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Leopard (Panthera pardus) density in southern Mozambique: Evidence from spatially explicit capture-recapture in Xonghile Game Reserve

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TITLE: Leopard (*Panthera pardus*) density in southern Mozambique: Evidence from spatially explicit capture-recapture in Xonghile Game Reserve

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ABSTRACT

Rigorous status estimates of large carnivore populations are necessary to inform their management and help evaluate the effectiveness of conservation interventions. The African leopard (*Panthera pardus*) faces rising anthropogenic pressures across most of its contracting sub-Saharan range, but the scarcity of reliable population estimates means that management decisions often have to rely on expert opinion or educated guesses. This is particularly true for Mozambique, where as a result of prolonged conflict very little is known on the ecology or conservation status of leopard populations across the country. We used camera trapping and spatially explicit capture-recapture models to provide a leopard density estimate in Xonghile Game Reserve, southern Mozambique, part of the Greater Limpopo Transfrontier conservation initiative. The estimated population density was of 2.60 (SE=±0.96) leopards per 100 km^2. Our study provides a baseline leopard density for the region, as well as the first empirical density estimate in southern Mozambique. In addition, our results suggest that current methods used to set trophy hunting quotas for leopard, both in Mozambique and elsewhere in Africa, might be leading to overinflated quotas, and highlight the importance of robust empirical data in guiding conservation policy.

INTRODUCTION

The leopard (*Panthera pardus*) is vulnerable to extinction in fragmented landscapes due to its low densities, large spatial requirements and potential for conflict with humans (Nowell & Jackson, 1996; Balme *et al.,* 2010). Leopard populations in Africa are increasingly threatened by growing anthropogenic pressures, leading to a rising conservation concern and calls for reliable population estimates to better inform conservation management (Jacobson *et al.,* 2016). In the absence of robust population estimates, management decisions are often reliant on expert opinion or educated guesses, making it difficult to identify areas of concern, prioritise conservation investments, and evaluate the effectiveness of interventions (Balme *et al.,* 2014; Gray & Prum, 2012).

In this context, density estimation, such as through capture-recapture modelling, has become a key process in wildlife ecology, conservation, and management (Gray & Prum, 2012). Initially, capture-recapture techniques estimated abundance rather than density, and relied on estimating the survey's effective sampled area to obtain the latter. However, no theoretical basis exists for this process, and the reliability of this approach is therefore questionable (Efford, 2004; Borchers & Efford, 2008; Royle *et al.,* 2009). Recently developed methodologies, know as spatially-explicit capture-recapture (SECR) overcome these issues by estimating density directly as an explicit parameter (Efford, 2004; Royle *et al.,* 2009)

Since being first applied to tiger populations in India (Karanth, 1995), capture-recapture techniques have been employed to obtain density estimates of most large carnivores, including for leopards in various African countries, such as South Africa (Balme *et al.,* 2009; Chase-Grey *et al.,* 2013; Swanepoel *et al.*, 2015), Gabon (Henschel, 2011), Tanzania (Cavallo, 1993), and Namibia (Stein *et al.,* 2011). Nevertheless, there is still paucity of such data across much of the continent, precluding effective conservation management (Balme *et al.,* 2014). This is particularly the case for Mozambique, where armed conflicts during much of the latter half of the 20th century contributed to large declines in wildlife populations across the country (Hatton *et al.* 2001), and considerably hindered conservation efforts. As a result, very little research has been conducted on the status, distribution or ecology of the leopard in Mozambique.

Leopards are legally hunted for trophies in several locations in Mozambique, with the current quota set at 120 permits per annum (CITES, 2007). This quota is based on efforts to estimate the overall abundance of leopards in Mozambique by Martin & de Meulenaer (1988), who employed a predictive model to estimate a country-wide population of 37,542 leopards, based on an average density of 0.10/km^2 (10 leopards per 100 km^2). Such estimates have been widely rejected as exaggerated for a number of reasons, including omitting from the model critical factors such as anthropogenic mortalities and prey availability, and relying on the assumption that leopards occur at maximum potential densities in all available habitats (Jackson, 1989; Balme *et al.,* 2010). Nevertheless, this approach was employed as a justification for the most recent increase in trophy hunting quota, with a lack of alternative in-country estimates of population densities cited as the principal reason for this (CITES, 2007). Consequently, more accurate assessments of leopard populations in Mozambique are needed to assess the reliability of current quota setting methods in the country, and to ensure that future changes in trophy hunting quotas are based on robust population data.

Here we use a closed-population SECR methodology to estimate density of leopards in Xonghile Game Reserve (XGR), a legally protected area in southern Mozambique. The aim of the study was to obtain the first empirical density estimate for a leopard population in southern Mozambique, and provide information that can guide management and act as a baseline to assess conservation interventions. Finally, the implications of findings for trophy hunting in Mozambique are explored.

STUDY AREA

Xonghile Game Reserve (Fig. 1) is a legally protected area in southern Mozambique. Its northern-most border is located approximately 13 km south of Limpopo National Park's (LNP) southern border, the country's largest national park. XGR is unfenced, bordering South Africa's Kruger National Park (KNP) to the west and unprotected land to the north, east and south. The reserve covers approximately 450 km^2, and is part of the Greater Limpopo Transfrontier Conservation Area (GLTFCA), a trans-boundary initiative where protected parks and reserves in Mozambique, South Africa and Zimbabwe are linked by non-protected areas. The predominant habitat in XGR consists of sand plains ('sandveld') characterized by low woodlands and thickets on deep sandy soils, as well as short-grass 'pans' (seasonally flooded depressions). Although large mammal populations in the region were severely depleted during the country's many years of armed conflicts (1964-1992; Hanks, 2000), the removal of fencing along the KNP border in recent years has provided the potential for movement of wildlife into the area. No human population permanently resides in XGR, with the main anthropogenic impacts coming from relatively low levels of poaching for bushmeat, anti-poaching efforts, and the low levels of tourism the reserve experiences (Andresen & Everatt; unpublished data). Trophy hunting does not currently take place in XGR.

Figure 1 here

METHODS

Camera Trapping

29 digital motion-activated cameras of multiple models (Reconyx HC500, Spy Point Tiny-W2, Bushnell Trophy Cam) were deployed at 26 stations over an area of c. 300 km^2 in XGR (Fig. 1),

between August 24 - November 23, 2012. Twenty-three stations had a single camera at the station, while at three stations two cameras were deployed.

The majority of stations were located at a distance of between 0.5-3 km from one other, ensuring that multiple cameras were likely to be present in an individual's home range. This was the case for all but three stations, which were placed between 5 and 6 km from the nearest station. While there was therefore a small possibility that an individual's home range did not contain a station, SECR models allow for the presence of such 'holes' in the trap array when estimating density (Borchers & Efford, 2008), and low prey densities in the study area (Andresen & Everatt, *unpublished data*) suggest this is unlikely. Cameras were set on trees along roads and game trails at a height of 35cm. The survey length of 92 days was considered adequate for assuming demographic closure, consistently with numerous previous studies of large felids (*e.g.* Karanth, 1995; Alexander *et al.*, 2015; Boron *et al.*, 2016).

Density Estimation

Density was modelled in a SECR framework, using the package secr (Efford, 2015) running in R v3.2.3 (R Core Development Team, 2015). A maximum-likelihood framework was chosen over a Bayesian one as it provides results comparable with other studies (Tobler & Powell, 2013; Noss *et al.,* 2013) with quicker computation times (Efford, 2015).

Leopards were identified from their pelage patterns and sexed by visual inspection of external genitalia. The flank with the greater number of captures (left) was chosen for identification of individual leopards. Individual spatial capture and trap effort histories were developed following the recommended procedures (Efford, 2015), with each day (24 hours) treated as a separate sampling occasion, as recommended by recent findings (Goldberg *et al.,* 2015). Information on varying effort from different camera stations (exact number of days active) was included in order to improve estimates of detection probability. The buffer width around the trapping grid was increased until density estimates stabilised, ensuring that no individual outside of the buffer area could be captured, and a half-normal detection function was fitted to the distance between home range centre and station. This is the most commonly used function in spatial capture-recapture analyses (Efford, 2004; Boron *et al.,* 2016), and describes the probability of capture (P) of an individual *i* at a trap *j* as a function of distance (*d*) from the activity centre of the individual to the trap, as follows: $Pij = g0 \exp(-dij^2/(2\sigma^2))$, where g0 is the probability of capture at exactly the home rang centre, and sigma (σ) is a spatial parameter related to home range size (Efford, 2004). A Bernoulli or binomial encounter model was fitted to the data, as this is most relevant to camera trapping studies; under this model, an individual can be recorded at different camera stations during one sampling occasion, but only once at each station (Royle *et al.,* 2009; Noss *et al.,* 2013).

Given that leopard populations have been shown to have unequal ranging patterns between sexes (Bailey, 1993; Kittle *et al.,* 2017), in turn potentially impacting capture parameters, sex was modelled as a covariate (Sollmann *et al.,* 2011; Tobler & Powell, 2013; Goldberg *et al.,* 2015). This was achieved by fitting a hybrid mixture model, which accommodates for individuals of unknown sex (Efford, 2015). The impact of sex on both parameters g0 and σ was tested through the comparison of four alternative models using the Akaike Information Criterion, adjusted for small sample size (AICc; Burnham & Anderson, 2002): "secr.0" (null model), "secr.sex.g0" (g0 varies between males and females), "secr.sex.σ" (σ varies between males and females), and "secr.sex" (both g0 and σ vary between males and females) (Efford, 2015; Boron *et al.*, 2016).

RESULTS

Sampling effort & capture success

A total sampling effort of 1,021 trap nights by 26 stations (mean trap nights per camera = 39.3) yielded 57 leopard capture events. Of these, 31 (54%) were used to identify nine individual leopards (five males, two females, two unsexed); the remaining 26 events (46%) were not suitable for identification (due to picture quality and/or wrong flank) and therefore discarded. Capture frequencies were 9, 3, 2, 2, and 1 for the five males; 6 and 4 for the two females; and 3 and 1 for the two unsexed individuals.

Density estimation

The best SECR model (AICc=360.36) did not allow either g0 or σ to vary with sex (secr.0), with the model receiving significantly more support than the next best alternative (secr.sex.σ, ΔAICc=10.47; Table 1).

The leopard density estimate of the best fitted model (secr.0) was 2.60 ± SE 0.96 adults per 100 km^2. Capture probability at home range centre (g_0) was estimated at 0.043 ± SE 0.013, and the scale parameter, σ, at 1,936 ± 279 m (Table 2). Buffer width stabilised at 10,000m, as reported by similar leopard density studies (Gray & Prum, 2012; Borah *et al.,* 2013).

Table 1 Here

Table 2 Here

DISCUSSION

Leopard density

Our study provides a baseline leopard density estimate for a relatively well-protected area of the region, which is also the first empirical estimate for a leopard population in Mozambique. Using SECR models, we estimated leopard density in XGR at 2.60 ± 0.96 adults per 100 km^2. While density estimates obtained in XGR are on the lower end of the spectrum relative to studies elsewhere in sub-Saharan Africa, they are nonetheless higher than estimates from other protected areas of southern Africa, including the densities of 0.60 leopards per 100 km^2 in the dry savannahs of the Kalahari Gemsbok National park (South Africa; Bothma & Le Riche, 1984); of 0.62 per 100 km^2 in the savannah/woodland Cederberg Wilderness Area (South Africa; Martins

& Harris, 2013); and of 1.50/100 km^2 in the savannah habitat of the Kaudom Game Reserve, Namibia (Stander *et al.,* 1997).

In South Africa's KNP, contiguous with XGR's western border, high leopard densities of 30.3/100 km^2 were reported for the Sabie riverine area (Bailey, 1993), and of 12.7/100 km^2 in the N'wantesi concession (Maputla *et al.,* 2013). We believe the observed differences are most likely a reflection of contrasting habitats, and consequently prey availability, between study sites. While density estimates from KNP came from highly productive riverine forests (Bailey, 1993) and savannah woodlands (Maputla *et al.,* 2013), XGR is predominantly comprised of nutrient-poor, lower-productivity sandveld that is able to sustain lower animal densities (Redfern *et al.,* 2003; Scholes *et al.,* 2003). Furthermore, the relatively high level of protection enjoyed by the reserve (Andresen & Everatt, *unpublished data.*) indicate that artificially low prey densities due to human hunting are unlikely.

Nonetheless, we cannot exclude the possibility that XGR could be acting as a population sink for leopards dispersing from KNP, through anthropogenic mortalities occurring in the adjacent non-protected areas (NPAs). While no estimates for anthropogenic leopard mortalities in the area are available, it is possible that individuals venturing into the NPAs adjoining the reserve could be suffering relatively high anthropogenic mortality rates, which in turn could attract leopards from surrounding areas (*e.g.* KNP). This 'vacuum effect' has been documented in large carnivores and in leopards in particular, and it may cause edge effects that affect the interior of even very large protected areas (Loveridge *et al.,* 2007). Indeed, multiple incidents of poisoned leopards have been recorded in nearby Limpopo National Park (Andresen & Everatt, *unpublished data*). Longer term camera trapping or GPS collaring efforts, combined with social surveys targeting the communities outside the reserve, are necessary to ascertain whether this is the case.

Methodological considerations and sex specific parameters

The majority of our stations comprised only one camera-trap, rather than the two-camera set-up (one for each flank) recommended (Karanth, 1995). Our strategy was a result of limited resources, allowing us to survey a larger area and thus increase the number of captured individuals. While we believe that in our case this was the best strategy, the trade-offs between surveying a larger area and obtaining higher identification rates should be considered on a case-by-case basis.

Interestingly, even though males commonly occupy territories overlapping with those of two to four females (Bailey, 1993), more males (n=5) than females (n=2) were captured during our study (although the gender of n=2 individuals could not be determined). Maputla *et al.* (2013) also recorded a marked male-bias in capture rates, and cited several potential reasons for this, as identified by Krebs (1999); heterogeneity in behaviour between genders in the vicinity of the trap, and in tendencies to use trap locations (*e.g.* roads), were suggested as particularly probable causes.

The SECR model which received the most support in the ranking was the model where sex did not influence neither the detection (g0) nor scale (σ) parameters. However, rather than indicating the absence of widely described sex-dependent heterogeneity in behaviour and ranging patterns (e.g. Bailey, 1993; Kittle *et al.,* 2017), we believe that the relatively small sample size did not provide enough data to allow for the inference and modelling of sex-specific differences in detectability and ranging patterns.

Implications for conservation policy in Mozambique

Trophy hunting has been shown to have substantial potential to foster conservation of large carnivores (Lindsey *et al.,* 2007; Loveridge *et al.,* 2007), and it is estimated that each leopard hunted in Mozambique has the potential to contribute in the region of $ 24,000 to the local and national economy (Jorge *et al.,* 2013). However, if poorly managed or additive to other source of anthropogenic mortality, excessive harvesting of a species can reduce numbers to such an extent that a population is no longer viable in the long term. Demonstrating that hunting practices, including quotas, are biologically sustainable is therefore essential if trophy hunting is to be considered an effective tool in the management and conservation of large African carnivores ((Swanepoel *et al.,* 2014; Braczkowski *et al.,* 2015).

Our results lead us to question the reliability of the estimates being employed to set leopard quotas in Mozambique. The study by Martin & de Meulenaer (1988), quoted as the primary justification for a recent trophy export quota increase in Mozambique (from 60 to 120 individuals per annum; CITES, 2007), states that up to 80% of Mozambique supports leopard at between 3-10 individuals per 100 km^2. In addition, it also suggests that only 3% of the country's total land area should exhibit leopard population densities lower than those found by the present study. However, our estimated of 2.60 per 100 km^2 in XGR, one of the better protected areas in the country, suggests that it is unlikely that many areas in Mozambique exhibit the densities cited in the quota revision application. Although some landscapes will yield higher primary productivity levels than XGR, it seems plausible that the high levels of anthropogenic disturbances common in much of the country (Hatton *et al.,* 2001) would often more than counteract this. Thus, while we appreciate that trophy hunting has not taken place in our study area in almost 10 years (Andresen & Everatt, *unpublished data.*), and we acknowledge the limitations of our study in terms of size and number of individuals encountered relative to the overall range and total population, we believe that it is unlikely that leopard densities as high as those cited in the quota increase application are common in the majority of areas where hunting currently takes place.

As a result, we recommend further assessments of leopard population status and densities across different habitats and land-use types across the country, in both hunting and potential protected source areas. This would be an important first step towards the development of a sustainable and empirical leopard trophy hunting quota allocation system in Mozambique, similar to that being currently developed for neighbouring South Africa, which includes age-based hunting regulations, adaptive management strategies, and dynamic, evidence-based quota systems (Department of Environmental Affairs, 2017). Camera trapping surveys such as ours would be a relatively rapid method to obtain robust estimates of leopard numbers at moderate cost (Balme *et al.,* 2009), and, if followed by effective management interventions, would play an important role in the species' successful recovery and conservation in many recuperating post-conflict landscapes across the country.

Finally, we believe the identified conservation problems are not exclusive to Mozambique, with both Tanzania and Namibia employing the Martin & de Meulenaer (1988) density estimates for justification in previous leopard quota modifications approved by CITES (CITES 2002, 2004). Our results reinforce the need for caution when setting leopard quotas, and the importance of reliable population estimates across its range. We suggest similar research be carried out in other regions where such estimates are used to set leopard harvest quotas, in the hope of a continent-wide shift towards evidence-based processes being employed to guide management and policy.

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AUTHOR CONTRIBUTIONS

Data was collected by LA and KE; analyses were performed by PS; write-up was a collaboration between all authors.

REFERENCES

Alexander, J.S., Gopalaswamy, A.M., Shi, K. & Riordan, P. (2015) Face Value: Towards Robust Estimates of Snow Leopard Densities. *PLoS One*, 10(8): e0134815.

Bailey, T.N. (1993) *The African leopard: ecology and behavior of a solitary felid*. Columbia University Press, New York, USA.

Balme, G., Slotow, R. & Hunter, L.T.B. (2010) Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation*, 13(3), 315–323.

Balme, G., Hunter, L.T.B. & Slotow, R. (2009) Evaluating Methods for Counting Cryptic Carnivores. *Journal of Wildlife Management*, 73(3), 433–441.

Balme, G. a., Lindsey, P. a., Swanepoel, L.H. & Hunter, L.T.B. (2014) Failure of research to address the rangewide conservation needs of large carnivores: Leopards in South Africa as a case study. *Conservation Lett*ers 7 (1), 3–11.

Borah, J., Sharma, T., Das, D., Rabha, N., Kakati, N., Basumatary, A., Firoz Ahmed, M. & Vattakaven, J. (2014) Abundance and density estimates for common leopard Panthera pardus and clouded leopard Neofelis nebulosa in Manas National Park, Assam, India. *Oryx*, *48*(01), 149-155.

Borchers, D. & Efford, M. (2008) Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, 64, 377–385.

Boron, V., Tzanopoulos, J., Gallo, J., Barragan, J., Jaimes-Rodriguez, L., Schaller, G. and Payán, E. (2016) Jaguar densities across human-dominated landscapes in Colombia: the contribution of unprotected areas to long term conservation. *PloS one*, *11*(5), p.e0153973.

Bothma, J. du P. & Le Riche, E.A. (1984) Aspects of the ecology and the behaviour of the leopard Panthera pardus in the Kalahari desert. *Koedoe*, 27(2), pp.259–279.

Braczkowski, A.R., Balme, G.A., Dickman, A., Macdonald, D.W., Fattebert, J., Dickerson, T., Johnson, P. and Hunter, L., (2015) Who Bites the Bullet First? The Susceptibility of Leopards Panthera pardus to Trophy Hunting. *Plos One*, 10(4), p.e0123100.

Burnham, K.P., Anderson, D.R (2002) Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer, New York, USA.

Cavallo, J. (1993) *A study of leopard behaviour and ecology in the Seronera Valley, Serengeti National Park*. Serengeti Wildlife Research Centre Scientific Report 1990- 1992, 33-43.

Chase Grey, J. N., Kent, V.T., Hill, R.A. (2013). Evidence of a high density population of harvested leopards in a montane environment. – PLoS ONE 8: e82832.

CITES, 2007. *Leopard Export Quotas for Mozambique*. Unpublished report. Fourteenth meeting of the Conference of the Parties, The Hague, Netherlands.

Efford, M.G. (2004) Density estimation in live-trapping studies. *Oikos*, 106(3), 598–610.

Efford M.G. (2015) Spatially explicit capture-recapture models. R package version 2.9.5. https://cran.r-project.org/package=secr.

Gardner, B., Royle, J.A. & Wegan, M.T. (2009). Hierarchical models for estimating density from DNA mark-recapture studies. Ecology 90, 1106–1115.

Goldberg, J. F., Tempa, T., Norbu, N., Hebblewhite, M., Mills, L. S., Wangchuk, T. R., & Lukacs, P. (2015). Examining Temporal Sample Scale and Model Choice with Spatial Capture-Recapture Models in the Common Leopard Panthera pardus. *PloS One*, 10 (11).

Gray, T.N.E. & Prum, S. (2012) Leopard density in post-conflict landscape, Cambodia: Evidence from spatially explicit capture-recapture. *Journal of Wildlife Management* , 76(1), 163–169.

Hanks, J. (2000) Southern Africa in the conservation of mammalian biodiversity. In *Priorities for the conservation of mammalian diversity: has the panda had its day?* (eds A. Entistle, N. Dunstone), pp 239. Cambridge University Press, Cambridge, UK.

Hatton, J., Couto, M. & Oglethorpe, J. (2001) *Biodiversity and war: a case study of Mozambique*. Unpublished report. Biodiversity Support Program, Washington D.C., USA

Henschel, P., Hunter, L.T.B., Coad, L., Abernethy, K.A. &Muhlenberg, M. (2011) Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. *Journal of Zoology*, 285(1), pp.11–20.

Jackson, P. (1989) A review by leopard specialists of the status of leopard in sub-Saharan Africa by Martin and de Meulenaer. Submitted to the seventh meeting of the CoP to CITES. Lausanne, Switzerland.

Jacobson, A.P., Gerngross, P., Lemeris Jr, J.R., Schoonover, R.F., Anco, C., Breitenmoser-Würsten, C., Durant, S.M., Farhadinia, M.S., Henschel, P., Kamler, J.F. and Laguardia, A. (2016). Leopard (Panthera pardus) status, distribution, and the research efforts across its range. *PeerJ*, *4*, p.e1974

Jorge, A.A., Vanak, A.T., Thaker, M., Begg, C. and Slotow, R. (2013) Costs and benefits of the presence of leopards to the sport□hunting industry and local communities in Niassa National Reserve, Mozambique. *Conservation Biology*, *27*(4), pp.832-843.

Karanth, K.U., (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71(3), 333–338.

Kittle, A.M., Watson, A.C. and Fernando, T.S.P. (2017) The ecology and behaviour of a protected area Sri Lankan leopard (Panthera pardus kotiya) population. *Tropical Ecology*, 58(1), pp.71-86.

Krebs, C.J. (1999) *Ecological Methodology*. 2nd edn. Addison Wesley Longman, Boston, USA.

Lindsey, P.A., Roulet, P.A., Romanach, S.S. (2007) Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological conservation*, 134(4), 455–469.

Loveridge, A.J., Searle, A.W., Murindagomo, G., Macdonald, D.W. (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, 134 (4), 548–558.

Maputla, N.W., Chimimba, C.T. & Ferreira, S.M. (2013) Calibrating a camera trap-biased mark-recture sampling design to survey the leopard population in the N'wanetsi concession, Kruger National Park, South Africa. *African Journal of Ecology*, 51(3), 422–430.

Martin, R.B. & De Meulenaer, T. (1988). *Survey of the status of the leopard (Panthera pardus) in Sub-Saharan Africa.* Report submitted to the Secretariat of the Convention on International Trade Endangered Species of Wild Fauna and Flora. Lausanne, Switzerland.

Martins, Q. and Harris, S. (2013) Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *African Journal of Ecology*, *51*(4), pp.571-579.

Nowell, K. & Jackson, P. (1996) *Wild cats: status survey and conservation action plan*. Burlington Press, Cambridge, UK.

Noss, A., Polisar, J., Maffei,. L, García, R., Silver,S. (2013) Evaluating jaguar densities with camera traps. WCS, New York, USA.

R Core Development Team (2014) R: A Language and Environment for Statistical Computing. Available: http://www. r-project.org.

Redfern, J. et al., 2003. Surface-water constraints on herbivore fogaring in the Kruger National Park, South Africa. *Ecology*, 84(8).

Royle JA, Nichols JD, Karanth KU (2009) A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology* ,46. 118–127.

Scholes, R.J., Bond, W.J. & Eckhardt, H.C. (2003) *Vegetation dynamics in the Kruger ecosystem*. The Kruger Experience. Island Press, Washington, D.C., USA.

Sollmann, R., Furtado, M., Gardner, B., Hofer, H., Jacomo, A., Torres, N. Silveira, L. (2011) Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture-recapture models for jaguars in central Brazil. *Biological Conservation,* 144. 1017–1024.

Stander, P.E., Haden, P.J., Kaqece, G. (1997) The ecology of asociality in Namibian leopards. *Journal of Zoology*, 242, 343-364.

Stein, A., Andreas, A., Aschernborn, O. (2011) *Namibian National Leopard Survey 2011, Final Report.* Unpublished report. Namibian Ministry of Environment and Tourism, Windhoek, Namibia.

Swanepoel, L., Lindsey, P., Somers, M.J., Van Hoven, W., Dalerum, F., (2014) The relative importance of trophy harvest and retaliatory killing of large carnivores: South African leopards as a case study. *South African Journal of Wildlife Research-subscription access*, *44*(2), 115-34.

Swanepoel, L., Somers, M., Dalerm, F. (2015) Density of leopards Panthera pardus on protected and non-protected land in the Waterberg Biosphere, South Africa. *Wildlife Biology,* 21 (5), 263-268.

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.

TABLES

Table 1

Table 1 Model selection parameters for Spatially Explicit Capture Recapture (SECR) models in R package 'secr'

Model	AICc	∆AICc	AIC wt	K	Dev.
g0 (.) sigma (.)	360.364	0.000	1	4	324.364
g0 (.) sigma (sex)	370.835	10.471	0	5	322.663
g0 (sex) sigma (.)	371.280	10.916	0	5	323.281
g0 (sex) sigma (sex)	394.663	34.299	0	6	322.835

AICc = Akaike Information Criterion, adjusted for small sample size; ∆AICc = difference in AICc values between each model and best ranking (lowest AIC) model; AICc wt = AICc model weights; K = number of model parameters; Dev. = Model deviances. g0 = probability of capture at home range centre; σ = spatial parameter related to home range size. secr.0: null model; secr.sex.g0: g0 varies between males and females; secr.sex: both g0 and σ vary between males and females; secr.sex.σ: σ varies between males and females.

Table 2

Table 2 Density and parameters estimated by the best Spatially Explicit Capture Recapture (SECR) model (secr.0)

	Value	SE	95% LCI	95% UCI
g0	0.043	0.013	0.024	0.078
Σ (m)	1963	279	1464	2562
D (N/100km^2)	**2.599**	**0.957**	**1.292**	**5.231**

SE = Standard error; LCI and UCI = lower and upper confidence intervals respectively; D = Density. g0 = probability of capture at the home range centre; σ = spatial parameter related to home range size

FIGURES

Figure 1

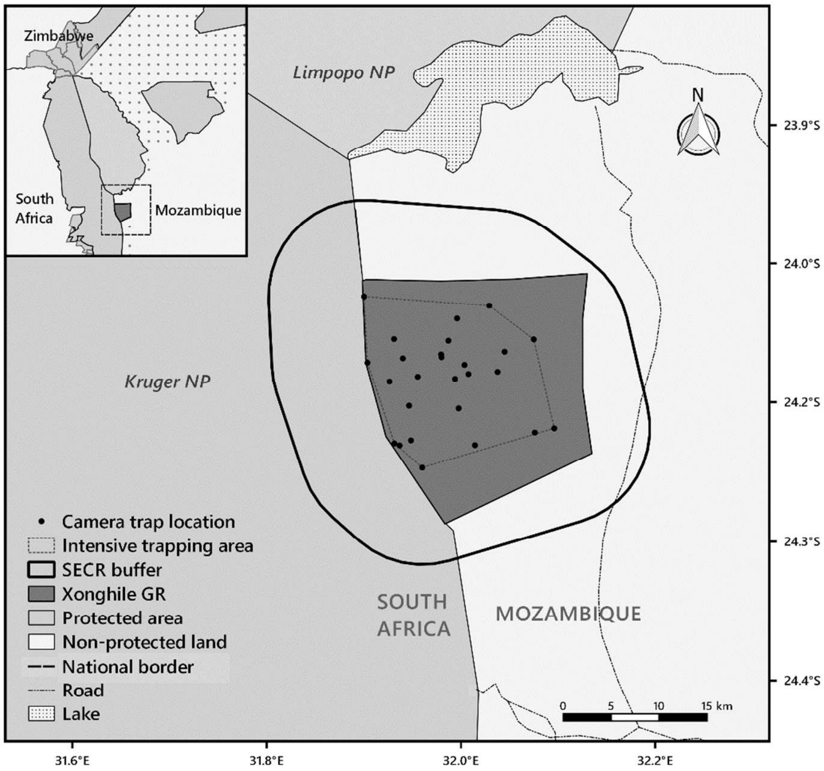

Figure 1 Legend

Fig.1 Xonghile Game Reserve (XGR), including camera locations and intensive trapping area within a 10 km buffer zone, as required by the SECR models. Inset map: XGR in the context of the wider GLTFCA, comprising both protected areas (grey) and non-protected lands (dotted).