



## LIMPOPO LEOPARD PROJECT 2013 ANNUAL REPORT

Ross Tyzack Pitman\*, Guy Balme

\*Corresponding email: [rosstyzackpitman@gmail.com](mailto:rosstyzackpitman@gmail.com)

### INTRODUCTION

Leopards (*Panthera pardus*) throughout Limpopo Province, South Africa, are heavily persecuted through legal and illegal practices (Ray, Hunter & Zigouris 2005; Swanepoel 2009). Even though a large proportion of Limpopo is considered suitable leopard habitat (63%; which comprises 32% of suitable leopard habitat in South Africa), there are uncertainties regarding leopard population viability, especially given that harvest practices are potentially unsustainable (Daly *et al.* 2005; Swanepoel *et al.* 2013). There exists the need to accurately monitor these populations at multiple scales so that reliable, long-term demographic data can facilitate sound management and conservation actions (Westgate, Likens & Lindenmayer 2013).

Small-scale site-specific studies have the advantage of collecting high resolution, precise data, but often lack the ability to generate accurate large-scale inferences; in contrast, large-scale multi-site studies are capable of determining relative, coarse demographic trends but sometimes lack the fine-resolution data necessary for management (Lindenmayer & Likens 2010). A marriage between these two approaches can provide a satisfying compromise (Hebblewhite *et al.* 2011). The Limpopo Leopard Project (LLP) aims to establish a reliable and easily repeatable method for monitoring leopards at the provincial scale in Limpopo to facilitate effective adaptive management. Such a method has applicability for leopard management elsewhere in South Africa, and more widely across the species' range.

The LLP will use simulation & spatial modeling alongside well-established survey methods to collect, manipulate and analyse leopard population and ecological data (Karanth & Nichols 1998; Karanth *et al.* 2006; Long *et al.* 2008; Balme, Hunter & Slotow 2009; Hebblewhite *et al.* 2011; O'Connell, Nichols & Karanth 2011; Robinson & DeSimone 2011). The LLP aims to consistently monitor the impact of legal and illegal killing of leopards throughout Limpopo, which will enable the Limpopo Department of Economic Development, Environment and Tourism (LEDET) to evaluate previous management decisions and provide a sound basis on which to develop future management plans.

The study will be conducted throughout Limpopo Province, South Africa. Data will be collected at different scales; specifically robust population abundance estimates will be collected at 5 surveillance sites, while relative population trends will be assessed across the entire province. Limpopo is the 5<sup>th</sup> largest province in South Africa (ca. 125 754 km<sup>2</sup>) and is generally characterized by dry deciduous/bushveld habitats (Mucina & Rutherford 2006). Climate differs throughout the Limpopo, but can be regarded as semi-arid. Temperatures average 21–22 °C in summer (peak – January), and fall to 11 °C in winter (peak – July). Precipitation averages 530 mm per annum (range: 200–1200 mm). In comparison to other provinces in South Africa, Limpopo contains extensive leopard habitat, with widespread leopard populations (Swanepoel *et al.* 2013). Limpopo awards the largest number of CITES permits (n = 52; 35% of the annual national quota) to individuals wishing to hunt leopards (Daly *et al.* 2005). Leopards can only be legally destroyed by a private individual who is in possession of a CITES tag or damage-causing animal (DCA) permit (also known as a destruction permit) issued by LEDET. The legal killing of leopards (both as trophies and as damage causing animals) in Limpopo is most likely eclipsed by illegal offtake of leopards by farmers and poachers (Chase-Grey 2011). Most anthropogenic pressure is centered on three main areas: the Waterberg, the Soutpansberg, and the southern-Mopani district (Lourens Swanepoel, *unpublished*). Instead of being evenly distributed across the province, these clustered, high mortality areas can create localized population sinks that can have devastating impact on metapopulation persistence (Robinson *et al.* 2008; Balme *et al.* 2010).

## **METHODS**

Leopard population trends will be assessed at a provincial scale using a number of relative abundance indices. These will be calibrated against rigorous population estimates at key surveillance sites.

### **Provincial Population Indices:**

1. *Harvest composition* - research on cougars suggest that changes in the population structure in the annual harvest is monotonically related to changes in population abundance (Anderson & Lindzey 2005). Because movement patterns vary predictably among cougar age and sex classes, some cohorts will likely be more exposed to hunting than others. We are exploring whether a similar relationship exists among leopards and determining a relative vulnerability index for the species (A. Braczkowski in prep.). The age of leopards hunted each year in Limpopo will be estimated using the detailed trophy photographs submitted to LEDET by hunting outfitters. Whenever possible, we will also examine trophies directly in the field or at local taxidermists to better estimate ages. In addition to tracking population trends, the age-sex composition of the harvest provides an indication of the impacts of trophy hunting on population viability. Several studies have shown that carnivore populations are resilient to disturbance if the reproductive female life-stage remains unaffected (Whitman *et al.* 2004). Hence, a localised increase of adult

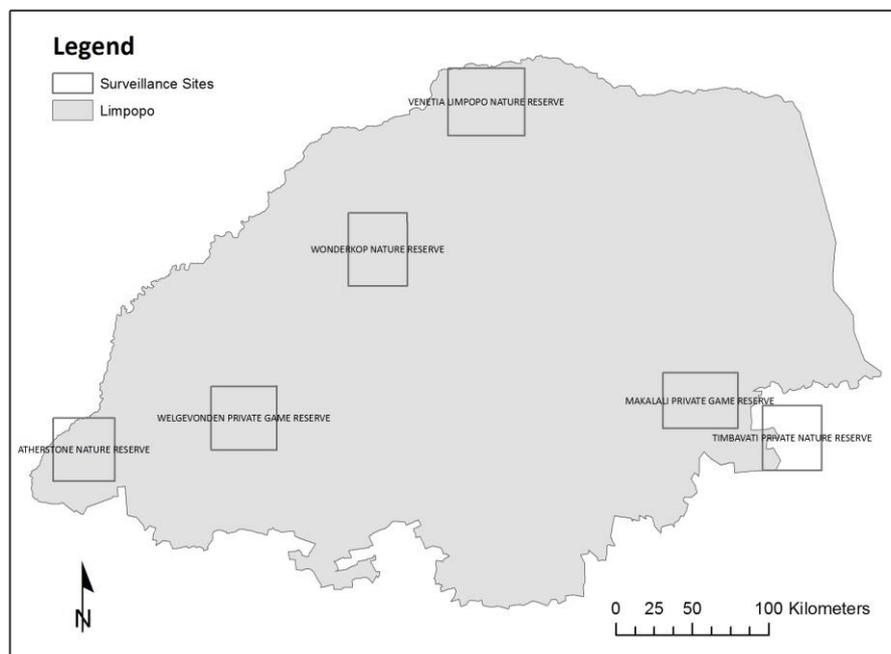
females in the harvest may require a localised reduction in quota the following year. Conversely, an increase in old (>7 years) trophy males could lead to an increase in quota the next year (Balme, Hunter & Braczkowski 2012).

2. *Catch-per-unit-effort* - in its simplest form, catch-per-unit-effort (CPUE) relies on the premise that a constant harvesting effort will remove a constant proportion of the population. An increase in the effort required to secure a trophy infers a proportional decrease in population size, and vice versa. CPUE is most commonly applied in fisheries management but it has also been used to monitor large carnivore populations (Edwards et al. in press). Our principal unit of effort will be the number of days required by hunters to successfully hunt a leopard. However, the success of leopard hunts is also affected by the number of baits deployed by hunters, the frequency that baits are replaced, whether an area was pre-baited, etc. These data are all included in the prescribed hunt return form that can be distributed to outfitters in Appendix I.
3. *Change in occupancy* - the melting-range hypothesis predicts that species' distributions should contract inward from low-quality, marginal habitats along range edges to the highest quality habitats in the range core (Brown 1984). We will use questionnaire surveys and site occupancy modelling to assess changes in distribution at the edges of leopard range in Limpopo (Zeller *et al.* 2011). A network of residents will be identified and visited in the first year of the project to establish a baseline of leopard occurrence in areas classified by Swanepoel et al. (2013). Questionnaires will be kept short; the primary goal is simply to determine the presence or absence of leopards on properties (Appendix 2). Grid cells of 400 km<sup>2</sup> will be used (to ensure sampling independence) and  $\pm 10$  interviews conducted per grid cell (these replicates enable the computation of detection probabilities; Mackenzie & Royle 2005). The same residents will be interviewed each year to assess changes in occupancy over time. However, after the first year, interviews will be conducted telephonically. Leopard occupancy and the factors influencing occupancy (biotic and abiotic) will be analysed using the software PRESENCE (Hines 2010). We selected environmental covariates hypothesized to influence the use of each grid by leopards. These covariates were derived from a 10-meter land use raster (Eskom 2009) and included the proportion of: recently cultivated land, built up urban areas, residential areas, tall tree cover, dense bush cover, bush cover, open bush cover, grassland, bare ground. Additional site covariates included road density (km<sup>-2</sup>; South African Department of Transport 2013), human population density (km<sup>-2</sup>; Statistics South Africa 2011), and mean habitat suitability index (Swanepoel *et al.* 2013). Probability of occupancy ( $\Psi$ ) and detection were modeled as a function of covariates using multinomial-logit link (*mlogit*) functions (MacKenzie *et al.* 2006; MacKenzie *et al.* 2009).

### Population estimation at surveillance sites:

We will estimate leopard population density on an annual basis at six key surveillance sites using systematic camera-trap surveys. The following list surveillance sites monitored by the LLP (Fig. 1), sites 1–3 and 6 (awaiting results) were monitored in 2013:

1. Welgevonden Private Game Reserve
2. Wonderkop Nature Reserve
3. Atherstone Nature Reserve
4. Makalali Private Game Reserve
5. Venetia Limpopo Nature Reserve
6. Timbavati Private Nature Reserve



**Figure 1.** Distribution of camera-trapping sites across Limpopo province, South Africa.

### CAMERA-TRAPPING METHODS

One hundred and fifty Panthera V4 camera traps are available for this study. The V4s are each fitted with a 2gb internal micro-SD card, capable of storing  $\pm 3000$  images. The V4s use a xenon flash that allows for extremely fast exposures ( $\pm 1/100^{\text{th}}$ ). The high-energy capacitor recharges the flash within 15 seconds (with good battery life). The V4s have a 'stealth' mode setting which allows the user to turn off any LED operating lights, and even the flash entirely, to prevent detection by poachers and thieves. The camera-traps (CTs) were fitted with high capacity (2000 mAh) low self discharge

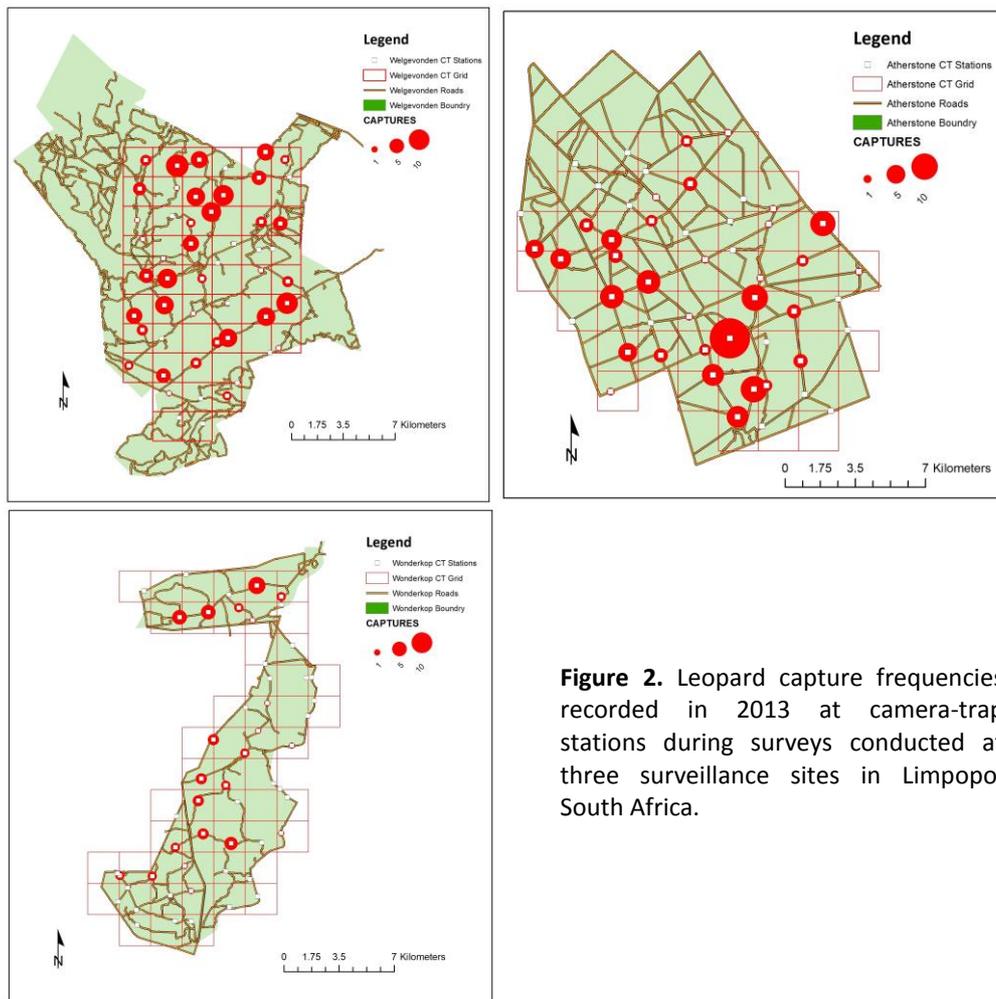
Tenergy™ Centura AA rechargeable batteries. Each CT was fitted with 3 AA batteries, which lasted approximately 15 days. For further details follow the link: <http://pantheracameratrap.org/Downloads/PantheraCameraTrap.pdf>

Camera-trapping began on the 18 March 2013, on Welgevonden Private Game Reserve. Cameras are deployed using 50 monitoring stations per survey (two cameras per station). Survey grid size was 4 km<sup>2</sup> (Fig. 2). We aimed to survey ±200 km<sup>2</sup> per surveillance site (i.e., ±50 CT stations; ±50 grid cells). This survey size ensures reduced bias of density estimates (Tobler & Powell 2013). Each surveillance site was investigated (for leopard tracks, sign, and suitable CT sites) prior to CT deployment. Surveillance sites were first mapped in a GIS using aerial photographs to determine site boundaries and access roads. Preliminary CT sites were chosen visually within survey grids and projected on a digital map. These preliminary CT sites were uploaded to a GPS device and navigated to in the field. Site selection depended on the actual suitability of each site (i.e., enabling high detection probability), which could only be determined once in the field. Actual site selection was kept within close proximity of preliminary CT sites to ensure suitable CT spacing. Maximum distance between CTs depends on female home range. GPS telemetry data from three female leopards in the Waterberg, Limpopo, recorded home ranges of ≥ 65 km<sup>2</sup> (range: 65–215 km<sup>2</sup>; LH Swanepoel, *unpublished*). Therefore, CT spacing of ≤ 4 km ensured no gaps were present in our study design (Tobler & Powell 2013). CTs were fixed using black ¼" shock cord to trees or onto metal-stakes driven into the ground using black, heavy duty cable ties. CTs were placed beside roads and well-used animal paths (Balme, Hunter & Slotow 2009). CT sites were cleared of excessive debris and vegetation that could inadvertently trigger the camera's motion sensor. CTs were installed at heights of 50–60 cm (shoulder height of a walking leopard) and positioned straight and level (Henschel & Ray 2003). CTs were offset by 2 m to prevent flash blinding, and placed at 1–3 m from the trail or road (O'Connell, Nichols & Karanth 2011).

In order to satisfy population closure, CT blocks were operational of short periods (±50 days). CTs were activated and then monitored periodically (±7–10 days) to change batteries and download images. Raw CT photos were imported from a USB stick to a personal computer using program CAMERA TRAP FILE MANAGER (CTFM). CT photos were then digitally marked using CTFM so that the appropriate EXIF data are stamped onto each image. Marked CT photos were then batch uploaded into program CAMERA BASE (Mathias Tobler; Microsoft Access Database). Each photo was assigned a code (NA = 0, human = 1, leopard = 2, lion = 3, etc.) and ancillary data collected for later analysis (e.g., sex, age, number of individuals, etc.). Capture histories were compiled from leopards identified from CT photos.

Capture probabilities and estimated population size were generated using a spatially-explicit capture-recapture (SECR) framework in program SPACECAP (Royle *et al.* 2009; Singh *et al.* 2010). The

SPACECAP program is run through the statistical software program R. CT data within CAMERA BASE can be read directly into R, and thus, directly into SPACECAP using the R binary package “RODBC” (Ripley 2012). SPACECAP uses a hierarchical modeling framework composed of (1) a point-process model describing the distribution of individuals in space and (2) a model describing the observation of individuals from traps. Thus, capture probabilities are a function of distance between individual home range centers and trap locations (Royle *et al.* 2009). Three input files are required for SECR analysis in SPACECAP: (1) “animal capture .csv file” comprising animal ID, trap location number, sampling occasion number; (2) “trap deployment .csv file” comprising trap spatial location, deployment activity, sampling occasion number; and (3) “state-space .csv file” comprising potential leopard home range centers (using spatial location and habitat suitability). We assessed model fitness in SPACECAP using the Bayesian P-value deduced from individual capture frequencies (a P-value close to 0 or 1 implies poor model fit; Gopaldaswamy *et al.* 2012). We also assessed whether the Markov-Chain Monte Carlo (MCMC) parameters reached convergence by visually examining the distribution of ‘N super’.



**Figure 2.** Leopard capture frequencies recorded in 2013 at camera-trap stations during surveys conducted at three surveillance sites in Limpopo, South Africa.

## RESULTS

We have not yet analyzed the harvest and hunter effort data for 2013, hence we report only on our camera-trap surveys and the preliminary occupancy survey.

A total area covered by camera-traps amounted to 554 km<sup>2</sup>. Our sampling effort comprised 7946 camera-trap days and yielded photographs of 58 individual leopards captured on 364 occasions (no individuals were captured at more than one surveillance site; Table 1). Leopards were photographed at 60% of camera-trap stations, with the lowest number of captures from Wonderkop Nature Reserve and the highest from Welgevonden Private Game Reserve. The Bayesian P-values in SPACECAP suggested that model fit was adequate for most surveys (Atherstone Nature Reserve resulted in high P-values) and the MCMC chains appeared to reach convergence in all cases. Estimated population density ranged from 3.2 ± 0.6 leopards/100 km<sup>2</sup> in Welgevonden Private Game Reserve to 6.2 ± 1.4 leopards/100 km<sup>2</sup> in Atherstone Nature Reserve (Table 2).

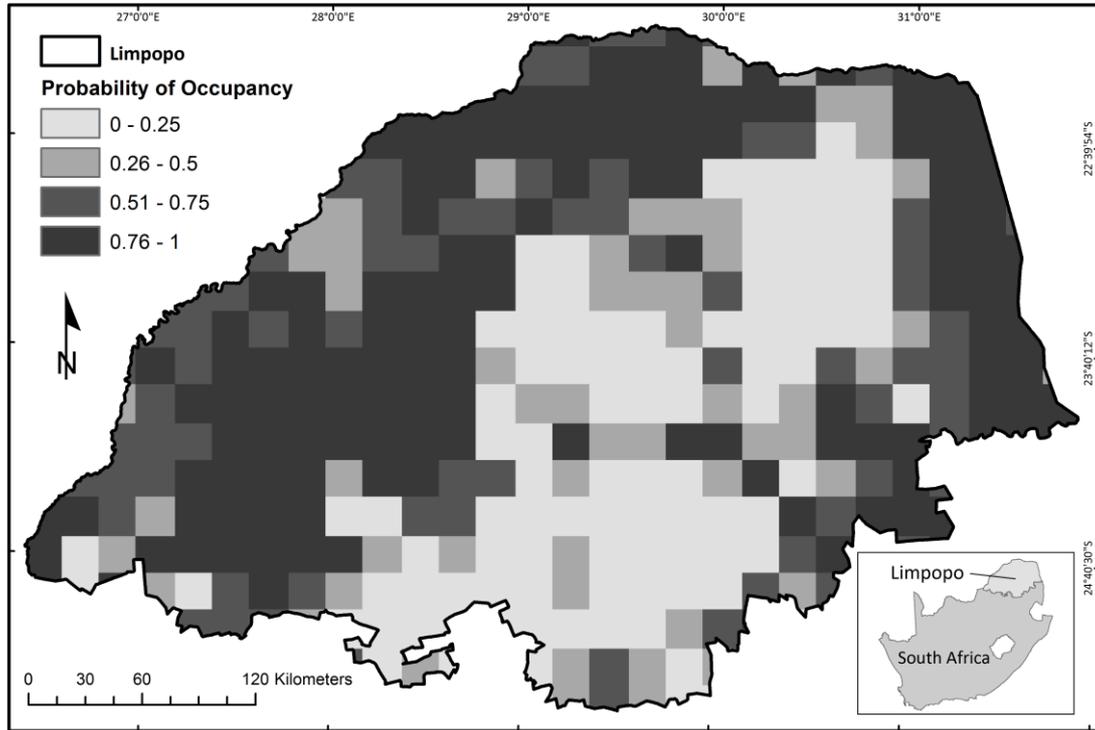
**Table 1.** Results of camera-trap surveys undertaken at leopard surveillance sites in Limpopo, South Africa during 2013.

SURVEILLANCE SITE	NO. OF CAMERA-TRAP STATIONS	AREA COVERED BY CAMERA-TRAP STATIONS (KM <sup>2</sup> )	SAMPLING EFFORT (NO. OF TRAP DAYS)	NO. OF LEOPARD CAPTURES	NO. OF INDIVIDUAL LEOPARD CAPTURES
Welgevonden Private Game Reserve	51	164	2694	169	21
Wonderkop Nature Reserve	52	217	2652	54	17
Atherstone Nature Reserve	50	173	2600	141	20

**Table 2.** Spatially-explicit capture-recapture model parameters estimating leopard population density from camera-trap surveys undertaken at three surveillance sites in Limpopo, South Africa during 2013.

SURVEILLANCE SITE	SIGMA	LAMBDA	PSI	N SUPER	DENSITY 100 KM <sup>2</sup> (± SD)
Welgevonden Private Game Reserve	3.40	0.03	0.33	75.35	3.2 ± 0.6
Wonderkop Nature Reserve	3.01	0.01	0.51	95.74	3.6 ± 0.9
Atherstone Nature Reserve	1.87	0.02	0.42	154.43	6.2 ± 1.4

We conducted 1020 questionnaire-based interviews over a 10-week period. Mean habitat suitability index (*MeanHSI*) and the proportion of bush cover (*Bush*) and tall tree cover (*TallTrees*) were positively correlated with  $\Psi$ , whilst human population density (*PeopleKM<sup>2</sup>*) and the proportion of recently cultivated land (*CultivRecent*) were negatively correlated with  $\Psi$  (Table 3; Fig. 3). Detection probability increased whenever the proportion of built up urban areas (*UrbanBultup*) and residential areas (*UrbanResid*) decreased, and whenever mean habitat suitability index (*MeanHSI*) increased (Table 3; Fig. 3).



**Figure 3.** Estimated probability of leopard *Panthera pardus* occupancy for Limpopo province, South Africa during 2013.

**Table 3.** Top three multi-state occupancy models with untransformed coefficients of covariates for leopard *Panthera pardus* across Limpopo province, South Africa for 2013.

Model <sup>a</sup>	$\Delta AIC_c$	AICc weight	No. of parameters	Untransformed coefficient of covariate $\pm SE^2$								
				Intercept	MeanHSI	PeopleKM <sup>2</sup>	CultivRecent	Bush	TallTrees	UrbanBuiltup	UrbanResid	MeanHSI
$\Psi(\text{MeanHSI} + \text{PeopleKM}^2 + \text{CultivRecent} + \text{Bush} + \text{TallTrees}), p(\text{UrbanBuiltup} + \text{UrbanResid})$	0	0.6838	15	-1.70 $\pm$ 0.88	4.20 $\pm$ 2.94	-0.02 $\pm$ 0.008	-18.72 $\pm$ 7.5	4.00 $\pm$ 3.39	97.87 $\pm$ 57.35	-1291.73 $\pm$ 641.98	-54.32 $\pm$ 23.9	—
$\Psi(\text{MeanHSI} + \text{PeopleKM}^2 + \text{CultivRecent} + \text{Bush} + \text{TallTrees}), p(\text{UrbanBuiltup} + \text{UrbanResid} + \text{MeanHSI})$	2.18	0.3362	16	-1.71 $\pm$ 0.88	4.08 $\pm$ 2.93	-0.02 $\pm$ 0.008	-18.71 $\pm$ 7.54	4.07 $\pm$ 3.38	100.08 $\pm$ 57.99	-1353.40 $\pm$ 651.85	-48.42 $\pm$ 24.72	0.85 $\pm$ 1.03 <sup>b</sup>
$\Psi(\text{MeanHSI} + \text{PeopleKM}^2 + \text{CultivRecent} + \text{Bush} + \text{TallTrees}), p(\text{UrbanBuiltup})$	4.14	0.1262	14	-1.74 $\pm$ 0.86	4.00 $\pm$ 2.90	-0.03 $\pm$ 0.008	-19.07 $\pm$ 7.58	4.45 $\pm$ 3.38	89.61 $\pm$ 56.44	-1300.84 $\pm$ 589.99	—	—

<sup>a</sup> Multistate models were modeled as a function of covariates in the 3<sup>rd</sup> state

<sup>b</sup> Non-significant covariates remained within a model if they had previously shown to influence leopard distribution

## DISCUSSION

The first year of the Limpopo Leopard Project has been a success with robust density estimates generated for four of the six key surveillance sites across Limpopo. Leopard populations appear relatively healthy in most surveillance sites; although their true status will only be known once surveys have been conducted over several years and trend data established. Nevertheless, our density estimates are at the mid- to upper-end of the scale documented for leopards (see Hunter et al. 2013 for review), though it must be noted that the reliability of many of these earlier estimates are

questionable. It is even problematic comparing our recent estimates derived using SECR models with historical estimates from camera-trap surveys using non-spatial methods (Balme, Slotow & Hunter 2009; Balme *et al.* 2010; Chapman & Balme 2010), as the latter have been shown to grossly overestimate population density, especially if surveyed areas are small (Noss *et al.* 2012).

The occupancy survey went far better than expected. Our sample size was fairly large and incorporated all major biomes within Limpopo, which ensured that our data adequately represented the province. The multi-state models neatly estimated leopard occupancy in areas that we suspected would have high and low levels of relative leopard abundance. We are currently analyzing harvest data that spans from 2002 to 2012 – the data are revealing some interesting patterns that fall in line with our occupancy results.

The real value of our monitoring project will hopefully be realised in time. In addition to tracking local leopard population trends, we will use the long-term capture data in combination with open SECR models to assess leopard demographic rates (i.e. mortality, reproduction, immigration, emigration) (Gardner *et al.* 2010). These life history data can be used in population viability analyses to better gauge the extinction risk of leopards in Limpopo and to predict the likely outcomes of management decisions. Inferences on landscape connectivity can also be made by integrating SECR models in a least-cost path framework (Royle *et al.* 2013). The annual camera-traps surveys benefit other species besides leopards; they also furnish data on the abundance of threatened wildlife such as spotted and brown hyenas, cheetahs and African wild dogs. While the primary goal of our project is to enable effective adaptive management of leopards in Limpopo, it has potential to act as a standard for monitoring a range of carnivore species in South Africa, and further afield.

## **ACKNOWLEDGEMENTS**

We are grateful to Panthera ([www.panthera.org](http://www.panthera.org)) and LEDET for making this research possible. We thank the owners and staff at all the reserves that allowed the LLP to conduct research on their properties. We are also grateful to Ms. Nstae Sekati and Ms. Dipolelo Mashabela for carrying out the occupancy fieldwork.

## **REFERENCES**

- Anderson, C.R. & Lindzey, F.G. (2005) Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. *Wildlife Society Bulletin*, **33**, 179–188.
- Balme, G.A., Hunter, L. & Braczkowski, A.R. (2012) Applicability of Age-Based Hunting Regulations for African Leopards. *PLoS ONE*, **7**.
- Balme, G.A., Hunter, L., Goodman, P., Ferguson, H., Craige, J. & Slotow, R. (2010) An adaptive management approach to trophy hunting of leopards *Panthera pardus*: a case study from KwaZulu-

- Natal, South Africa. *Biology and Conservation of Wild Felids* (eds D.W. Macdonald & A. Loveridge), pp. 341–352. Oxford University Press, Oxford.
- Balme, G.A., Hunter, L.T.B. & Slotow, R. (2009) Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management*, **73**, 433–441.
- Balme, G.A., Slotow, R. & Hunter, L.T.B. (2009) Impact of conservation interventions on the dynamics and persistence of a persecuted leopard *Panthera pardus* population. *Biological Conservation*, **142**, 2681–2690.
- 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 African Journal of Wildlife Research*, **40**, 114–120.
- Chase-Grey, J. (2011) Leopard population dynamics, trophy hunting and conservation in the Soutpansberg Mountains, South Africa. PhD, Durham University.
- Daly, B., Power, J., Camacho, G., Traylor-Holzer, K., Barber, S., Catterall, S., Fletcher, P., Martins, Q., Martins, N., Owen, C., Thal, T. & Friedmann, Y. (2005) Leopard (*Panthera pardus*) PHVA. Workshop Report. Conservation Breeding Specialist Group (SSC / IUCN) / CBSG South Africa. Endangered Wildlife Trust.
- Gardner, B., Reppucci, J., Lucherini, M. & Royle, J.A. (2010) Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology*, **91**, 3376–3383.
- Hebblewhite, M., Miquelle, D.G., Murzin, A.A., Aramilev, V.V. & Pikunov, D.G. (2011) Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. *Biological Conservation*, **144**, 2403–2413.
- Henschel, P. & Ray, J. (2003) Leopards in African rainforests: survey and monitoring techniques. *Wildlife Conservation Society, Global Carnivore Program*. New York, USA.
- Hines, J.E. (2010) PRESENCE – Software to estimate patch occupancy and related parameters v.6.2. USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/doc/presence/presence.html>
- Hunter, L., Henschel, P. & Ray, J.C. (2013) *Panthera pardus*. *The Mammals of Africa: carnivores, pangolins, rhinos, and equids*. Academic Press, Amsterdam, The Netherlands.
- Karanth, K.U. & Nichols, J.D. (1998) Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, **79**, 2852–2862.
- Karanth, K.U., Nichols, J.D., Kumar, N.S. & Hines, J.E. (2006) Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology*, **87**, 2925–2937.
- Lindenmayer, D.B. & Likens, G.E. (2010) The science and application of ecological monitoring. *Biological Conservation*, **143**, 1317–1328.
- Long, R.A., MacKay, P., Zielinski, W.J. & Ray, J.C. (2008) *Noninvasive Survey Methods for Carnivores*. Island Press.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.A. & Hines, J.E. (2006) *Occupancy Modeling and Estimation: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, San Diego, CA.
- MacKenzie, D.I., Nichols, J.D., Seamans, M.E. & Gutierrez, R.J. (2009) Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology*, **823**–835.

- Mucina, L. & Rutherford, M.C. (2006) *The vegetation of South Africa, Lesotho and Swaziland*. Sterlitzia 19: South African National Biodiversity Institute, Pretoria, South Africa.
- Noss, A.J., Gardner, B., Maffei, L., Cuéllar, E., Montañó, R., Romero-Muñoz, A., Sollman, R., O'Connell, A.F. & Altwegg, R. (2012) Comparison of density estimation methods for mammal populations with camera traps in the Kaa-lya del Gran Chaco landscape. *Animal Conservation*, **15**, 527-535.
- O'Connell, A.F., Nichols, J.D. & Karanth, K.U. (2011) *Camera Traps in Animal Ecology: Methods and Analyses*. Springer.
- R Core Team (2013) R: A language and environment for statistical computing <http://www.R-project.org/>
- Ray, J.C., Hunter, L. & Zigouris, J. (2005) *Setting conservation and research priorities for large African carnivores*. Wildlife Conservation Society, New York.
- Ripley, B. (2012) RODBC: ODBC Database Access. R package version 1.3.6 <http://CRAN.R-project.org/package=RODBC>
- Robinson, H.S. & DeSimone, R.M. (2011) The Garnet Range Mountain Lion Study: Characteristics of a Hunted Population in West-central Montana (Final Report). Montana Department of Fish, Wildlife & Parks, Wildlife Bureau, Helena, MT. 102 pp.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S. & Cooley, S.W. (2008) Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications*, **18**, 1028–1037.
- Royle, J.A., Chandler, R.B., Gazenski, K.D. & Graves, T.A. (2013) Spatial capture-recapture models for jointly estimating population density and landscape connectivity. *Ecology*, **94**, 287–294.
- Royle, J.A., Karanth, K.U., Gopalaswamy, A.M. & Kumar, N.S. (2009) Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, **90**, 3233–3244.
- Singh, P., Gopalaswamy, A.M., Royle, J.A., Kumar, N.S. & Karanth, K.U. (2010) SPACECAP: a program to estimate animal abundance and density using Bayesian spatially-explicit capture-recapture models
- Swanepoel, L.H. (2009) Ecology and conservation of leopards *Panthera pardus* on selected game ranches in the Waterberg region, Limpopo, South Africa. MSc MSc, University of Pretoria.
- Swanepoel, L.H., Lindsey, P., Somers, M.J., Hoven, W., Dalerum, F., Pettorelli, N. & Penteriani, V. (2013) Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation*, **16**, 41–50.
- Tobler, M.W. & Powell, G.V.N. (2013) Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation*, **159**, 109–118.
- Westgate, M.J., Likens, G.E. & Lindenmayer, D.B. (2013) Adaptive management of biological systems: A review. *Biological Conservation*, **158**, 128–139.
- Whitman, K., Starfield, A.M., Quadling, H.S. & Packer, C. (2004) Sustainable trophy hunting of African lions. *Nature*, **428**, 175-178.
- Zeller, K.A., Nijhawan, S., Salom-Pérez, R., Potosme, S.H. & Hines, J.E. (2011) Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. *Biological Conservation*, **144**, 892–901.