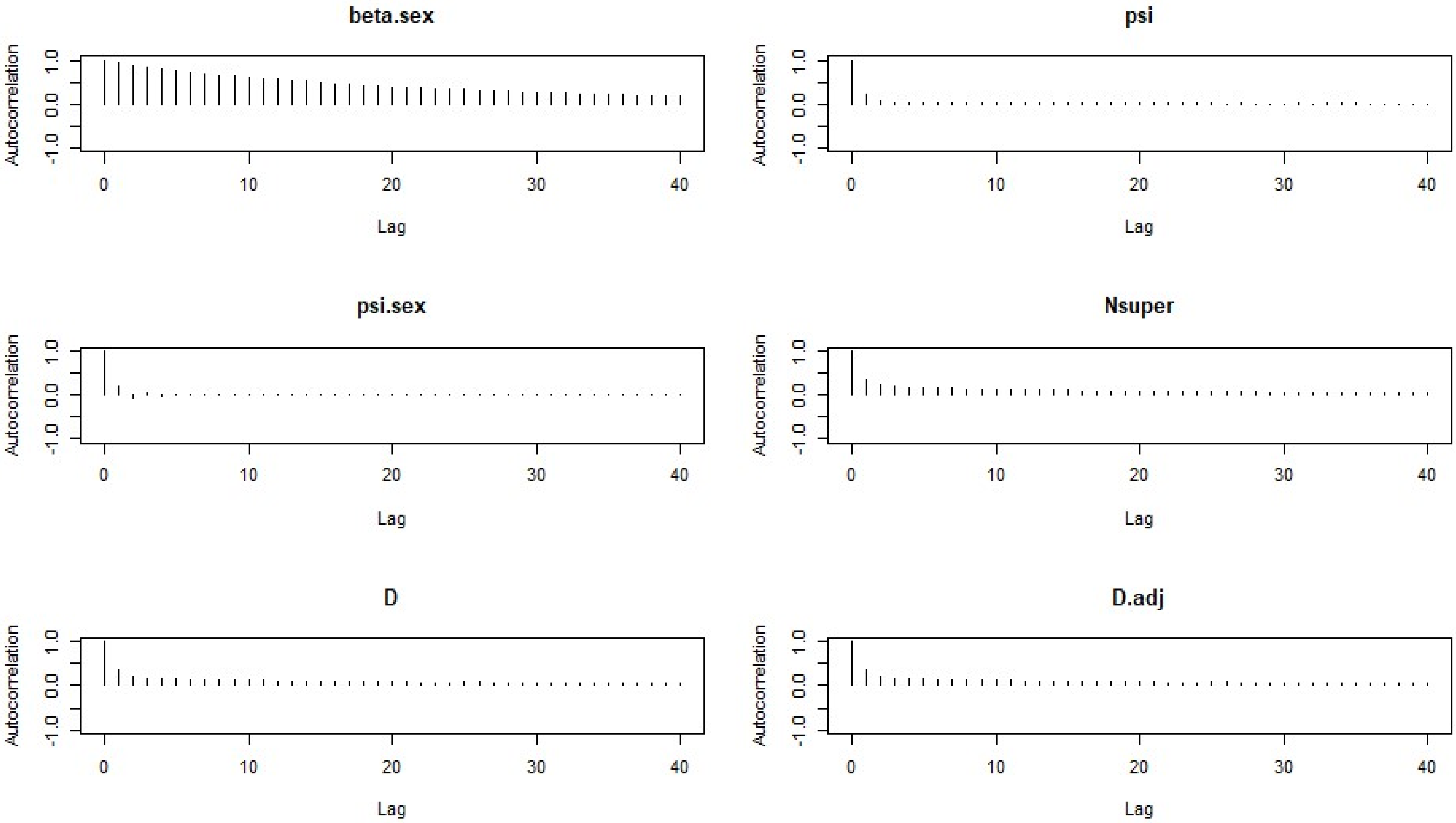


Figure S.4. Model 4

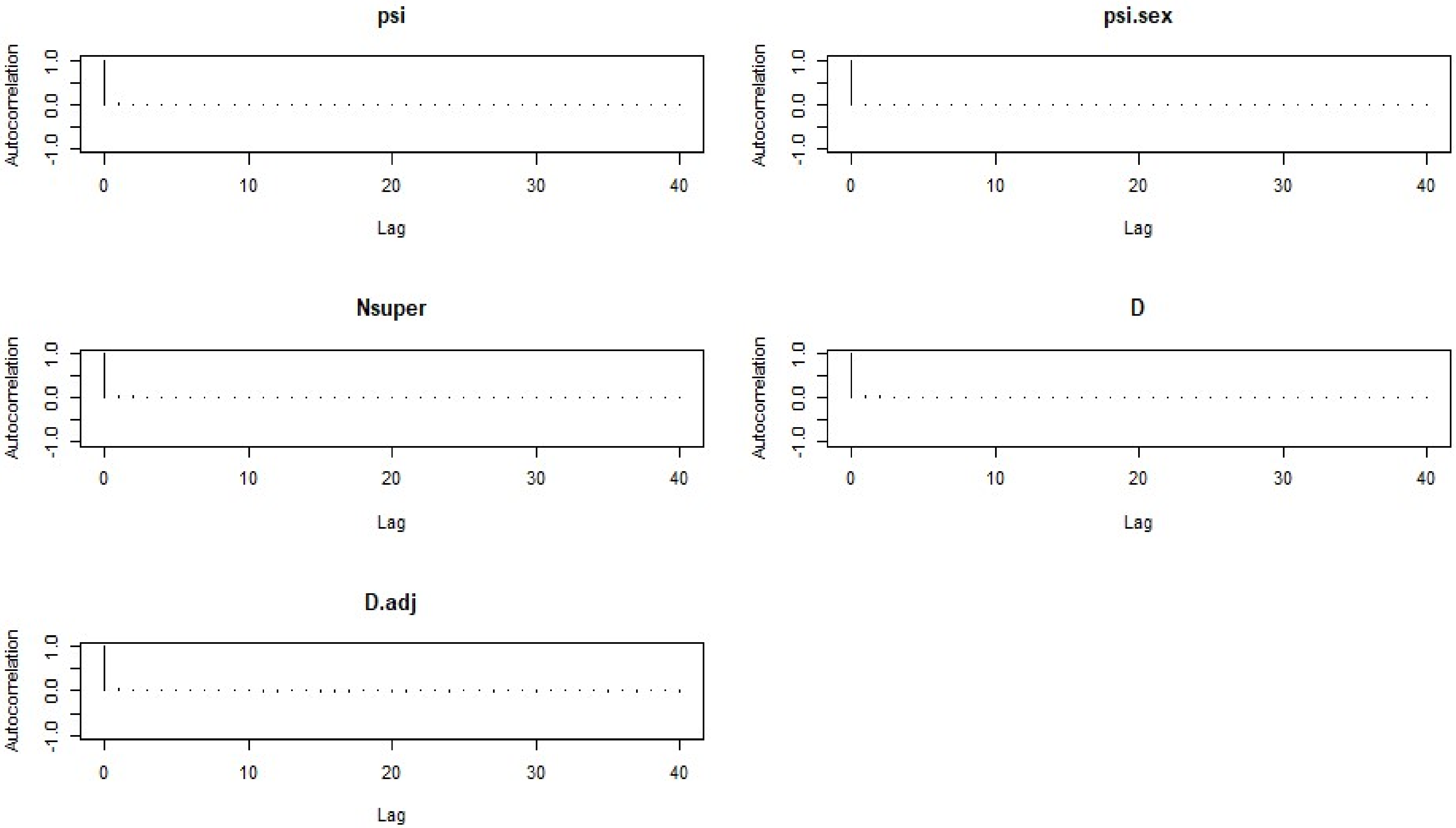


Figure S.4. Model 5

Figure S5. Model 1-5. Pairwise plots between estimated parameters from the posterior MCMC draws. We used these to visually assess covariance and parameter redundancy (or identifiability) issues as a result of model overfitting relative to sample size. Since abundance (N_{super}) and density (*D.adj*) were the parameters of primary interest to our study, we were particularly concerned to assess whether there were correlations between these parameters and any other parameter.

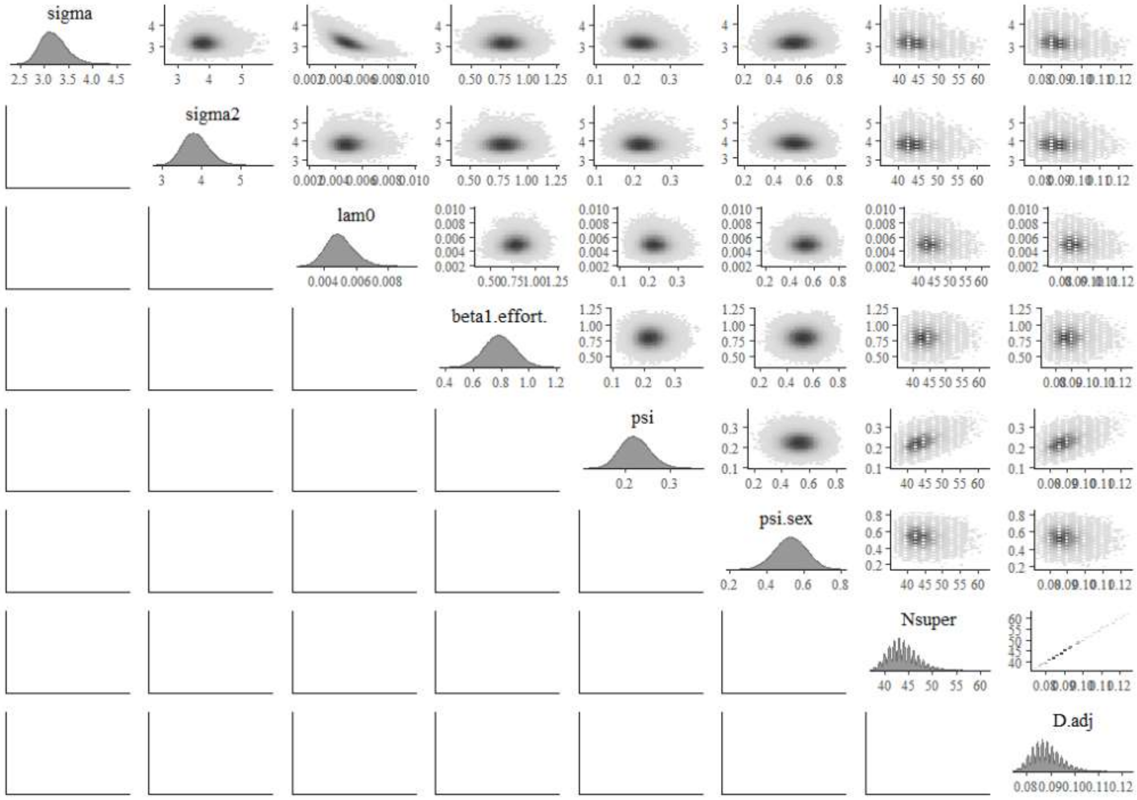


Figure S.5. Model 1

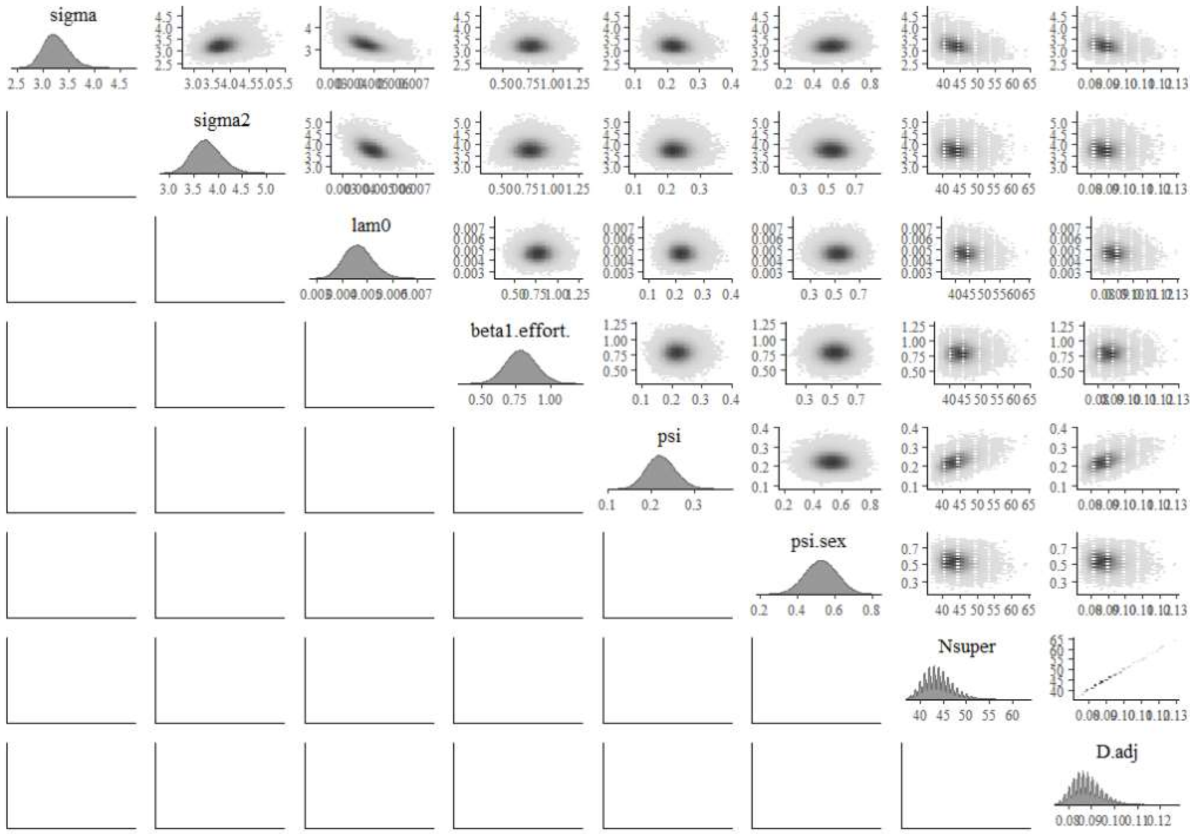


Figure S.5. Model 2

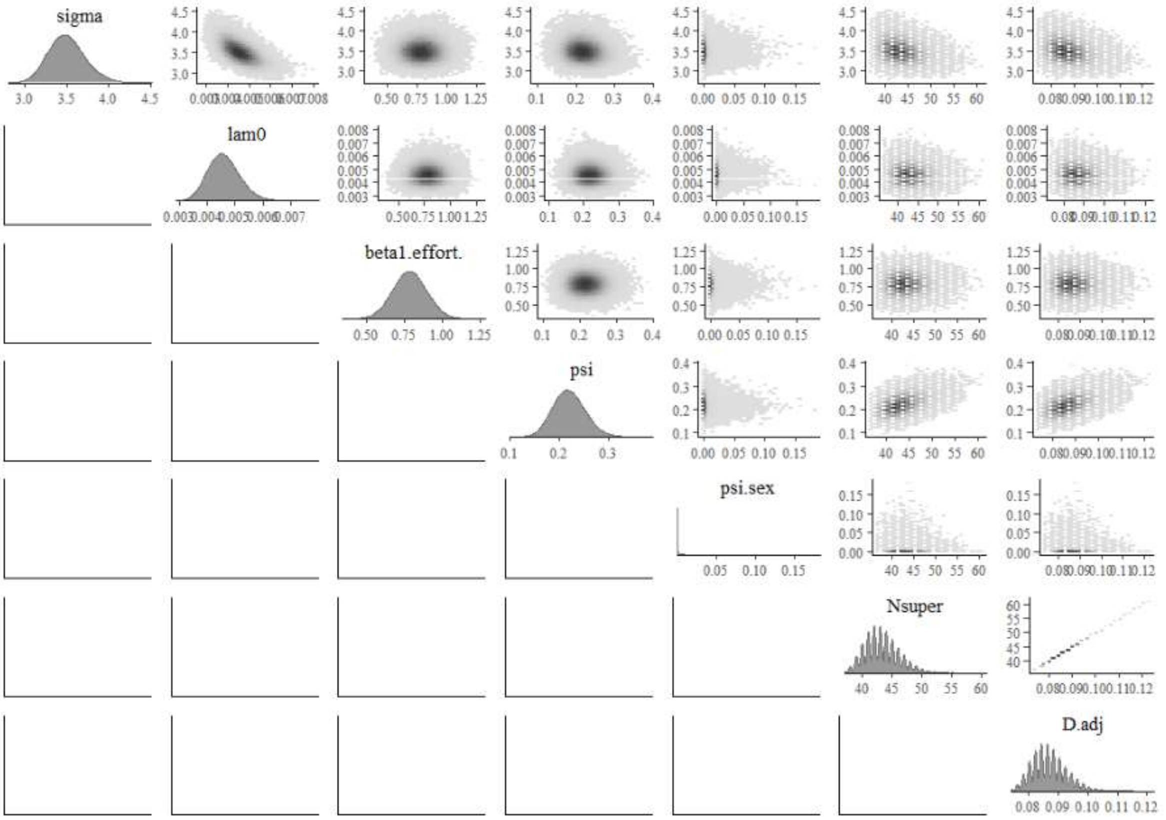


Figure S.5. Model 3

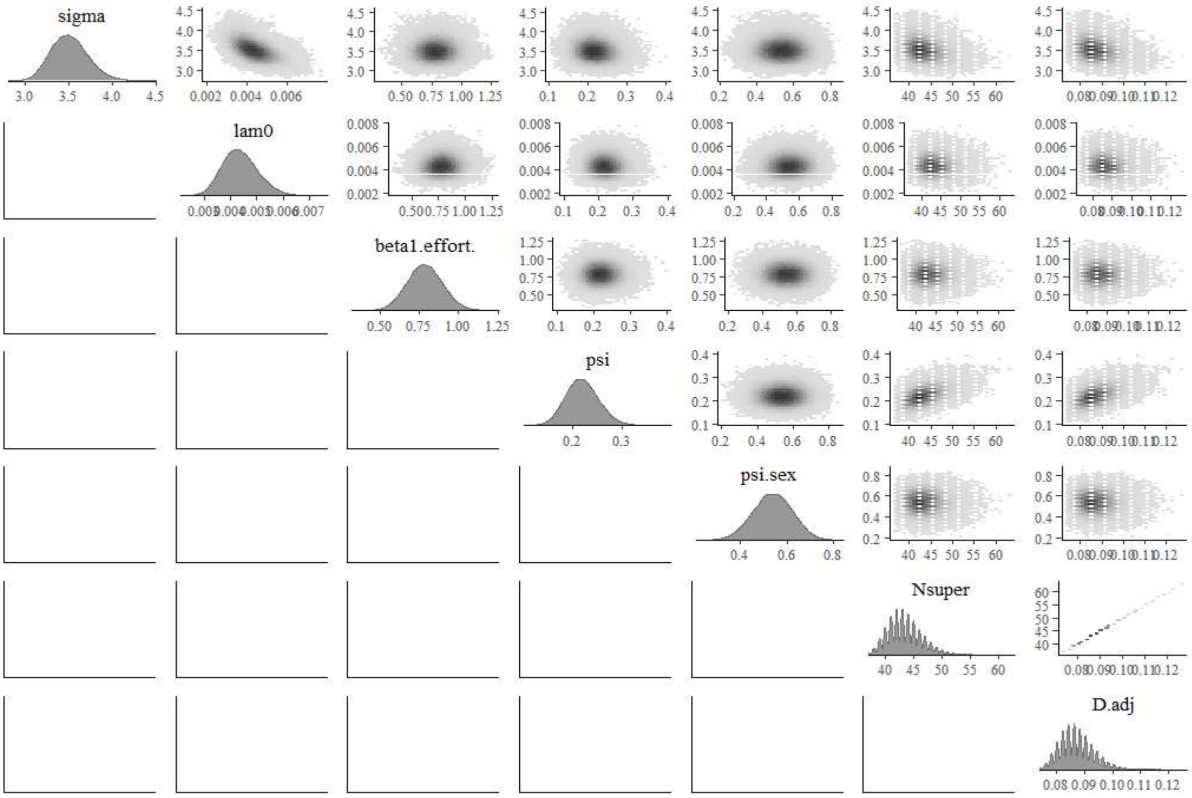


Figure S.5. Model 4

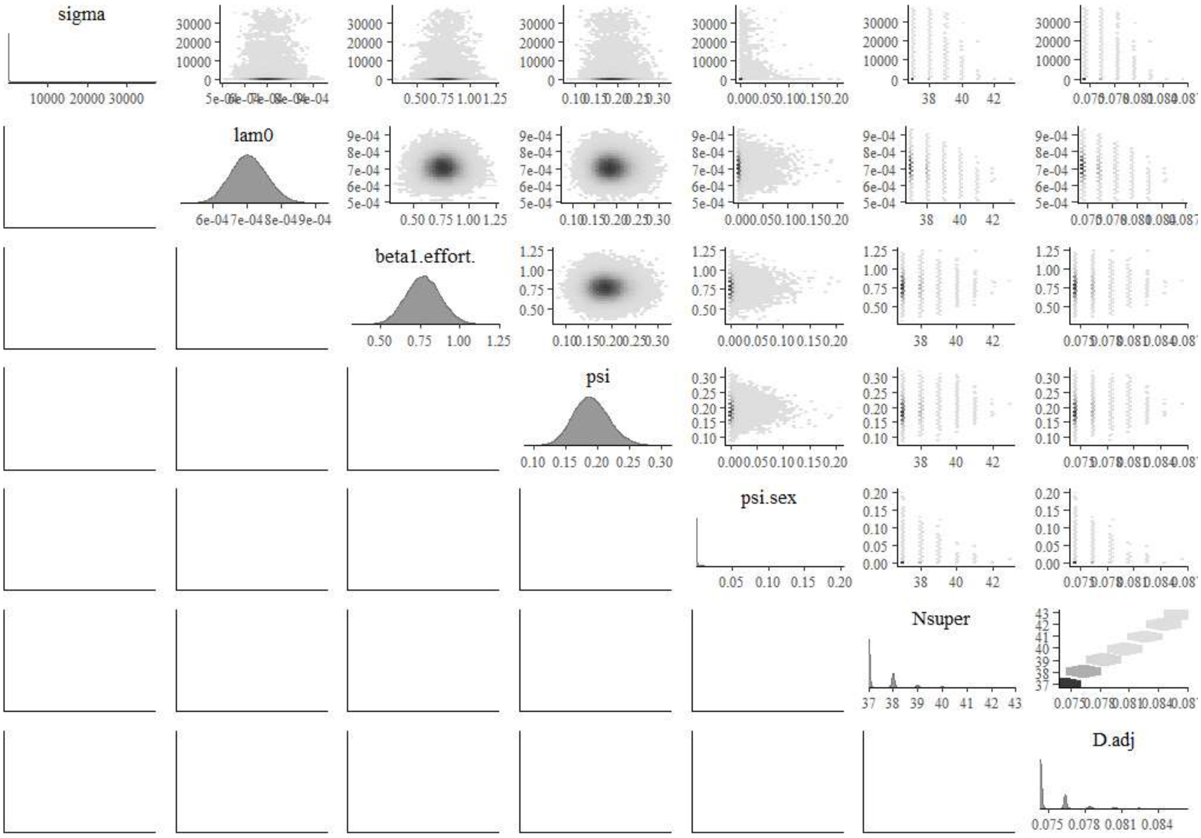


Figure S.5. Model 5

Table S.2. Posterior estimates of parameters for Models 1-5. Model 1 was selected for reporting due to (a) Bayesian *p* value lying within the extremities (0.15-0.85), (b) minimal pairwise correlations and (c) the highest marginal likelihood value.

Table S.2. Model specifications and diagnostics of model 1-5.

	Model 1	Model 2	Model 3	Model 4	Model 5
Model Specifications	**Setting**	**Setting**	**Setting**	**Setting**	**Setting**
M_{sex}	1	0	0	1	0
$M_{sexsigma}$	1	1	0	0	0
M_{sigma}	1	1	1	1	0
Theta	1	1	1	1	1
Nz	200	200	200	200	200
Chains	4	4	4	4	4
Iterations	31 000	31 000	31 000	31 000	31 000
Burn	1 000	1 000	1 000	1 000	1 000
Post Hoc Burn	0	1 600	1 400	1 400	0
Model Diagnostics					
Bayes P-Value	0.696	0.686	0.672	0.679	0.999
Marginal Likelihood	-9342	-7387	-7627	-7910	-8113

Table S.3. Model 1-5 Parameter estimates. Look for how different median is to the mean. This indicates nature of the posterior distribution. Ideally, we would like them to be nearly the same.

Table S.3. Model 1

	Mean	Monte Carlo SE	Median	Mode	Post. SD	Lower 95% HPDI	Upper 95% HPDI
σ_F	3.189	0.006	3.166	3.079	0.273	2.676	3.732
σ_M	3.854	0.007	3.834	3.756	0.332	3.233	4.521
λ_0	0.005	0.000	0.005	0.005	0.001	0.003	0.007
β_{eff}	0.790	0.001	0.789	1.110	0.111	0.569	1.001
β_{sex}	-0.130	0.006	-0.133	-0.329	0.246	-0.611	0.354
ψ	0.222	0.000	0.221	0.194	0.033	0.161	0.288
ψ_{sex}	0.529	0.000	0.530	0.586	0.083	0.366	0.689
N_{super}	43.854	0.025	44.000	43.000	3.054	38.000	49.000
D	0.088	0.000	0.088	0.086	0.006	0.078	0.101

Table S.3. Model 2

	Mean	Monte Carlo SE	Median	Mode	Post. SD	Lower 95% HPDI	Upper 95% HPDI
σ_F	3.249	0.005	3.232	3.591	0.247	2.787	3.743
σ_M	3.767	0.006	3.748	4.193	0.303	3.192	4.369
λ_0	0.005	0.000	0.005	0.004	0.001	0.004	0.006
β_{eff}	0.786	0.001	0.784	0.700	0.112	0.569	1.009
ψ	0.222	0.000	0.221	0.258	0.033	0.158	0.287
ψ_{sex}	0.529	0.000	0.529	0.483	0.084	0.366	0.691
N_{super}	43.856	0.026	44.000	43.000	3.078	38.000	49.000
D	0.088	0.000	0.088	0.086	0.006	0.078	0.101

Table S.3. Model 3

	Mean	Monte Carlo SE	Median	Mode	Post. SD	Lower 95% HPDI	Upper 95% HPDI
σ_F	3.503	0.006	3.492	3.230	0.218	3.092	3.944
σ_M							
λ_0	0.005	0.000	0.005	0.005	0.001	0.004	0.006
β_{eff}	0.786	0.001	0.785	0.769	0.111	0.566	1.003
ψ	0.220	0.000	0.218	0.180	0.032	0.158	0.284
ψ_{sex}	0.002	0.000	0.000	0.002	0.007	0.000	0.014
N_{super}	43.317	0.025	43.000	42.000	2.902	37.000	48.000
D	0.087	0.000	0.086	0.084	0.006	0.078	0.101

Table S.3. Model 4

	Mean	Monte Carlo SE	Median	Mode	Post. SD	Lower 95% HPDI	Upper 95% HPDI
σ_F	3.513	0.005	3.502	3.571	0.215	3.104	3.937
σ_M							
λ_0	0.004	0.000	0.004	0.005	0.001	0.003	0.006
β_{eff}	0.784	0.001	0.783	0.492	0.112	0.561	0.997
β_{sex}	0.108	0.004	0.108	-0.070	0.192	-0.272	0.479
ψ	0.220	0.000	0.219	0.226	0.033	0.158	0.285
ψ_{sex}	0.538	0.000	0.539	0.532	0.083	0.373	0.696
N_{super}	43.451	0.025	43.000	42.000	2.967	38.000	49.000
D	0.087	0.000	0.086	0.084	0.006	0.078	0.101

Table S.3. Model 5

	Mean	Monte Carlo SE	Median	Mode	Post. SD	Lower 95% HPDI	Upper 95% HPDI
σ_F σ_M	629.52	400.01	20.77	6.06	2649.97	0.052	3462.38
λ_0	0.001	0.000	0.001	0.001	0.000	0.001	0.001
β_{eff}	0.769	0.001	0.768	0.971	0.108	0.562	0.984
ψ	0.190	0.000	0.189	0.184	0.028	0.136	0.245
ψ_{sex}	0.003	0.000	0.000	0.000	0.008	0.000	0.016
N_{super}	37.296	0.002	37.000	37.000	0.558	37.000	38.000
D	0.075	0.000	0.074	0.074	0.001	0.074	0.076

Table S.4. 41 protected areas (small, medium, and large) where the light grey colour is fenced protected areas. The figure describes lion densities per km^2 throughout Africa's continent which was assessed in different years (Elliot et al., 2020; C. Packer, Loveridge, et al., 2013).

Park names	**Size**	**Lion Density**	**Year assessment**	**Reference**
Nairobi National Park, Kenya	117 km^2	23.93	2009	
Ol Pejeta Conservancy, Kenya	303 km^2	22.77	2012	
Ngorongoro Crater, Tanzania	8 288 km^2	22.6	2012	
Hluhluwe iMfolozi Park, South Africa	960 km^2	20.83	2010	
Maasai Mara Game Reserve, Kenya	1 530 km^2	18.68	2005	
Serengeti National Park, Tanzania	14 763 km^2	15.3	2012	
Tembe Private Nature Reserve, South Africa	300 km^2	14.67	2010	
Matambwe (Selous Game Reserve), Tanzania	4 4800 km^2	14	2009	
Makalali Private Wildlife Reserve, South Africa	203 km^2	13.81	2010	
Kwandwe Private Wildlife Reserve, South Africa	185 km^2	13.51	2009	
Lower Sabie – Kruger National Park, South Africa	19 485 km^2	13.48	1995	
Phinda Private Wildlife Reserve, South Africa	246 km^2	12.28	2009	
Central district- Kruger National Park, South Africa	19 485 km^2	11.45	2006	
Malilangwe Private Nature Reserve, Zimbabwe	399 km^2	9.76	2011	
Pilanesberg National Park, South Africa	550 km^2	8.8	2020	(Northwest Parks Tourism board, Unpublished data, 2020)
Taragire National Park, Tanzania	2 850 km^2	8.2	2010	

Samburu/Buffalo Springs Nature Reserve, Kenya	296 km^2	7.77	2011	
Welgevonden Private Wildlife Reserve, South Africa	370 km^2	7	2007	
Save Valley Conservancy, Zimbabwe	2 439 km^2	6.88	2011	
Ongava Game Reserve, Namibia	300 km^2	6.77	2009	
Nakuru National Park, Kenya	188 km^2	6.75	2019	(Elliot *et al*, 2020)
Moremi Game Reserve, Botswana	5 000 km^2	6.67	2009	
Laikipia District, Kenya	3 100 km^2	6.47	2003	
Madikwe Game Reserve, South Africa	620 km^2	5.32	2021	(Northwest Parks Tourism board, Unpublished data, 2021)
Bubye Conservancy, Zimbabwe	3 440 km^2	4.94	2012	
Murchison Falls National Park, Uganda	3 480 km^2	3.79	2009	
Shasha - Queen Elizabeth National Park, Uganda	1 978 km^2	3.39	2008	
Tau, Xudem area, Botswana	5 000 km^2	2.86	2008	
Kavati National Park, Tanzania	4 471 km^2	2.53	2010	
Taita Conservancy, Kenya	690 km^2	2.25	2008	
Niassa-Riparian, Mozambique	42 000 km^2	2	2008	
Hwange National Park, Zimbabwe	14 600 km^2	1.7	2011	
Pendjari National Park, Benin	4 711 km^2	1.6	2009	
Kgalagadi Transfrontier Park, South Africa	36 000 km^2	1.23	2001	
Faro National Park, Cameroon		1.15		
Niassa- Watershed, Mozambique	42 000 km^2	1	2008	
Mbirikani Group Ranch, Kenya	1 230 km^2	0.89	2009	
Bouda Ndjida National Park, Cameroon	2 114 km^2	0.63	2010	
Waza National Park, Cameroon	1 700 km^2	0.53	2008	
Benoue National Park, Cameroon	1 980 km^2	0.36	2010	
Kunene Conservancy, Namibia	40 381 km^2	0.3	2009	

CHAPTER 4

How much sampling effort is required when using Bayesian spatial explicit capture-recapture models to estimate African lion populations in small fenced protected areas?

Isabella A Bettings[a], David G Marneweck[a,b], Nicholas B Elliot[c], Arjun M Gopalaswamy[d,e], Herve Fritz[a,f], and Jan A Venter[a,f]

[a]*Department of Conservation Management, Faculty of Science, George Campus, Nelson Mandela University*

[b]*Endangered Wildlife Trust, Johannesburg, South Africa*

[c]*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxfordshire, OX13 5QL, UK*

[d]*Carnassials Global, 44/1, Regus Supreme, K.R. Road, 7th Block, Jayanagar, Bengaluru – 560070, Karnataka, India*

[e]*Wildlife Conservation Society, Global Conservation Programs, 2300, Southern Boulevard, Bronx, New York, 10460*

[f]*REHABS International Research Laboratory, CNRS-Université Lyon 1-Nelson Mandela University, George Campus, Madiba drive 6531 George, South Africa*

Abstract

Reliable large carnivore population estimates, which generally require time and an associated high cost, are important for effective management in fenced protected areas. Large carnivores are known to be elusive, requiring considerable effort to produce reliable and accurate population estimates. Long-term monitoring methods increase management's understanding of the large carnivore's abundance, behaviour, movement, and effect on prey species. We used direct observation which incorporated driving effort and high-resolution photographs to estimate the abundance, sex ratio, and range size of lions through Bayesian spatially explicit capture-recapture (SECR) models. We were interested in setting a replicable population survey design for trend and estimates of vital rates, to establish a well-designed multi-year data and long-term monitoring programme. We focused on the trade-off between the robustness of the estimates and the field costs of surveys. Applying the SECR sampling design, we used the empirical data to explore the influence of sampling efforts on the relative precision and bias of density estimates of lions in Pilanesberg National Park. A survey completed in 2020 generated these precise estimates. The analyses were repeated with subsamples of the data and compared the estimates from the reduced datasets to those based on the full datasets. All the data was analysed through the Bayesian SECR approach, which was divided in seven, 1 000 km increments and three models. Increment 7 000 km was the benchmark result. We expected that moderate to high driving effort would produce the most accurate data. We concluded that 4 000 km is a sufficient distance in order to estimate lion abundance and density in small fenced protected areas, with a reasonable degree of precision. Management should not reduce their effort of the suggested survey as it can compromise the outputs of the models.

Key words: Bayesian spatial explicit capture-recapture, African lion, monitoring, sampling effort.

Introduction

The decline of wildlife populations remains a global conservation problem, especially for large carnivores (Ripple et al., 2014). Large carnivores are particularly difficult to monitor because they are elusive, nocturnal, and live at relatively low densities (Balme et al., 2009). Ongoing methods for monitoring large carnivores vary in accuracy, cost, and reliability (Gese, 2001; Lahoz-Monfort, Harris, Morgan, Freeman, & Wanless, 2014).

In the early 1990s, fenced protected areas containing mega-herbivores and large carnivores became popular in South Africa due to the growing tourism sector and decreasing wildlife habitats (Hayward, O'Brien, et al., 2007; Miller et al., 2013; Miller & Funston, 2014). These fenced protected areas became essential in the conservation of wildlife of South Africa, especially for large carnivore species (Miller & Funston, 2014). In many fenced protected areas, lions quickly reached their estimated carrying capacity (Packer, Loveridge, et al., 2013).

Monitoring large carnivore populations is not always simple, even if the protected area is fenced (Jiménez et al., 2017). Traditional monitoring methods include spoor tracking and call-up stations, but there are, in many cases, large uncertainties associated with density estimates derived from these methods. Over the last decade, multiple novel tools have been developed to monitor large carnivore populations. These methods not only allow us to compare data on abundance, but also on behaviour, and distribution (Gese, 2001; Jiménez et al., 2017). Advanced analytical inference-based procedures have been created to estimate densities using spatial explicit frameworks (Jiménez et al., 2017). It links the abundance with location by estimating the latent variable, which represents an individual's activity centre and is known as the spatial explicit capture recapture (SECR) approach (Dey, Delampady, & Gopalaswamy, 2019; Gopalaswamy et al., 2012; Jiménez et al., 2017). SECR facilitates robust animal density estimation and is regularly used for estimating population abundance and vital rates of large carnivores (Braczkowski, Gopalaswamy, Elliot, et al., 2020; Broekhuis & Gopalaswamy, 2016). It is important for a survey design to match the analytical technique used to enable precise and accurate estimation of relevant parameters. When density estimates are robust, it can be compared through space and time (Harmsen et al., 2020). Therefore, in SECR surveys, there must be enough detected individuals, sufficient effort/coverage, and an adequate number of recaptures for inferences on animal density. Novel developments using the SECR approach also enables researchers to estimate other important ecological parameters, such as sex ratio, sex-specific movement, and home range size (Braczkowski, Gopalaswamy, Mustafa, et al., 2020). In the long term , SECR approaches enable the estimation of critical vital rates, such as survival and recruitment (Braczkowski, Gopalaswamy, Elliot, et al., 2020). Long term monitoring is vital for numerous conservation programmes, management decisions, and ecological studies (Lahoz-Monfort et al., 2014).

Pilanesberg National Park (PNP) management has encountered challenges in monitoring their lion population. These challenges include resources, time, and manpower. In the previous chapter, we found that the population size is 44 individuals, with a density of 8.8 per 100 km^2 (see previous chapter). We collected data using unstructured spatial sampling in an SECR framework. However, this method is costly, takes time (~90 continuous days) and requires considerable effort (~7,100km) to produce reliable estimates. In order to ensure census cost-effectiveness, we were interested in what is required to produce reasonably accurate and precise results while minimising costs . Here we present an investigation of the influence of varied sampling effort on relative bias and precision of population estimates calculated with SECR, in order to inform future sampling designs. We expected that little driving effort would produce low lion detections and recaptures, considering that moderate to high driving effort would produce an increase in lion detections and recaptures. We also expected detection rates to increase and estimates to become more reliable as effort increases.

Methods

Study area

The Pilanesberg National Park (PNP) (25°08’ to 25°22’S; 26°57’ to 27°13’E) is located in the Northwest Province, South Africa, and covers approximately 550 km^2 (Figure 1). The park is a fenced protected area (Tambling & du Toit, 2005; Vanak et al., 2010). According to Mucina et al., (2006) the park falls under the savanna biome and consists of Pilanesberg Mountain Bushveld. It covers a unique ecotone of wetter Bushveld vegetation and Kalahari Thornveld known as Sour Bushveld (Kidwai et al., 2019; Vanak et al., 2010; Woolley et al., 2011). Further, vegetation in the park is mainly broad leaf bushveld, mixed Acacia, and patches of open grasslands and thickets due to past mining operations and agricultural practices (Rutherford et al., 2006; Van Dyk & Slotow, 2003). The PNP falls under a summer rainfall region with an average rainfall of 632 mm per year (la Grange et al., 2009; Van Dyk and Slotow, 2003). The mean temperature during the summer varies between (19°C and 31°C) and in winter between (3°C and 21°C) (la Grange et al., 2009).

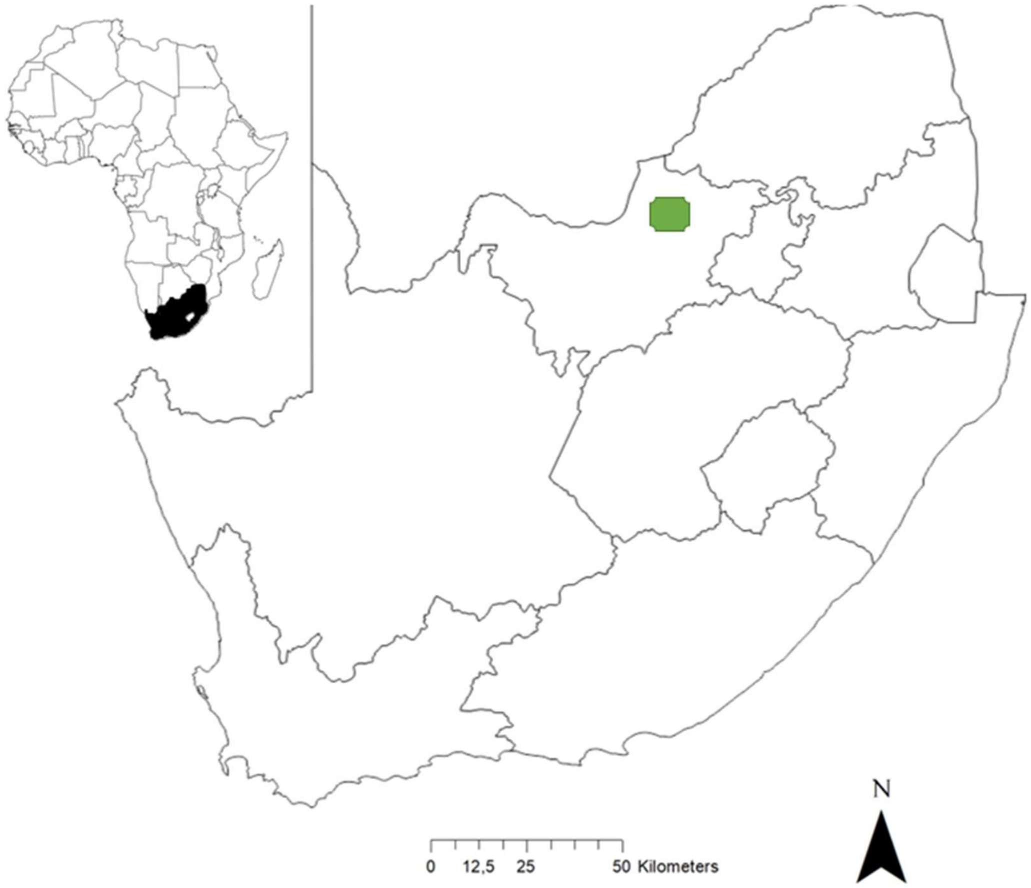


Figure 1. The location (indicated in green) of Pilanesberg National Park, a 550 km^2 fenced protected area within the North West province of South Africa.

Field sampling

I conducted a lion survey from 25 August to 10 December 2020, which covered 90 survey days in total. A total of 7 349.81 km driving effort was invested. The survey was conducted shortly after the dry season. I made observations form a 4x4 vehicle during the daily lion searches (Braczkowski, Gopalaswamy, Mustafa, et al., 2020). The road network of PNP is extensive, however, it does not cover the whole park (Figure 2). I kept an average speed of 15 km per hour twice a day a) sunrise from 05:00-10:30 and

b) late afternoon 16:00 - 18:30 when lions were most active (Lehmann, Funston, Owen, & Slotow, 2008a, 2008b). I used Cybertracker (v3) application (www.cybertracker.org), which was installed on an android smartphone (BlackView), to record the lion detection data. This application has a built in Global Positioning System (GPS) and was set to record my location every 10 seconds. I recorded the following data during a lion encounter, number of individuals, age class (adult, sub-adult, cub), sex (male, female), activity (hunting, sleeping, moving), habitat (woodlands, open grasslands, riverine), field notes, and precise location. I recorded lions of all ages during the survey, but lions < 1-year were discarded from the data set since their mortality rate is high (Packer et al., 1988).

I allocated five road segments, west, south, east, north, and central sections in PNP. At the end of every day, set routes were selected which was driven the following sunrise and afternoon to ensure evenly distributed driving effort (Elliot & Gopalaswamy, 2017). After completing the set route for the day, I used citizen science via radio call ins from guides and social media to collect additional lion detections (Rafiq et al., 2019). Search effort was the most important aspect to record throughout the study to avoid any bias during the study. Through appropriate effort, an adequate amount of precise data can be generated, which are useful to the park manager (Tarugara et al., 2019). Aiming to search each of the 1 km x 1 km trap can improve the detection of lions in all traps. Through increased search effort the data set improves (Boitani et al., 2012; Tarugara et al., 2019). I created Cybertracker heatmaps to review where more effort was needed, to ensure sample effort across the 1 km x 1 km traps.

I created identification (ID) kits for each individual lion that was detected during the lion survey (Figure 3). A 5D Canon camera and Sigma 150-600hmm F/5-6,3 DG OS HSM-Canon Sigma lens was used to take photographs (Braczkowski, Gopalaswamy, Mustafa, et al., 2020). Taking lion photographs at different angles are vital for identifying individuals and creating a profile for each individual (Brink et al., 2012). Primarily, each ID kit consisted of, if possible, 1) left, right, and full body, 2) left, right, and front side of face, and 3) additional scars and marks to create an ID profile for each lion, see (Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Brink et al., 2012; Creel & Creel, 1997; Elliot et al., 2020; Hatfield, 2014; Kane et al., 2015; Pennycuick & Rudnai, 1970). The emphasis of the photographs was to determine which individual were detected at each sighting without making any conjecture, since lions have a fission-fusion social dynamic (Mbizah et al., 2019). External validation was done on the capture history by one of the authors not involved in the fieldwork. Discrepancies between the original and validated data were discussed, and a consensus was agreed upon and produced a final validated capture history that was analysed through Bayesian SECR model.

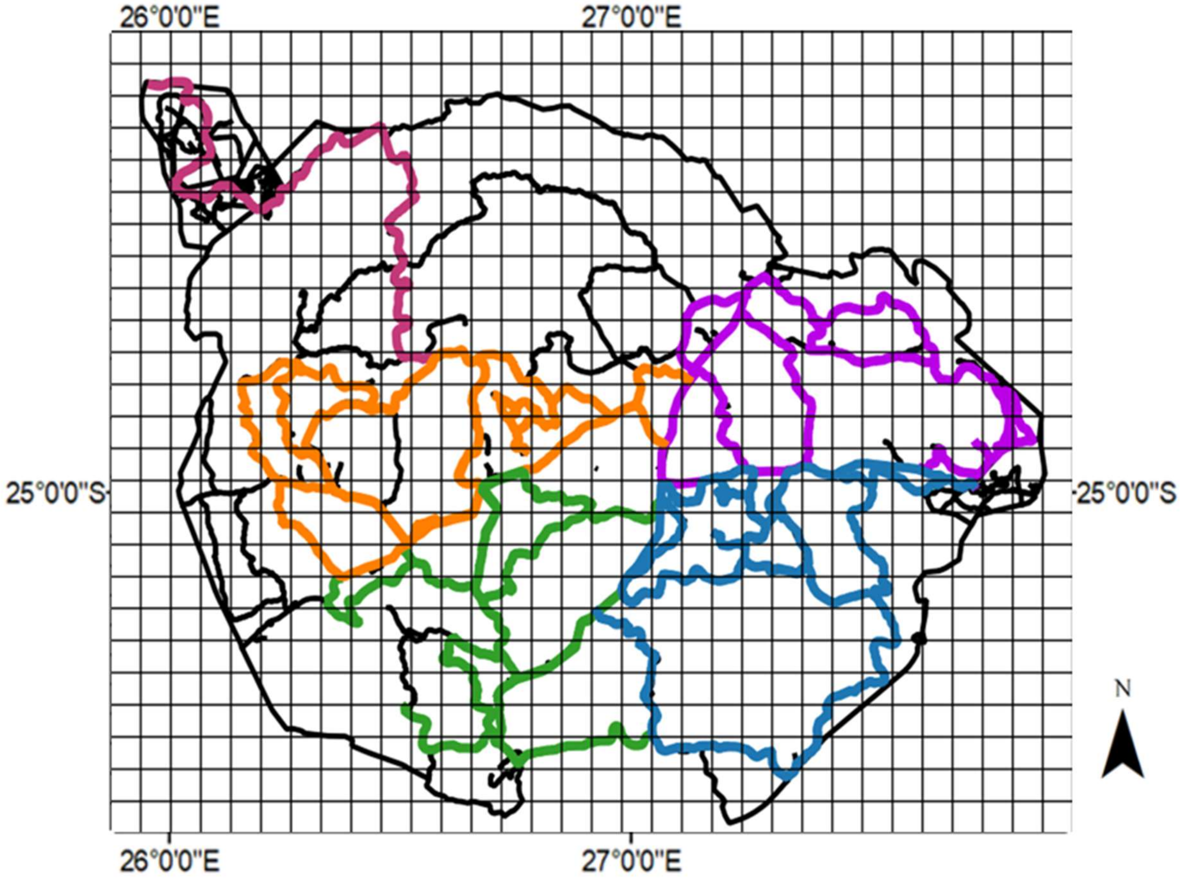


Figure 2. The survey routes during the lion survey in Pilanesberg National Park. The five distinctive colours represent a route driven once or twice a week. The border of the park is illustrated as a black line. The other blackline within the border is old roads that cannot be driven due to erosion. The size of the grid squares is 1 km x 1 km.

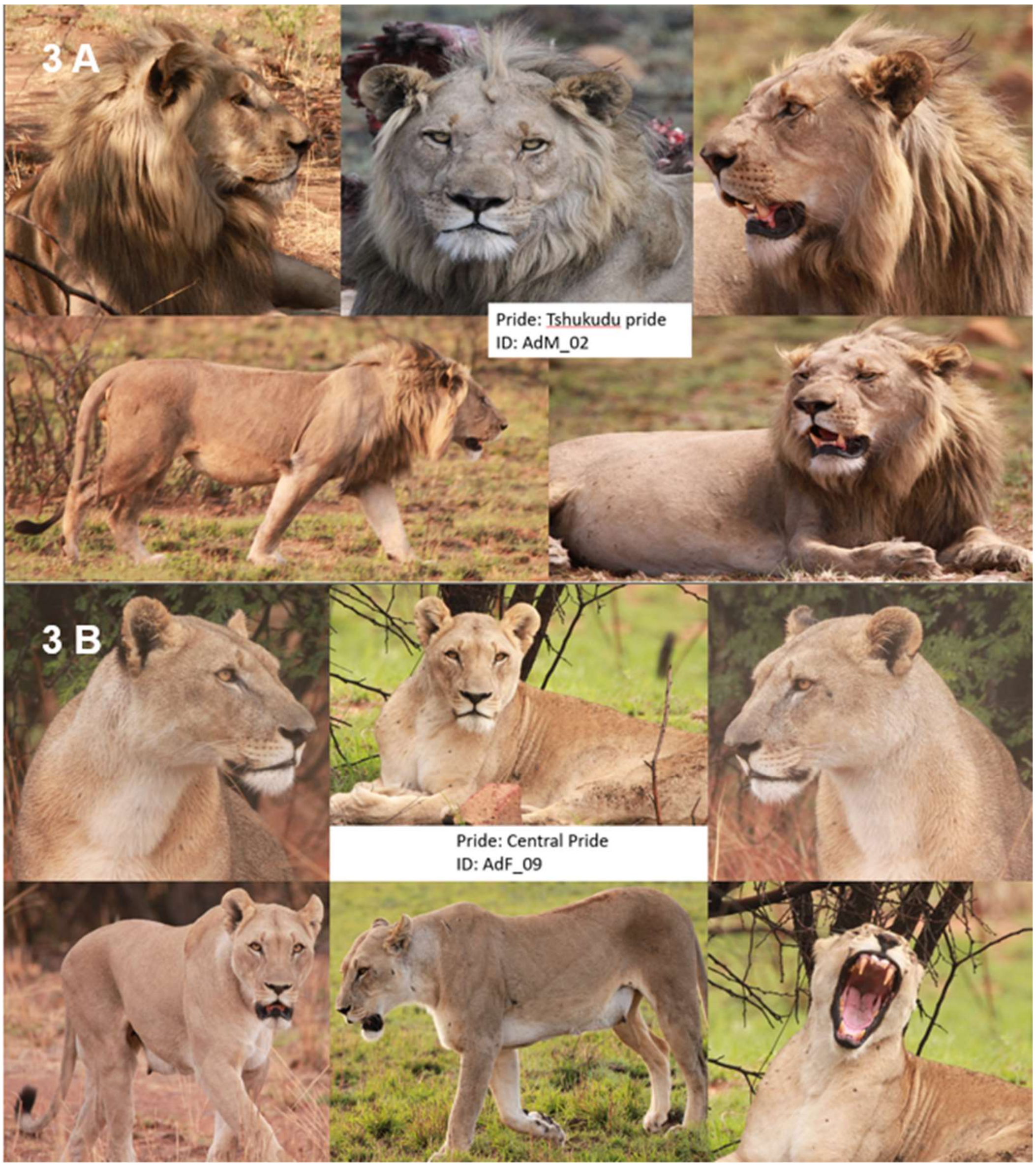


Figure 3. Example of Pilanesberg National Park lion ID kits showing A) one adult male lion and B) one adult female recorded during the survey.

Analytical framework

We used the lion survey data that were collected in 2020 and performed a subsampling experiment to understand how to reduce sampling effort affects the precise and bias of our estimate. Accuracy is how researchers measure how close the estimate is to the true population size (Gese, 2001). We used the kilometres driven in 2020, 7 349.81 km, and divided it into seven 1 000 increments. Regarding the spatial distribution of lions (state process), we generated a state space that essentially needed to be 2.5 times larger than the expected spatial scale parameter sigma (σ) (Elliot et al., 2020). Our potential activity centres, which are represented by evenly spaced pixels of 0.5

km^2, were spread over 707 km^2 to form the state space (Elliot & Gopalaswamy, 2017; Gopalaswamy et al., 2012; Royle & Converse, 2014). PNP is a fully fenced and electrified protected area which prevents dangerous animals from escaping (Pekor et al., 2019). Hence our study population can be considered as closed for our modelling exercise. We set the data augmentation value *M* at 300 for the first three models, thereafter it was 200.

Pertaining to the way in which individual animals were detected during our driving effort survey (observation process), we followed the measures described by Elliot & Gopalaswamy, (2017). This demanded a compiled standard SECR that consisted of individuals, sampling occasions, and trap locations (0.5 km^2). Seeing that highly sampled traps could possibly increase the number of detections, we included an effort covariate (logarithm of kilometres driven) per trap per day. Therefore, we expected that little driving effort would produce low lion detections and recaptures, whereas moderate to high driving effort would produce an increase in lion detections and recaptures (Braczkowski, Gopalaswamy, Mustafa, et al., 2020). The unstructured sampling of the SECR approach could only be implemented if the effort covariate were included (Elliot et al., 2020). The inclusion of spatial heterogeneity in detection probability made the SECR models much more reliable than the capture-recapture model (Royle et al., 2009). This is crucial since the probability of detecting an individual lion declined with increasing distance between its activity center and a searched pixel (Royle et al., 2013). Males and females have various home range sizes, which might have an effect on the observation process in the SECR models for that reason, we incorporated a sex specific covariate (Elliot & Gopalaswamy, 2017). Lastly, we estimated sex, ratio through different detection probabilities (Elliot et al., 2020).

Candidate model

I drove 7 349.81 km during the 2020 lion survey (rounded down to a total of 7 000 km). As a result, driving effort was divided into seven 1 000 km increments to investigate how much effort was needed to be precise and bias enough to estimate lion abundance and density. Each increment is represented, by having covered all the five road segments twice. Each increment had either one or three models, which gave the estimated results. All newly tested increments 1 000 – 6 000 km with their models (1 -

3 model) illustrated their posterior outputs which were compared with the benchmark results (7 000 km).

We described 3 priori models and compared their posterior outputs (Elliot et al., 2020). The detection function parameter theta (θ) was set to 1, throughout the study. The complementary log-log function of covariates described below, illustrated the probability of detecting lion *i* in pixel *j* on sampling occasion *k* (π_{ijk}) (Gopalaswamy et al., 2012; Royle & Converse, 2014):

$$\lambda 0+\beta_{eff}\left[\log\left(Effort_{jk}\right)\right]+\beta_{sex}\left(sex_{i}\right)-f\left[dist\left(i,j\right)\middle|\theta,\sigma_{sex}\right.$$
$$cloglog\left(\pi_{ijk}\right)=\log$$

The function *f* [dist.(*i,j*)| θ, σ_{sex}] defines how the detection rate is a function of distance between the activity center of individual *i,* and pixel *j*, which are conditional on θ and σ_{sex}. We ran three variations of this traditional model, which follows as;

Model 1 – *N*(.), λ_0(sex + effort), σ (sex): The basal encounter rate and the spatial scale parameter is sex-specific.

Model 2 – *N*(.), λ_0(effort), σ (sex): the spatial scale parameter is sex-specific, but the basal encounter rate is independent of sex.

Model 3 - N(.), λ_0(effort), σ (.): The spatial scale parameter and the basal encounter rate are independent of sex.

We formatted all data to analyse three prior models using the statistical adaption package SCRbayes (https://github.com/jaroyle/SCRbayes) which were carried out in the data processing environment R (R Development Core Team 2021, version 4.1.2) (Elliot & Gopalaswamy, 2017; Mcevoy, 2019; Royle & Converse, 2014). I used a distinct R script developed by Elliot et al., (2020). The main functions that run throughout the script were Bayesian Markov Chain Monte Carlo (MCMC) and Metropolis Hasting algorithms (Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Vega Yon & Marjoram, 2019). During the diagnostics phase of each model, in the respected increment, the MCMC got examined for convergence by adding trace plots for each parameter of interest (Vega Yon & Marjoram, 2019). The calculated values of Gelman-Rubin should be below 1.1 to reach convergence for each parameter (Gelman & Rubin, 1992; López-Bao et al., 2018; Vega Yon & Marjoram, 2019). If convergence has not been reached, one can either a) perform a post ad hoc iterations burn-in or b) add longer chains, which would require a re-run of the whole model's analysis (Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Elliot et al., 2020). This process continues until convergence has been accomplished (Elliot et al., 2020). To choose the correct model, three inferences were used a) goodness-of-fit assessment by using the Bayesian *p* value evaluation to examine individual encounter frequencies (Elliot et al., 2020; López-Bao et al., 2018). The Bayesian *p* values have extremities (0.15-0.85) that indicated whether a model is a good or poor fit. The Bayesian *p* value tool is used as model rejection criteria (Elliot et al., 2020). b) Pair-wise correlation plots were created which is situated between the estimated parameters of the posterior MCMC draws. Although, it is vital to examine whether the correlations are influencing the abundance parameters. c) The harmonic mean estimator of the logarithm of the marginal likelihood was used as the a model selection tool for the Bayesian SECR models (Broekhuis et al., 2021; Elliot et al., 2020; Elliot & Gopalaswamy, 2017). We calculated the home range size, through the formulation bivariate normal kernel estimator: $\pi(\sigma\ \sqrt{}5.99)^2$) (Braczkowski, Gopalaswamy, Mustafa, et al., 2020; Broekhuis et al., 2021). All the diagnostics parameter output is illustrated in Table S.2-5, see appendix. Additionally, we calculated the coefficient of variance and relative bias, the percentage of the standard deviation to the mean, which indicated the level of variability between each model in respective increments (Arnholt & Herbert, 1995; Kazemi & Jafari, 2020). We calculated the coefficient of variance (CV) using a formula $(CV = \frac{\sigma}{\mu})$. CV is an analysis of data points dispersed around the mean. The benchmark is often used to compare data dispersion between distinct data series (Arnholt & Herbert, 1995). For relative bias, consider the true value of a parameter to be the posterior mean estimate of that parameter of the full dataset, 7 000 km. Taking the posterior mean estimate of that same parameter at the increment datasets, 1 000 km, 2 000 km etc is value partial. The formula that we used is (value partial - value full)/(value full) to calculate the relative bias (Figure S.2.1 and S.2.2, see appendix).

Results

Model diagnostics

Increment 1 000 km to 3 000 km had very few recaptures which is reflected in the output results since it was difficult to get convergence, especially in increment 1 000 km. The total lion detections (in parentheses) from the increments were: 1 000 km

(20), 2 000 km (57), 3 000 km (76), 4 000 km (112), 5 000 km (134), 6 000 km (157), and 7 000 km (184) increased as driving effort increased. Similarly with the total recaptures per increment 1 000 km (2), 2 000 km (29), 3 000 km (46), 4 000 km (81), 5 000 km (103), 6 000 km (123), and 7 000 km (147) confirmed that more driving effort produced better datasets and earlier convergence without the need to evaluate additional chains.

Posterior density and abundance estimates

Based on model 2 (increment 4 000 km), the PNP population size 45 (mode = 44, posterior *SD* = 5.247, 95% highest posterior density interval = 35 - 55). The mean lion density (individuals >1-year-old/100 km^2) is 9.1 (mode = 8.8, posterior *SD* = 1.1, 95% highest density interval = 7 - 11.1). The estimated sex ratio produced by ψ_{sex} was 1♀:1♂. The movement of lions was measured by the σ parameter of model 2. The σ for females was 2.918 and σ for males was 3.501. We calculated the home range size, through the formulation: $\pi(\sigma\sqrt{5.99})^2)$ (Royle et al., 2013). Based on this, the average home range estimate of female lions was 160 km^2 with a range of (103 – 232 km^2) and 230 km^2 with a range of (147 – 348 km^2) for males. These results can be compared with the original results which are the 7 000-increment model 1 (i.e., data chapter 1). The results are as follow, 44 individuals (mode = 43, posterior *SD* = 3.054, 95% highest posterior density interval = 38 – 49). The mean lion density (individuals >1 year old/100 km^2) is 8.8 (mode = 8.6, posterior *SD* = 0.6%, 95% highest posterior density interval = 7.8 – 10.1). The estimated sex ratio produced by ψ_{sex} was 0.9♀:1♂. The movement of lions was measured by the σ parameter of model 1. The σ for males and females were 3.854 and 3.189, respectively. Based on this, the average home range estimate of male lions was 279 km^2 with a range of (197 – 385 km^2) and 191 km^2 with a range of (135 – 262 km^2) for female lions.

Discussion

Our results showed that the minimum driving effort of 4 000 km was needed to accurately estimate lion population parameters in PNP. However, increased effort after the 4 000 km is exceptional as it further improves confidence. Many managers and researchers are often aiming for the most cost-effective way to monitor lions. Systems similar to PNP, would require just over half of the full effort, to get the minimum data required to gain a good understanding of the lion population size, sex ratio, home range size. When effort is increased, more detections and recaptures will be obtained which produce precise data. When effort is lower than i.e., < 4 000 km increment, it could produce unreliable results. Consequently, management could make decisions that might have a bad impact on the health of the ecosystem. Therefore, we strongly recommend managers to consider the amount of effort required to get reliable estimates.

The first increment 1 000 km did not have enough data to produce converging models, which was expected with limited number of iterations. Increments of 2 000 and 3 000 km did produce models which satisfied the Bayesian *p* value criterion. But the coefficient of variance indicated that the results of the first three increments showed a great deal of dispersion around the mean, whereas increment four to seven did correlate around the mean, see Figure S.2.1 appendix. Acceptable reliability levels commenced at 4 000 km and increased in reliability as it moved closer to 7 000 km effort. The 1 000 – 3 000 km effort did not have enough detections and recaptures to allow for reliable estimates.

In parks like PNP (fenced, small, with tourist-habituated lions), this method is useful for a survey i.e., 4 000 km ~ 51 days of effort, to count lions. This can be applied to other small fenced protected areas where reliable estimates are not available and continuous monitoring not an option. Repeated SECR surveys over long-term, have the capability to provide vital insight of the lion population dynamic and guide conservation interventions (Braczkowski, Gopalaswamy, Elliot, et al., 2020). Comparing annual results will contribute to detecting a fluctuation within a certain carnivore or herbivore population and assist with conservation decision making (Durant et al., 2011).

References

Alibhai, S., Jewell, Z., & Evans, J. (2017). The challenge of monitoring elusive large carnivores: An accurate and cost-effective tool to identify and sex pumas (Puma concolor) from footprints. *PloS one*, *12*(3), e0172065. https://doi.org/10.1371/journal.pone.0172065

Arnholt, A. T., & Herbert, J. (1995). Estimating the mean with known coefficient of variation. *The American Statistician*, *49*(4), 367–369.

Auffray, J.-C., Renaud, S., & Claude, J. (2009). Rodent Biodiversity in Changing Environments. *Kasetsart Journal, Natural Science*, *43*(1), 83–93. Retrieved from https://www.researchgate.net/publication/228350392

Balme, G. A., Hunter, L. T. B., & Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, *73*(3), 433–441. https://doi.org/10.2193/2007-368

Barthold, J. A., Loveridge, A. J., Macdonald, D. W., Packer, C., & Colchero, F. (2016). Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, *53*(2), 295–304. https://doi.org/10.1111/1365-2664.12594

Bauer, H., & Van Der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, *38*(1), 26–31. https://doi.org/10.1017/S0030605304000055

Bauer, Hans., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., … Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *PNAS*, *112*(48), 14894–14899. https://doi.org/10.1073/pnas.1500664112

Belant, J. L., Bled, F., Mkasanga, I. J., Wilton, C. M., Mwampeta, S. B., Beyer, D. E., … Fyumagwa, R. (2019). Track surveys do not provide accurate or precise lion density estimates in Serengeti. *Global Ecology and Conservation*, *19*, e00651. https://doi.org/10.1016/j.gecco.2019.e00651

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, *90*, 171–180. https://doi.org/10.1016/j.anbehav.2014.01.030

Boitani, L., Ciucci, P., & Mortelliti, A. (2012). Designing carnivore surveys. In *Carnivore ecology and management: a handbook of techniques* (pp. 8–29). https://doi.org/10.1093/acprof

Borchers, D. (2012). A non-technical overview of spatially explicit capture-recapture models. *Journal of Ornithology*, *152*(2), 435–444. https://doi.org/10.1007/s10336-010-0583-z

Borchers, D., Distiller, G., Foster, R., Harmsen, B., & Milazzo, L. (2014). Continuous-time spatially explicit capture-recapture models, with an application to a jaguar camera-trap survey. *Methods in Ecology and Evolution*, *5*(7), 656–665. https://doi.org/10.1111/2041-210X.12196

Botai, C. M., Botai, J. O., Dlamini, L. C., Zwane, N. S., & Phaduli, E. (2016). Characteristics of droughts in South Africa: A case study of Free State and North West provinces. *Water*, *8*(10), 439. https://doi.org/10.3390/w8100439

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., … Allan, J. R. (2020). Restoring Africa’s lions: Start with good counts. *Frontiers in Ecology and Evolution*, *8*, 138. https://doi.org/10.3389/fevo.2020.00138

Braczkowski, A., Gopalaswamy, A. M., Mustafa, N., Allan, J., Biggs, D., & Maron, M. (2020). Detecting early warnings of pressure on an African lion (*Panthera leo*) population in the Queen Elizabeth Conservation Area , Uganda. *Ecological Solution Eviddence*, *1*, e12015. https://doi.org/10.1002/2688-8319.12015

Briers-Louw, W. D. (2017). Ecology of three apex predators in Majete Wildlife Reserve, Malawi (Doctoral dissertation). Stellenbosch University, Stellenbosch.

Brink, H., Smith, R. J., & Skinner, K. (2012). Methods for lion monitoring: A comparison from the Selous Game Reserve, Tanzania. *African Journal of Ecology*, *51*(2), 366–375. https://doi.org/10.1111/aje.12051

Broekhuis, F., Elliot, N. B., Keiwua, K., Koinet, K., Macdonald, D. W., Mogensen, N., … Gopalaswamy, A. M. (2021). Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography*, *44*(3), 358–369. https://doi.org/10.1111/ecog.05154

Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PloS one*, *11*(5), 1–15. https://doi.org/10.1371/journal.pone.0153875

Caravaggi, A., Banks, P. B., Burton, C. A., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., … Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109–122. https://doi.org/10.1002/rse2.48

Carbone, C., Teacher, A., & Rowcliffe, M. J. (2007). The costs of carnivory. *PLoS Biology*, *5*(2), 0363–0368. https://doi.org/10.1371/journal.pbio.0050022

Carruthers, J. (2011). Pilanesberg National Park, North West Province, South Africa: Uniting economic development with ecological design – A history, 1960s to 1984. *Koedoe*, *53*(1), 1–10. https://doi.org/10.4102/koedoe.v53i1.1028

Clark, T. J., Horne, J. S., Hebblewhite, M., & Luis, A. D. (2021). Stochastic predation exposes prey to predator pits and local extinction. *Oikos*, *130*(2), 300–309. https://doi.org/10.1111/oik.07381

Comley, J., Joubert, C. J., Mgqatsa, N., & Parker, D. M. (2020). Battle of the Large Carnivores: Spatial Partitioning in a Small, Enclosed Reserve? *African Journal of Wildlife Research*, *50*(1), 176–189. https://doi.org/10.3957/056.050.0176

Cooper, D. M., Dugmore, A. J., Kitchener, A. C., Metzger, M. J., & Trabucco, A. (2021). A kingdom in decline: Holocene range contraction of the lion (*Panthera leo*) modelled with global environmental stratification. *PeerJ*, *9*, e10504. https://doi.org/10.7717/peerj.10504

Creel, S., Becker, M. S., Durant, S. M., M'Soka, J., Matandiko, W., Dickman, A. J., … Zimmermann, A. (2013). Conserving large populations of lions - the argument for fences has holes. *Ecology Letters*, *16*(11), 1413-e3. https://doi.org/10.1111/ele.12145

Creel, Scott., & Creel, N. M. (1997). Lion density and population structure in the Selous Game Reserve: Evaluation of hunting quotas and offtake. *African Journal of Ecology*, *35*(2), 83–93. https://doi.org/10.1111/j.1365-2028.1997.062-89062.x

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., … Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS one*, *13*(7), e0196213. https://doi.org/10.1371/journal.pone.0196213

De Boer, W. F., Vis, M. J. P., De Knegt, H. J., Rowles, C., Kohi, E. M., van Langevelde, F., … Prins, H. H. T. (2010). Spatial distribution of lion kills determined by water dependency of prey species. *Journal of Mammalogy*, *91*(5), 1280–1286. https://doi.org/10.1644/09-MAMM-A-392.1

de Manuel, M., Barnett, R., Sandoval-Velasco, M., Yamaguchi, N., Vieira, F. G., Mendoza, L. Z. M., … Gilbert, T. M. (2020). The evolutionary history of extinct and living lions. PNAS, *117*(20), 10927–10934. https://doi.org/10.1073/pnas.1919423117

Dey, S., Delampady, M., & Gopalaswamy, A. M. (2019). Bayesian model selection for spatial capture–recapture models. *Ecology and Evolution*, *9*(20), 11569–11583. https://doi.org/10.1002/ece3.5551

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, S. R., & Frank, L. (2014). A metapopulation approach to African lion (*Panthera leo*) conservation. *PloS one*, *9*(2). https://doi.org/10.1371/journal.pone.0088081

Dröge, E., Creel, S., Becker, M. S., Loveridge, A. J., Sousa, L. L., & Macdonald, D. W. (2020). Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecology and Evolution*, *10*(7), 3276–3292. https://doi.org/10.1002/ece3.6065

Durant, S. M., Craft, M. E., Hilborn, R., Bashir, S., Hando, J., & Thomas, L. (2011). Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *Journal of Applied Ecology*, *48*(6), 1490–1500. https://doi.org/10.1111/j.1365-2664.2011.02042.x

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion - conservation stronghold. *Density and Distribution*, *25*, 870–879. https://doi.org/10.1111/ddi.12905

Edwards, S., Cooper, S., Uiseb, K., Hayward, M., Wachter, B., & Melzheimer, J. (2018). Making the most of by-catch data: Assessing the feasibility of utilising non-target camera trap data for occupancy modelling of a large felid. *African Journal of Ecology*, *56*(4), 885–894. https://doi.org/10.1111/aje.12511

Elliot, N. B., Bett, A., Chege, M., Sankan, K., de Souza, N., Kariuki, L., … Gopalaswamy, A. M. (2020). The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice*, 1–11. https://doi.org/10.1111/csp2.217

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., & Macdonald, D. W. (2014). Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, *95*(10), 2860–2869. https://doi.org/10.1890/13-1793.1

Elliot, N. B., & Gopalaswamy, A. M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, *31*(4), 934–943. https://doi.org/10.1111/cobi.12878

Elliot, N. B., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos*, *123*(9), 1049–1056. https://doi.org/10.1111/oik.01266

Estes, R. D. (2012). Lion (*Panthera leo*). In *The behaviour guide to African mammals* (pp. 369–377). London and Los Angeles and Berkeley: The University of California Press.

Everatt, K. T., Kokes, R., & Pereira, C. L. (2019). Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation*, *28*(14), 4099–4114. https://doi.org/10.1007/s10531-019-01866-w

Ferreira, S. M., Beukes, O. B., Haas, T. C., & Radloff, F. G. T. (2020). Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park. *African Journal of Ecology*, *58*(3), 348–360. https://doi.org/10.1111/aje.12728

Ferreira, S. M., & Funston, P. J. (2010). Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, *37*(3), 194–206. https://doi.org/10.1071/WR09030

Ferreira, S. M., & Hofmeyr, M. (2014). Managing charismatic carnivores in small areas: Large felids in South Africa. *South African Journal of Wildlife Research*, *44*(1), 32–42.

Forsyth, D. M., Ramsey, D. S. L., & Woodford, L. P. (2019). Estimating abundances, densities, and interspecific associations in a carnivore community. *The Journal of Wildlife Management*, *83*(5), 1090–1102. https://doi.org/10.1002/jwmg.21675

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M., & Clobert, J. (2011). A food web perspective on large herbivore community limitation. *Ecography*, *34*(2), 196–202. https://doi.org/10.1111/j.1600-0587.2010.06537.x

Funston, P J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., … Ferreira, S. M. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, *281*(1), 56–65. https://doi.org/10.1111/j.1469-7998.2009.00682.x

Funston, P J., & Levendal, M. (2015). *Biodiversity management plan for the lion (Panthera leo) in South Africa. Government Gazette, 2*. Retrieved from www.gpwonline.co.za

Funston, P J., & Mills, M. G. L. (2006). The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *African Journal of Wildlife Research*, *36*(1), 9–22.

Funston, P J., Mills, M. G. L., & Biggs, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, *253*(4), 419–431.

Funston, Paul J. (2011). Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, *41*(1), 1–10.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–511.

Gese, E. M. (2001). Monitoring of terrestrial carnivore populations. *Conservation Biology Series- Cambridge-*, 372–396.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, *10*(1), 57–63. https://doi.org/10.1007/BF00296396

Gomez, D., Sommaro, L., Steinmann, A., Chiappero, M., & Priotto, J. (2011). Movement distances of two species of sympatric rodents in linear habitats of Central Argentine agro-ecosystems. *Mammalian Biology*, *76*, 58–63.

https://doi.org/10.1016/j.mambio.2010.02.001

Goodall, V. L., Ferreira, S. M., Funston, P. J., & Maruping-Mzileni, N. (2019). Uncovering hidden states in African lion movement data using hidden Markov models. *Wildlife Research*, *46*(4), 296–303. https://doi.org/10.1071/WR18004

Gopalaswamy, A. M., Delampady, M., Karanth, U. K., Kumar, S. N., & Macdonald, D. W. (2015). An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods in Ecology and Evolution*, *6*(9), 1055–1066. https://doi.org/10.1111/2041-210X.12351

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program SPACECAP: Software for estimating animal density using spatially explicit capture-recapture models. *Methods in Ecology and Evolution*, *3*(6), 1067–1072. https://doi.org/10.1111/j.2041-210X.2012.00241.x

Groom, R. J., Funston, P. J., & Mandisodza, R. (2014). Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: What is driving the population collapse? *Oryx*, *48*(3), 385–393. https://doi.org/10.1017/S0030605312001457

Gusset, M., & Burgener, N. (2005). Estimating larger carnivore numbers from track counts and measurement. *African Journal of Ecology*, *43*, 320–324.

Harmsen, B. J., Foster, R. J., & Quigley, H. (2020). Spatially explicit capture recapture density estimates: Robustness, accuracy and precision in a long-term study of jaguars (*Panthera onca*). *PloS one*, *15*(6), e0227468. https://doi.org/10.1371/journal.pone.0227468

Hatfield, R. (2014). Population dynamics of the African lion (*Panthera leo*) within the Maasai Mara region of southern Kenya. *Kaleidoscope*, *11*(1), 70.

Hayward, M. W., Adendorff, J., O'Brien, J., Sholto-douglas, A., Bissett, C., Moolman, L. C., … Kerley, G. I. H. (2007). Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eatern Cape Province. *The Open Conservation Biology Journal*, *1*(1), 1–11.

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, Ullas K., Mackenzie, D. I., … Yarnell, R. W. (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, *52*(2), 286–290.

https://doi.org/10.1111/1365-2664.12408

Hayward, M. W., Hayward, G. J., Druce, D. J., & Kerley, G. I. H. (2009). Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity Conservation*, *18*, 887–904. https://doi.org/10.1007/s10531-008-9452-y

Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, *267*, 309–322. https://doi.org/10.1017/S0952836905007508

Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, *139*(1–2), 219–229. https://doi.org/10.1016/j.biocon.2007.06.018

Holekamp, K. E., & Sawdy, M. A. (2019). The evolution of matrilineal social systems in fissiped carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1780), 20180065. https://doi.org/10.1098/rstb.2018.0065

Hrabar, H., & du Toit, J. T. (2005). Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conservation*, *8*(3), 259–267. https://doi.org/10.1017/S1367943005002234

Jewell, Z. (2013). Effect of monitoring technique on quality of conservation science. *Conservation Biology*, *27*(3), 501–508. https://doi.org/10.1111/cobi.12066

Jiménez, J., Nuñez-Arjona, J. C., Rueda, C., González, L. M., Garciá-Domínguez, F., Munõz-Igualada, J., & López-Bao, J. V. (2017). Estimating carnivore community structures. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/srep41036

Kane, M. D., Morin, D. J., & Kelly, M. J. (2015). Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodiversity and Conservation*, *24*(14), 3527–3541. https://doi.org/10.1007/s10531-015-1012-7

Karanth, U. K., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, *79*(8), 2852–2862. https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2

Kazemi, M. R., & Jafari, A. A. (2020). Small sample inference for the common coefficient of variation. *Communications in Statistics: Simulation and Computation*, *49*(1), 226–243. https://doi.org/10.1080/03610918.2018.1484474

Keet, D. F. (2010). Lions. In *Game Ranch Management* (Fith Editi, pp. 295–312). Van Schaik Publication.

Kettles, R., & Slotow, R. (2009). Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research*, *39*(1), 23–33. Retrieved from https://journals.co.za/docserver/fulltext/wild/39/1/wild_v39_n1_a3.pdf?expires=1560189647&id=id&accname=guest&checksum=514349490088AEF9B952A9F9167F8569

Kidwai, Z., Jimenez, J., Louw, C. J., Nel, H. P., & Marshal, J. P. (2019). Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (*Diceros bicornis*) populations from aerial counts. *Global Ecology and Conservation*, *19*, e00687. https://doi.org/10.1016/j.gecco.2019.e00687

Kiffner, C., Meyer, B., Mühlenberg, M., & Waltert, M. (2009). Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania? *Oryx*, *43*(1), 52–59. https://doi.org/10.1017/S0030605307002335

Kissui, B. M., & Packer, C. (2004). Top-down population regulation of a top predator: Lions in the Ngorongoro Crater. Proceedings of *the Royal Society of London*, *271*, 1867–1874. https://doi.org/10.1098/rspb.2004.2797

la Grange, M., Kellner, K., Cilliers, S. S., & Götze, A. R. (2009). Vegetation classification of the proposed Heritage Park, North-West Province, South Africa (North-West University; Vol. 75). https://doi.org/10.1016/j.sajb.2009.02.149

Lahoz-Monfort, J. J., Harris, M. P., Morgan, B. J. T., Freeman, S. N., & Wanless, S. (2014). Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. *Journal of Applied Ecology*, *51*(2), 534–543. https://doi.org/10.1111/1365-2664.12214

le Roux, E., Marneweck, D. G., Clinning, G., Druce, D. J., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2019). Top–down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography*, *42*(6), 1115–1123. https://doi.org/10.1111/ecog.03791

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008a). Feeding behaviour of lions (*Panthera leo*) on a small reserve. *African Journal of Wildlife Research*, *38*(1), 66–78.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008b). Home range utilisation and territorial behavior of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PloS one*, *3*(12), e3998. https://doi.org/10.1371/journal.pone.0003998

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008c). Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. *African Zoology*, *43*(2), 230–236. https://doi.org/10.3377/1562-7020-43.2.230

Lesilau, F., Verschueren, S., van't Zelfde, M., Musters, K. C. J. M., de Snoo, G. R., & de Iongh, H. H. (2021). Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: The case study of Nairobi National Park, Kenya. *Mammalia*, *85*(3), 198–207. https://doi.org/10.1515/mammalia-2020-0116

Lindner, E., & Fuelling, O. (2002). Marking methods in small mammals: ear-tattoo as an alternative to toe-clipping. *The Zoological Society of London*, *256*, 159–163.

Lindsey, P. A., Petracca, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., … Hunter, L. T. B. (2017). The performance of African protected areas for lions and their prey. *Biological Conservation*, *209*, 137–149. https://doi.org/10.1016/j.biocon.2017.01.011

López-Bao, J. V., Godinho, R., Pacheco, C., Lema, F. J., García, E., Llaneza, L., … Jiménez, J. (2018). Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. *Scientific Reports*, *8*(1), 1–8. https://doi.org/10.1038/s41598-018-20675-9

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, *54*(3), 815–825. https://doi.org/10.1111/1365-2664.12794

Macdonald, D. W., Loveridge, A. J., & Nowell, K. (2010). Dramatis personae: an introduction to the wild felids. In *The biology and conservation of wild felids* (First Edit, pp. 3–59). Oxford University Press (OUP).

Magome, H., Cain, J. W., Owen-Smith, N., & Henley, S. R. (2008). Forage selection of sable antelope in Pilanesberg Game Reserve, South Africa. *African Journal of Wildlife Research*, *38*(1), 35–41. https://doi.org/10.3957/0379-4369-38.1.35

Mari, L., Gatto, M., & Casagrandi, R. (2008). Local resource competition and the skewness of the sex ratio: A demographic model. *Mathematical Biosciences and Engineering*, *5*(4), 813–830. https://doi.org/10.3934/mbe.2008.5.813

Massey, A. L., King, A. A., & Foufopoulos, J. (2014). Fencing protected areas: A long-term assessment of the effects of reserve establishment and fencing on African mammalian diversity. *Biological Conservation*, *176*, 162–171. https://doi.org/10.1016/j.biocon.2014.05.023

Mbizah, M. M., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2019). Applying the resource dispersion hypothesis to a fission–fusion society: A case study of the African lion (*Panthera leo*). *Ecology and Evolution*, *9*(16), 9111–9119. https://doi.org/10.1002/ece3.5456

Mcevoy, O. K. (2019). *The management of lions (Panthera leo) in small, fenced wildlife reserves*. (Doctoral dissertation) Grahamstown, South Africa: Rhodes University.

Mcevoy, O. K., Ferreira, S. M., & Parker, D. M. (2021). The influence of population demographics on lion (*Panthera leo*) growth rates in small, fenced wildlife reserves. *African Journal of Wildlife Research*, *51*(1), 75–89.

Midlane, N., O’Riain, M. J., Balme, G. A., Robinson, H. S., & Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, *172*, 101–108. https://doi.org/10.1016/j.biocon.2014.02.006

Midlane, Niel., O’Riaain, J. M., Balme, G. A., & Hunter, L. T. B. (2015). To track or to call: comparing methods for estimating population abundance of African lions *Panthera leo* in Kafue National Park. *Biodiversity and Conservation*, *24*(6), 1311–1327. https://doi.org/10.1007/s10531-015-0858-z

Miller, S. M., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D. J., … Zimmermann, D. (2013). Management of reintroduced lions in small, fenced reseved in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research*, *43*(2), 138–154.

Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: A management dilemma. *South African Journal of Wildlife Research*, *44*(1), 43–55.

Miller, S. M., Riggio, J., Funston, P. J., Power, R. J., Williams, V., & Child, M. F. (2016). A conservation assessment of *Panthera leo*. In *The red list of mammals of South Africa*. Swaziland and Lesotho.

Milleret, C., Dupont, P., Chipperfield, J., Turek, D., Brøseth, H., Gimenez, O., … Bischof, R. (2020). Estimating abundance with interruptions in data collection using open population spatial capture–recapture models. *Ecosphere*, *11*(7), 1–14. https://doi.org/10.1002/ecs2.3172

Mondol, S., Karanth, U. K., Kumar, S. N., Gopalaswamy, A. M., Andheria, A., & Ramakrishnan, U. (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation*, *142*(10), 2350–2360. https://doi.org/10.1016/j.biocon.2009.05.014

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, *78*(2), 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024

Mucina, L., Rutherford, M. C., & Powrie, W. (2006). Vegetation atlas of South Africa, Lesotho and Swaziland. In L. Mucina & M. C. Rutherford (Eds.), *Vegetation Map of Southern Africa, Lesotho and Swaziland* (pp. 750–760). Pretoria: South Africa National Biodiversity Institute.

Noack, J., Heyns, L., Rodenwoldt, D., & Edwards, S. (2019). Leopard density estimation within an enclosed reserve, namibia using spatially explicit capture-recapture models. *Animals*, *9*(10), 724. https://doi.org/10.3390/ani9100724

Packer, C., Herbst, L., Pusey, A., Bygott, A., Hanby, J. P., Cairns, S. J., & Borgerhoff-Mulder, M. (1988). *Reproduction success of lions: studies of individual variation in contrasting breeding systems* (T. Clutton-Brock, Ed.). Chicago: University of Chicago Press.

Packer, C., Loveridge, A. J., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., … Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology*

Letters, *16*(5), 635–641. https://doi.org/10.1111/ele.12091

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups : Food is not enough. *The American Naturalist*, *136*(1), 1–19.

Packer, C., Swanson, A., Canney, S., Loveridge, A., Garnett, S., Pfeifer, M., … Macnulty, D. (2013). The case for fencing remains intact. *Ecology Letters*, *16*(11), 7–8. https://doi.org/10.1111/ele.12171

Packer, Craig. (2019). The African lion: A long history of interdisciplinary research. *Frontiers in Ecology and Evolution*, *7*(259), 1–6. https://doi.org/10.3389/fevo.2019.00259

Pekor, A., Miller, J. R. B., Flyman, M. V., Kasiki, S., Kesch, M. K., Miller, S. M., … Lindsey, P. A. (2019). Fencing Africa's protected areas: Costs, benefits, and management issues. *Biological Conservation*, *229*, 67–75. https://doi.org/10.1016/j.biocon.2018.10.030

Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, *160*(4), 497–508. https://doi.org/10.1111/j.1469-7998.1970.tb03093.x

Périquet, S., Fritz, H., & Revilla, E. (2015). The lion king and the hyaena queen: Large carnivore interactions and coexistence. *Biological Reviews*, *90*(4), 1197–1214. https://doi.org/10.1111/brv.12152

Pfeffer, S. E. (2016). *Comparison of three different indirect methods to evaluate ungulate population densities*. Swedish university of africultural science.

Power, R. J. (2002). Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe*, *45*(2), 67–75. https://doi.org/10.4102/koedoe.v45i2.32

Prox, L., & Farine, D. (2020). A framework for conceptualizing dimensions of social organization in mammals. *Ecology and Evolution*, *10*(2), 791–807. https://doi.org/10.1002/ece3.5936

Pusey, A. E., & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, *101*(4), 275–310.

Rafiq, K., Bryce, C. M., Rich, L. N., Coco, C., Miller, D. A. W., Meloro, C., … Hayward,

M. W. (2019). Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Current Biology*, *29*(14), R681–R682. https://doi.org/10.1016/j.cub.2019.05.056

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., … Pimm, S. (2013). The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation*, *22*(1), 17–35. https://doi.org/10.1007/s10531-012-0381-4

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Royle, A. J., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture-recapture*. Academic Press.

Royle, A. J., & Converse, S. J. (2014). Hierarchical spatial capture-recapture models: Modelling population density in stratified populations. *Methods in Ecology and Evolution*, *5*(1), 37–43. https://doi.org/10.1111/2041-210X.12135

Royle, A. J., Fuller, A. K., & Sutherland, C. (2018). Unifying population and landscape ecology with spatial capture–recapture. *Ecography*, *41*(3), 444–456. https://doi.org/10.1111/ecog.03170

Royle, A. J., Karanth, U. K., Gopalaswamy, A. M., & Kumar, S. N. (2009). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, *90*(11), 3233–3244. https://doi.org/10.1890/08-1481.1

Royle, A. J., Sutherland, C., Fuller, A. K., & Sun, C. C. (2015). Likelihood analysis of spatial capture-recapture models for stratified or class structured populations. *Ecosphere*, *6*(2), 1–11. https://doi.org/10.1890/ES14-00148.1

Rutherford, M. C., Mucina, L., Lötter, C., Bredenkamp, G. J., Jacobus, H. L., Scott-shaw, C. R., … Hurter, P. J. H. (2006). Savanna Biome. In *The vegetation of South Africa, Lesotho and Swaziland.* (pp. 440–529). Pretoria: South Africa National Biodiversity Institute.

Schaller, G. B. (1972). The Serengeti Lion. Chicago: Univeristy of Chicago Press. https://doi.org/10.1017/CBO9781107415324.004

Silk, J. B. (1984). Local resource competition and the evolution of male-biased sex ratio. *Journal of Theoretical Biology*, *108*(2), 203–213.

Skinner, J. D., & Chimimba, C. T. (2005). Lion. In *The mammals of the Southern African sub-region* (Third Edit, pp. 390–396). Cambridge University Press.

Slotow, R., & Hunter, L. T. B. (2009). Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: The African lion in South Africa. In *Reintroduction of Top-Order Predators, (5), 43*. https://doi.org/10.1002/9781444312034.ch3

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), 20142711. https://doi.org/10.1098/rspb.2014.2711

Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., & Harwood, J. (2010). The functional response of a generalist predator. *PloS one*, *5*(5). https://doi.org/10.1371/journal.pone.0010761

Snyman, A., Jackson, C. R., & Funston, P. J. (2015). The effect of alternative forms of hunting on the social organization of two small populations of lions *Panthera leo* in Southern Africa. *Oryx*, *49*(4), 604–610. https://doi.org/10.1017/S0030605313001336

Sobratee, N., & Slotow, R. (2019). A critical review of lion research in South Africa: The impact of researcher perspective, research mode, and power structures on outcome bias and implementation gaps. *Frontiers in Ecology and Evolution*, *7*(81), 1–17. https://doi.org/10.3389/fevo.2019.00081

Spong, G. (2002). Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology*, *52*(4), 303–307. https://doi.org/10.1007/s00265-002-0515-x

Stander, P. E. (2019). Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia. *Namibian Journal of Environment*, *3*, 1–10.

Stoffelen, A., Adiyia, B., Vanneste, D., & Kotze, N. (2020). Post-apartheid local sustainable development through tourism: an analysis of policy perceptions among “responsible” tourism stakeholders around Pilanesberg National Park, South Africa. *Journal of Sustainable Tourism*, *28*(3), 414–432. https://doi.org/10.1080/09669582.2019.1679821

Tambling, C. J., & du Toit, J. T. (2005). Modelling wildebeest population dynamics: Implications of predation and harvesting in a closed system. *Journal of Applied Ecology*, *42*, 431–441. https://doi.org/10.1111/j.1365-2664.2005.01039.x

Tarugara, A., Clegg, B. W., Gandiwa, E., & Muposhi, V. K. (2019). Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population. *Global Ecology and Conservation*, *18*, e00627. https://doi.org/10.1016/j.gecco.2019.e00627

Tende, T., Ottosson, U., Hansson, B., & Bensch, S. (2008). Population density and abundance of Lions in Yankari Game Reserve, 2008. Unpublish report, Lund University, Sweden.

Trinkel, M., Fleischmann, P. H., & Slotow, R. (2017). Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population. *Journal of Zoology*, *301*(1), 41–50. https://doi.org/10.1111/jzo.12387

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation*, *13*(4), 374–382. https://doi.org/10.1111/j.1469-1795.2009.00344.x

Trinkel, Martina., & Angelici, F. M. (2016). The decline in the Lion population in Africa and possible mitigation measures. In F. M. Angelici (Ed.), *Problematic Wildlife* (Edition 1, pp. 45–68). https://doi.org/10.1007/978-3-319-22246-2

Tumenta, P. N., van’t Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., Udo de Haes, H. A., & De Iongh, H. H. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology*, *78*(6), 461–469. https://doi.org/10.1016/j.mambio.2013.08.006

Van de Kerk, M., de Kroon, H., Conde, D. A., & Jongejans, E. (2013). Carnivora population dynamics are as slow and as fast as those of other mammals: Implications for their conservation. *PloS one*, *8*(8), e70354. https://doi.org/10.1371/journal.pone.0070354

Van Dyk, G., & Slotow, R. (2003). The effects of fences and lions on the ecology of African wild dogs reintroduced to Pilanesberg National Park, South Africa. *African Zoology*, *38*(1), 79–94. https://doi.org/10.1080/15627020.2003.11657196

Van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (Panthers, leo). *Journal of Zoology*, *206*(1), 97–112. https://doi.org/10.1111/j.1469-7998.1985.tb05639.x

Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, *143*(11), 2631–2637. https://doi.org/10.1016/j.biocon.2010.07.005

VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, *77*(4), 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028

Vega Yon, G. G., & Marjoram, P. (2019). fmcmc: A friendly MCMC framework. *The Journal of Open Source Software*, *4*(39), 1427. https://doi.org/10.2307/2334940

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion’s mane. *Science*, *297*(5585), 1339–1343. https://doi.org/10.1126/science.1073257

Wijers, M., Trethowan, P., Du Preez, B., Chamaillé-Jammes, S., Loveridge, A. J., Macdonald, D. W., & Markham, A. (2021). Vocal discrimination of African lions and its potential for collar-free tracking. *Bioacoustics*, *30*(5), 575–593. https://doi.org/10.1080/09524622.2020.1829050

Wild, G., & West, S. A. W. (2009). Genomic imprinting and sex allocation. *American Naturalist*, *173*(1), 1–14. https://doi.org/10.1086/593305

Winterbach, H. E. K., Winterbach, C. W., Somers, M. J., & Hayward, M. W. (2013). Key factors and related principles in the conservation of large African carnivores. *Mammal Review*, *43*(2), 89–110. https://doi.org/10.1111/j.1365-2907.2011.00209.x

Witmer, G. W. (2005). Wildlife population monitoring: some practical considerations. *Wildlife Research*, *32*, 259–263.

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation*, *3*(2), 165–173.

https://doi.org/10.1017/S136794300000086X

Woolley, L. A., Page, B., & Slotow, R. (2011). Foraging strategy within African elephant family units: Why body size matters. *Biotropica*, *43*(4), 489–495. https://doi.org/10.1111/j.1744-7429.2010.00733.x

Appendix

Table S2.2 The specification and diagnostics of increment 1, which include models 1, 2, and 3.

Search effort driven	**1 000 km**					
N. individuals	18					
N. recaps	2					
Total detections	20					
N. indiv. recaptured	2					
Indiv. at more than 1 trap	2					
Average spatial recaps	1.11					
New detections	25					
End date	2020/09/06					
SO’s	13					
Recapture Index	1.11					
Model setting	**Model 1**		**Model 2**		**Model 3**	
M	300		300		300	
Iterations	100 000		100 000		100 000	
Chains	5		5		5	
Diagnostic						
Post-hoc burn-ins	1		10 000		1	
Chains	5		5		5	
Max GR	1.29		1.3		1.08	
Baye P	0.60		0.57		0.50	
Likelihood	-6532		-12503		-5507	
Estimates	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**
Sigma	7.07	17.54	62093502016186.40	713980210547546.00	5.26	4.70
Sigma2	3.71	18.30	1188438170.75	13891367560.49	5.26	4.70
Lam0	0.00	0.00	0.00	0.00	0.00	0.00
Beta1.effort	0.36	0.29	0.19	0.26	0.19	0.26
Beta.sex	3.74	2.89	NA	NA	NA	NA
Psi	0.66	0.20	0.55	0.24	0.57	0.22
Psi.sex	0.59	0.20	0.49	0.18	0.00	0.00
Nsuper	199	61	165	71	170	66

Table S.2.3. The specification and diagnostics of increment 2 000 km and 3 000 km, which includes models 1, 2, and 3.

Search effort driven	**2 000 km**						**3 000 km**					
N. indiv	28						30					
N. recaps	29						46					
Total detections	57						76					
N. indiv. recaptured	21						29					
Indiv. at more than 1 trap	21						24					
Average spatial recaps	2.04						2.37					
New detections	37						19					
End date	2020/09/19						2020/10/05					
SO's	26						42					
Recapture Index	2.04						2.53					
Model setting	**Model 1**		**Model 2**		**Model 3**		**Model 1**		**Model 2**		**Model 3**	
M	200		200		200		200		200		200	
Iterations	100 000		30 000		30 000		30 000		30 000		30 000	
Chains	5		4		4		4		4		4	
Diagnostic												
Post-hoc Burn-ins	40 000		5 000		5 000		1		5 000		5 000	
Chains	2		4		4		4		4		4	
Max GR	1.1		1		1		1		1		1	
Baye P	0.54		0.51		0.43		0.49		0.47		0.41	
Likelihood	-1464		-1538		-2357		-7473		-3228		-4591	
Estimates	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**

Sigma	4.80	2.84	4.17	1.41	4.24	1.17	3.08	0.65	3.27	0.52	3.28	0.45
Sigma2	4.66	1.78	4.74	1.71	4.24	1.17	3.86	1.06	3.37	0.56	3.28	0.45
Lam0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Beta1.effort	0.63	0.19	0.63	1.07	0.63	0.19	0.88	0.18	0.87	0.18	0.87	0.17
Beta.sex	0.12	0.66	NA	NA	NA	NA	-0.44	0.49	NA	NA	NA	NA
Psi	0.29	0.07	0.29	0.07	0.27	0.06	0.27	0.05	0.26	0.05	0.26	0.05
Psi.sex	0.44	0.12	0.44	0.12	0.00	0.01	0.50	0.10	0.50	0.10	0.00	0.01
Nsuper	57	13	57	13	53	10	53	8	53	8	51	8

Table S.2.4. The specification and diagnostics of increment 4 and 5, which includes models 1 and 2.

Search effort driven	**4 000 km**				**5 000 km**			
N. Indiv.	31				31			
N. recaps	81				103			
Total detections	112				134			
N. indiv. recaptured	29				29			
Indiv. at more than 1 trap	27				27			
Average spatial recaps	3.29				4.00			
New detections	36				22			
End date	2020/10/17				2020/11/11			
SO's	54				79			
Recapture Index	3.61				4.32			
Model setting	**M1**		**M2**		**M1**		**M2**	
M	200		200		200		200	
Iterations	30 000		30 000		30 000		30 000	
Chains	4		4		4		4	
Diagnostic								
Post-hoc Burn-ins	1		1		1		1	
Chains	4		4		4		4	
Max GR	1		1		1		1	
Baye P	0.66		0.65		0.71		0.72	
Likelihood	-6103		-11618		-8169		-6170	
Estimates	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**
Sigma	2.92	0.38	2.92	0.30	3.16	0.34	3.24	0.33
Sigma2	3.58	0.46	3.50	0.39	4.33	0.51	4.21	0.45
Lam0	0.01	0.00	0.01	0.00	0.01	0.00	0.00	0.00
Beta1.effort	0.58	0.14	0.58	0.13	0.67	0.12	0.66	0.12
Beta.sex	-0.07	0.34	NA	NA	-0.16	0.30	NA	NA
Psi	0.23	0.04	0.23	0.04	0.21	0.03	0.21	0.04
Psi.sex	0.49	0.10	0.49	0.10	0.48	0.09	0.48	0.09
Nsuper	45	5	45	5	41	4	41	4

Table S.2.5. The specification and diagnostics of increment 6 and 7, which includes models 1 and 2.

Search effort driven	**6 000 km**	**7 000 km**
N. Indiv.	34	37
N. recaps	123	147
Total detections	157	184
N. Indiv. recaptured	29	30

Indiv. at more than 1 trap	27				28			
Average spatial recaps	4.26				4.59			
New detections	23				27			
End date	2020/11/24				2020/12/10			
SO's	92				108			
Recapture Index	4.62				4.97			
Model setting	**M1**		**M2**		**M1**		**M2**	
M	200		200		200		200	
Iterations	30 000		30 000		30 000		30 000	
Chains	4		4		4		4	
Diagnostic								
Post-hoc Burn-ins	1		1		1		1	
Chains	4		4		4		4	
Max GR	1		1		1		1	
Baye P	0.75		0.76		0.70		0.69	
Likelihood	-6808		-8702		-9343		-7388	
Estimates	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**	**EST**	**PSD**
Sigma	2.953	0.262	3.06	0.256	3.19	0.27	3.25	0.25
Sigma2	3.861	0.389	3.71	0.327	3.85	0.33	3.77	0.30
Lam0	0.006	0.001	0.01	0.001	0.00	0.00	0.00	0.00
Beta1.effort	0.757	0.120	0.75	0.122	0.79	0.11	0.79	0.11
Beta.sex	-0.261	0.269	NA	NA	-0.13	0.25	NA	NA
Psi	0.216	0.034	0.22	0.034	0.22	0.03	0.22	0.03
Psi.sex	0.513	0.088	0.51	0.088	0.53	0.08	0.53	0.08
Nsuper	43	4	43	4	44	3	44	3

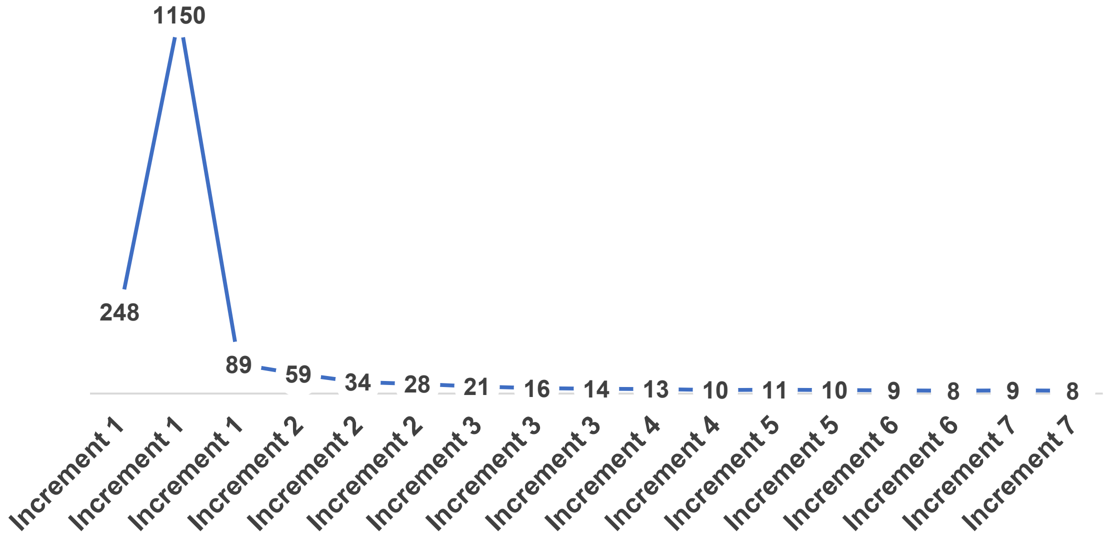


Figure S.2.1. The coefficient of variance from increment 1 000 – 7 000 km. The results indicate that increment 1 000 to 3 000 have a great level of dispersion around the mean, while increments 4 000 to 7 000 km are lower which indicates precision as it gets closer to the mean (Kazemi & Jafari, 2020).

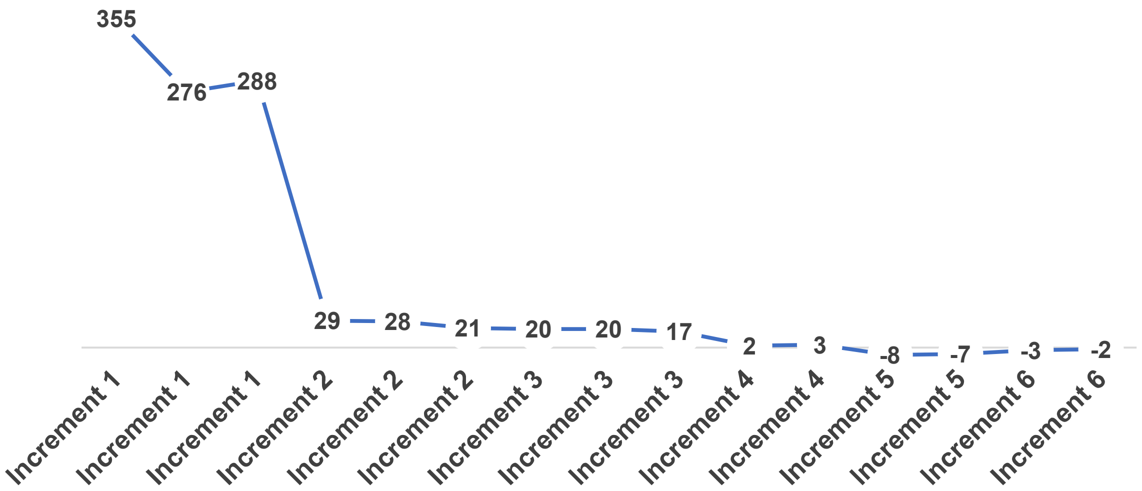


Figure S.2.2. The relative bias of the posterior estimate. The true value of the posterior mean estimate is the full set of increment 7 000 km.

CHAPTER 5

SYNTHESIS

Introduction

The African lion (*Panthera leo*) is considered an important apex predator and tourism species on the African continent (Funston & Levendal, 2015; Ripple et al., 2014). In recent years, lions throughout Africa underwent dramatic declines despite their ecological, social, and economic value (Bauer et al., 2015). The declines are caused by human wildlife conflict, prey depletion, and habitat transformation (Lesilau et al., 2021; Riggio et al., 2013). In South Africa, lions declined during the 1900’s due too ? (Miller & Funston, 2014). lions were reintroduced to small protected areas during the late 1900’s, where their numbers increased and stabilized in span of 20-years (Miller et al., 2016).

Managing lions in a fenced protected area does not come without a cost as it limits, ecological, and behavioural processes (Miller et al., 2013; Noack et al., 2019). Because lions have a high population growth rate, conservation managers often struggle to keep track of lion numbers. Lions are top predators, which have a notable effects on the ecosystem, consequently, prey populations, and other smaller predators can decline because of this (Lindsey et al., 2017; Ripple et al., 2014). To effectively manage lion numbers in fenced protected areas efficient population monitoring is required (Miller et al., 2013, 2016; Miller & Funston, 2014; Packer, Loveridge, et al., 2013). By monitoring the spatio-temporal fluctuations in lion population’s, mangers can produce reliable estimations on the size and structure of their lion prides However, estimating lion populations can be challenging as it requires time, human resources, and funding (Gese, 2001; Milleret et al., 2020).

Previous studies used spoor tracking and call up stations to survey population sizes (Everatt et al., 2019; Funston et al., 2010; Midlane et al., 2015). It was found that these types of methods can be problematic since indices can fluctuate and lions become habituated to sounds (Belant et al., 2019; Elliot, & Gopalaswamy, 2017). Estimating the precise population size, are beneficial for the ecosystem’s future and management decisions.

If protected areas do not have an active monitoring program in place they cannot detect changes in the ecosystem (e.g. fluctuations in herbivore population due to large carnivore effects). Braczkowski et al., (2020), showed the Bayesian spatial explicit capture recapture method is a reliable method for solving the unreliable and inaccurate abundance and density of large carnivores. This method does include a spatial factor which helps the researcher understand the movement patterns of the studied species. This method can be time consuming and expensive, which may be a reason why researchers are reluctant to implement it .

Research findings

The abundance of lions at Pilanesberg National Park was unknown for many years. Management faced challenges in determining the actual population size as well as associated population control methods. Subsequent high lion numbers potentially played a role in the decline in prey species. My first research objective was to determine how many lions Pilanesberg National Park had. Along with my first objective, I had three hypotheses. Firstly, I hypothesised, based on the assumption of an unmonitored, growing lion population, that the lion density would be high in PNP. Secondly, I hypothesised that the estimated sex ratio would be unequal (skewed towards females) on account of their mating system (polygyny) and the aggressiveness between territorial males normally expected from lion populations. Lastly, I hypothesised that males would have much larger home range sizes than females with predicted home ranges overlapping females.

I performed a 90-day intensive lion search. I used direct observation and driving effort to estimate the lion population. The results were analysed by the Bayesian spatial explicit spatial capture recapture model. The estimated lion number of lions was 44, using the Bayesian spatial explicit capture recapture model. The estimated number was much lower compared to the last count (50) in the 2001, during a time when the high number of caused a decline in the blue wildebeest population (Tambling & du Toit, 2005). The lion density in PNP was 8.8 individuals per 100 km^2. The density of PNP was compared with 20 other protected areas in Southern Africa and have a slightly higher density compared to an average of 7.8 per 100 km^2.

I found that the sex ratio was skewed towards males (0.9♀:1♂). This was different compared to a sex ratio of 2♀:1♂ expected in more natural unfenced systems (Périquet et al., 2015). In several protected areas the sex ratio is skewed towards females. For example in Venetia Limpopo Nature Reserve the sex ratio was 4.5♀:2.7♂, Kgalagadi Transfrontier Park the sex ratio was 1.2♀:0.82♂, and North Tuli Game Reserve the sex ratio was 3.9♀:2.3♂ (Creel & Creel, 1997; Ferreira et al., 2020; Snyman et al., 2015). Factors that could influence the skewed sex ratio towards females are infanticide, human wildlife conflict, the breaking away of sub adult males from their pride which often gets killed by older males, and nomadic males gets killed when catching prey (Elliot, Cushman, Loveridge, Mtare, & Macdonald, 2014; Ferreira et al., 2020; Mcevoy, 2019; Miller, & Funston, 2014). Many of these factors do not affect male lions in PNP, since human wildlife conflict and trophy hunting are not present. This potentially could explain the high numbers of male lions, (see Miller & Funston, 2014). The lion males had an average home range size of 279 km^2, which is much larger than the female lion with an average of 191 km^2, which was expected. Primarily, male lions have a much bigger area to protect, while females have smaller home ranges to protect their cubs (Lehmann et al., 2008b; Lesilau et al., 2021). The study only looked at home range sizes for 90 days, compare to other home ranges which are monitored for a year.

I also determined what the influence of varied sampling on the precision of estimates and bias, and future sampling designs. We used the completed lion survey data of chapter one, which was analysed and repeated with subsamples of the data and compared the estimates from the reduced datasets to those of the full dataset. The data analysed were divided into 7, 1000 km increments and three models of the Bayesian SECR. It was concluded that 4 000 km is the necessary minimum effort to estimate lion abundance, density, and movement patterns in small fenced protected areas.

Discussion and recommendations

Managing lions in fenced protected areas is challenging and requires constant effort, time, money, and attention (Slotow & Hunter, 2009). Making decisions based on inadequate information, increases risks not only towards lions but also to other species in the system (Miller & Funston, 2014; Packer, Loveridge, et al., 2013; Pekor et al., 2019; Slotow & Hunter, 2009). Through active management, a protected area will be able to meet its objectives (e.g., knowing the status of lion and prey population, their movement, and social dynamic). The precise estimate of lion population size within a small fenced protected area is vital for management.

Understanding the factors that regulate natural variation in population size and structure, movement, and demographic rates, are important for conservation, and future management decisions (Royle, Fuller, & Sutherland, 2018). The SECR model incorporates the spatial information of inference. The location where an individual is recorded/trapped are important for the model to run successfully. The SECR is an appropriate model that can be altered for methods such as camera trapping, DNA methods, and cage trapping (Borchers, 2012; Royle, Sutherland, Fuller, & Sun, 2015). All these methods can obtain recaptures, which is an important aspect of the SECR. Further, the SECR incorporates the parameters that vary within populations such as sex and age to rationalise the difference in space use by individual or encounter rate (Royle et al., 2015).

During this study I was able to determine important population parameters (e.g., numbers, sex ratios and ranges using the SECR method with enough accuracy useful for conservation management purposes). I also determined the minimum effort required for a reliable survey of this nature. For future management PNP should incorporate the SECR when estimating lions to ensure precise population data on a regular basis.

Study constraints

The topography (white blocks on the map) of PNP can be considered a massive constraint. It can be viewed as bias since these areas could have contain lions which might not be recorded. Knowing the preferred prey is plains game, most of the lions might not move into the mountainous areas for too long as they will not find the preferred prey. However, the buffalo does move into these mountainous areas, but it is not often seen that they lay on a buffalo carcass. The areas that is not survey will not affect the accuracy since lions constantly move throughout the park. If there were little recaptures the study would have had a different approach. This would have meant that the search effort needed to be increased and that the lions might be roaming in the inaccessible areas. Using one observer who is also the driver could have affected detection rates. An extra observer might have increased lion detections and recaptures, since an extra pair of eyes can examine the other side of the vehicle. Pilanesberg is open to self-drive and guided tourists. Because of this it is always busy at PNP. Visitors often disturb lions, and they move away from roads which is another factor that could have influenced detectability.

Future research

The detectability of lions is vital when the population size needs to be estimated (Funston et al., 2001). During the rainfall season, PNP has tall grass. During the dry season, fires are common, which enhances the detectability of predators (Belant et al., 2019). However, all areas are not burned and could influence data collection. This potential issue needs to be investigated, to see whether it has an effect when collecting data. Thereafter, the potential error can be quantified into future monitoring efforts.

References

Alibhai, S., Jewell, Z., & Evans, J. (2017). The challenge of monitoring elusive large carnivores: An accurate and cost-effective tool to identify and sex pumas (Puma concolor) from footprints. *PloS one*, *12*(3), e0172065. https://doi.org/10.1371/journal.pone.0172065

Arnholt, A. T., & Herbert, J. (1995). Estimating the mean with known coefficient of variation. *The American Statistician*, *49*(4), 367–369.

Auffray, J.-C., Renaud, S., & Claude, J. (2009). Rodent Biodiversity in Changing Environments. *Kasetsart Journal, Natural Science*, *43*(1), 83–93. Retrieved from https://www.researchgate.net/publication/228350392

Balme, G. A., Hunter, L. T. B., & Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, *73*(3), 433–441. https://doi.org/10.2193/2007-368

Barthold, J. A., Loveridge, A. J., Macdonald, D. W., Packer, C., & Colchero, F. (2016). Bayesian estimates of male and female African lion mortality for future use in population management. *Journal of Applied Ecology*, *53*(2), 295–304. https://doi.org/10.1111/1365-2664.12594

Bauer, H., & Van Der Merwe, S. (2004). Inventory of free-ranging lions *Panthera leo* in Africa. *Oryx*, *38*(1), 26–31. https://doi.org/10.1017/S0030605304000055

Bauer, Hans., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., … Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *PNAS*, *112*(48), 14894–14899. https://doi.org/10.1073/pnas.1500664112

Belant, J. L., Bled, F., Mkasanga, I. J., Wilton, C. M., Mwampeta, S. B., Beyer, D. E., … Fyumagwa, R. (2019). Track surveys do not provide accurate or precise lion density estimates in Serengeti. *Global Ecology and Conservation*, *19*, e00651. https://doi.org/10.1016/j.gecco.2019.e00651

Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, *90*, 171–180. https://doi.org/10.1016/j.anbehav.2014.01.030

Boitani, L., Ciucci, P., & Mortelliti, A. (2012). Designing carnivore surveys. In *Carnivore ecology and management: a handbook of techniques* (pp. 8–29). https://doi.org/10.1093/acprof

Borchers, D. (2012). A non-technical overview of spatially explicit capture-recapture models. *Journal of Ornithology*, *152*(2), 435–444. https://doi.org/10.1007/s10336-010-0583-z

Borchers, D., Distiller, G., Foster, R., Harmsen, B., & Milazzo, L. (2014). Continuous-time spatially explicit capture-recapture models, with an application to a jaguar camera-trap survey. *Methods in Ecology and Evolution*, *5*(7), 656–665. https://doi.org/10.1111/2041-210X.12196

Botai, C. M., Botai, J. O., Dlamini, L. C., Zwane, N. S., & Phaduli, E. (2016). Characteristics of droughts in South Africa: A case study of Free State and North West provinces. *Water*, *8*(10), 439. https://doi.org/10.3390/w8100439

Braczkowski, A., Gopalaswamy, A. M., Elliot, N. B., Possingham, H. P., Bezzina, A., Maron, M., … Allan, J. R. (2020). Restoring Africa's lions: Start with good counts. *Frontiers in Ecology and Evolution*, *8*, 138. https://doi.org/10.3389/fevo.2020.00138

Braczkowski, A., Gopalaswamy, A. M., Mustafa, N., Allan, J., Biggs, D., & Maron, M. (2020). Detecting early warnings of pressure on an African lion (*Panthera leo*) population in the Queen Elizabeth Conservation Area , Uganda. *Ecological Solution Eviddence*, *1*, e12015. https://doi.org/10.1002/2688-8319.12015

Briers-Louw, W. D. (2017). Ecology of three apex predators in Majete Wildlife Reserve, Malawi (Doctoral dissertation). Stellenbosch University, Stellenbosch.

Brink, H., Smith, R. J., & Skinner, K. (2012). Methods for lion monitoring: A comparison from the Selous Game Reserve, Tanzania. *African Journal of Ecology*, *51*(2), 366–375. https://doi.org/10.1111/aje.12051

Broekhuis, F., Elliot, N. B., Keiwua, K., Koinet, K., Macdonald, D. W., Mogensen, N., … Gopalaswamy, A. M. (2021). Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography*, *44*(3), 358–369. https://doi.org/10.1111/ecog.05154

Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PloS one*, *11*(5), 1–15. https://doi.org/10.1371/journal.pone.0153875

Caravaggi, A., Banks, P. B., Burton, C. A., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., … Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109–122. https://doi.org/10.1002/rse2.48

Carbone, C., Teacher, A., & Rowcliffe, M. J. (2007). The costs of carnivory. *PLoS Biology*, *5*(2), 0363–0368. https://doi.org/10.1371/journal.pbio.0050022

Carruthers, J. (2011). Pilanesberg National Park, North West Province, South Africa: Uniting economic development with ecological design – A history, 1960s to 1984. *Koedoe*, *53*(1), 1–10. https://doi.org/10.4102/koedoe.v53i1.1028

Clark, T. J., Horne, J. S., Hebblewhite, M., & Luis, A. D. (2021). Stochastic predation exposes prey to predator pits and local extinction. *Oikos*, *130*(2), 300–309. https://doi.org/10.1111/oik.07381

Comley, J., Joubert, C. J., Mgqatsa, N., & Parker, D. M. (2020). Battle of the Large Carnivores: Spatial Partitioning in a Small, Enclosed Reserve? *African Journal of Wildlife Research*, *50*(1), 176–189. https://doi.org/10.3957/056.050.0176

Cooper, D. M., Dugmore, A. J., Kitchener, A. C., Metzger, M. J., & Trabucco, A. (2021). A kingdom in decline: Holocene range contraction of the lion (*Panthera leo*) modelled with global environmental stratification. *PeerJ*, *9*, e10504. https://doi.org/10.7717/peerj.10504

Creel, S., Becker, M. S., Durant, S. M., M'Soka, J., Matandiko, W., Dickman, A. J., … Zimmermann, A. (2013). Conserving large populations of lions - the argument for fences has holes. *Ecology Letters*, *16*(11), 1413-e3. https://doi.org/10.1111/ele.12145

Creel, Scott., & Creel, N. M. (1997). Lion density and population structure in the Selous Game Reserve: Evaluation of hunting quotas and offtake. *African Journal of Ecology*, *35*(2), 83–93. https://doi.org/10.1111/j.1365-2028.1997.062-89062.x

Cushman, S. A., Elliot, N. B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., … Loveridge, A. J. (2018). Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. *PloS one*, *13*(7), e0196213. https://doi.org/10.1371/journal.pone.0196213

De Boer, W. F., Vis, M. J. P., De Knegt, H. J., Rowles, C., Kohi, E. M., van Langevelde, F., … Prins, H. H. T. (2010). Spatial distribution of lion kills determined by water dependency of prey species. *Journal of Mammalogy*, *91*(5), 1280–1286. https://doi.org/10.1644/09-MAMM-A-392.1

de Manuel, M., Barnett, R., Sandoval-Velasco, M., Yamaguchi, N., Vieira, F. G., Mendoza, L. Z. M., … Gilbert, T. M. (2020). The evolutionary history of extinct and living lions. PNAS, *117*(20), 10927–10934. https://doi.org/10.1073/pnas.1919423117

Dey, S., Delampady, M., & Gopalaswamy, A. M. (2019). Bayesian model selection for spatial capture–recapture models. *Ecology and Evolution*, *9*(20), 11569–11583. https://doi.org/10.1002/ece3.5551

Dolrenry, S., Stenglein, J., Hazzah, L., Lutz, S. R., & Frank, L. (2014). A metapopulation approach to African lion (*Panthera leo*) conservation. *PloS one*, *9*(2). https://doi.org/10.1371/journal.pone.0088081

Dröge, E., Creel, S., Becker, M. S., Loveridge, A. J., Sousa, L. L., & Macdonald, D. W. (2020). Assessing the performance of index calibration survey methods to monitor populations of wide-ranging low-density carnivores. *Ecology and Evolution*, *10*(7), 3276–3292. https://doi.org/10.1002/ece3.6065

Durant, S. M., Craft, M. E., Hilborn, R., Bashir, S., Hando, J., & Thomas, L. (2011). Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *Journal of Applied Ecology*, *48*(6), 1490–1500. https://doi.org/10.1111/j.1365-2664.2011.02042.x

Dures, S. G., Carbone, C., Loveridge, A. J., Maude, G., Midlane, N., Aschenborn, O., & Gottelli, D. (2019). A century of decline: Loss of genetic diversity in a southern African lion - conservation stronghold. *Density and Distribution*, *25*, 870–879. https://doi.org/10.1111/ddi.12905

Edwards, S., Cooper, S., Uiseb, K., Hayward, M., Wachter, B., & Melzheimer, J. (2018). Making the most of by-catch data: Assessing the feasibility of utilising non-target camera trap data for occupancy modelling of a large felid. *African Journal of Ecology*, *56*(4), 885–894. https://doi.org/10.1111/aje.12511

Elliot, N. B., Bett, A., Chege, M., Sankan, K., de Souza, N., Kariuki, L., … Gopalaswamy, A. M. (2020). The importance of reliable monitoring methods for the management of small, isolated populations. *Conservation Science and Practice*, 1–11. https://doi.org/10.1111/csp2.217

Elliot, N. B., Cushman, S. A., Loveridge, A. J., Mtare, G., & Macdonald, D. W. (2014). Movements vary according to dispersal stage, group size, and rainfall: The case of the African lion. *Ecology*, *95*(10), 2860–2869. https://doi.org/10.1890/13-1793.1

Elliot, N. B., & Gopalaswamy, A. M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, *31*(4), 934–943. https://doi.org/10.1111/cobi.12878

Elliot, N. B., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos*, *123*(9), 1049–1056. https://doi.org/10.1111/oik.01266

Estes, R. D. (2012). Lion (*Panthera leo*). In *The behaviour guide to African mammals* (pp. 369–377). London and Los Angeles and Berkeley: The University of California Press.

Everatt, K. T., Kokes, R., & Pereira, C. L. (2019). Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation*, *28*(14), 4099–4114. https://doi.org/10.1007/s10531-019-01866-w

Ferreira, S. M., Beukes, O. B., Haas, T. C., & Radloff, F. G. T. (2020). Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park. *African Journal of Ecology*, *58*(3), 348–360. https://doi.org/10.1111/aje.12728

Ferreira, S. M., & Funston, P. J. (2010). Estimating lion population variables: Prey and disease effects in Kruger National Park, South Africa. *Wildlife Research*, *37*(3), 194–206. https://doi.org/10.1071/WR09030

Ferreira, S. M., & Hofmeyr, M. (2014). Managing charismatic carnivores in small areas: Large felids in South Africa. *South African Journal of Wildlife Research*, *44*(1), 32–42.

Forsyth, D. M., Ramsey, D. S. L., & Woodford, L. P. (2019). Estimating abundances, densities, and interspecific associations in a carnivore community. *The Journal of Wildlife Management*, *83*(5), 1090–1102. https://doi.org/10.1002/jwmg.21675

Fritz, H., Loreau, M., Chamaillé-Jammes, S., Valeix, M., & Clobert, J. (2011). A food web perspective on large herbivore community limitation. *Ecography*, *34*(2), 196–202. https://doi.org/10.1111/j.1600-0587.2010.06537.x

Funston, P J., Frank, L., Stephens, T., Davidson, Z., Loveridge, A., Macdonald, D. M., … Ferreira, S. M. (2010). Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *Journal of Zoology*, *281*(1), 56–65. https://doi.org/10.1111/j.1469-7998.2009.00682.x

Funston, P J., & Levendal, M. (2015). *Biodiversity management plan for the lion (Panthera leo) in South Africa. Government Gazette, 2*. Retrieved from www.gpwonline.co.za

Funston, P J., & Mills, M. G. L. (2006). The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *African Journal of Wildlife Research*, *36*(1), 9–22.

Funston, P J., Mills, M. G. L., & Biggs, H. C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, *253*(4), 419–431.

Funston, Paul J. (2011). Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research*, *41*(1), 1–10.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–511.

Gese, E. M. (2001). Monitoring of terrestrial carnivore populations. *Conservation Biology Series- Cambridge-*, 372–396.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, *10*(1), 57–63. https://doi.org/10.1007/BF00296396

Gomez, D., Sommaro, L., Steinmann, A., Chiappero, M., & Priotto, J. (2011). Movement distances of two species of sympatric rodents in linear habitats of Central Argentine agro-ecosystems. *Mammalian Biology*, *76*, 58–63. https://doi.org/10.1016/j.mambio.2010.02.001

Goodall, V. L., Ferreira, S. M., Funston, P. J., & Maruping-Mzileni, N. (2019). Uncovering hidden states in African lion movement data using hidden Markov models. *Wildlife Research*, *46*(4), 296–303. https://doi.org/10.1071/WR18004

Gopalaswamy, A. M., Delampady, M., Karanth, U. K., Kumar, S. N., & Macdonald, D. W. (2015). An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods in Ecology and Evolution*, *6*(9), 1055–1066. https://doi.org/10.1111/2041-210X.12351

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program SPACECAP: Software for estimating animal density using spatially explicit capture-recapture models. *Methods in Ecology and Evolution*, *3*(6), 1067–1072. https://doi.org/10.1111/j.2041-210X.2012.00241.x

Groom, R. J., Funston, P. J., & Mandisodza, R. (2014). Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: What is driving the population collapse? *Oryx*, *48*(3), 385–393. https://doi.org/10.1017/S0030605312001457

Gusset, M., & Burgener, N. (2005). Estimating larger carnivore numbers from track counts and measurement. *African Journal of Ecology*, *43*, 320–324.

Harmsen, B. J., Foster, R. J., & Quigley, H. (2020). Spatially explicit capture recapture density estimates: Robustness, accuracy and precision in a long-term study of jaguars (Panthera onca). *PloS one*, *15*(6), e0227468. https://doi.org/10.1371/journal.pone.0227468

Hatfield, R. (2014). Population dynamics of the African lion (*Panthera leo*) within the Maasai Mara region of southern Kenya. *Kaleidoscope*, *11*(1), 70.

Hayward, M. W., Adendorff, J., O'Brien, J., Sholto-douglas, A., Bissett, C., Moolman, L. C., … Kerley, G. I. H. (2007). Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eatern Cape Province. *The Open Conservation Biology Journal*, *1*(1), 1–11.

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, Ullas K., Mackenzie, D. I., … Yarnell, R. W. (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, *52*(2), 286–290. https://doi.org/10.1111/1365-2664.12408

Hayward, M. W., Hayward, G. J., Druce, D. J., & Kerley, G. I. H. (2009). Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. *Biodiversity Conservation*, *18*, 887–904. https://doi.org/10.1007/s10531-008-9452-y

Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (Panthera leo). *Journal of Zoology*, *267*, 309–322. https://doi.org/10.1017/S0952836905007508

Hayward, M. W., O'Brien, J., & Kerley, G. I. H. (2007). Carrying capacity of large African predators: Predictions and tests. *Biological Conservation*, *139*(1–2), 219–229. https://doi.org/10.1016/j.biocon.2007.06.018

Holekamp, K. E., & Sawdy, M. A. (2019). The evolution of matrilineal social systems in fissiped carnivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1780), 20180065. https://doi.org/10.1098/rstb.2018.0065

Hrabar, H., & du Toit, J. T. (2005). Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conservation*, *8*(3), 259–267. https://doi.org/10.1017/S1367943005002234

Jewell, Z. (2013). Effect of monitoring technique on quality of conservation science. *Conservation Biology*, *27*(3), 501–508. https://doi.org/10.1111/cobi.12066

Jiménez, J., Nuñez-Arjona, J. C., Rueda, C., González, L. M., Garciá-Domínguez, F., Munõz-Igualada, J., & López-Bao, J. V. (2017). Estimating carnivore community structures. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/srep41036

Kane, M. D., Morin, D. J., & Kelly, M. J. (2015). Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodiversity and Conservation*, *24*(14), 3527–3541. https://doi.org/10.1007/s10531-015-1012-7

Karanth, U. K., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, *79*(8), 2852–2862. https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2

Kazemi, M. R., & Jafari, A. A. (2020). Small sample inference for the common coefficient of variation. *Communications in Statistics: Simulation and Computation*, *49*(1), 226–243. https://doi.org/10.1080/03610918.2018.1484474

Keet, D. F. (2010). Lions. In *Game Ranch Management* (Fith Editi, pp. 295–312). Van Schaik Publication.

Kettles, R., & Slotow, R. (2009). Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research*, *39*(1), 23–33. Retrieved from https://journals.co.za/docserver/fulltext/wild/39/1/wild_v39_n1_a3.pdf?expires=1560189647&id=id&accname=guest&checksum=514349490088AEF9B952A9F9167F8569

Kidwai, Z., Jimenez, J., Louw, C. J., Nel, H. P., & Marshal, J. P. (2019). Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (*Diceros bicornis*) populations from aerial counts. *Global Ecology and Conservation*, *19*, e00687. https://doi.org/10.1016/j.gecco.2019.e00687

Kiffner, C., Meyer, B., Mühlenberg, M., & Waltert, M. (2009). Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania? *Oryx*, *43*(1), 52–59. https://doi.org/10.1017/S0030605307002335

Kissui, B. M., & Packer, C. (2004). Top-down population regulation of a top predator:

Lions in the Ngorongoro Crater. Proceedings of *the Royal Society of London*, *271*, 1867–1874. https://doi.org/10.1098/rspb.2004.2797

la Grange, M., Kellner, K., Cilliers, S. S., & Götze, A. R. (2009). Vegetation classification of the proposed Heritage Park, North-West Province, South Africa (North-West University; Vol. 75). https://doi.org/10.1016/j.sajb.2009.02.149

Lahoz-Monfort, J. J., Harris, M. P., Morgan, B. J. T., Freeman, S. N., & Wanless, S. (2014). Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. *Journal of Applied Ecology*, *51*(2), 534–543. https://doi.org/10.1111/1365-2664.12214

le Roux, E., Marneweck, D. G., Clinning, G., Druce, D. J., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2019). Top–down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography*, *42*(6), 1115–1123. https://doi.org/10.1111/ecog.03791

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008a). Feeding behaviour of lions (*Panthera leo*) on a small reserve. *African Journal of Wildlife Research*, *38*(1), 66–78.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008b). Home range utilisation and territorial behavior of lions (*Panthera leo*) on Karongwe Game Reserve, South Africa. *PloS one*, *3*(12), e3998. https://doi.org/10.1371/journal.pone.0003998

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008c). Reproductive biology of a pride of lions on Karongwe Game Reserve, South Africa. *African Zoology*, *43*(2), 230–236. https://doi.org/10.3377/1562-7020-43.2.230

Lesilau, F., Verschueren, S., van't Zelfde, M., Musters, K. C. J. M., de Snoo, G. R., & de Iongh, H. H. (2021). Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: The case study of Nairobi National Park, Kenya. *Mammalia*, *85*(3), 198–207. https://doi.org/10.1515/mammalia-2020-0116

Lindner, E., & Fuelling, O. (2002). Marking methods in small mammals: ear-tattoo as an alternative to toe-clipping. *The Zoological Society of London*, *256*, 159–163.

Lindsey, P. A., Petracca, L. S., Funston, P. J., Bauer, H., Dickman, A., Everatt, K., … Hunter, L. T. B. (2017). The performance of African protected areas for lions and their prey. *Biological Conservation*, *209*, 137–149. https://doi.org/10.1016/j.biocon.2017.01.011

López-Bao, J. V., Godinho, R., Pacheco, C., Lema, F. J., García, E., Llaneza, L., … Jiménez, J. (2018). Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. *Scientific Reports*, *8*(1), 1–8. https://doi.org/10.1038/s41598-018-20675-9

Loveridge, A. J., Valeix, M., Elliot, N. B., & Macdonald, D. W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology*, *54*(3), 815–825. https://doi.org/10.1111/1365-2664.12794

Macdonald, D. W., Loveridge, A. J., & Nowell, K. (2010). Dramatis personae: an introduction to the wild felids. In *The biology and conservation of wild felids* (First Edit, pp. 3–59). Oxford University Press (OUP).

Magome, H., Cain, J. W., Owen-Smith, N., & Henley, S. R. (2008). Forage selection of sable antelope in Pilanesberg Game Reserve, South Africa. *African Journal of Wildlife Research*, *38*(1), 35–41. https://doi.org/10.3957/0379-4369-38.1.35

Mari, L., Gatto, M., & Casagrandi, R. (2008). Local resource competition and the skewness of the sex ratio: A demographic model. *Mathematical Biosciences and Engineering*, *5*(4), 813–830. https://doi.org/10.3934/mbe.2008.5.813

Massey, A. L., King, A. A., & Foufopoulos, J. (2014). Fencing protected areas: A long-term assessment of the effects of reserve establishment and fencing on African mammalian diversity. *Biological Conservation*, *176*, 162–171. https://doi.org/10.1016/j.biocon.2014.05.023

Mbizah, M. M., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2019). Applying the resource dispersion hypothesis to a fission–fusion society: A case study of the African lion (*Panthera leo*). *Ecology and Evolution*, *9*(16), 9111–9119. https://doi.org/10.1002/ece3.5456

Mcevoy, O. K. (2019). *The management of lions (Panthera leo) in small, fenced wildlife reserves*. (Doctoral dissertation) Grahamstown, South Africa: Rhodes University.

Mcevoy, O. K., Ferreira, S. M., & Parker, D. M. (2021). The influence of population demographics on lion (*Panthera leo*) growth rates in small, fenced wildlife reserves. *African Journal of Wildlife Research*, *51*(1), 75–89.

Midlane, N., O'Riain, M. J., Balme, G. A., Robinson, H. S., & Hunter, L. T. B. (2014). On tracks: A spoor-based occupancy survey of lion *Panthera leo* distribution in Kafue National Park, Zambia. *Biological Conservation*, *172*, 101–108. https://doi.org/10.1016/j.biocon.2014.02.006

Midlane, Niel., O'Riaain, J. M., Balme, G. A., & Hunter, L. T. B. (2015). To track or to call: comparing methods for estimating population abundance of African lions *Panthera leo* in Kafue National Park. *Biodiversity and Conservation*, *24*(6), 1311–1327. https://doi.org/10.1007/s10531-015-0858-z

Miller, S. M., Bissett, C., Burger, A., Courtenay, B., Dickerson, T., Druce, D. J., … Zimmermann, D. (2013). Management of reintroduced lions in small, fenced reseved in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research*, *43*(2), 138–154.

Miller, S. M., & Funston, P. J. (2014). Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: A management dilemma. *South African Journal of Wildlife Research*, *44*(1), 43–55.

Miller, S. M., Riggio, J., Funston, P. J., Power, R. J., Williams, V., & Child, M. F. (2016). A conservation assessment of *Panthera leo*. In *The red list of mammals of South Africa*. Swaziland and Lesotho.

Milleret, C., Dupont, P., Chipperfield, J., Turek, D., Brøseth, H., Gimenez, O., … Bischof, R. (2020). Estimating abundance with interruptions in data collection using open population spatial capture–recapture models. *Ecosphere*, *11*(7), 1–14. https://doi.org/10.1002/ecs2.3172

Mondol, S., Karanth, U. K., Kumar, S. N., Gopalaswamy, A. M., Andheria, A., & Ramakrishnan, U. (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation*, *142*(10), 2350–2360. https://doi.org/10.1016/j.biocon.2009.05.014

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, *78*(2), 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024

Mucina, L., Rutherford, M. C., & Powrie, W. (2006). Vegetation atlas of South Africa, Lesotho and Swaziland. In L. Mucina & M. C. Rutherford (Eds.), *Vegetation Map of Southern Africa, Lesotho and Swaziland* (pp. 750–760). Pretoria: South Africa National Biodiversity Institute.

Noack, J., Heyns, L., Rodenwoldt, D., & Edwards, S. (2019). Leopard density estimation within an enclosed reserve, namibia using spatially explicit capture-recapture models. *Animals*, *9*(10), 724. https://doi.org/10.3390/ani9100724

Packer, C., Herbst, L., Pusey, A., Bygott, A., Hanby, J. P., Cairns, S. J., & Borgerhoff-Mulder, M. (1988). *Reproduction success of lions: studies of individual variation in contrasting breeding systems* (T. Clutton-Brock, Ed.). Chicago: University of Chicago Press.

Packer, C., Loveridge, A. J., Canney, S., Caro, T., Garnett, S. T., Pfeifer, M., … Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology Letters*, *16*(5), 635–641. https://doi.org/10.1111/ele.12091

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups : Food is not enough. *The American Naturalist*, *136*(1), 1–19.

Packer, C., Swanson, A., Canney, S., Loveridge, A., Garnett, S., Pfeifer, M., … Macnulty, D. (2013). The case for fencing remains intact. *Ecology Letters*, *16*(11), 7–8. https://doi.org/10.1111/ele.12171

Packer, Craig. (2019). The African lion: A long history of interdisciplinary research. *Frontiers in Ecology and Evolution*, *7*(259), 1–6. https://doi.org/10.3389/fevo.2019.00259

Pekor, A., Miller, J. R. B., Flyman, M. V., Kasiki, S., Kesch, M. K., Miller, S. M., … Lindsey, P. A. (2019). Fencing Africa's protected areas: Costs, benefits, and management issues. *Biological Conservation*, *229*, 67–75. https://doi.org/10.1016/j.biocon.2018.10.030

Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology*, *160*(4), 497–508. https://doi.org/10.1111/j.1469-7998.1970.tb03093.x

Périquet, S., Fritz, H., & Revilla, E. (2015). The lion king and the hyaena queen: Large carnivore interactions and coexistence. *Biological Reviews*, *90*(4), 1197–1214. https://doi.org/10.1111/brv.12152

Pfeffer, S. E. (2016). *Comparison of three different indirect methods to evaluate ungulate population densities*. Swedish university of africultural science.

Power, R. J. (2002). Prey selection of lions *Panthera leo* in a small, enclosed reserve. *Koedoe*, *45*(2), 67–75. https://doi.org/10.4102/koedoe.v45i2.32

Prox, L., & Farine, D. (2020). A framework for conceptualizing dimensions of social organization in mammals. *Ecology and Evolution*, *10*(2), 791–807. https://doi.org/10.1002/ece3.5936

Pusey, A. E., & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, *101*(4), 275–310.

Rafiq, K., Bryce, C. M., Rich, L. N., Coco, C., Miller, D. A. W., Meloro, C., … Hayward, M. W. (2019). Tourist photographs as a scalable framework for wildlife monitoring in protected areas. *Current Biology*, *29*(14), R681–R682. https://doi.org/10.1016/j.cub.2019.05.056

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., … Pimm, S. (2013). The size of savannah Africa: A lion's (*Panthera leo*) view. *Biodiversity and Conservation*, *22*(1), 17–35. https://doi.org/10.1007/s10531-012-0381-4

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Royle, A. J., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture-recapture*. Academic Press.

Royle, A. J., & Converse, S. J. (2014). Hierarchical spatial capture-recapture models: Modelling population density in stratified populations. *Methods in Ecology and Evolution*, *5*(1), 37–43. https://doi.org/10.1111/2041-210X.12135

Royle, A. J., Fuller, A. K., & Sutherland, C. (2018). Unifying population and landscape ecology with spatial capture–recapture. *Ecography*, *41*(3), 444–456. https://doi.org/10.1111/ecog.03170

Royle, A. J., Karanth, U. K., Gopalaswamy, A. M., & Kumar, S. N. (2009). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, *90*(11), 3233–3244. https://doi.org/10.1890/08-1481.1

Royle, A. J., Sutherland, C., Fuller, A. K., & Sun, C. C. (2015). Likelihood analysis of spatial capture-recapture models for stratified or class structured populations. *Ecosphere*, *6*(2), 1–11. https://doi.org/10.1890/ES14-00148.1

Rutherford, M. C., Mucina, L., Lötter, C., Bredenkamp, G. J., Jacobus, H. L., Scott-shaw, C. R., … Hurter, P. J. H. (2006). Savanna Biome. In *The vegetation of South Africa, Lesotho and Swaziland.* (pp. 440–529). Pretoria: South Africa National Biodiversity Institute.

Schaller, G. B. (1972). The Serengeti Lion. Chicago: Univeristy of Chicago Press. https://doi.org/10.1017/CBO9781107415324.004

Silk, J. B. (1984). Local resource competition and the evolution of male-biased sex ratio. *Journal of Theoretical Biology*, *108*(2), 203–213.

Skinner, J. D., & Chimimba, C. T. (2005). Lion. In *The mammals of the Southern African sub-region* (Third Edit, pp. 390–396). Cambridge University Press.

Slotow, R., & Hunter, L. T. B. (2009). Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: The African lion in South Africa. In *Reintroduction of Top-Order Predators, (5), 43*. https://doi.org/10.1002/9781444312034.ch3

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), 20142711. https://doi.org/10.1098/rspb.2014.2711

Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., & Harwood, J. (2010). The functional response of a generalist predator. *PloS one*, *5*(5). https://doi.org/10.1371/journal.pone.0010761

Snyman, A., Jackson, C. R., & Funston, P. J. (2015). The effect of alternative forms of hunting on the social organization of two small populations of lions *Panthera leo* in Southern Africa. *Oryx*, *49*(4), 604–610. https://doi.org/10.1017/S0030605313001336

Sobratee, N., & Slotow, R. (2019). A critical review of lion research in South Africa:

The impact of researcher perspective, research mode, and power structures on outcome bias and implementation gaps. *Frontiers in Ecology and Evolution*, *7*(81), 1–17. https://doi.org/10.3389/fevo.2019.00081

Spong, G. (2002). Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioural Ecology and Sociobiology*, *52*(4), 303–307. https://doi.org/10.1007/s00265-002-0515-x

Stander, P. E. (2019). Lions (*Panthera leo*) specialising on a marine diet in the Skeleton Coast National Park, Namibia. *Namibian Journal of Environment*, *3*, 1–10.

Stoffelen, A., Adiyia, B., Vanneste, D., & Kotze, N. (2020). Post-apartheid local sustainable development through tourism: an analysis of policy perceptions among “responsible” tourism stakeholders around Pilanesberg National Park, South Africa. *Journal of Sustainable Tourism*, *28*(3), 414–432. https://doi.org/10.1080/09669582.2019.1679821

Tambling, C. J., & du Toit, J. T. (2005). Modelling wildebeest population dynamics: Implications of predation and harvesting in a closed system. *Journal of Applied Ecology*, *42*, 431–441. https://doi.org/10.1111/j.1365-2664.2005.01039.x

Tarugara, A., Clegg, B. W., Gandiwa, E., & Muposhi, V. K. (2019). Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population. *Global Ecology and Conservation*, *18*, e00627. https://doi.org/10.1016/j.gecco.2019.e00627

Tende, T., Ottosson, U., Hansson, B., & Bensch, S. (2008). Population density and abundance of Lions in Yankari Game Reserve, 2008. Unpublish report, Lund University, Sweden.

Trinkel, M., Fleischmann, P. H., & Slotow, R. (2017). Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population. *Journal of Zoology*, *301*(1), 41–50. https://doi.org/10.1111/jzo.12387

Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C., & Slotow, R. (2010). Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation*, *13*(4), 374–382.

https://doi.org/10.1111/j.1469-1795.2009.00344.x

Trinkel, Martina., & Angelici, F. M. (2016). The decline in the Lion population in Africa and possible mitigation measures. In F. M. Angelici (Ed.), *Problematic Wildlife* (Edition 1, pp. 45–68). https://doi.org/10.1007/978-3-319-22246-2

Tumenta, P. N., van't Zelfde, M., Croes, B. M., Buij, R., Funston, P. J., Udo de Haes, H. A., & De Iongh, H. H. (2013). Changes in lion (*Panthera leo*) home range size in Waza National Park, Cameroon. *Mammalian Biology*, *78*(6), 461–469. https://doi.org/10.1016/j.mambio.2013.08.006

Van de Kerk, M., de Kroon, H., Conde, D. A., & Jongejans, E. (2013). Carnivora population dynamics are as slow and as fast as those of other mammals: Implications for their conservation. *PloS one*, *8*(8), e70354. https://doi.org/10.1371/journal.pone.0070354

Van Dyk, G., & Slotow, R. (2003). The effects of fences and lions on the ecology of African wild dogs reintroduced to Pilanesberg National Park, South Africa. *African Zoology*, *38*(1), 79–94. https://doi.org/10.1080/15627020.2003.11657196

Van Orsdol, K. G., Hanby, J. P., & Bygott, J. D. (1985). Ecological correlates of lion social organization (Panthers, leo). *Journal of Zoology*, *206*(1), 97–112. https://doi.org/10.1111/j.1469-7998.1985.tb05639.x

Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, *143*(11), 2631–2637. https://doi.org/10.1016/j.biocon.2010.07.005

VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour*, *77*(4), 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028

Vega Yon, G. G., & Marjoram, P. (2019). fmcmc: A friendly MCMC framework. *The Journal of Open Source Software*, *4*(39), 1427. https://doi.org/10.2307/2334940

West, P. M., & Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science*, *297*(5585), 1339–1343. https://doi.org/10.1126/science.1073257

Wijers, M., Trethowan, P., Du Preez, B., Chamaillé-Jammes, S., Loveridge, A. J., Macdonald, D. W., & Markham, A. (2021). Vocal discrimination of African lions and its potential for collar-free tracking. *Bioacoustics*, *30*(5), 575–593.

https://doi.org/10.1080/09524622.2020.1829050

Wild, G., & West, S. A. W. (2009). Genomic imprinting and sex allocation. *American Naturalist*, *173*(1), 1–14. https://doi.org/10.1086/593305

Winterbach, H. E. K., Winterbach, C. W., Somers, M. J., & Hayward, M. W. (2013). Key factors and related principles in the conservation of large African carnivores. *Mammal Review*, *43*(2), 89–110. https://doi.org/10.1111/j.1365-2907.2011.00209.x

Witmer, G. W. (2005). Wildlife population monitoring: some practical considerations. *Wildlife Research*, *32*, 259–263.

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation*, *3*(2), 165–173. https://doi.org/10.1017/S136794300000086X

Woolley, L. A., Page, B., & Slotow, R. (2011). Foraging strategy within African elephant family units: Why body size matters. *Biotropica*, *43*(4), 489–495. https://doi.org/10.1111/j.1744-7429.2010.00733.x