

Leopard Density Estimates Across the Highly Modified Human Dominated Landscape of the Western Cape, South Africa

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SUMMARY

Apex predators maintain a critical role in the health of ecosystems, however, they are highly susceptible to landscape changes, such as habitat degradation and loss, as well as human caused mortality. The leopard (*Panthera pardus*) is the last free-roaming large carnivore in the Western Cape, South Africa. From 2011 to 2015, we carried out a camera trap survey across three regions covering an area of about 30,000 km² of the Western Cape. Our survey comprised 151 camera sites sampling nearly 14,000 active camera trap nights, resulting in the identification of 71 individuals. We used two spatially explicit capture-recapture (SECR) methods (program secr and SPACECAP) to provide a comprehensive density analysis capable of incorporating environmental and anthropogenic factors. Leopard density estimates varied between 0.35 (secr) and 1.18 leopards/ 100 km² (SPACECAP) respectively, with leopard population size predicted to be between 102 and 345 individuals for our three study regions. With these estimates and the predicted available leopard habitat for the province, we extrapolated that the Western Cape supports an estimated 175 to 588 individuals. Providing a comprehensive baseline population density estimate is critical to understanding population dynamics across a mixed landscape, and helping to determine the most appropriate conservation actions. SECR methods are unbiased by edge effects and

superior to traditional capture-mark-recapture (CMR) methods when estimating animal densities. Consequently, our recommendation is for further utilisation of robust spatial methods as they continue to be advanced.

Keywords: camera trapping, carnivore conservation, leopard, SECR, SPACECAP, spatial capture-recapture, *Panthera pardus*

INTRODUCTION

The exponential growth of the human population is threatening all levels of biodiversity, including carnivore diversity, which has reportedly declined by 77% (Estes et al. 2011; Ripple et al. 2014). Large carnivores are uniquely vulnerable to extinction because of their small population sizes, slow reproductive rates, complex social structures and requirement of large and contiguous habitat (with sufficient prey presence) (Ripple et al. 2014). These characteristics, compounded by human-carnivore conflict, have driven range declines for some of the most wide-ranging carnivores (Ray, Hunter & Zircouris 2005; Swanepoel et al. 2013; Wolf & Ripple, 2017).

While leopards are considered the most adaptable large carnivore worldwide (Hunter & Balme 2004; Ripple et al. 2014), range declines of 63-75% globally, 48-67% in Africa and 28-51% in southern Africa indicate that leopard populations are not as resilient to anthropogenic influences as previously believed (Jacobson et al. 2016). Major anthropogenic threats to leopards include ongoing habitat loss and fragmentation (Harcourt et al. 2001; Crooks 2002; Swanepoel et al. 2015), depletion of prey resources (Woodroffe 2000; Karanth & Chellam 2009), unsustainable harvest levels (Woodroffe 2000; Harcourt et al. 2001), and direct persecution by people (Harcourt et al. 2001; Treves & Karanth 2003; Treves et al. 2004; Treves

& Naughton-Treves 2005; McManus et al. 2014; Swanepoel et al. 2015). The loss of habitat often results in human-carnivore conflict, which is exacerbated by resource competition with people (Woodroffe 2000). Persecution often includes indiscriminate use of lethal methods to manage livestock depredation by carnivores, e.g. snares, poisoned carcasses, gin-traps (leg-hold traps), gun-traps, live-trapping, and targeted (often retaliatory) hunting (McManus et al. 2014).

Estimating density of a species across various types of land cover (i.e. habitat and vegetation type) and land uses (i.e. residential/urban land, cultivated land, commercial and recreational land and protected conservation areas) can help determine how population numbers are affected by landscape features. Density estimates are not equally robust and under or over-estimating populations can have substantial implications for conservation management and policy (Foster & Harmsen 2012; Hayward et al. 2015). For example, Soisalo and Cavalcanti (2006) demonstrated how overestimating jaguar (*Panthera onca*) populations by five individuals per 100 km² inflated the overall population estimate by 7,000 individuals across their 140,000 km² study region. Density estimation also depends upon data quality, with a large enough sample size and capture probability for the chosen analysis method (Foster & Harmsen 2012).

Conservationists and ecologists constantly try to redefine and improve the methodology of estimating animal population abundances and densities (Griffiths and van Schaik 1993; Karanth & Nichols 1998; Karanth & Nichols 2000). The use of camera traps and capture-recapture analysis is a common and effective non-invasive wildlife monitoring tool for obtaining data on the population dynamics of species, particularly rare or elusive species (Foster & Harmsen 2012). The leopard, like many other large felids, is challenging to monitor due to their large home ranges, low population density and primarily solitary and elusive nature (Karanth & Nichols 2000; Treves & Karanth 2003). The leopard's expansive geographical distribution and

global population estimates do not account for the health and sustainability of smaller isolated regional metapopulations across a variety of habitat types, countries and levels of human landscape modification and pressure.

Capture-Recapture

Camera trap surveys have become an important data collection method for population and density studies because of their non-invasiveness, practicality and affordability (Karanth 1995; Karanth & Nichols 1998; Foster & Harmsen 2012). The capture-recapture method relies on individuals being identifiable (Karanth 1995; Silver et al. 2004) and has been the predominant approach used in felid density studies.

Spatially Explicit Capture-Recapture Method

More recently, spatial capture-recapture (SCR) or spatially explicit capture-recapture (SECR) methods have become popular because they provide comprehensive analyses that can incorporate environmental and anthropogenic factors when estimating animal densities. These methods enable density analyses to include spatiotemporal data from capture histories, providing direct estimates of population density that remain unbiased by edge effects (Chase Grey et al. 2013). By allowing for flexibility in individual heterogeneity with the consideration of capture probability relative to trap location, spatial covariates like habitat and intrinsic factors like sex and age (Foster & Harmsen 2012; Efford & Fewster 2013), SECR models are increasingly robust and comprehensive.

These statistical and methodological advances provide multiple options that can be applied to specific density study analysis questions while making species population density estimates increasingly reliable. Inaccurate density estimates can lead to biased population

estimates, the consequences of which could have serious implications for conservation management (Soisalo & Cavalcanti 2006).

The estimation of a baseline population density for leopards in the Western Cape is fundamental to understanding how this population responds to landscape-scale threats and changes. By estimating densities across landscapes of varying resource availability and threats to the leopard's persistence, we can further understand drivers of regional density variation and improve conservation management for disjunct and discontinuous populations.

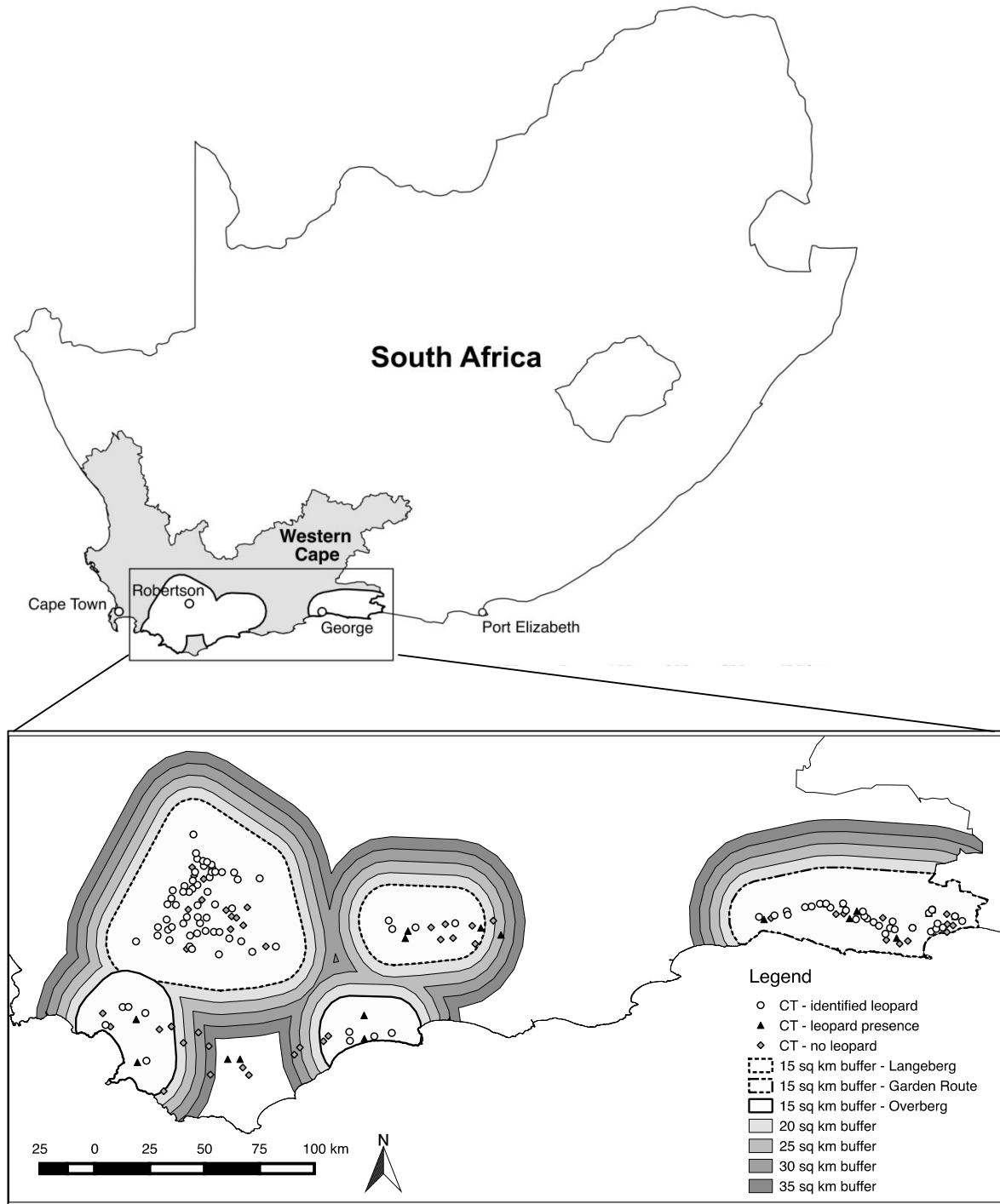
MATERIALS AND METHODS

Study Area

Camera trap surveys were undertaken from June 2011 to March 2015 covering an area of about 30,000 km² focusing on three regions (Langeberg, Overberg and Garden Route) in the Western Cape, South Africa (Figure 1). We conducted seven large-scale camera trap surveys with placement focused on likely presence of leopards inside and outside of protected areas and across different agricultural land use zones (livestock, crops, forestry). Topography varied from the Cape Fold Mountain peaks >1,600 m that extend 1,000 km east to west to coastal and low-lying valleys less than 500 m above sea level (Thamm & Johnson, 2006). Sample biomes present included Thicket, Afro temperate forest (Forest), Sandstone fynbos (Fynbos), Nama-Karoo, Succulent-Karoo and Savanna (Mucina & Rutherford, 2006).

In the Langeberg, we deployed camera traps in the greater Riversdale/Heidelberg area on the southern slopes of Langeberg Mountain Range, greater Greyton area on the southern slope of Rivieronderend Mountain Range, and the Robertson Wine Valley (Breede River Valley) situated between the Langeberg and Rivieronderend Mountain Ranges. In the Overberg region, we surveyed the greater Hermanus area to the west, the greater Cape Agulhas and Arniston areas

Figure 1. Map illustrating the camera trap surveys conducted across the Langeberg (19,063 km²), Garden Route (6,680 km²) and Overberg (7,910 km²) regions in the Western Cape, South Africa. Data from camera stations with identified leopards were analysed with SPACECAP and program secr various buffers.



to the south along the coast and the greater De Hoop Nature Reserve area to the eastern extent of surveyed region. In the Garden Route region, we surveyed temperate forest along the southern slopes of the Outeniqua and Tsitsikamma Mountains from George in the west to the Bloukrans River in Plettenberg Bay to the east.

Research Design

We used Cuddeback™ Attack IR (Wisconsin, USA; www.cuddeback.com) digital infrared cameras to photograph leopards that were then individually identified by their fur patterns. We calculated density estimates using two SECR methods, i.e. the maximum likelihood based estimator program secr (Efford et al. 2009; Efford 2011) version 2.10.3 (Efford 2016), which is a more robust version of program DENSITY (Efford 2011), and the Bayesian estimator program SPACECAP (Gopalaswamy et al. 2012) version 1.1.0 (Gopalaswamy et al. 2014) within the programming environment R version 3.4.0 (R Development Core Team 2017). SECR methods for density analyses are generally recognized as being more comprehensive and reliable than traditional capture-recapture analyses (Borchers & Efford, 2008; Kalle et al. 2011; Gopalaswamy et al. 2012; Chase Grey et al. 2013; Thapa et al. 2014). They also produce lower density estimates than non-spatial methods (Obbard et al. 2010; Gerber et al. 2011; Gopalaswamy et al. 2012; Noss et al. 2012; Brackzkowski et al. 2016). Previous studies have applied these two SECR programs to compare density estimates (Kalle et al. 2011; Thapa et al. 2014) and to compare results of SECR with non-spatial methods (Noss et al. 2012; Brackzkowski et al. 2016). We used these programs for comparison of SECR methods and to determine the most robust and inclusive density estimate range for each region.

Field Methods – Camera Trapping Surveys

Site Selection

We selected camera trap locations based on the highest likelihood of leopard activity as determined by physical evidence (scat, spoor and territorial scent and scratch markings on trees), as well as habitat type and conditions (Karanth et al. 2000). Two camera traps were positioned to capture both flanks of a passing leopard. These camera stations were placed 3-5 km apart to achieve even sampling area coverage and to ensure at least one station was located within the minimum average daily distance walked by leopards in the Western and Eastern Cape (McManus 2009; Devens and Tshabalala et al. 2018). Camera stations remained active for a minimum of three months to ensure maximum likelihood of leopard activity being captured without violating the closed population assumption (Karanth & Nichols, 1998; Devens and Tshabalala et al. 2018).

Capture-Recapture Identification from Camera Traps

Individual identification is best established from capture events with clear photographs of an individual's flanks and unique rosette markings. Leopard identification from single flank photos would have to be based upon the observation of characteristics like neck girth, size, injuries or scars. While such characteristics may be useful, incorrectly identified individuals could bias density estimates, resulting in overestimation of the population if individual flank photos were erroneously assigned two IDs. We only utilized double flank capture events for identification with confidence.

DATA ANALYSIS

Program secr

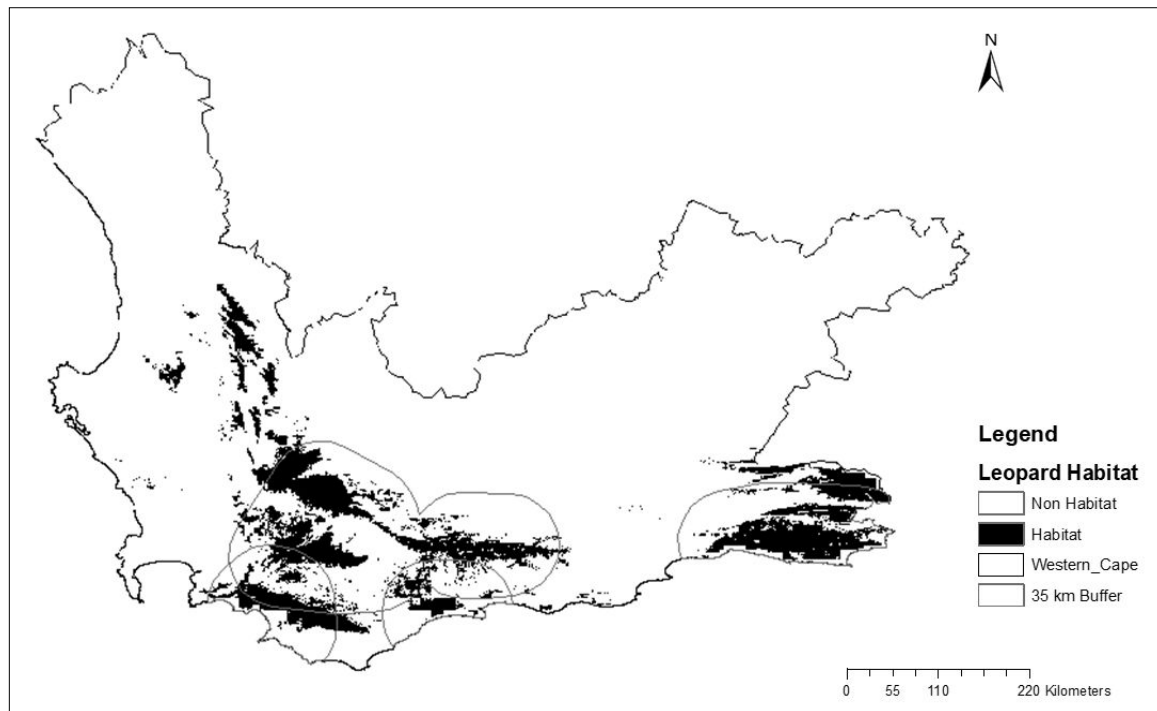
Program secr's analysis was conducted in RStudio (0.99.467) (RStudio Team 2015). We categorised camera traps as 'count' detectors, which allows repeat detections in secr. Count data

can result from devices such as automatic camera traps. Count detectors record the presence of an animal at a trap location without restricting movement and allow >1 detection of an individual at a particular site on any occasion. The secr.fit function was run for each regional survey phase using models of time ($g_0 \sim T$) and behavioural response ($g_0 \sim b$), as well as buffers of 15, 20, 25, 30 and 35 km. These buffers ensured inclusion of all leopard home ranges within reach of camera traps (Kalle et al. 2011) and increased density estimation reliability by determining the point at which the density estimate stabilized (Kalle et al. 2011; Chase Grey et al. 2013).

Program SPACECAP

SPACECAP was also run within RStudio estimating abundance and density using spatially-explicit capture-recapture models to derive spatial Bayesian estimate with trap response. A grid of equally spaced points 1 km apart was generated within QGIS version 2.8 (QGIS Development Team 2013) and clipped to the state-space at buffer distances of 15, 20, 25, 30 and 35 km. These points represent all potential home range centres of all the leopards within the survey. The potential home range centres file includes the UTM coordinates of each of these generated points within the state-space as well as the habitat suitability of each point. Habitat suitability was determined using Maxent software (v. 3.3.3) (Phillips et al. 2006) model output comprised of environmental variables including eight WorldClim bioclimatic variables (v. 1.4) (<http://www.worldclim.org>), human footprint index (Last of the Wild Data Version 2, 2005), altitude, anthropogenic biomes (Ellis & Ramankutty 2008), Globcover 2009 (Food and Agriculture Organization of the United Nations 2012) SANBI ecosystem status of vegetation types (Rouget et al. 2004) and a subset of GPS collar data from two locally collared leopard individuals. The Natural Breaks function (Jenks 1967) in ArcMap (v. 10.3.1) was used to reclassify the model output into two classes from 0 (not suitable = 0 - 0.189171) to 1 (suitable =

Figure 2. Map illustrating the Maxent probability distribution model of leopard habitat suitability in the Western Cape and considering the study's 35 km buffers. Distribution model is reclassified with Natural Breaks function.



0.189172 - 0.775). The habitat suitability generated (Jenks method) for these points (0 or 1) is recorded for each point and a home range centre input file is generated for each region's buffer distances (Figure 2).

SPACECAP was run with a 1 km² pixel area, and the model definitions were set to 'Trap response present' (the equivalent of Mb behavioural response model), 'Spatial Capture-Recapture', 'half normal' detection function and the capture encounters 'Bernoulli's process'. The 'Trap response present' option implements a "trap-specific" behavioural response in which the probability of capture at that specific location increases (or decreases) after the initial capture. The 'spatial capture-recapture' option runs a SECR analysis. The Markov-Chain Monte Carlo (MCMC) settings varied between study regions and buffers. MCMC iterations were set between 60,000 and 100,000 with a burn-in period between 10,000 and 65,000 iterations and a thinning rate of 1. The data augmentation numbers were approximately 20 to 40 times the number of animals identified in each regional survey and varied between 170 and 1500. Chain convergence was assessed with the Geweke diagnostic test produced within the SPACECAP output in the form of z-score values. Z-scores between -1.6 and +1.6 implied adequate convergence and confirmed that the MCMC analysis was run with a sufficiently long burn-in period. The SPACECAP output also produces a Bayesian P-value to provide additional assessment of the model fit where P-values close to 0 or 1 imply that the model is inadequate. The adequacy of the data augmentation number can be checked in the 'density plot for psi' and 'density plot for N' files included within the output files. All densities obtained with SPACECAP produced z-scores that achieved convergence, as well as sufficient model fit and data augmentation number. The output also included pixel density estimates (animals per km²)

with which we were able to create a pixel density map of the study regions and compare leopard densities across various land covers and uses to illustrate relationship with anthropogenic factors.

RESULTS

Camera Trap Data – Sampling Effort

The total sampling effort for the Overberg survey region from November 2011 to March 2012 was 2,880 active camera trap nights across a total of 32 camera trap locations (64 cameras). This yielded 118 leopard photographs (captures) of eight individuals. Leopards were uniquely identified in 40 of the 118 photographs, and these individuals were detected at nine of the 32 camera trap sites (Table 1).

The total sampling effort for the two phases of the Langeberg survey region between April 2012 and December 2012 consisted of 9,480 active camera trap nights across a total of 79 camera trap locations (158 cameras). This yielded 454 leopard photographs (captures), from which 42 individual leopards were identified. Leopards were uniquely identified in 250 of the 454 photographs, and these individuals were detected at 58 of the 79 camera trap sites (Table 1).

The total sampling effort for the three phases of the Garden Route survey region from May 2013 to December 2014 consisted of 3,600 active camera trap nights across a total of 40 camera trap locations (80 cameras). This yielded 142 leopard photographs (captures), of which 21 individual leopards were identified. Leopards were uniquely identified in 86 of the 142 photographs, and these individuals were detected at 33 of the 40 camera trap sites (Table 1).

This yields a total sampling effort of 13,590 active camera trap nights across 151 camera trap locations (302 cameras) with 714 leopard photos and 71 total identified individuals (Table 1).

Density Estimates

Table 1. Summary of capture-recapture camera trap survey sampling effort and leopard capture results across three regions in the Western Cape, South Africa.

Sampled site	Date	Survey phase duration (active nights)	Regional phases	Camera trap stations	Camera trap stations with leopard IDs	Total camera trap nights	Total leopard pictures	Total leopard pictures enabling leopard ID	Identified leopards
Overberg	July 2011 - Sept 2012	90	1	32	9	2,880	118	40	8
Garden Route	Oct 2012 - March 2015	90	3	40	33	3,600	142	86	21
Langeberg	April 2012 - Jan 2013	90	2	79	58	7,110	454	250	42
Average		90		42	33	4,530	238	125	24
Total	July 2011 – March 2015	270	6	151	100	13,590	714	376	71

The SECR density estimates varied by region and between regional phases, and program secr density estimates were lower than SPACECAP's estimates. The effect of using various buffers within the two programs, especially SPACECAP, demonstrated the sensitivity to buffer width and data augmentation size (Kalle et al. 2011). We calculated average density estimates from stabilized buffer values to ensure the study area was large enough with no probability of capturing any individuals residing outside the buffered region during the survey.

In the Overberg, density estimates were stable at 0.17 leopards/ 100 km² (CI: 0.06-0.48), with buffers from 30 to 35 km. Both of the phases in the Langeberg had density estimates that were stable across all five buffers with a phase one density estimate of 0.29 leopards/ 100 km² (CI: 0.2-0.41) and a phase two estimate of 0.7 leopards/ 100 km² (CI: 0.57-1.76). The Garden Route's first phase had an estimated density of 0.5 leopards/ 100 km² (CI: 0.19-1.32) with densities stable across all buffers, while phase two had an estimated density of 0.34 leopards/ 100 km² (CI: 0.18-0.63) stabilizing between buffers 25 and 35 km. The third phase produced a density estimate of 0.29 leopards/ 100 km² (CI: 0.13-0.67), which stabilized between buffers of 20 and 35 km (Table 2). We averaged multi-phase densities within each region to provide one regional density estimate for comparison between sites, which resulted in the Overberg's density of 0.17 leopards/ 100 km² compared to the average densities of the Langeberg at 0.5 leopards/ 100 km² (CI: 0.39-1.09) and Garden Route at 0.38 leopards/ 100 km² (CI: 0.17-0.87). The highest estimated density was Langeberg's phase two with 0.7 leopards/ 100 km² and the lowest was in the Overberg at 0.17 leopards/ 100 km² (Table 2).

SPACECAP produced an Overberg density estimate of 0.69 leopards/ 100 km² (CI: 0.39-1.28) with estimates stabilizing between buffers of 25 and 35 km. The Langeberg region's phase one and two density estimates were 1.67 (CI: 1.21-2.18) and 2.11 (CI: 1.46-2.82) leopards/ 100

Table 2. Posterior summaries from program secr and SPACECAP (abbreviated to SC) with SE and SD, lower (LCI) and upper (UCI) confidence intervals, buffer range of means' stabilization, area of regional 35 km buffer, number of leopards estimated within surveyed area (N) with lower and upper confidence intervals and the Bayesian P value for model fit. The area total is without 35 km land overlap between regional surveys.

Site	Survey Phase	Posterior mean (100km ²)		SE estimate	Posterior SD	95% LCI		95% UCI		Stabilized buffer range		35 km buffer area (km ²)	N		N LCI		N UCI		P
		secr	SC			secr	SC	secr	SC	secr	SC		secr	SC	secr	SC	secr	SC	SC
Langeberg	1	0.29	1.67	0.05	0.26	0.2	1.21	0.41	2.18	15-35	15-30								0.86
	2	0.7	2.11	0.15	0.35	0.57	1.46	1.76	2.82	15-35	25-35								0.55
	regional avg	0.5	1.89	0.1	0.30	0.39	0.89	1.09	2.50			19,063.42	93.41	360.30	74.35	169.66	205.88	476.59	0.71
Garden Route	1	0.5	1.44	0.26	0.58	0.19	0.55	1.32	2.54	15-35	20-30								0.47
	2	0.34	0.92	0.11	0.16	0.18	0.65	0.63	1.22	25-35	20-35								0.73
	3	0.29	0.51	0.13	0.10	0.13	0.36	0.67	0.70	20-35	15-35								0.60
	regional avg	0.38	0.96	0.17	0.28	0.17	0.52	0.87	1.49			6,680.34	25.39	64.13	11.36	34.74	58.12	99.54	0.60
Overberg	1	0.17	0.69	0.1	0.30	0.06	0.39	0.48	1.28	30-35	25-35	7,910.04	13.45	54.58	4.75	30.85	37.97	101.25	0.63
Average		0.35	1.18	0.12	0.29	0.21	0.60	0.81	1.76			11,217.93	44.08	159.67	30.15	78.42	100.66	225.79	0.65
Total (no overlap)												29,258.43	132.25	479.01	90.46	235.25	301.97	677.38	

km² respectively. Phase one's estimate stabilized between 15 and 30 km and phase two between 25 and 35 km. The Garden Route phase one survey had an estimated density of 1.44 leopards/ 100 km² (CI: 0.55-2.54) with densities stabilizing between buffers of 20 and 30 km, while phase two had an estimated density of 0.92 leopards/ 100 km² (CI: 0.16-1.22) stabilizing between 20 and 35 km and phase three produced an estimate of 0.51 leopards/ 100 km² (CI: 0.36-0.7), which remained stable across all buffers. Again, we averaged multi-phase densities within each region and the Overberg density was 0.69 leopards/ 100 km² compared to the average densities of the Langeberg at 1.89 leopards/ 100 km² CI: 0.89-2.5) and Garden Route at 0.96 leopards/ 100 km² (CI: 0.52-1.49) (Table 2).

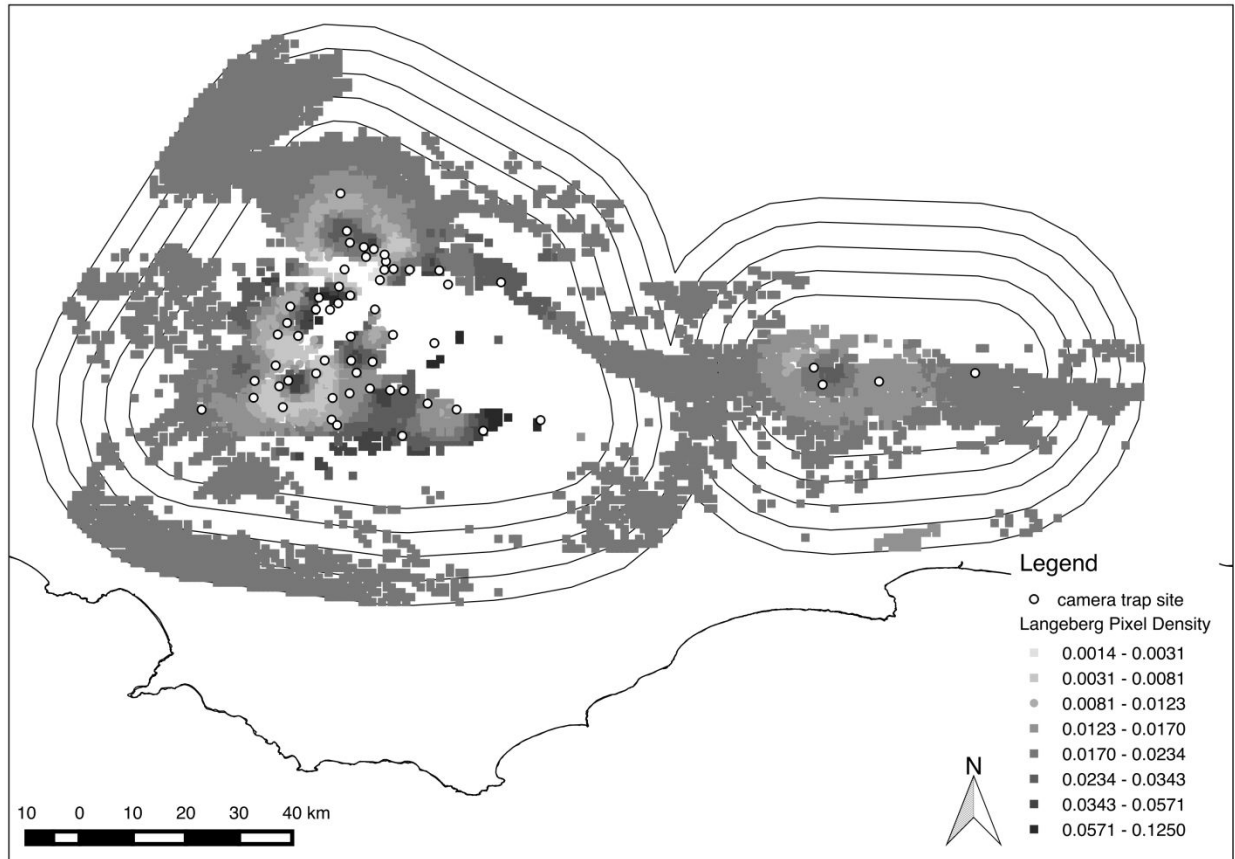
SPACECAP calculated an overall leopard density of 1.18 leopards/ 100 km² (CI: 0.60-1.76), while secr calculated an overall density estimate of 0.35 leopards/ 100 km² (CI: 0.21-0.81). SPACECAP's output includes a pixel density file, which was converted into a fine-scale map using QGIS, showing the variation of estimated animal densities across each of the potential home range centres (Figure 3). Using these pixel density values, we also created regional graphs depicting the sum of pixel densities across land cover categories (CapeNature 2014) and protected areas (Department of Environmental Affairs 2017) (Figure 4).

Estimated Population Numbers

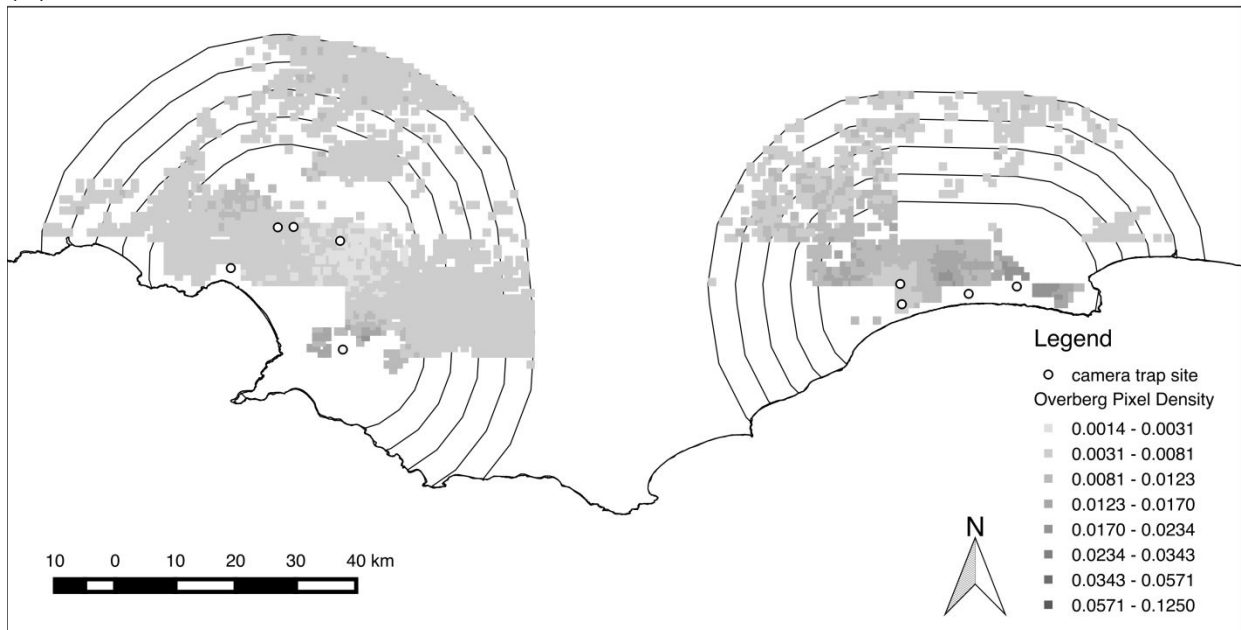
Using this study's total area with each region's 35 km buffer width (Garden Route 6,680.34 km²; Overberg 7,910.04 km²; Langeberg 19,063.42 km²) and the regional secr average density estimates results in an estimate of 25 leopards (CI: 11.4-58.1) in the Garden Route, 13 leopards (CI: 4.7-38.0) in the Overberg and 93 leopards (CI: 74.3-205.9) in the Langeberg region (Table 2). The total estimate for all areas combined is 132 leopards (CI: 90.4-302.0) (Table 3). In comparison, the total non-overlapping area (km²) of all three study regions' 35 km buffers

Figure 3. Pixelated (1 km²) SPACECAP leopard density maps showing the A) Langeberg; B) Overberg; C) Garden Route study regions. White regions represent unsuitable habitat. Camera traps shown are analyzed sites with identified leopards.

(A)



(B)



(C)

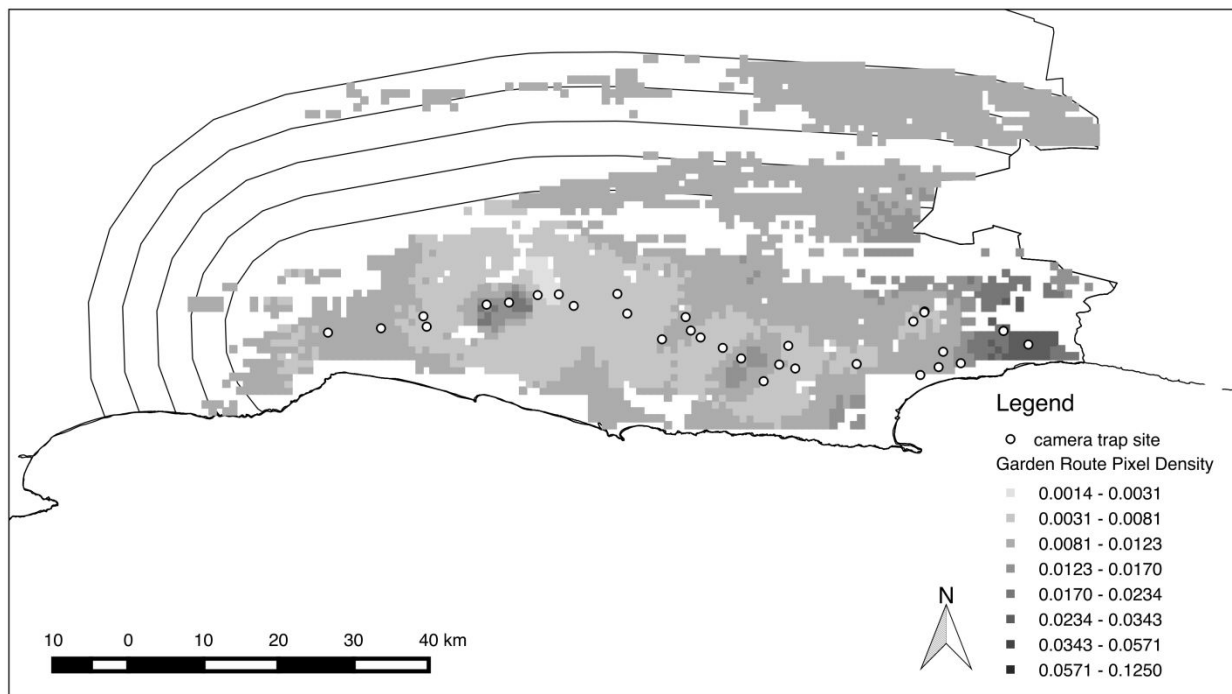


Table 3. Summary of estimated leopard population sizes in each surveyed region using secr and SPACECAP density estimates.

Survey region	Program	Density estimate (per/ 100 km ²)	Estimated population size
Langeberg	secr	0.5	93.4 (CI: 74.3 - 205.9)
	SPACECAP	1.89	360.3 (CI: 169.7 - 476.6)
Garden Route	secr	0.38	25.4 (CI: 11.4 - 58.1)
	SPACECAP	0.96	64.1 (CI: 34.7 - 99.5)
Overberg	secr	0.17	13.4 (CI: 4.7 - 38.0)
	SPACECAP	0.69	54.6 (CI: 30.8 - 101.2)
Average	secr	0.35	44.1 (CI: 30.2 - 100.7)
	SPACECAP	1.18	159.7 (CI: 78.4 - 225.8)
Total	secr		132.2 (CI: 90.4 - 302.0)
	SPACECAP		479.0 (CI: 235.3 - 677.4)

Table 4. Comparison of estimated population size of leopards per/ 100 km² using the total area within study's 35 km buffer distance (without regional survey overlap) and Swanepoel et al.'s (2013) suitable Western Cape habitat estimate.

Areas (km ²)	secr (0.35 leopard/ 100 km ²)	SPACECAP (1.18 leopard/ 100 km ²)
Total buffered area (29,258.43 km ²)	102.4 (CI: 61.44 - 237.0)	345.25 (CI: 175.6 - 515.0)
Suitable WC habitat (49,850 km ²) (Swanepoel et al. 2013)	174.5 (CI: 104.7 - 403.8)	588.2 (CI: 299.1 - 877.4)

(29,258.43 km²) and the overall secr average density produces a total study area population estimate of 102 leopards (CI: 61.4-237.0) (Table 4).

Using the regional SPACECAP average density estimates, we estimate that there would be approximately 64 leopards (CI: 34.7-99.5) in the Garden Route, 55 leopards (CI: 30.8-101.2) in the Overberg and 360 leopards (CI: 169.7-476.6) in the Langeberg regions (Table 2), yielding a total estimate of 479 leopards (CI: 235.3-677.4) (Table 3). Comparatively, using the total area of all three regions' 35 km buffers (without overlap) and the overall SPACECAP averaged density provides a population estimate of 345 leopards (CI: 175.6-515.0) (Table 4).

Our study area of 29,258.43 km² is 23% of the Western Cape's total area (129,460 km²). While our leopard population estimates are useful for regional comparisons, they are unable to provide a provincial population outlook. We extrapolated an ecologically useful Western Cape abundance estimate using our secr and SPACECAP average density estimates and Swanepoel et al.'s (2013) estimated 49,850 km² of suitable remaining Western Cape leopard habitat (38% of province). Using this habitat estimate in conjunction with our secr and SPACECAP estimates suggest that the entire Western Cape harbours as few as 175 (CI: 104.7 - 403.8) and as many as 588 (CI: 299.1-877.4) leopards respectively (Table 4).

DISCUSSION

This study covered about 30,000 km² and is the most extensive leopard camera trap density estimate survey conducted in the Western Cape. We compared the use of two SECR density estimating methods for a critically endangered disjunct leopard population, which is isolated in the Western Cape of South Africa. Our comprehensive density analysis investigated leopard persistence in a predominately human-modified and privately-owned landscape with varying degrees of conflict and persecution.

It is important to reiterate that our study area incorporates variation across vegetation types, landscape topography and degree of landscape modification and fragmentation. Due to its diversity of agricultural activities (mainly grain production and livestock farming), the Overberg region is considered the ‘breadbasket’ of the Western Cape. The Langeberg region’s Breede River Valley is encircled by the Cape Fold Mountain ranges and is dominated by fynbos, vineyards and fruit production, while the Garden Route is a long stretch of the south-western coast situated between mountains to the north and the Indian Ocean to the south and unique mixture of Cape fynbos and indigenous temperate forest. Each region’s agricultural land is utilized by leopards, as evidenced by capture and recapture locations and suitable habitat extending beyond natural vegetation (Figure 4) and protected area boundaries (Figure 5). None of our identified territorial adult leopards remained strictly within protected areas, and most did not utilize any protected land within their home range. While PAs play a crucial role in the conservation of natural landscapes, they do not necessarily encompass the entirety of remaining natural vegetation or existing leopard habitat. In the Western Cape, 79% of conservation areas contain suitable leopard habitat, while only 30% of leopard habitat occurs within conservation areas (Swanepoel 2013). These findings, in addition to estimated leopard densities within highly modified, cultivated and non-protected land (Figures 4 and 5), suggest that non-protected private land plays a role in sustaining the Western Cape leopard population. Both SECR methods suggest that the characteristics of the Langeberg winelands region host the highest leopard density and the Overberg’s agricultural landscape hosts the lowest. Langeberg leopards have higher densities on agricultural land than the other two regions (Figure 4), which can be attributed to the predominantly non-conflict crop cultivation (vineyard and orchard) in a valley surrounded by natural mountain vegetation. The proportion of leopard density in natural and

Figure 4. Sum of SPACECAP leopard pixel density estimates (animal per km²) for each classified land cover in Western Cape study regions. 'Agriculture' includes cultivated commercial fields, orchards and plantations. 'Urban' includes residential and urban commercial land and 'other' includes dams, roads and railways.

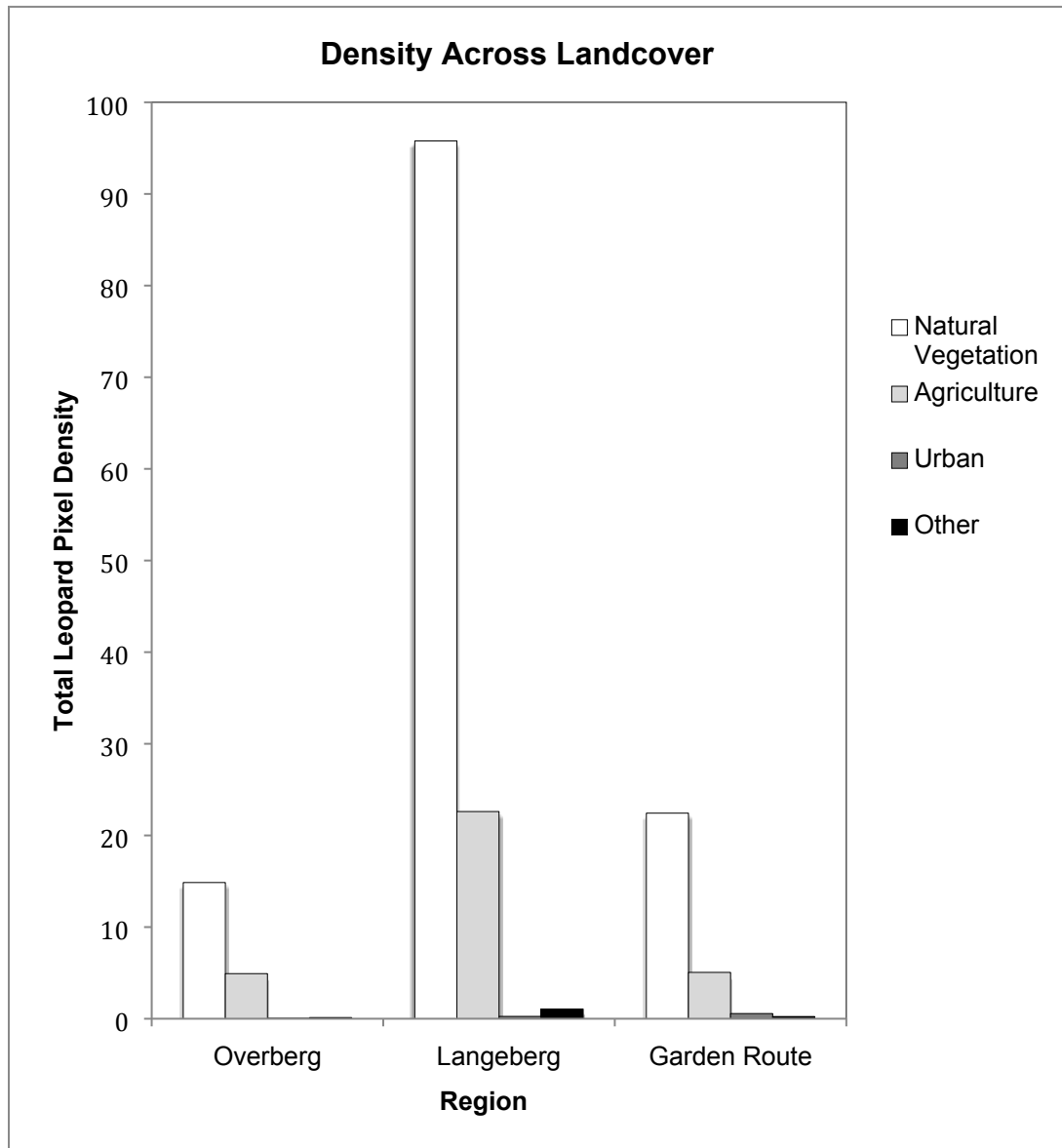
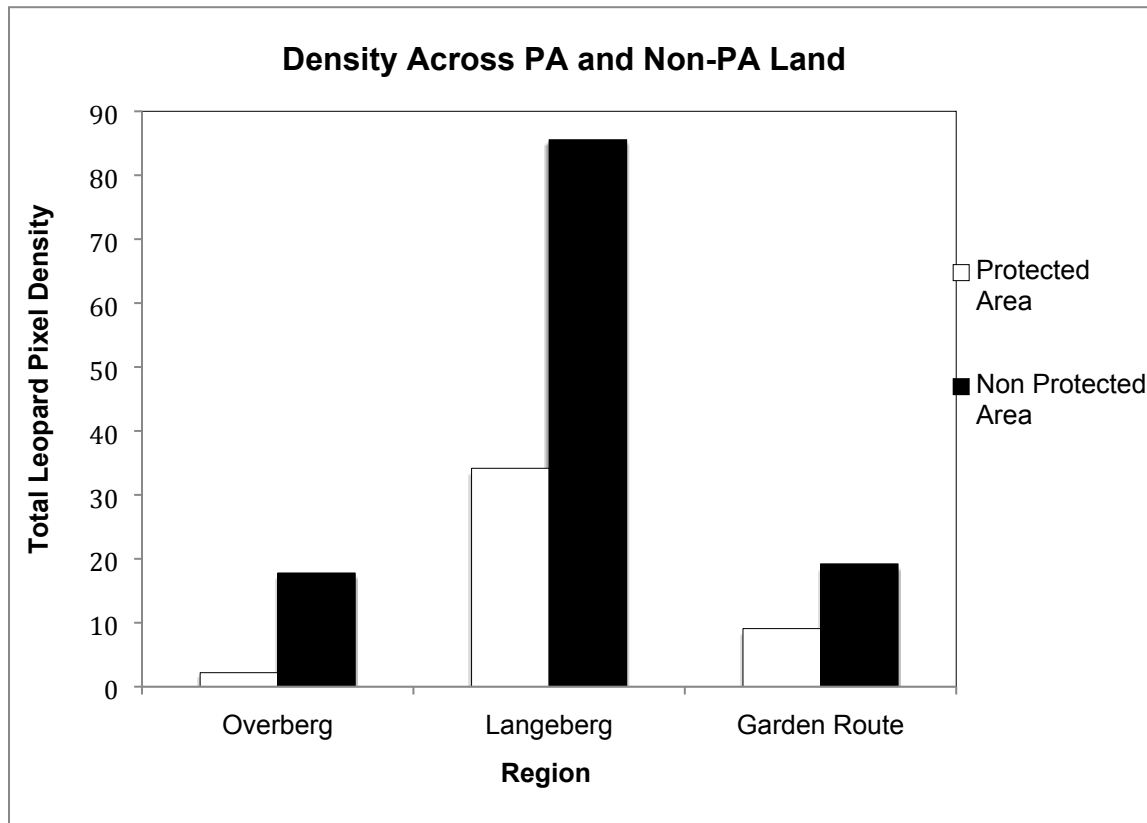


Figure 5. Sum of SPACECAP leopard pixel density estimates (animal per km²) for suitable leopard habitat within protected and non-protected areas for each study region, Western Cape.



cultivated land is closest in the Overberg, likely due to the highly fragmented habitat.

Our secr and SPACECAP estimates represent some of the lowest national density estimates for leopard and are comparable to the other three Western Cape studies (Devens and Tshabalala et al. 2018; Mann 2014; Martins 2010) (Table 5). Our SECR estimates differed more than expected, which could be partially attributed to the extra Maxent habitat mask covariate modelling incorporated into the SPACECAP analyses. The likelihood method requires substantially less computation time than the Bayesian approach (seconds/minutes versus hours/days), is less sensitive to buffer width and data augmentation size and has **greater convenience and versatility** for customization with covariates and models. SPACECAP entails checks to verify that convergence is achieved, model fit is sufficient, and data augmentation is adequate. Hence, it is more appropriate and robust for small sample sizes. Our mean SPACECAP density estimate of 1.18 leopards/ 100 km² respectively is directly comparable to Devens and Tshabalala et al.'s (2018) SPACECAP and two GPS methods with mean density estimates of 0.95 leopards/ 100 km² and 0.9-1.11 leopards/ 100 km² respectively (Table 5). These GPS methods used data from 21 collared leopards with home range size (home range density estimate (HRDE)) and home range overlap of same-sex neighbouring leopards (socially considerate density estimate (SCDE)). Therefore, we would suggest our SPACECAP results are more accurate and reliable at determining the spatial requirements of species. We recommend SECR methods for future research, with the specific incorporation of GPS collar data, because these methods are more robust at capturing a species' spatial ecology within a population.

We extrapolated an ecological density (number of individuals per useable area) using our density estimates and a prediction of 49,850 km² suitable remaining Western Cape leopard

Table 5. Published South African leopard population density estimates for data collected after 2000 and the analysis program used.

Region	Source	Density Estimate (leopards/100 km ²)	Program
Various (Western Cape)	present study	0.17 - 0.5 (0.35 average)	secr
		0.69 - 1.89 (1.18 average)	SPACECAP
Various (Western Cape, Eastern Cape)	Devens and Tshabalala et al. 2018	0.24 - 1.89 (0.95 average)	SPACECAP
		0.9	HRDE
		1.11	SCDE
Little Karoo (Western Cape)	Mann 2014	0.5	CAPTURE
		1.18	DENSITY
Cederberg Mountains (Western Cape)	Martins 2010	1.8 - 2.3	CAPTURE
Phinda-Mkhuze Complex (Kwazulu-Natal)	Balme et al. 2010	2.49 - 11.11	CAPTURE
Zululand Rhino Reserve (Kwazulu-Natal)	Chapman and Balme 2010	2.5 - 7	CAPTURE
Phinda Private Game Reserve (Kwazulu-Natal)	Brackowski et al. 2016	3.4	secr
		3.65	SPACECAP
		7.28 - 9.28	CAPTURE
Waterberg Mountains (Limpopo)	Swanepoel et al. 2015	4.56 - 6.59	secr
Phinda Private Game Reserve (Kwazulu-Natal)	Balme et al. 2009a	6.97	CAPTURE
Phinda Private Game Reserve (Kwazulu-Natal)	Balme et al. 2009b	7.17 - 11.21	CAPTURE
Soutpansberg Mountains (Limpopo)	Chase Grey et al. 2013	10.7	SPACECAP
N'wanetsi concession (Kruger National Park)	Maputla et al. 2013	12.7	CAPTURE

habitat (Swanepoel et al. 2013). Our findings suggest that there are between 175 and 588 leopards remaining (Table 4), however this may be an optimistic estimation. Habitat modelling is not infallible and identified suitable habitat is not necessarily useable for wide ranging species like leopard. The available habitat estimate included fragmented habitat, small isolated pockets of habitat and areas of habitat subject to edge effects and anthropogenic pressures. These factors can negatively affect populations and cause areas of habitat to not be viable to accommodate populations (Woodroffe & Ginsberg 1998). Additionally, our maximum Western Cape population estimate of 588 individuals is well below the minimum viable population size necessary to maintain genetic diversity (Traill et al. 2007). Genetic population structure of the Western and Eastern Cape provinces indicates very low to moderate gene flow between three subpopulations (McManus et al. 2015).

While highly adaptable, the leopard is a widely persecuted species, experiencing varying levels of anthropogenic threat and habitat loss. Our results suggest that protected areas are inadequate to ascertain the long-term conservation of leopards in the Western Cape. By establishing density and population size estimates in an increasingly fragmented and modified landscape, we increase the understanding of how leopards can persist in human-dominated areas, influencing the species' conservation planning. For adaptive and wide-ranging species like large carnivores, non-protected human-dominated areas may become increasingly important for genetic dispersal and landscape connectivity (Boron 2016). The threats and conservation conflicts affecting the leopard of the Cape region are affecting all top trophic level carnivores around the world. The need for accurate density estimates is widespread and critically important as various anthropogenic interests and threats continue to compete for and conflict with leopard resources and habitat.

Authors' contribution

CD, BS and JM conceived the ideas; CD designed the methodology, collected the data and wrote the manuscript; CD and TT analysed the data; MS, MH, AD, TT and BS provided revisions of important intellectual content to manuscript drafts. All authors contributed critically to the drafts and gave final approval for publication.

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Conflicts of interest

None.

Ethical standards

All authors have abided by the Oryx code of conduct and camera trapping fieldwork was conducted ethically with the necessary approvals and permits from appropriate institutions and statutory authorities. Cape Nature Research Permit to collect fauna specimens for scientific

research in the Western Cape was granted to Carolyn H. Devens in August 2014 (permit no.: AAA007-00130-0056) and prior camera trap data was covered under a Cape Nature Permit for co-author Jeannine McManus. These permits were granted for the purposes of collaring leopards. Carolyn H. Devens also was granted an Animal Ethics Committee Approval Certificate from the University of Pretoria in February 2014 – December 2016 (Project Number: EC005-14). This paper only uses camera trap data and not the collection of specimens, but all fieldwork was conducted ethically with the cooperation of local conservation authorities and landowners.

Statement for data archiving:

We agree to archive the data with one of the recommended public archive (i.e. Dryad, TreeBASE, etc.), which will be determined upon acceptance of this manuscript.

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