

Population density estimate of leopards (*Panthera pardus*) in north-western Mpumalanga, South Africa, determined using spatially explicit capture–recapture methods

Declan R. Morris^{1,*}, Wayne S. J. Boardman¹, Lourens H. Swanepoel^{2,3}, Greg Simpson⁴, Jannie Coetzee⁵, Gerrie J. Camacho⁵, Todd J. McWhorter¹

¹ School of Animal and Veterinary Sciences, University of Adelaide, Roseworthy, SA 5371, Australia

² Department of Zoology, University of Venda, Thohoyandou 0950, Limpopo, South Africa

³ African Institute for Conservation Ecology, Levubu 0929, Limpopo, South Africa

⁴ Department of Production Animal Studies, University of Pretoria, Onderstepoort 0110, Gauteng, South Africa

⁵ Mpumalanga Tourism and Parks Agency, Nelspruit 1200, Mpumalanga, South Africa

*Correspondence to Declan R. Morris. Email: declanmorris743@gmail.com

Abstract

The African leopard (*Panthera pardus pardus*) has lost much of its historical range within South Africa. The remaining suitable habitat for the species includes both protected and unprotected areas in a fragmented landscape mosaic, bringing the species into close contact with human settlements. In order to make successful management decisions for the conservation of the species, more information is needed on leopard populations that exist in these highly fragmented habitats. The aim of our study was to determine the density of a population of leopards on Loskop Dam Nature Reserve (LDNR), Mpumalanga, South Africa. LDNR is located in a highly fragmented landscape and is surrounded by a variety of human settlements including game farms, livestock farms and rural towns. There are several smaller reserves 20–45 km away from LDNR, which may allow leopard movement and connectivity within the region. We determined population density by running a 164-day camera trap survey that covered a total area of 148.77 km² within the reserve. Leopard density was estimated using Spatially Explicit Capture–Recapture models implemented in the program ‘secr’ in R using four different models. The most supported model was a sex-based model that allowed for differences in detection probabilities between males and females. The population density estimated with this model was 7.7 ± 2.0 (range 4.7–12.6) leopards per 100 km². This density estimate in LDNR is comparable to other leopard populations in protected areas with similar habitat types and fragmented landscapes within South Africa. This study highlights that isolated, protected natural areas have the potential to harbour significant populations of leopards, which is important for the management and conservation of the species.

Keywords: Camera trap; Density; Leopard; Mpumalanga; Population; South Africa; Spatially Explicit Capture–Recapture (SECR)

Introduction

Large carnivore species throughout the world are under threat with 64% currently facing extinction and 80% exhibiting a declining population trend (Wolf and Ripple [2018](#)). Anthropogenic factors such as habitat destruction and fragmentation, retaliatory killings and poorly managed harvest quotas are the biggest threats (Swanepoel et al. [2015b](#); Williams et al. [2017](#)). Typically, large carnivores occur at low densities, have large home ranges and disperse over large distances (Cardillo et al. [2005](#)); thus, habitat loss and fragmentation due to expanding urbanisation and agricultural enterprises affects both the extent of available habitat and the connectivity between populations (Crooks et al. [2011](#)). Widespread habitat destruction and fragmentation has contributed to a sharp increase in human-carnivore interactions leading to an increased frequency of livestock (domestic and game species) loss (Treves and Karanth [2003](#)). This real or perceived threat to livelihood and livestock often results in the lethal persecution of carnivores (Treves and Karanth [2003](#)). An additional threat that arises from closer human interaction is the introduction of diseases that can be transmitted from livestock and other domestic species to free ranging carnivores (Miller et al. [2013](#)). Finally, carnivores also face the risk of over utilisation from trophy hunting in cases where robust scientific data does not exist on population size or viability (Braczkowski et al. [2015](#)).

The African subspecies of leopard (*Panthera pardus pardus*, Fig. [A1](#)) is currently listed as Vulnerable on the IUCN Red List of Threatened Species (Stein et al. [2020](#)). The subspecies has lost an estimated 48–67% of its historical home range across the African continent with much of this loss occurring in western Africa and South Africa (Jacobson et al. [2016](#)). Across the continent, leopards are thought to exist as one large, continuous population, but display genetically structured meta-populations at regional scales (Anco et al. [2018](#)). This observation is thought to be due to a combination of both geographic separation and an inability of animals to move across the landscape, which has led to slight differences in the genetic makeup of the metapopulations (Anco et al. [2018](#)). The leopard population within South Africa displays genetic differentiation on a smaller, local scale (McManus et al. [2015](#); Ropiquet et al. [2015](#)). Genetic differentiation of populations within close geographic proximity, as observed in areas of South Africa, generally suggests that movement and connectivity between the leopard population units has been reduced or impeded (McManus et al. [2015](#)). Within South Africa, only 20% of the land is regarded as suitable leopard habitat, much of which is highly fragmented and located outside of protected areas (Swanepoel et al. [2013](#)). In studies conducted in the Limpopo and KwaZulu-Natal provinces, leopard density fell by over 10% over a 4- to 7-year period (Swanepoel et al. [2016](#)). Leopard population estimates for the Mpumalanga province are 338–1851 individuals (203–1111 mature adults) (Swanepoel et al. [2011](#)).

In order for governments, non-government organisation (NGOs) and management authorities to make effective management decisions, there needs to be reliable up-to date information regarding the status and viability of distinct leopard populations. As leopards are elusive animals that are notoriously difficult to study due to their shy, solitary behaviour and ability

to persist in secluded hard-to-access habitats, camera trapping surveys have emerged as a vital technique to collect robust information on their populations (Balme et al. [2009](#)). Camera trapping allows researchers to collect large amounts of data with relatively little associated cost and is minimally invasive for the animals (Rowcliffe et al. [2008](#)). Camera trap data can be used to make inferences about several ecologically-relevant parameters including species occupancy, abundance, density, activity, behaviour and competition (Caravaggi et al. [2017](#); Sollmann [2018](#)).

Information on population density has become an important tool in large carnivore conservation as it can be an indication of population status and viability (Jędrzejewski et al. [2017](#)). Density estimates that note a declining population can highlight the need to prevent local extinction, which can lead to deleterious trophic cascade events (Schmitz et al. [2000](#); Ripple et al. [2014](#)). Population density is also used for effective conservation management plans, such as leopard trophy hunting quotas which are currently based on density and abundance estimates in South Africa (Trouwborst et al. [2019](#)).

Spatially explicit capture-recapture (SECR) modelling is a recently developed method of estimating population density for animals that can be individually identified (Efford [2004](#)). This analysis can estimate density by calculating the spatial movements of individual animals based on when and where they were identified on camera traps. SECR provides more accurate density estimates than traditional capture-recapture methodologies by accounting for individual animal movement and allows more sophisticated analysis of spatial parameters (Borchers and Efford [2008](#)). SECR analysis is now the most commonly used method for estimating carnivore population density (Grey et al. [2013](#); Strampelli et al. [2018](#)). SECR studies have been utilised for a variety of leopard subspecies including the Amur leopard *P. p. orientalis* (Qi et al. [2015](#)), Indochinese leopard *P. p. delacouri* (Gray and Prum [2012](#); Hedges et al. [2015](#)) Indian leopard *P. p. fusca* (Kalle et al. [2011](#)), Javan leopard *P. p. melas* (Rahman et al. [2018](#)) and the African leopard *P. p. pardus* (Grey et al. [2013](#); Swanepoel et al. [2015a](#)).

As much of the remaining leopard habitat exists outside of protected areas and in areas where they are in close contact with human settlements (especially agricultural industries such as game and livestock farms), research on leopard populations that persist in these areas should receive priority for research (Balme et al. [2014](#)). Mpumalanga province has currently lost 36% of the total natural area due to conversion of land for use in agriculture, mining and manufacturing (Ferrari [2007](#)). Loskop Dam Nature Reserve (LDNR) is a protected area in the province of Mpumalanga, South Africa, that is surrounded by both agricultural industries and human settlements. The reserve is known to have a leopard population, however this population has been little studied except for inclusion in national level species management reports (Mann et al. [2017](#)). The reserve is located close to several smaller nature reserves including Mabusa Game Reserve which lies 20 km north-west of LDNR, Mdala Nature Reserve 45 km to the north-west, Kwaggavoetpad Nature Reserve 40 km to the north-east and Ezemvelo Nature Reserve 35 km to the south. Connectivity between these reserves is yet to be studied however, due to the close proximity it is highly likely that regular movements are occurring. The Drakensberg Mountain range lies approximately 130 km east of the reserve and has the potential to be acting as a barrier to leopard movement further east to the province. Kruger National Park is located approximately 185 km east of LDNR across the

escarpment. There is a pressing need for reserves such as LDNR to be studied to better understand the population dynamics of leopards in highly fragmented landscapes.

The aim of our study was to estimate the leopard population density on Loskop Dam Nature Reserve, Mpumalanga province, South Africa. We achieved this by using camera trap surveys and analysed the data using a maximum likelihood spatially explicit capture-recapture (SECR) framework. The aims were to (i) provide baseline information so the LDNR leopard population can be monitored over time, (ii) compare the density estimate with other leopard populations from other areas around southern Africa (iii) contribute data to making informed management plans for the LDNR leopard population.

Methods

Study area

Loskop Dam Nature Reserve (LDNR) is a 228.5 km² nature reserve under the authority of the provincial government entity, the Mpumalanga Tourism and Parks Agency (MTPA). It is located in the north-western region of Mpumalanga province in South Africa and abuts the Limpopo border (Fig. 1). The closest town, Groblersdal, is 30 km north of the reserve and Middleburg is situated 55 km south. The reserve exists in a fragmented landscape surrounded by local community settlements and villages to the north and a variety of agricultural enterprises (mostly game farms, sheep/cattle farms and citrus farms) on the eastern, western and southern boundaries. The main river flowing through the reserve is the Olifants River that flows from Mpumalanga to Mozambique through Kruger National Park. The Loskop dam was originally constructed in 1938 for irrigation purposes and area around the dam was declared a nature reserve later in 1942 with additional land reclaimed and added to the reserve over time (MTPA 2014). The surface of the reservoir covers a total area of approximately 23 km².

The climate of the reserve is characterised by hot, rainy summers (October–March; 650 mm of rainfall; daily average maximum in December is 29.8 °C) and cool dry winters (April–September; daily average minimum in July is 8.1 °C) (MTPA 2014). The terrain is mountainous and rocky which has led to the formation of deep drainage lines and cliffs. The elevation of the reserve varies from 990 to 1450 m above sea level (MTPA 2014). The higher altitude areas are characterised by large flat plateaus with a vegetation type classed as grassland biome. The lower lying regions are characterised by deep drainage lines, a large valley, rolling hills and cliffs of varying steepness and the reservoir. The vegetation type of the lower lying areas is classed as mixed bushveld within the savannah biome. The reserve is home to a number of large mammal species including buffalo (*Syncaerus caffer*), white rhinoceros (*Ceratotherium simum*), the common hippopotamus (*Hippopotamus amphibius*), giraffe (*Giraffa camelopardalis*), plains zebra (*Equus quagga*) and sable antelope (*Hippotragus niger*). A number of carnivores are found on the reserve including leopard, brown hyaena (*Hyaena brunnea*), caracal (*Caracal caracal*), black-backed jackal (*Canis mesomelas*) and serval (*Leptailurus serval*). The absence of other large carnivores such as lions makes the leopard the apex predator of this system. Common leopard prey species found on the reserve include impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*), baboon (*Papio ursinus*), vervet monkey (*Chlorocebus pygerythrus*), bushbuck (*Tragelaphus sylvaticus*) and mountain reedbuck (*Redunca fulvorufula*) (Hayward et al. 2006).

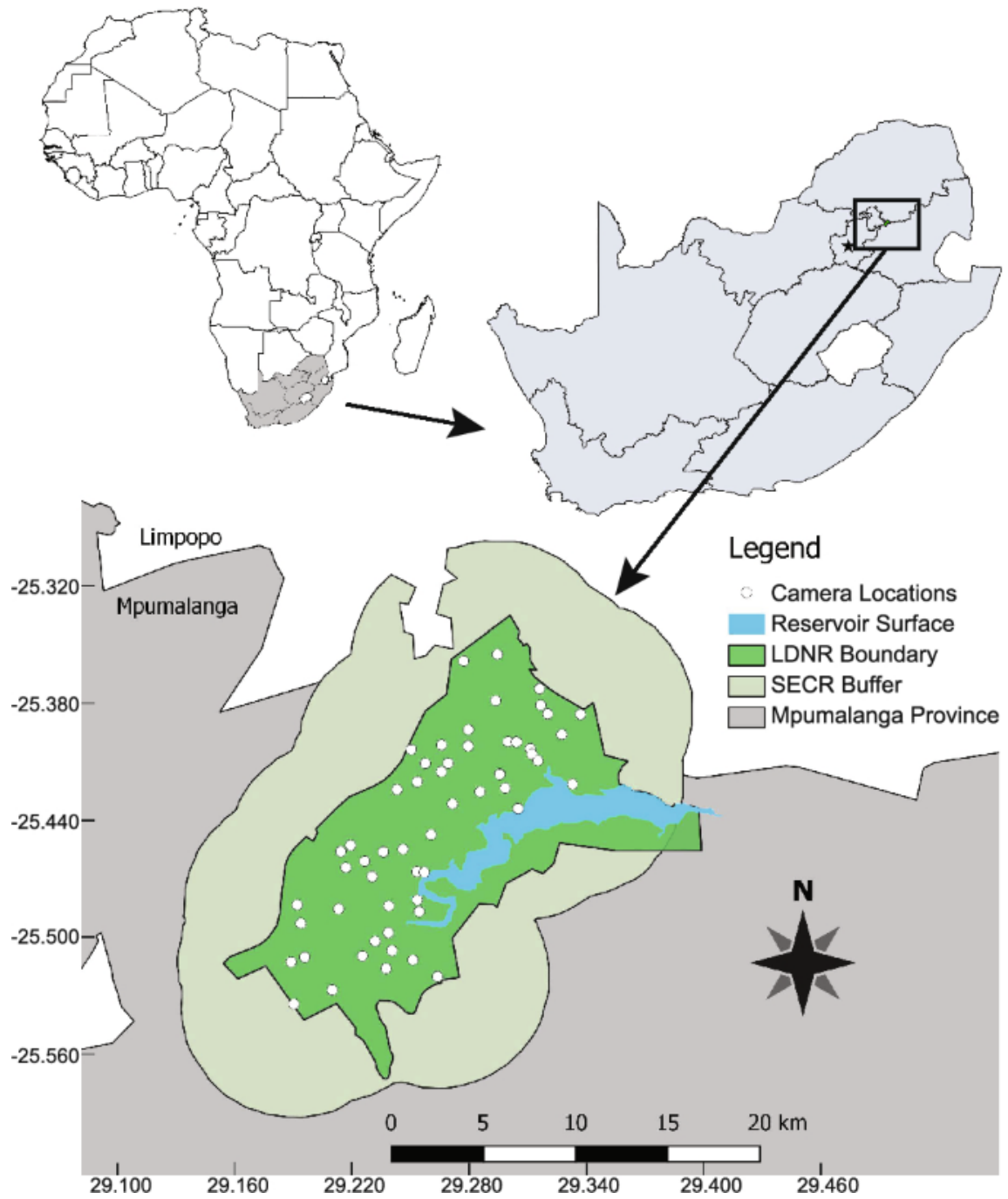


Fig. 1. Location of Loskop Dam Nature Reserve within South Africa where a spatially explicit capture-recapture camera trap survey was conducted for 6 months in early 2018. The map highlights the reservoir surface, the border of the nature reserve, the SECR buffer and the locations in which camera stations were active over the survey period

Camera trapping and leopard identification

The camera trap survey ran for a 6-month period from the 9th of February to the 23rd of July 2018 (164 days). We used 26 Cuddeback Professional Colour strobe flash cameras (Model 1347; Non Typical, Inc., Green Bay, WI, USA). Two cameras were used at each station and set on both sides of the target path in order to attempt to capture both flanks of animals for identification purposes. Camera trap stations were set on roads, game paths, drainage lines and along dam edge paths where leopards were most likely to frequent. Sites were also selected where signs of leopard (tracks and scats) were observed. Cameras were secured in steel cases and attached to either trees or metal posts at a height of 35–40 cm from the ground. Thirteen stations were active at a time, and then they were moved approximately every 4 weeks in order to cover the entire reserve. Camera stations were set 0.5–2 km apart from each other in order to ensure that there was a probability that every individual in the population could be captured. Minimum female leopard home range has been recorded at 14 km² in a similar reserve so setting the camera stations this close together meant there were multiple stations located within an individual's home range (Balme et al. [2009](#)). The total area polygon that we sampled measured 148.77 km². This is important for SECR analysis as the detector polygon must be larger than the maximum home range of the target species (Efford [2011](#)). For male leopards in similar habitats and regions, home ranges can vary between 28 and 56 km² (Hayward et al. [2008](#); Ray-Brambach et al. [2018](#)). Leopards were individually identified based on their rosette patterns and by any other unique identifying features such as scars. Leopards were sexed based on the appearance of external genitalia and dew lap size (Balme et al. [2012](#)). Cubs were not recorded as a capture for purposes of the density analysis.

As described in Karanth and Nichols ([2002](#)) and Karanth et al. ([2004](#)), we concatenated the data by splitting the capture data set evenly into two blocks, drawing one day sequentially from each block, then combining the two days of data to form one capture occasion. This meant that one capture occasion represented two real life days and resulted in a total of 82 capture occasions for the analysis.

Leopard density estimation

Leopard density was estimated using spatially explicit capture-recapture (SECR) models within a maximum likelihood framework (Borchers and Efford [2008](#)). Analysis was performed in 'R' version 3.4.3 (R Core Team, 2017 using the package 'secr' (V3.2.0) (Efford [2019](#)). Data was fitted with a Bernoulli (binomial encounter) model. This model specifies that individuals can be captured at several different stations over one sampling occasion, but only once at each station on a given sampling occasion (Royle et al. [2009](#), [2014](#)).

For the SECR analysis, a habitat mask is used to define the total area in which density will be estimated. This generally has areas of non-habitat excluded and an adequately sized buffer that allows for animal movement outside of the detector polygon. A habitat mask was created that included a buffer distance of 6000 m and excluded areas of non-habitat. A 6000 m buffer was selected by running multiple tests while increasing buffer width to determine when the density estimates stabilised (estimates stabilised at 5700 m), and by using the SECR programs buffer estimation functions. For all individual animals captured within the detector polygon,

in this case the reserve, it was possible that the animal had a home range that extended outside of the detector polygon. The buffer ensures that the regions outside of the detector polygon are taken into consideration in the analysis. It is important to exclude areas of non-habitat for SECR analysis as the density estimate will be underestimated. In our project, we removed the entire reservoir water surface area and the nearby densely populated towns of Thabakhubedu and Elandsdoorn.

The data were analysed with sex as a covariate for each individual. Male and female leopards have been found to display different spatial behaviours and have different home range sizes (Mizutani and Jewell [1998](#)). Fitting sex as a covariate in SECR analysis has been shown to improve density estimates (Sollmann et al. [2011](#); Tobler and Powell [2013](#)).

In SECR analysis, the data must also be fit with a detection function model. An assumption of SECR models is that the further an individual is from its activity centre, the lower the probability of detecting that individual (Efford [2019](#)). The detection function model estimates the degree to which that probability changes as the distance (d) from the activity centre changes. The half normal (HN) spatial capture detection function was selected for the data as it is the most commonly used detection function for this type of spatial analysis and makes our data comparable to other leopard density studies (Efford [2004](#); Boron et al. [2016](#)). The HN detection function has two parameters: g_0 and sigma (σ). The parameter g_0 is the probability of capturing an individual at the exact centre of its home range while σ is a spatial parameter related to home range size (Efford [2004](#)). The HN detection function describes the probability of capture (P) of an individual (i) at a trap (j) as $P_{ij} = g_0 \exp(-d_{ij}^2/2\sigma^2)$ (Efford [2004](#)).

We compared four models to estimate density and investigate the impact sex had on the parameters g_0 and σ . Models were compared using Akaike Information Criterion, adjusted for smaller sample sizes (AICc). Model 1 was a null model where sex was not set to have an impact on either spatial parameter. Model 2 was set where only σ differed between sexes and Model 3 was set so that only g_0 differed between sexes. The final model, Model 4, was set so that both the σ and g_0 spatial parameters differed between sexes.

Results

Camera trapping

The survey resulted in a total of 1132 cumulative trap days over 47 trap stations with a mean of 24.1 ± 6.2 (mean \pm SD, range 15–38) days per station. The average distance between camera traps was 1206 m. There was a total of 84 leopard detections over the survey period, from which we identified 19 individual leopards (12 females, six males and one individual that could not be sexed based on photographs). A total of eight detections (9.5%) were removed from the study; six were removed as they were unidentifiable (tail picture, white flushed photography) and two for only having pictures of cubs. There were a significant number of individual recaptures with five males (83%), eight females (67%) and the one unknown sex individual (100%) having been recaptured at other camera trap stations and on different occasions. A total of 14 (74%) animals were recaptured. Figure [2](#) highlights how many times each individual leopard was captured over the survey period.

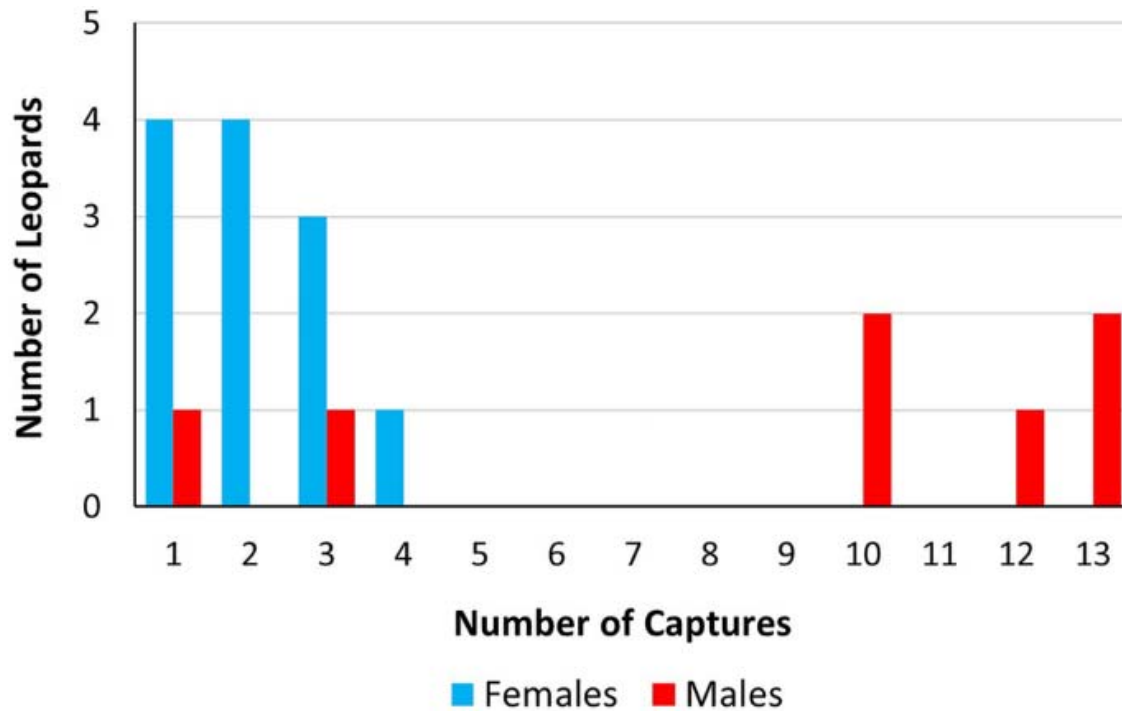


Fig. 2. Number of individual leopard recaptures during a camera trap survey that ran from February to July 2018 on Loskop Dam Nature reserve, South Africa

Density estimates

The model with the lowest AIC_c was model 3 ($AIC_c = 959.783$). This model specified that detection probability (g_0) was dependant on sex. The overall leopard density estimate for model 3 was 7.7 ± 2.0 (95% CI 4.7–12.6) leopards per 100 km² (Table [1](#)). The density for females was 5.5 ± 1.7 (95% CI 3.0–10.0) and males was 1.8 ± 0.8 (95% CI 0.8–4.0) leopards per 100 km². The detection probability (g_0) was 0.028 ± 0.006 (0.018–0.041) for males and 0.006 ± 0.002 (0.004–0.012) for females (Table [1](#)). The σ was the same for both sexes due to the model: 1808 ± 148 m (1541–2121 m).

Table 1. Density and spatial parameter estimations and their variations based on sex of the leopard population on Loskop Dam Nature Reserve according to various Spatially Explicit Capture–Recapture Models

| Model (M) | Model specification | AIC _c value | ΔAIC _c | AIC _c Weight | Density (D) ± SE | Density 95% CI | Sex | Density by Sex ± SE | 95% CI (D) | σ ± SE | 95% CI (σ) | g ₀ ± SE | 95% CI (g ₀) |
|---|------------------------------|------------------------|-------------------|-------------------------|------------------|----------------|-----|---------------------|------------|------------|------------|---------------------|--------------------------|
| 3—g ₀ varies by sex | g ₀ ~ Sex | 959.783 | 0 | 0.734 | 7.7 ± 2.0 | 4.7–12.6 | M | 1.8 ± 0.8 | 0.8–4.0 | 1808 ± 148 | 1541–2121 | 0.028 ± 0.006 | 0.018–0.041 |
| | | | | | | | F | 5.5 ± 1.7 | 3.0–10.0 | | | 0.006 ± 0.002 | 0.004–0.012 |
| 4—both g ₀ and σ vary by sex | g ₀ ~ Sex σ ~ Sex | 962.290 | 2.507 | 0.210 | 8.2 ± 2.1 | 5.0–13.4 | M | 1.8 ± 0.7 | 0.8–3.9 | 1887 ± 175 | 1574–2262 | 0.026 ± 0.006 | 0.017–0.040 |
| | | | | | | | F | 6.0 ± 1.9 | 3.3–11.0 | 1509 ± 245 | 1100–2070 | 0.009 ± 0.003 | 0.004–0.019 |
| 2—σ varies by sex | σ ~ Sex | 964.912 | 5.129 | 0.057 | 7.9 ± 1.9 | 4.9–12.6 | M | 1.7 ± 0.7 | 0.8–3.8 | 2043 ± 197 | 1692–2466 | 0.019 ± 0.004 | 0.013–0.028 |
| | | | | | | | F | 5.7 ± 1.7 | 3.2–10.2 | 1221 ± 119 | 1009–1478 | | |
| 1—Null model | g ₀ ~ 1 | N/A | N/A | N/A | 6.2 ± 1.5 | 3.9–10 | N/A | | | | | | |

Models are ranked in order of AIC_c values (lowest to highest)

D density, *g*₀ detection probability at centre of home range, *sigma* (*σ*) spatial parameter related to home range size, AIC_c Akaike information criterion adjusted for small sample size, ΔAIC_c difference from the lowest AIC_c score, SE Standard Error, CI Confidence Interval, M Male, F Female

Discussion

Leopard density

The total density of leopards on Loskop Dam Nature Reserve was estimated to be 7.7 ± 2.0 leopards per 100 km² (4.7–12.6) using model 3. Model 3 was selected as it has the lowest AIC_c score (959.783) and carried the majority of the model selection weight (73.4%). Density for males under model 3 was 1.8 ± 0.8 (0.8–4.0) leopards per 100km² and the density of females was 5.5 ± 1.7 (3.0–10.0) leopards per 100 km². Model 3 allowed for the spatial parameter (g_0) to vary based on sex while σ remained constant across sexes. Male leopards on LDNR had a higher detection probability at their activity centres than females (g_0 ; Table 1), reflecting lower recapture rates in females (1–4 captures/individual) compared to males (1–13 captures/individual; Fig. 2). Male leopards generally display more territorial behaviours than females and actively patrol their established home ranges more frequently than females (Mizutani and Jewell 1998). This could explain why we captured more male activity on the camera traps compared to females. As the two sexes have different ranging and behavioural traits, including sex as a covariate in the models gives more accurate density estimates (Sollmann et al. 2011; Tobler and Powell 2013).

While model 3 was the most supported model based on AIC_c scores, model 4 (AIC_c = 962.29) only had a delta AIC_c score of 2.507. Model 4 was the model that allowed both g_0 and σ to vary based on sex. We expected that σ (spatial parameter closely related to home range size) would also vary as male leopard home ranges are generally larger than females (Mizutani and Jewell 1998). In model 4, the σ value for males was 1887 ± 175 m and for females was 1509 ± 245 m. The overall density of leopards estimated when using model 4 was 8.2 ± 2.1 leopards per 100 km² (5.0–13.4). The σ estimate of model 3 was similar to that for model 4 for males but larger than that for females, which is likely to have caused the overall density estimate to be slightly higher in model 4. We suggest that this could explain why model 3 was more supported by AIC_c scores and is thus, the more robust model for the density estimates.

In SECR analysis, one of the main assumptions is that the population remains closed over the sampling period (Dupont et al. 2019). This assumption aims to minimise the chance that immigration, emigration or deaths bias density estimates. Some researchers have suggested that shorter time periods ensure that the population is closed (Tobler and Powell 2013), while others suggest that for some species, such as wide-ranging large carnivores, longer sampling surveys provide more accurate density estimates (Jędrzejewski et al. 2017; Devens et al. 2019; Dupont et al. 2019; Harmsen et al. 2020). Due to the large area of the reserve and the limited number of camera traps, we decided to run a longer survey period (6 months) to increase the likelihood of capturing all adult leopards present on the reserve. This was achieved by ensuring that the camera trapping polygon covered the vast majority of the reserve. We followed the methods in Karanth et al. (2004) to concatenate data from the divided dataset and defined one sampling occasion as 2 real-life camera trap days. This resulted in a dataset that consisted of 82 capture sampling occasions. This was done in order to help meet the final requirements of population closure (Karanth and Nichols 2002; Balme et al. 2009).

Comparison to other regions

The estimated density on LDNR (model 3: 7.7 ± 2.0 leopards per 100 km²) is similar to the density of leopard populations found in other areas across southern Africa that also have a mixture of grassland and mixed bushveld biomes (Table 2). SECR studies on leopard populations from these regions on protected areas and reserves found a density found a density between 7.0 - 10.8 leopards per 100 km on various protected nature reserves in KwaZulu-Natal (KZN), South Africa (Balme et al. 2010; Chapman and Balme 2010; Braczkowski et al. 2016). Population densities between 7.4 and 8.4 leopards per 100 km² were recorded across the St Lucia Wetlands Reserve in KZN (Ramesh et al. 2017). Leopard densities were recorded to be lower in unprotected areas, despite having similar habitat. Balme et al. (2010) reported a density of only 2.5 leopards per 100 km² for the unprotected regions surrounding the reserves studied in KZN. Densities ranged from 4.6 to 6.6 leopards per 100 km² in unprotected regions in Limpopo (Swanepoel et al. 2015a).

Areas of southern Africa that displayed the highest leopard density estimates (between 11.8 and 14.5 leopards per 100 km²) are protected areas where savannah and woodland biomes are present (Maputla et al. 2013; Balme et al. 2019). The two highest density estimates from South Africa are from Kruger National Park (KNP) and Sabi Sands Game Reserve (SSGR). SSGR is a private game reserve that is open to KNP and forms part of the Greater Kruger National Park area. The largest leopard density estimates on unprotected land was 10.7 leopards per 100 km² in the western Soutpansberg, Limpopo, South Africa (Grey et al. 2013), while the lowest density estimates were observed in the Eastern and Western Cape provinces of South Africa (Devens et al. 2018, 2019). Density estimates range from 0.2 to 1.9 leopards per 100 km² in these regions (Table 2). The major biomes present in these areas are Fynbos and Karoo and the studies were conducted on either unprotected or partially protected land.

Both habitat type and protection status appear to be linked to leopard density (Table 2). Habitat can affect both prey species and prey density which in turn can affect leopard density. Prey species generally occur at lower densities in drier areas such as fynbos and karoo biomes, due to the lower availability of food. This directly impacts the ecosystem's carnivore species carrying capacity. Noack et al. (2019) noted that the Okonjima Nature Reserve, which has the highest leopard density estimate of 14.5 leopards per 100 km² has an unusually large number of game species, which ensures a high density of animals for tourism purposes. While areas that are protected generally have the highest leopard densities, other protected areas like LDNR in Mpumalanga and the St Lucia Wetlands Park/Phinda-Mkhuze complex in KZN exist in highly fragmented, human dominated, agricultural landscapes. Leopards in these areas are more likely to cause conflicts with humans due to predation on livestock and game. This can often threaten livelihoods and lead to negative perceptions within communities (Thorn et al. 2012; Constant et al. 2015). Retaliatory killings due to livestock predation has been identified as the biggest threat to the conservation of the species (Treves and Karanth 2003). This might explain why protected areas that occur within fragmented landscapes close to human settlements, only display a moderate population density. Much of the only remaining suitable leopard habitat within South Africa is located in these unprotected and/or highly fragmented landscapes (Swanepoel et al. 2013).

Table 2. Leopard density estimates reported across various areas in southern Africa

| Location | Density (leopards/100 km ²) | Habitat type | Protected (Y/N) | Density estimation methods | Reference |
|--|--|--|-----------------|----------------------------|---|
| Langeberg Garden Route Overberg Western Cape, South Africa | 0.5 ± 0.1 0.4 ± 0.2 0.2 ± 0.1 | Thicket/Fynbos/Succulent Karoo/Savannah | Partially | SECR | (Devens et al. 2019) |
| Angulhas Baviaanskloof Garden Route Langeberg Eastern/Western Cape | 0.7 ± 0.3 0.2 ± 0.1 1.0 ± 0.3 1.9 ± 0.3 | Thicket/Afro-temperate forest/Fynbos /Succulent Karoo | Partially | SECR | (Devens et al. 2018) |
| Cederberg Mountains, Western Cape, South Africa | 0.6–0.9 | Fynbos/Succulent Karoo | N | CR | (Martins 2010) |
| Little Karoo, Western Cape, South Africa | 1.3 ± 0.3 | Sub-tropical Thicket/Succulent Karoo/Fynbos | N | SECR | (Mann et al. 2020) |
| Xonghile Game Reserve, Mozambique | 2.6 ± 1.0 | Sandveld | Y | SECR | (Strampelli et al. 2018) |
| Surrounding Farmlands Waterberg Plateau Park Namibia | 3.6 1.0 | Acacia Scrubland/Woodland Bush Savannah/Woodland | N Y | CR | (Stein et al. 2011) |
| Welgevonden Lapalala Farming Matrix Waterberg Biosphere, Limpopo, South Africa | 4.6 ± 1.4 5.2 ± 2.8 6.6 ± 5.2 | Waterburg Mountain Bushveld | N | SECR | (Swanepoel et al. 2015a) |
| Kwalusi Mazunga Bubye Valley Conservancy, Matabeleland South Province, Zimbabwe | 5.5 ± 1.1 2.8 ± 0.7 | Acacia scrub and Woodland/Grassland | Y | SECR | (du Preez et al. 2014) |
| Mangwe District, Zimbabwe | 5.1 ± 0.6 | Savannah Bushveld, Grassland/Woodlands | N | SECR | (Grant 2012) |

| | | | | | |
|---|--------------------------------------|--|-------------|------|---|
| Zululand Rhino Reserve, KwaZulu-Natal, South Africa | 7.0 ± 2.6 | Bushveld/Open Savannah Thornveld | Y | CR | (Chapman and Balme 2010) |
| Phinda Private Game Reserve Mkhuze Game Reserve Non-protected area surrounding Phinda and Mkhuze KwaZulu-Natal, South Africa | 7.2 ± 1.1 10.8 ± 1.8 2.5 ± 0.9 | Woodland/Grassland | Y Y N | CR | (Balme et al. 2010) |
| Phinda Private Game Reserve, KwaZulu-Natal, South Africa | 7.3 ± 2 9.3 ± 2.9 | Woodland/Grassland | Y | SECR | (Brackowski et al. 2016) |
| Loskop Dam Nature Reserve, Mpumalanga, South Africa | 7.7 ± 2.0 | Grassland/Mixed Bushveld | Y | SECR | Current Study |
| Western Shores Eastern Shores St Lucia Wetland Park | 8.4 (6.8–10.4) 7.4 (6.1–9.1) | Dry Forest and Thicket/Grassland Grassland/Coastal Dune Forest | Y Y | SECR | (Ramesh et al. 2017) |
| Tembe Elephant Reserve Ndumo Game Reserve KwaZulu-Natal, South Africa | 4.8 (3.8–5.7) 1.6 (1.3–2.9) | Woodland/Sand Forest Broadleaf Woodland/Sand Forest/Makatini Clay Thicket | Y Y | | |
| Western Soutpansberg, Limpopo, South Africa | 10.7 | Montane Woodland | N | SECR | (Grey et al. 2013) |
| Sabi Sands Game Reserve, Mpumalanga, South Africa | 11.8 ± 2.6 | Savannah/Grassland | Y | SECR | (Balme et al. 2019) |
| N'wanetsi concession Kruger National Park, South Africa | 12.7 | Savannah Woodland | Y | CR | (Maputla et al. 2013) |
| Okonjima Nature Reserve, Namibia | 14.5 | Savannah | Y | SECR | (Noack et al. 2019) |

Density estimation methods were either Capture-Recapture (CR) or Spatially Explicit Capture-Recapture (SECR)

Management implications

Data are lacking on leopard population dynamics in the Loskop region of Mpumalanga, but it is likely that the leopards would be experiencing similar threats faced on other reserves across southern Africa. Retaliation killings, habitat destruction/fragmentation, accidental or deliberate poisoning and road kills, often exacerbated by the edge effects that occur when protected areas are densely surrounded by human enterprises, all contribute to reduced population viability (Balme et al. [2010](#); Swanepoel et al. [2015b](#)). The matrix of protected reserves occurring in the greater Loskop region, including nearby protected regions such as Mabusa Game Reserve, Mdala Nature Reserve and Ezemvelo Nature reserve are all separated by high concentrations and densities of human settlements. From a national perspective, a map of suitable leopard habitat highlights that leopards from LDNR are likely to be most connected to regions to the north (Limpopo) and east (KNP/Mozambique), however leopard movements and connectivity from Loskop to and between these regions have yet to be studied (Swanepoel et al. [2013](#)).

Despite the large number of potential threats to leopards in the region, we found a moderate density of leopards on Loskop Dam Nature Reserve, which was comparable to other protected areas within similar human dominated landscapes with similar biomes in the neighbouring provinces of Limpopo and KZN. This study highlights that isolated protected natural areas, even in highly fragmented landscapes, have the potential to harbour significant populations of leopards. These populations will be important in the management and conservation of the species and play a key role in leopard meta-population dynamics. Further studies on leopard movements between protected reserves and population genetic analyses are needed to characterise the connectivity of isolated protected leopard populations across Mpumalanga province.

Availability of data and material

Raw data and material are either published in the manuscript or available in data repository DANS (<https://doi.org/10.17026/dans-zvs-betq>).

Code availability

All analyses were performed in R and the codes are attached as supplementary material.

Acknowledgements

We would like to thank the Mpumalanga Tourism and Parks Agency for their support, especially Jannie Du Bruyn, Dr. Hannes Botha, Delecia Gunn, Tommie Steyn, Juan De Beer, Johan Eksteen & the MTPA game capture team. Special thanks to Jeanette Wentzel for her assistance with logistical planning and support throughout the project. We would also like to thank Dr. Philip Stott for his input into the project development. Thanks also to the students Herman Viviers, Tora-Lee Axelson, Max Peters, Parris Jeffries, Marco Gouws, Olivia Rynders and Mosa Molapo who assisted with field work activities.

Funding

This study was funded from PhD student operating funds available from the School of Animal and Veterinary Sciences at The University of Adelaide.

Contributions

DRM: project planning, field work, analysis and manuscript preparation/editing WSJB: project planning, analysis, manuscript editing LHS: analysis, manuscript editing GS: project planning, field work, manuscript editing JC: project planning, field work, manuscript editing, GJC: project planning, field work, manuscript editing, TJM: project planning, analysis, manuscript editing.

Conflict of interest

The authors declare that there is no conflict of interest nor competing interests.

Ethics approval

Ethics approval was received from the University of Adelaide Animal Ethics Committee (S-2016-023) and the permit to conduct research on Loskop Dam Nature Reserve was given by the provincial municipality Mpumalanga Tourism and Parks Agency (TS3/11).

References

- Anco C, Kolokotronis SO, Henschel P, Cunningham SW, Amato G, Hekkala E (2018) Historical mitochondrial diversity in African leopards (*Panthera pardus*) revealed by archival museum specimens. Mitochondrial DNA Part A 29:455–473. <https://doi.org/10.1080/24701394.2017.1307973>
- Balme GA, Hunter LT, Slotow R (2009) Evaluating methods for counting cryptic carnivores. J Wildl Manag 73:433–441. <https://doi.org/10.2193/2007-368>
- Balme GA, Slotow R, Hunter LTB (2010) Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. Anim Conserv 13:315–323. <https://doi.org/10.1111/j.1469-1795.2009.00342.x>
- Balme GA, Hunter L, Braczkowski AR (2012) Applicability of age-based hunting regulations for African leopards. PLoS One. <https://doi.org/10.1371/journal.pone.0035209>
- Balme GA, Lindsey PA, Swanepoel LH, Hunter LTB (2014) Failure of research to address the rangewide conservation needs of large carnivores: leopards in South Africa as a case study. Conserv Lett 7:3–11. <https://doi.org/10.1111/conl.12028>
- Balme G, Rogan M, Thomas L, Pitman R, Mann G, Whittington-Jones G, Midlane N, Broodryk M, Broodryk K, Campbell M, Alkema M, Wright D, Hunter L (2019) Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. Popul Ecol 61:256–267. <https://doi.org/10.1002/1438-390x.1023>

- Borchers DL, Efford MG (2008) Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64:377–385. <https://doi.org/10.1111/j.1541-0420.2007.00927.x>
- Boron V, Tzanopoulos J, Gallo J, Barragan J, Jaimes-Rodriguez L, Schaller G, Payan E (2016) Jaguar densities across human-dominated landscapes in Colombia: the contribution of unprotected areas to long term conservation. *PLoS One*. <https://doi.org/10.1371/journal.pone.0153973>
- Braczkowski AR, Balme GA, Dickman A, Macdonald DW, Fattebert J, Dickerson T, Johnson P, Hunter L (2015) Who bites the bullet first? The susceptibility of leopards *Panthera pardus* to trophy hunting. *PLoS One*. <https://doi.org/10.1371/journal.pone.0123100>
- Braczkowski AR, Balme GA, Dickman A, Fattebert J, Johnson P, Dickerson T, Macdonald DW, Hunter L (2016) Scent lure effect on camera-trap based leopard density estimates. *PLoS One*. <https://doi.org/10.1371/journal.pone.0151033>
- Caravaggi A, Banks PB, Burton AC, Finlay CM, Haswell PM, Hayward MW, Rowcliffe MJ, Wood MD (2017) A review of camera trapping for conservation behaviour research. *Remote Sens Ecol Conserv* 3:109–122. <https://doi.org/10.1002/rse2.48>
- Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds OR, Sechrest W, Orme CDL, Purvis A (2005) Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241. <https://doi.org/10.1126/science.1116030>
- Chapman S, Balme G (2010) An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South Afr J Wildl Res* 40:114–120. <https://doi.org/10.3957/056.040.0202>
- Constant N, Bell S, Hill R (2015) The impacts, characterisation and management of human–leopard conflict in a multi-use land system in South Africa. *Biodivers Conserv* 24:2967–2989. <https://doi.org/10.1007/s10531-015-0989-2>
- Crooks KR, Burdett CL, Theobald DM, Rondinini C, Boitani L (2011) Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Phil Trans R Soc B* 366:2642–2651. <https://doi.org/10.1098/rstb.2011.0120>
- Devens C, Tshabalala T, McManus J, Smuts B (2018) Counting the spots: the use of a spatially explicit capture-recapture technique and GPS data to estimate leopard (*Panthera pardus*) density in the Eastern and Western Cape, South Africa. *Afr J Ecol* 56:850–859. <https://doi.org/10.1111/aje.12512>
- Devens CH, Hayward MW, Tshabalala T, Dickman A, McManus JS, Smuts B, Somers MJ (2019) Estimating leopard density across the highly modified human-dominated landscape of the Western Cape, South Africa. *Oryx*. <https://doi.org/10.1017/S0030605318001473>

du Preez BD, Loveridge AJ, Macdonald DW (2014) To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. *Biol Conserv* 176:153–161. <https://doi.org/10.1016/j.biocon.2014.05.021>

Dupont P, Milleret C, Gimenez O, Bischof R (2019) Population closure and the bias-precision trade-off in spatial capture-recapture. *Methods Ecol Evol* 10:661–672. <https://doi.org/10.1111/2041-210X.13158>

Efford M (2004) Density estimation in live-trapping studies. *Oikos* 106:598–610. <https://doi.org/10.1111/j.0030-1299.2004.13043.x>

Efford MG (2011) Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. *Ecology* 92:2202–2207. <https://doi.org/10.1890/11-0332.1>

Efford M (2019) secr 3.2-spatially explicit capture-recapture in R (2019). <https://cran.r-project.org/web/packages/secr/vignettes/secr-overview.pdf>. Accessed 1 Nov 2019

Ferrar AA, Lötter MC (2007) Mpumalanga Biodiversity Conservation Plan Handbook. Mpumalanga Tourism and Parks Agency, Nelspruit

Grant T (2012) Leopard population density, home range size and movement patterns in a mixed landuse area of the Mangwe District of Zimbabwe. M.Sc. Thesis, Rhodes University

Gray TNE, Prum S (2012) Leopard density in post-conflict landscape, Cambodia: evidence from spatially explicit capture-recapture. *J Wildl Manag* 76:163–169. <https://doi.org/10.1002/jwmg.230>

Grey JNC, Kent VT, Hill RA (2013) Evidence of a high density population of harvested leopards in a montane environment. *PLoS One*. <https://doi.org/10.1371/journal.pone.0082832>

Harmsen BJ, Foster RJ, 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:e0227468. <https://doi.org/10.1371/journal.pone.0227468>

Hayward MW, Henschel P, O'Brien J, Hofmeyr M, Balme G, Kerley GIH (2006) Prey preferences of the leopard (*Panthera pardus*). *J Zool* 270:298–313. <https://doi.org/10.1111/j.1469-7998.2006.00139.x>

Hayward MW, Hayward GJ, Druce DJ, Kerley GIH (2008) 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 Afr Biodivers Conserv* 18:887. <https://doi.org/10.1007/s10531-008-9452-y>

Hedges L, Lam WY, Campos-Arceiz A, Rayan DM, Laurance WF, Latham CJ, Saaban S, Clements GR (2015) Melanistic leopards reveal their spots: infrared camera traps provide a population density estimate of leopards in Malaysia. *J Wildl Manag* 79:846–853. <https://doi.org/10.1002/jwmg.901>

Jacobson AP, Gerngross P, Lemeris JR, Schoonover RF, Anco C, Breitenmoser-Wursten C, Durant SM, Farhadinia MS, Henschel P, Kamler JF, Laguardia A, Rostro-Garcia S, Stein AB, Dollar L (2016) Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. PeerJ. <https://doi.org/10.7717/peerj.1974>

Jędrzejewski W, Puerto MF, Goldberg JF, Hebblewhite M, Abarca M, Gamarra G, Calderón LE, Romero JF, Vilorio ÁL, Carreño R, Robinson HS, Lampo M, Boede EO, Biganzoli A, Stachowicz I, Velásquez G, Schmidt K (2017) Density and population structure of the jaguar (*Panthera onca*) in a protected area of Los Llanos, Venezuela, from 1 year of camera trap monitoring. Mamm Res 62:9–19. <https://doi.org/10.1007/s13364-016-0300-2>

Kalle R, Ramesh T, Qureshi Q, Sankar K (2011) Density of tiger and leopard in a tropical deciduous forest of Mudumalai Tiger Reserve, southern India, as estimated using photographic capture-recapture sampling. Acta Theriol 56:335–342. <https://doi.org/10.1007/s13364-011-0038-9>

Karanth KU, Chundawat RS, Nichol JD, Kumar NS (2004) Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture-recapture sampling. Anim Conserv 7:285–290. <https://doi.org/10.1017/s1367943004001477>

Karanth KU, Nichols JD (2002) Monitoring tigers and their prey: a manual for wildlife researchers, managers and conservationists in tropical Asia. Centre for Wildlife Studies, Bangalore, India

Mann GKH, O’Riain MJ, Parker DM (2020) A leopard’s favourite spots: habitat preference and population density of leopards in a semi-arid biodiversity hotspot. J Arid Environ 181:104218. <https://doi.org/10.1016/j.jaridenv.2020.104218>

Mann G, Pitman R, Whittington-Jones G, Thomas L, Broadfield J, Taylor J, Rogan M, Balme G (2017) South African Leopard Monitoring Project. Annual report on monitoring activities in 2017

Maputla NW, Chimimba CT, Ferreira SM (2013) Calibrating a camera trap-based biased mark-recapture sampling design to survey the leopard population in the N’wanetsi concession, Kruger National Park, South Africa. Afr J Ecol 51:422–430. <https://doi.org/10.1111/aje.12047>

Martins QE (2010) The ecology of the leopard *Panthera pardus* in the Cederberg Mountains. University of Bristol, Bristol, UK

McManus JS, Dalton DL, Kotze A, Smuts B, Dickman A, Marshal JP, Keith M (2015) Gene flow and population structure of a solitary top carnivore in a human-dominated landscape. Ecol Evol 5:335–344. <https://doi.org/10.1002/ece3.1322>

Miller RS, Farnsworth ML, Malmberg JL (2013) Diseases at the livestock-wildlife interface: status, challenges, and opportunities in the United States. Prev Vet Med 110:119–132. <https://doi.org/10.1016/j.prevetmed.2012.11.021>

Mizutani F, Jewell PA (1998) Home-range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. *J Zool* 244:269–286. <https://doi.org/10.1017/s0952836998002118>

Mpumalanga Tourism and Parks Agency (MTPA) (2014) Integrated management plan: Ioskop dam nature reserve, South Africa. In: Dereck M, Peter V (eds) MTPA, Nelspruit

Noack J, Heyns L, Rodenwoldt D, Edwards S (2019) Leopard density estimation within an enclosed reserve, Namibia using spatially explicit capture-recapture models. *Animals* 9:724–732. <https://doi.org/10.3390/ani9100724>

Qi JZ, Shi QH, Wang GM, Li ZL, Sun Q, Hua Y, Jiang GS (2015) Spatial distribution drivers of Amur leopard density in northeast China. *Biol Cons* 191:258–265. <https://doi.org/10.1016/j.biocon.2015.06.034>

Rahman DA, Rianti P, Muhiban M, Muhtarom A, Rahmat UM, Santosa Y, Aulagnier S (2018) Density and spatial partitioning of endangered sympatric Javan leopard (Felidae) and dholes (Canidae) in a tropical forest landscape. *Folia Zool* 67:207–219. <https://doi.org/10.25225/fozo.v67.i3-4.a8.2018>

Ramesh T, Kalle R, Rosenlund H, Downs CT (2017) Low leopard populations in protected areas of Maputaland: a consequence of poaching, habitat condition, abundance of prey, and a top predator. *Ecol Evol* 7:1964–1973. <https://doi.org/10.1002/ece3.2771>

Ray-Brambach RR, Stommel C, Rodder D (2018) Home ranges, activity patterns and habitat preferences of leopards in Luambe National Park and adjacent Game Management Area in the Luangwa Valley, Zambia. *Mamm Biol* 92:102–110. <https://doi.org/10.1016/j.mambio.2017.11.002>

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP (2014) Status and ecological effects of the world's largest carnivores. *Science* 343:151–162. <https://doi.org/10.1126/science.1241484>

Ropiquet A, Knight AT, Born C, Martins Q, Balme G, Kirkendall L, Hunter L, Senekal C, Matthee CA (2015) Implications of spatial genetic patterns for conserving African leopards. *CR Biol* 338:728–737. <https://doi.org/10.1016/j.crv.2015.06.019>

Rowcliffe JM, Field J, Turvey ST, Carbone C (2008) Estimating animal density using camera traps without the need for individual recognition. *J Appl Ecol* 45:1228–1236. <https://doi.org/10.1111/j.1365-2664.2008.01473.x>

Royle JA, Nichols JD, Karanth KU, Gopalaswamy AM (2009) A hierarchical model for estimating density in camera-trap studies. *J Appl Ecol* 46:118–127. <https://doi.org/10.1111/j.1365-2664.2008.01578.x>

Royle JA, Chandler RB, Sollmann R, Gardner B (2014) Chapter 6—Likelihood analysis of spatial capture-recapture models. In: Royle JA, Chandler RB, Sollmann R, Gardner B (eds) *Spatial capture-recapture*. Academic Press, Boston, pp 171–196. <https://doi.org/10.1016/B978-0-12-405939-9.00006-2>

Schmitz OJ, Hambäck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am Nat* 155:141–153. <https://doi.org/10.1086/303311>

Sollmann R (2018) A gentle introduction to camera-trap data analysis. *Afr J Ecol* 56:740–749. <https://doi.org/10.1111/aje.12557>

Sollmann R, Furtado MM, Gardner B, Hofer H, Jacomo ATA, Torres NM, Silveira L (2011) Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biol Cons* 144:1017–1024. <https://doi.org/10.1016/j.biocon.2010.12.011>

Stein AB, Fuller TK, DeStefano S, Marker LL (2011) Leopard population and home range estimates in north-central Namibia. *Afr J Ecol* 49:383–387. <https://doi.org/10.1111/j.1365-2028.2011.01267.x>

Stein AB, Athreya V, Gerngross P, Balme G, Henschel P, Karanth U, Miquelle D, Rostro-Garcia S, Kamler JF, Laguardia A, Khorozyan I, Ghoddousi A (2020) *Panthera pardus* (amended version of 2019 assessment). IUCN Red List of Threatened Species. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T15954A50659089.en>

Strampelli P, Andresen L, Everatt KT, Somers MJ, Rowcliffe JM (2018) Leopard *Panthera pardus* density in southern Mozambique: evidence from spatially explicit capture–recapture in Xonghile Game Reserve. *Oryx*. <https://doi.org/10.1017/S0030605318000121>

Swanepoel LH, Lindsey P, Somers MJ, Van Hoven W, Dalerum F (2011) The relative importance of trophy harvest and retaliatory killing of large carnivores: South African leopards as a case study. *Afr J Wildl Res* 44:115–134. <https://doi.org/10.3957/056.044.0210>

Swanepoel LH, Lindsey P, Somers MJ, van Hoven W, Dalerum F (2013) Extent and fragmentation of suitable leopard habitat in South Africa. *Anim Conserv* 16:41–50. <https://doi.org/10.1111/j.1469-1795.2012.00566.x>

Swanepoel LH, Somers MJ, Dalerum F (2015a) Density of leopards *Panthera pardus* on protected and non-protected land in the Waterberg Biosphere, South Africa. *Wildl Biol* 21:263–268. <https://doi.org/10.2981/wlb.00108>

Swanepoel LH, Somers MJ, van Hoven W, Schiess-Meier M, Owen C, Snyman A, Martins Q, Senekal C, Camacho G, Boshoff W, Dalerum F (2015b) Survival rates and causes of mortality of leopards *Panthera pardus* in southern Africa. *Oryx* 49:595–603. <https://doi.org/10.1017/s0030605313001282>

Swanepoel L, Balme G, Williams S, Power R, Snyman A, Gaigher I, Seneka C, Martins Q, Child M (2016) A conservation assessment of *Panthera pardus*. In: Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT (eds) *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa, pp 1–13. <https://doi.org/10.13140/RG.2.2.17803.69921>

Thorn M, Green M, Dalerum F, Bateman PW, Scott DM (2012) What drives human–carnivore conflict in the North West Province of South Africa? *Biol Conserv* 150:23–32. <https://doi.org/10.1016/j.biocon.2012.02.017>

Tobler MW, Powell GVN (2013) Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. *Biol Conserv* 159:109–118. <https://doi.org/10.1016/j.biocon.2012.12.009>

Treves A, Karanth KU (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv Biol* 17:1491–1499. <https://doi.org/10.1111/j.1523-1739.2003.00059.x>

Trouwborst A, Loveridge AJ, Macdonald DW (2019) Spotty data: managing international leopard (*Panthera pardus*) trophy hunting quotas amidst uncertainty. *J Environ Law* 32:253–278. <https://doi.org/10.1093/jel/eqz032>

Williams ST, Williams KS, Lewis BP, Hill RA (2017) Population dynamics and threats to an apex predator outside protected areas: implications for carnivore management. *R Soc Open Sci*. <https://doi.org/10.1098/rsos.161090>

Wolf C, Ripple WJ (2018) Rewilding the world’s large carnivores. *R Soc Open Sci*. <https://doi.org/10.1098/rsos.172235>