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Density of leopards *Panthera pardus* on protected and non-protected land in the Waterberg Biosphere, South Africa

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Data on the population size and trends of large carnivores remains the cornerstone of effective management and conservation programs. However, such data are rarely available for the majority of large carnivore species. Furthermore, large carnivore research is often directed towards formally protected areas. There is therefore a need to improve our knowledge regarding the population ecology of large carnivores in non-protected areas. In this study we use camera trapping in conjunction with spatially explicit mark–recapture models to estimate leopard *Panthera pardus* density across different land use types in the Waterberg Biosphere, South Africa. Estimated densities (mean ± SE) ranged from 6.59 (± 5.2/100 km²) on a matrix of commercial game and livestock farms to 5.35 (± 2.93/100 km²) and 4.56 (± 1.35/100 km²) on two protected areas (Lapalala and Welgevonden respectively). Although density estimates had large confidence intervals we suggest that these results indicate similar densities across the three sites. These results support other studies suggesting that non-protected areas can harbour as dense leopard populations as protected areas, and can therefore not be neglected in the management of leopards.

Effective management and conservation of free ranging animals depend on an understanding of their population sizes (Karanth and Nichols 2002). This is especially true for rare and elusive species that are subjected to commercial exploitation. Large carnivore species are typically both elusive and rare due to their secretive nature, low population densities and wide ranging behaviour (Purvis et al. 2000). Large carnivores are also sought after species for the trophy hunting and fur trade industries (Packer et al. 2009), and they are central in human–carnivore conflict (Treves and Karanth 2003). Large carnivores are also important components in terrestrial ecosystems. They therefore play an important role in biodiversity conservation and management (Ray et al. 2005, Ripple et al. 2014). Despite their economic and ecological importance, data on population sizes remains inadequate for many large carnivore species (Ray et al. 2005), while inappropriate reliance on indices of abundance has led to poor management suggestions (Hayward et al. 2015).

The leopard *Panthera pardus* is a large felid that persist throughout most of its formal range, including much of Africa and tropical Asia (Henschel et al. 2008). In South Africa leopards are found throughout the country, and the majority of suitable leopard habitat is in non-protected areas (Swanepoel et al. 2013). South African leopards are commercially important through trophy hunting and eco-tourism (Balme et al. 2012). They are also often featured in human carnivore conflict (Thorn et al. 2012), simlar to in other parts of their range (Athreya et al. 2011). However, there appears to be a discrepancy between leopard research and information necessary for conservation and management actions, with a bias towards basic ecological questions and research in formally protected areas (Balme et al. 2014).

Different land-uses generate contrasting opportunities for leopards to persist. A large portion of the South African leopard population probably live on un-protected land, and only a small proportion of suitable leopard habitat in South Africa is located in formally protected areas (Swanepoel et al. 2013). Land use has been directly linked to contrasting mortality in leopard populations (Swanepoel et al. 2014), and sociological and cultural factors appear to influence the attitude of land-owners to leopards (Thorn et al. 2012). Commercial game reserves may provide habitat and levels of persecution similar to those found inside formally protected areas, whereas other commercial land use types, such as cattle farming or crop fields may provide directly unsuitable environments for leopards. However, there is currently limited data on the effect of different land uses on leopard densities in South Africa.

During the past two decades camera trapping has emerged as an effective method to survey elusive and rare species (O'connell et al. 2011). Where species have unique marking or coat patterns, recently developed spatially explicit

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models provides possibilities to directly calculate densities from mark–recapture data (Sollmann et al. 2011, Efford and Fewster 2013). In this study we aimed to increase our knowledge regarding the population ecology of leopards in South Africa by utilizing data from camera trapping surveys in conjunction with spatially explicit mark recapture models to derive leopard density data across different land use types in the Waterberg Biosphere, South Africa.

Methods

Study area

Since our aim was to quantify leopard density across different land uses in the Waterberg Biosphere, we conducted camera trapping surveys at three different sites that are representative for the major categories of land uses within the Waterberg Biosphere (Fig. 1); 1) large reserve containing all the big five species (which include lion *Panthera leo*, leopard *Panthera pardus*, African elephant *Loxodonta africana*, rhinoceros *Ceratotherium simum* and African buffalo *Syncerus caffer*, 2) large reserve not containing all the big five species and 3) a matrix of small farms dedicated to different land uses (including livestock, game, lifestyle resorts, cropping or various mixtures of these; De Klerk 2003). Welgevonden Private Game Reserve (Welgevonden) represents a large reserve with the big five. Welgevonden is a syndicated private game reserve of 375 km² (24°10′–24°25′S, 27°45′–27°56′E) established in 2003 which focusses on conservation and ecotourism. Lapalala Wilderness (Lapalala) represents a large reserve not containing all the big five, as it had no lions, no elephant, and had buffalo only in a smaller area fenced off from the rest of the reserve. Lapalala is a privately-owned reserve of 360 km² established in 1981 (23°44′–23°57′S, 28°09′–28°25′E) which is dedicated to conservation, environmental education and ecotourism (Dalerum and Belton 2015). To get a representative sample of the farming areas, we placed a polygon of similar size to the large reserves over an area of small farms and gained permission from individual land owners to do camera trapping. This site consisted of seven farms dedicated to ecotourism, eight hunting game farms and 11 livestock farms. The total size of this site was approximately 350 km² (Farming Matrix; 28°23′E, 24°64′S; Fig. 1).

All three sites have abundant and diverse communities of ungulates, ranging in size from giraffe *Giraffa camelopardalis*, Burchell's zebra *Equus burchelli*, blue wildebeest *Connochaetes taurinus* and greater kudu *Tragelaphus strepsiceros* to smaller ungulates like impala *Aepyceros melampus*, mountain reedbuck *Redunca fulvorufula* and common duiker *Sylvicapra grimmia*. Similarly, carnivores like brown hyena *Hyaena brunnea*, black-backed jackal *Canis mesomelas*, caracal *Caracal caracal* and African civet *Civettictis civetta* were well represented in all three study sites (Ramnanan et al. 2013). However, only Welgevonden has a full complement of large carnivores including lion *Panthera leo*, cheetah *Acinonyx jubatus* and spotted hyenas *Crocuta crocuta*, while wild dogs *Lycaon pictus* are only present on Lapalala (Ramnanan et al. 2013). Topographies at all sites were characterised by undulating mountains with elevated plateaus, while the vegetation is classified as Waterberg Mountain Bushveld (Mucina and Rutherford 2006).

Camera trap methods

We followed camera trapping protocols for closed population mark recapture studies on large carnivores (Karanth and Nichols 2002). Camera traps were set out in pairs in a grid with a cell size of 6.25 km², which corresponds to approximately half the smallest home range diameter for leopards in mountainous areas (10 km²; Smith 1978). This resulted

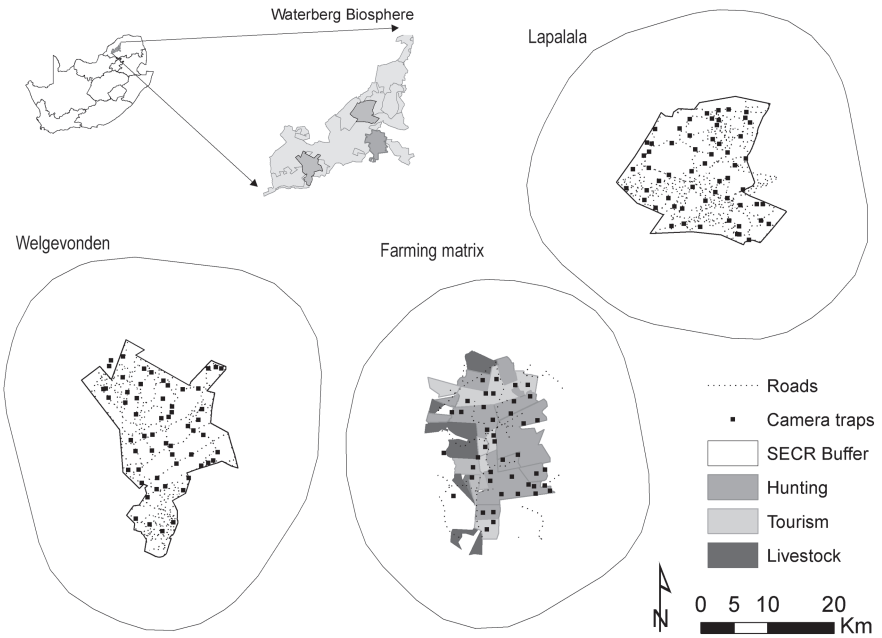


Figure 1. Location of the study sites within the Waterberg Biosphere, South Africa and camera locations within each study site as well as the buffer used in the spatially explicit mark recapture models. Shaded areas in the farming matrix indicated the different land use types.

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in camera trap density of between 17 to 20 camera traps/ 100 km². Although the total number of grid cells for each site was 45–65, we surveyed 13–15 grid cells simultaneously for 18–20 days and then moved to the next 13–15 until each study site had been completely covered. Lapalala and Welgevonden were camera trapped during the same period; May 2009 untill July 2009. Due to a shortage of camera traps the farming matrix was camera trapped later (August 2009 untill September 2009). The total period to cover each specific study site ranged from 40 to 90 days, which is within a time period generally regarded to satisfy assumptions of demographic population closure for large carnivores (Karanth et al. 2004).

We used Moultrie I40 (Moultrie Feeders) digital infrared camera traps at Welgevonden and a combination of these and film (Trailmasters, TM 1550; Goodson Associates Inc., Lenexa, KS, USA, DeerCam DC100; Non Typical Inc., Wisconsin, USA, Stealth Cam MC2-GV; Stealth Cam, Grand Prairie, USA) camera traps at Lapalala and the farming matrix. Due to a slow camera trap trigger speed for digital cameras, we baited (rotten eggs and fermented fish) all camera stations every five days to increase the probability that a visit by a leopard resulted in a useful photograph for identification (Gerber et al. 2012). Camera trap delays were set at 1 min for digital camera traps. For film camera traps we used an 8 min delay to prevent wastage of film on group living animals (e.g. baboons *Papio ursinus*). Film cameras were loaded with Fujifilm ISO 400 film and all sites were visited every 4–5 days to check cameras, re-bait and change films. Camera traps were place 50 cm above ground and the majority of camera traps (99%) were place on the existing vehicle road network, while the remaining traps were set on animal paths.

We identified individual leopards by examining spots on flanks and limbs and facial scars and/or any other distinctive markings. To determine the sex of leopards we followed the guidelines from Balme et al. (2012) and use the presence or absence of external genitalia, the size of the dew lap and the overall size of the animal to sex individuals. At all study sites we had extensive databases of leopard pictures taken by tourists, guides, landowners (e.g. many landowners have their own camera traps) or from pilot studies that aided in the identification and conformation of sex of leopards that were only photographed once (or partial pictures). All leopards were identified and triple checked by the same person.

Density estimation

We estimated density by fitting maximum likelihood based spatially explicit capture recapture (SECR) models to the capture data (Efford et al. 2008). In SECR models the detection probability of each individual is modelled using a spatial detection function (Efford 2004). The half normal spatial detection function is commonly used and has two parameters; g_0 which is the encounter rate at activity center (similar to detection probability) and σ, which is a scale parameter describing how the encounter rate declines with increased distance from the activity center and is related to the home range of the animal (Efford et al. 2009, Tobler and Powell 2013).

We fitted the half normal detection function by maximising the conditional likelihood in which the scale parameter (σ) and the detection probability (g_0) were modelled using biologically plausible hypotheses. Previous work has shown that including sex as a covariate can improve density estimates (Sollmann et al. 2011). We therefore created two different models including sex as a covariate. In the first model (M_{sex1}) the detection probability (g_0) varied by sex but the scale parameter (σ) was kept constant, where we in the second model (M_{sex2}) allowed both the detection probability (g_0) and the scale parameter (σ) to vary between the sexes. We also created a model that takes variation in detection probability among individuals into account (M_h; heterogeneity in detection probability). Such a model permits a different capture probability for each individual which is expected because of biases in biology of the species (e.g. sex, age and social status) and sampling (e.g. camera trap locations; Foster and Harmsen 2012). Lastly we created a null model (M_0) where both the detection probability (g_0) and the scale parameter (σ) were held constant (Efford 2004). We set the buffer width for analysis at 15 km and selected the most parsimonious model based on Akaike's information criterion corrected for small sample sizes (AIC_c; Akaike 1974, Burnham and Anderson 2002).

We used species accumulation curves to evaluate whether we captured all individuals during surveys (Estimate S 9.0, Colwell 2013). We also calculated effort by expressing the increase in new leopards per unit of effort (e.g. camera trap days; Wegge et al. 2004). The program CloseTest was used to test for population closure (Stanley and Richards 2005), and the user contributed R package 'secr' to implement the likelihood based SECR models (Efford 2012).

Accumulation curves for mean number of individual leopards observed did not reach an asymptote for any of the study sites. However, the increase in the number of new leopards per unit sampling effort were less than 10% for the latter half of the camera trapping period (Lapalala = 4.19% ;

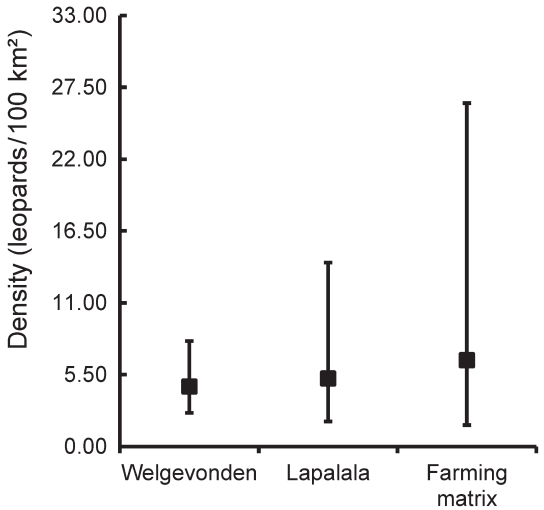


Figure 2. Leopard density estimates and asymmetric 95% confidence intervals estimated from spatially explicit mark–recapture models for three different study sites in the Waterberg Biosphere, South Africa during May to September 2009.

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Table 1. Summary of leopard camera trapping at three sites in the Waterberg Biosphere Reserve, Limpopo, South Africa from May to September 2009. *No. of camera trap nights, values in brackets indicate trap nights/km². **Female to male ratio.

Study site	Survey intensity*	Survey area (km²)	Camera stations	Trapping days	Recaptures	Male	Female	Sex ratio**
Welgevonden	1330 (4.0)	333	58	95	41	5	13	2.60
Lapalala	936 (3.2)	296	59	71	26	7	5	0.70
Farming matrix	849 (3.3)	257	43	64	26	6	6	1.00

Welgevonden = 8.75% ; farming matrix = 6.96%), suggesting adequate effort (Wegge et al. 2004). The assumption of population closure was supported for Lapalala ($Z = 0.843$, $p = 0.800$) Welgevonden ($Z = 1.791$, $p = 0.963$), and the farming matrix ($Z = 1.186$, $p = 0.882$).

Results

Based on the most parsimonious models, the highest estimated leopard density was for the farming matrix (6.59 ± SE 5.2/100 km²), followed by Lapalala (5.35 ± 2.93/100 km²) and Welgevonden (4.56 ± 1.35/100 km²) (Fig. 2). However, the observed estimates were characterised by low precision, making inferences about density differences between sites difficult. In total we identified 18 leopards at Welgevonden, 12 at Lapalala and 12 in the farming matrix (Table 1). Most of the individuals were only captured once (Fig. 3). The observed sex ratio was female biased in Welgevonden, male biased in Lapalala, and unbiased in the farming matrix (Table 1).

Including sex as a covariate to both the encounter rate parameter (g_0) and scale parameter (σ) produced the most parsimonious models for both Lapalala and Welgevonden, whereas the most parsimonious model for the farming matrix included sex as a covariate only in the encounter rate parameter (Table 2). The encounter rate at Lapalala was similar among sexes (males; 0.035 ± 0.027, females; 0.034 ± 0.014), while at Welgevonden females had a higher (0.028 ± 0.010) encounter rate than males (0.012 ± 0.005). At the farming matrix females had a substantially lower encounter rate (0.003 ± 0.003) compared to males (0.039 ± 0.016).

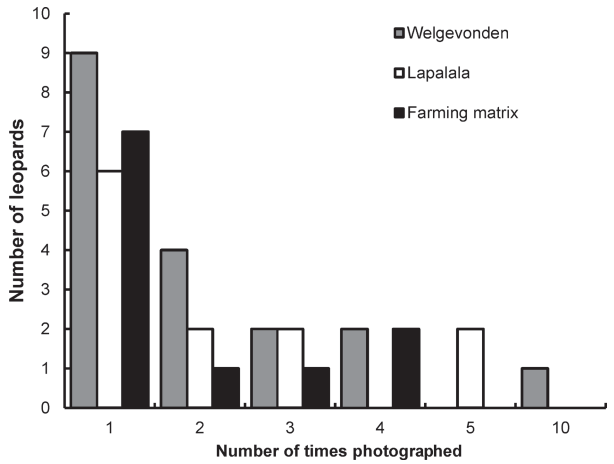


Figure 3. Capture frequencies for different individual leopards captured at different study sites in the Waterberg Biosphere, South Africa during May to September 2009.

Similarly sex affected the scale parameter (σ) at Lapalala (males; 1.043 km ± 0.276 km, females; 3.55 km ± 0.694 km) and Welgevonden (males; 5.615 km ± 1.600 km, females; 1.577 km ± 0.257 km).

Discussion

Although our density estimates had low precision, we suggest that our results reflect similar densities across the three sites. Such an interpretation would indicate that non-protected areas can harbour as viable leopard populations as protected areas. This result stand in contrast to research from other parts (KwaZulu-Natal) of South Africa where lower leopard densities were reported in non-protected farming areas (2.49 ± 0.87/100 km²) compared to the edge (7.17 ± 1.12 /100 km²) or inside protected areas (11.11 ± 1.31/100 km²; Balme et al. 2010). Nontheless our results do however support suggestions from Swanepoel et al. (2013) that non-protected land may play an important role in leopard conservation and can harbour viable leopard populations (Chase Grey et al. 2013).

Our density estimates, i.e. 4.5–6.5/100 km², were higher than previous estimates from the Waterberg area (1.9 leopards/100 km²; Grimbeek 1992, 3.2/100 km²; Gusset and Burgener 2005, 2.5/100 km²; Swanepoel 2009). This suggested increase in leopard density could have been caused by land use and attitudinal changes that occurend in the Waterberg Biosphere during the last century (De Klerk 2003). For example there has been a large increase in the number of game farms in the Waterberg Biosphere (De Klerk 2003, Anonymous 2005). Such an increase in game farming should coincide with an increase in leopard prey with an associated density increase (Hayward et al. 2007). However, different density estimates may also arise from methodological inconsistencies, such as spatially explicated mark–recapture versus spoor counts versus home range overlap.

In our secr models the inclusion of sex as a covariate improved model fit. This result concur with observations on another large solitary felid, the jaguar *Panthera onca* (Sollmann et al. 2011, Tobler and Powell 2013), and highlight that mark–recapture models may benefit from incorporating sex differences home range sizes and movement patterns (Tobler and Powell 2013). For example, because male leopards have large home ranges, they will spend a proportion of their time outside the trapping grid. This does not only reduce their encounter rate, but also lead to a larger scale parameter values than for females (Bailey 2005, Sharma et al. 2010). Females typically have smaller home ranges, which could lead to higher encounter rates and lower scale parameter values. We suggest that our observation from Lapalala, where females had higher scale parameters than males, may reflect sampling bias where the majority of the

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Table 2. Complete density esitimation models incorporating detection problabily variation of leopards in the Waterberg Biosphere, South Africa. Models are ranked according to AICc. †Half normal spatial capture probability function. *g_0, detection probability at center of home range. ** σ, sigma, a function of the scale of animal movement. ¥ '.' indicates a constant value.

Study site	Name	Model specification	AIC_c	delta AIC_c	AICweight	parameters	density (± SE)
Welgevonden	M_{sex2}	half normal† g_0*(sex) σ**(sex)	465.35	0	1	4	4.57 (±1.35)
	M_{null}	half normal g_0(.)¥ σ(.)	478.63	13.28	0	2	3.02 (±0.86)
	M_{sex}	half normal g_0(sex) σ(.)	479.03	13.68	0	3	3.34 (±1.00)
	M_h	half normal g_0(h2) σ(.)	481.41	16.06	0	4	4.00 (±1.54)
Lapalala	M_{sex2}	half normal g_0(sex) σ(sex)	275.55	0	0.82	4	5.18 (±2.83)
	M_{sex}	half normal g_0(sex) σ(.)	278.78	3.23	0.16	3	3.59 (±1.90)
	M_{null}	half normal g_0(.) σ(.)	283.72	8.17	0.01	2	2.33 (±0.78)
	M_h	Half normal g_0(h2) σ(.)	303.10	27.55	0	4	2.70 (±1.00)
Farming matrix	M_{sex}	half normal g_0(sex) σ(.)	280.62	0.00	0.85	3	6.59 (±5.2)
	M_{sex2}	half normal g_0(sex) σ(sex)	284.65	4.03	0.11	4	8.96 (±7.70)
	M_{null}	half normal g_0(.) σ(.)	286.89	6.26	0.03	2	2.70 (±0.90)
	M_h	half normal g_0(h2) σ(.)	Algorithm failed to converge				

males were either detected only once or repeatedly detected at the same camera trap location. In the farming matrix, female leopards had lower encounter rates compared to in the two protected areas. This observation suggests that some external factor influenced female movements in the farming matrix, for instance factors related to human carnivore conflict (Swanepoel 2009, Tobler et al. 2013) such as persecution (Wegge et al. 2004).

Despite significant survey effort density results from our study had low precision. This exemplifies the logistical difficulties in deriving accurate density estimates of large, free ranging carnivores. We suspect that the lack of precision in our estimates were caused by a number of different reasons, not necessary mutually exclusive. First, since secr models estimate density directly they include uncertainty and process variation in abundance and area estimation that is not normally taken into account, or underestimated, in traditional buffer strip methods (Gerber et al. 2012). Secr models will therefore have lower precision than other mark–recapture models (Gerber et al. 2012). Secondly, we could have misidentified some individuals that could have induced bias and uncertainty in our results (Link et al. 2010). Thirdly, since the number of unique individual leopard photo captured during the survey periods did not reach an asymptote, we may not have had an adequate sampling effort (Foster and Harmsen 2012). However, the low number of individuals added to the surveys during their latter parts contradicts that sampling effort was the sole reason for low precision. Our efforts were also comparable to those suggested for large solitary carnivores (4 trap nights/km²; Sharma et al. 2010).

Conclusion

We found that leopard densities in the Waterberg Biosphere, northern South Africa, were comparable between three land-use types. Furthermore, our results show what inclusion of sex as a covariate can improve the performance of spatially explicit mark–recapture models. Since non-protected areas in the Waterberg seem to harbour as dense leopard populations as protected areas, our study support previous studies that have highlighted the importance of non-protected areas for southern African leopard conservation.

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