The importance of refugia, ecological traps and scale for large carnivore management

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Abstract Management zones feature prominently in conservation planning, particularly at large spatial scales, but prioritization of areas of concern is required to focus efforts and limited resources. Human-mediated mortality constitutes a major threat to species persistence, particularly for widespread carnivores that undergo harvest and population control, such as the leopard (*Panthera pardus*). In this study, we evaluated the extent and spatial distribution of legal anthropogenic offtake of leopards to identify de facto refugia and ecological traps across Limpopo Province, South Africa. We defined refugia as management units with offtake levels below an established sustainable harvest rate, and ecological traps as management units with offtake exceeding the sustainable harvest rate. We assessed offtake at three geographical scales using trophy hunting permit records alone, and then in combination with problem leopard permit records to investigate the compounding effect of additional forms of offtake and the potential for management scale mismatching. Across Limpopo Province, high leopard offtake created fewer areas of refuge than ecological traps. Refugia were smaller in size and within close proximity of ecological traps. Human-mediated leopard mortality occurred mostly in prime leopard habitat. Finer-scaled management units resulted in fewer ecological traps and more refugia, and enables authorities to focus conservation attention in areas of concern. Human-mediated leopard mortality exceeded the annual offtake rate considered sustainable. Our study highlights the importance of assessing both the scale and distribution of the harvest, whilst also considering alternative forms of offtake, when devising harvest management strategies. Management scale mismatching and high human-mediated leopard mortality is of particular concern in Limpopo Province, as such, we propose an adaptive, science-based regulatory framework aimed at improving leopard harvest strategies.

Keywords Leopard · *Panthera pardus* · Human-carnivore conflict · Harvest rates · Trophy hunting · Problem animal

Introduction

Large-scale management decisions are seldom supported by science-based evidence (Sutherland et al. 2004). Given the rapid decline of global biodiversity (Sala et al. 2000), conservation planning requires a systematic and adaptive approach where the implementation of scientifically informed management zones feature prominently (Margules and Pressey 2000; Westgate et al. 2013). Understanding the spatio-temporal dynamics that underpin the distribution of animal populations within and across management zones, and how these are influenced by ecological and anthropogenic factors, is key to effective conservation planning (Delsink et al. 2013; Hansen 2011). Habitat quality is one factor affecting how animals interact with their environment (Pearson et al. 2011), and is a commonly explored theme in ecological studies (Battin 2004; Turner et al. 2001). High-quality habitats generally yield fitness benefits through increased opportunities for survival and reproduction, whereas low-quality habitats carry fitness costs due to increased mortality or reduced reproduction (Delibes et al. 2001; Franklin et al. 2000). This conceptual framework forms the basis of source–sink theory (Pulliam 1988) and is considered a mechanistic foundation for landscape ecology (Wiens et al. 1993). Subsequent refinement of the source–sink model has enabled the inclusion of two essential concepts. First, habitats that exhibit relatively high survival due to the low risk of human-mediated mortality (Naves et al. 2003), but low reproduction due to suboptimal habitat, are considered 'refugia' (Stoner et al. 2013). In contrast, 'ecological traps' are characterized by high-quality habitat that exhibits reduced survival (Sanchez-Mercado et al. 2014; Schlaepfer et al. 2002), often due to human activity such as over-hunting or excessive retaliatory killing (Delibes et al. 2001; Hansen 2011; Naves et al. 2003). These scenarios can lead to maladaptive habitat selection by animals, which may threaten their long-term persistence (Battin 2004; Gilroy and Sutherland 2007; Schlaepfer et al. 2002).

Identifying refugia and ecological traps is critical to enable conservation practitioners to focus resources in areas of concern (Naves et al. 2003; Stoner et al. 2013). Although a number of empirical studies have demonstrated the existence of such areas (e.g., Woodward et al. 2001; Weldon and Haddad 2005; van der Meer et al. 2014), few have done so at the spatial scales required to inform management (Robertson and Hutto 2006). Scale mismatching (i.e., where the implementation of conservation research and actions do not reflect the scale of the conservation problem) occurs frequently in natural resource management, resulting in inefficiencies, a loss of system components, and failure to achieve management objectives (Cumming et al. 2006; Guerrero et al. 2013). Many of the problems arising in conservation are a consequence of the mismatch between the scale of the management intervention and the scale of the ecological processes being managed (Delsink et al. 2013).

The leopard (*Panthera pardus)* typifies the challenges faced in conservation. Leopards are the most widely distributed felid, occurring across much of sub-Saharan African, the Middle East and tropical Asia (Hunter et al. 2013). This extensive distribution, together with their wide-ranging movements, dictate that management of leopards occurs at large spatial scales. Despite their ubiquity, leopards are habitat selective (Balme et al. 2007; Pitman et al. 2013), which may lead to maladaptive behaviour in human affected landscapes. Like most large carnivores, leopards are frequently implicated in conflict centered around livestock and game depredation (Kissui 2008; Thorn et al. 2013), often leading to retaliatory killing of putative problem individuals (Hunter et al. 2013; Thorn et al. 2013). Leopards are also legally trophy hunted in many parts of Africa (Balme et al. 2010a). Most range states lack science-based guidelines on how to effectively manage leopard hunting and problem animal control, particularly at the scales relevant to leopard conservation and that take into consideration the suitability of leopard habitat (Balme et al. 2014).

We use an approach previously applied to cougar (*Puma concolor*) (Stoner et al. 2013) to identify de facto refugia and ecological traps among leopard populations at multiple scales in Limpopo Province, South Africa. We use historical trophy hunting and problem leopard permit records to assess the relationship between human-mediated leopard

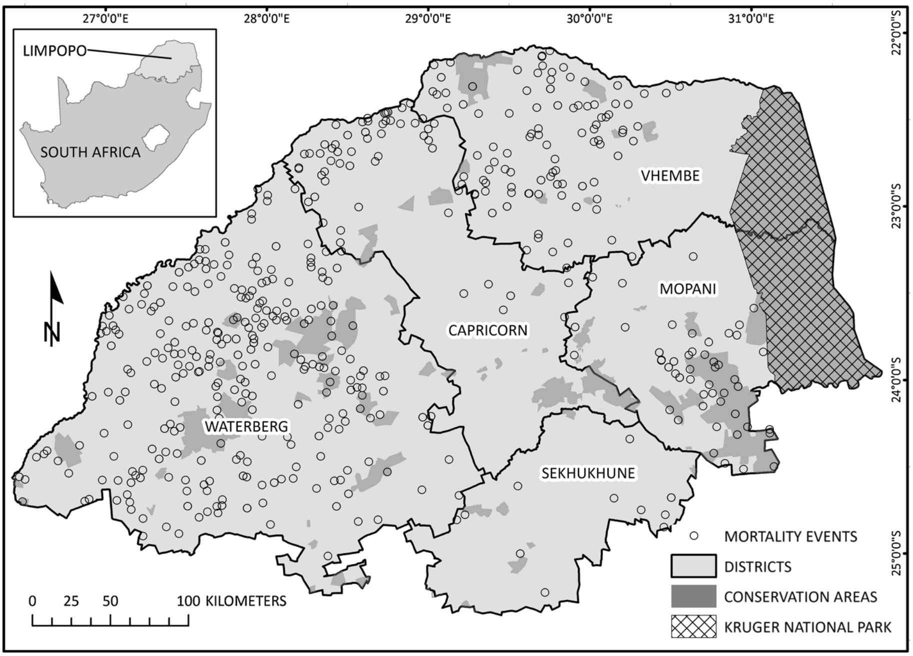

Fig. 1 Distribution of leopard (*Panthera pardus*) mortality events ($N = 757$) from January 2007 to December 2012 across Limpopo Province, South Africa. The Kruger National Park (cross-hatched) was removed from all analyses; *dark-grey* areas represent the remaining conservation areas

mortality and habitat quality. Due to past ad-hoc regulation, we predict that the highest levels of offtake will be focused in the most suitable leopard habitat, likely leading to a predominance of ecological traps which may threaten the persistence of the wider provincial leopard population. We assess these relationships at three geographical scales using trophy hunting permits records alone, and then in combination with problem leopard permit records to (1) investigate the compounding effect of additional forms of offtake on leopard harvesting, and (2) to investigate the potential for management scale mismatching. Finally, we propose an adaptive, science-based regulatory framework aimed at improving leopard management practices in Limpopo, but which has broader applicability for the management of other large carnivores exposed to trophy hunting or population control.

Materials and methods

Study area

Limpopo (ca. 125,977 km^2; Fig. 1) represents the most suitable, contiguous leopard habitat across South Africa (Swanepoel et al. 2013), and is likely the most important province in South Africa for leopard conservation (Daly et al. 2005). To legally hunt a leopard, a person must be in possession of a trophy hunting permit issued by the Limpopo Department of Economic Development, Environment and Tourism (LEDET). The LEDET also award problem leopard permits, which are required by landowners for the removal of putative problem individuals. Limpopo award the most trophy hunting and problem leopard permits of any province in South Africa (Daly et al. 2005; Lindsey et al. 2011).

Sampling units and leopard offtake rates

Variation in leopard offtake rates were evaluated at three scales: (1) from a provincial district scale ($N = 5$) representing the current administrative unit used by the LEDET to manage leopard, (2) from a municipal scale ($N = 25$) which offers a finer and more intuitive administrative unit for management (Statistics South Africa 2011), and (3) from a quaternary catchment scale ($N = 194$) on the premise that catchment zones provide a more ecologically meaningful management unit than municipalities or districts (South African Department of Agriculture, Forestry and Fisheries 2013). We excluded the Kruger National Park (Limpopo region = 9879 km^2) from all analyses since it is neither administered by the LEDET, nor open to leopard hunting or retaliatory killing (Fig. 1). All other 'conservation areas' were included in our analyses because many of these areas are open to leopard hunting or retaliatory killing and their small size (range: 1–1922 km^2) renders them vulnerable to edge effects (Balme et al. 2010b).

Data were compiled from trophy hunting ($N = 354$) and problem leopard ($N = 403$) permit records issued by the LEDET between January 2007 and December 2012 ($N = 757$; Fig. 1). In Limpopo, trophy hunted leopard are usually targeted using camera-traps at baited sites; whilst problem leopard are destroyed in an ad hoc fashion using gin traps, cages, poison or lured to baited sites where they are shot (LEDET, unpublished data). Leopard offtake rates were defined as the average number of leopard killed per year per 100 km^2 at all three scales. Unsuccessful hunts were removed from all analyses ($N = 76$). Mortality events were accurate to the property-level (Cadastral Spatial Information, Pre-toria). Illegal hunting of leopard in Limpopo likely eclipses legal hunting (St John et al.

2012), but given the challenges in accurately monitoring these activities they could not be included in our analyses.

Habitat quality, de facto refugia and ecological traps

A map of leopard habitat suitability derived from maximum entropy-based (MaxEnt) habitat models was used as a predictor of habitat quality and potential leopard density (Swanepoel et al. 2013). Approximately 63 % of Limpopo is considered suitable leopard habitat, which was grouped into four classes following Swanepoel et al. (2013): low quality (habitat suitability index = 0–0.22), medium quality (0.23–0.50), high quality (0.60–0.75), and very high quality (>0.75). Leopard densities were derived from Swanepoel et al.(2014) such that low-, medium-, high- and very high-quality habitat were assigned population densities of 0.56 ± 0.02, 1.97 ± 0.12, 3.29 ± 0.14, and 3.81 ± 0.09 leopard per 100 km^2, respectively. These densities agreed with previous estimates for regional leopard population sizes in Limpopo (Daly et al. 2005; Norton 1990). Since sampling units often comprised >1 habitat class, leopard densities were multiplied by the area of each habitat class in each sampling unit to obtain an estimated leopard population size per sampling unit. Caro et al. (2009) used age-sex structured density independent models to determine maximum sustainable harvest for leopard; removal of ≤3.6 % of the estimated population is considered sustainable for populations where both male and female leopard are hunted (Caro et al. 2009). Given that information on local context sustainability is not known, we set Limpopo's annual sustainable offtake to 3.6 %, and used this value to categorically distinguish refugia (annual offtake rates ≤3.6 %) from ecological traps (annual offtake rates >3.6 %) following Stoner et al. (2013).

Statistical analysis

Friedman tests were used to evaluate the distribution of leopard trophy hunts and problem leopard offtake at the district-scale from 2007 to 2012. A generalized linear model (GLM) based on a zero-inflated probability distribution was used to examine the effect of habitat quality on leopard offtake rates at all scales. A two-factor analysis of variance (ANOVA) with replication was used to assess the size of refugia and ecological traps at all scales. A single-factor ANOVA was used to assess the distances between 'spatially aggregated' refugia (i.e., refugia that only abut other refugia) and their closest ecological trap. The sizes of refugia and ecological traps, and Euclidean distances between refugia and ecological traps, were square-root transformed to meet assumptions of normality. All statistical analyses were conducted in R v.3.0.2 (R Core Team 2014). Spatial analyses were conducted in ArcGIS v.10.1 (ESRI, Redlands, USA). Unless otherwise stated, we present means with 95 % confidence intervals (CI) as a measure of precision.

Results

Leopard offtake rates

On average, 67 ± 2 leopard were trophy hunted each year in Limpopo, and 59 ± 3 were legally killed as putative problem animals. Problem leopard offtake differed significantly (FRIEDMAN: $\chi^2_6 = 14.3$, $P = 0.03$; Fig. 2a) among districts from 2007 to 2012, whereas

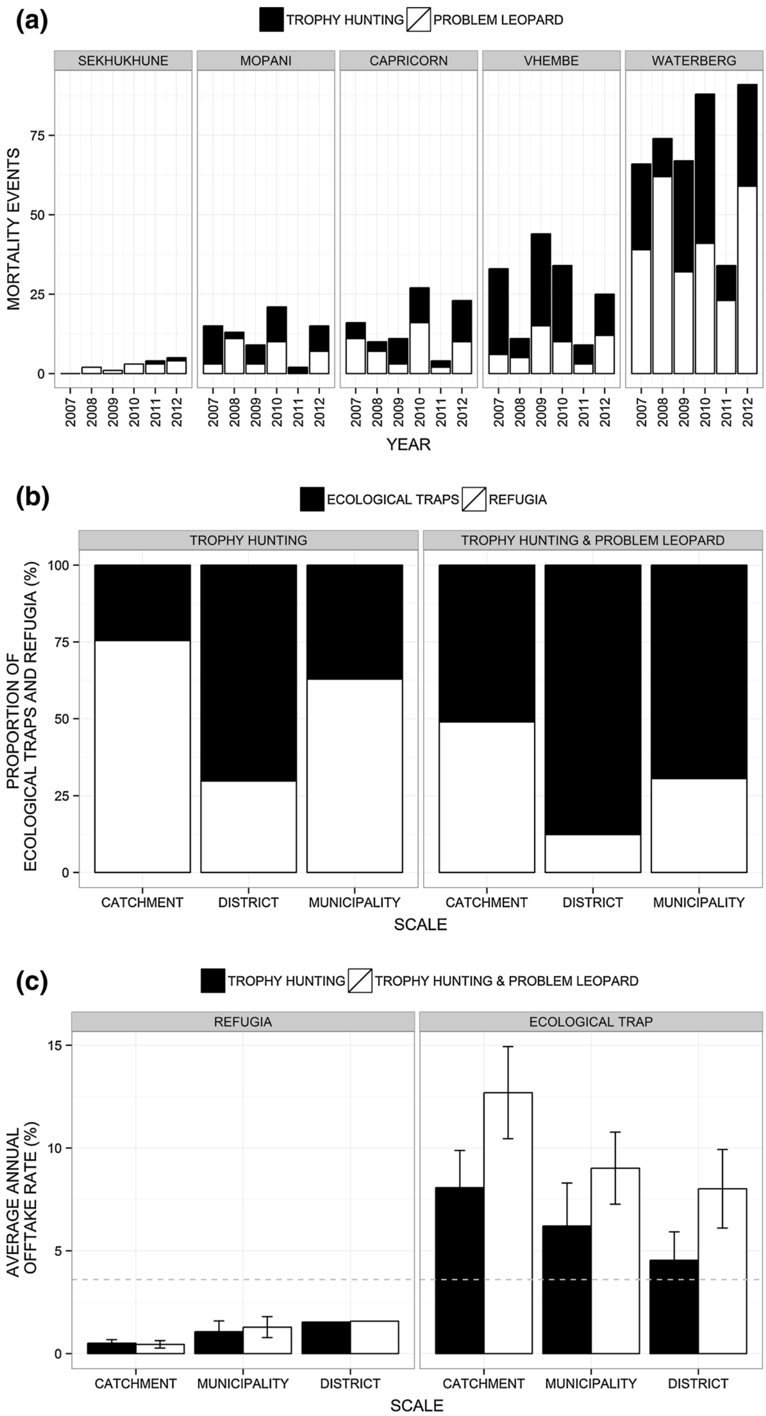

Fig. 2 Leopard (Panthera pardus) mortality events from trophy hunting and problem leopard permits distributed temporally across the five current management districts of Limpopo Province, South Africa from 2007 to 2012 (a); proportion of de facto refugia and ecological traps at three geographical scales under two offtake scenarios for Limpopo Province, South Africa from 2007 to 2012 (b); and average annual leopard offtake rates (95 % CI) at three geographical scales (dashed line depicts the 3.6 % sustainable offtake rate) under two offtake scenarios for Limpopo Province, South Africa from 2007 to 2012 (c)

trophy hunting offtake approached significance (FRIEDMAN: $\chi^2_6 = 12.1$, $P = 0.06$; Fig. 2a). The Waterberg district accounted for the vast majority (55 %) of leopard mor-tality events, followed by Vhembe (21 %), Capricorn (12 %), Mopani (10 %), and Sekhukhune (2 %). Across all districts, total leopard offtake was greatest in 2010 ($N = 173$) and 2012 ($N = 159$). Problem leopard offtake was greatest in 2008 ($N = 87$) and 2012 ($N = 92$), while trophy hunting offtake peaked in 2009 ($N = 78$), 2010 ($N = 93$) and 2012 ($N = 67$).

Habitat quality and mortality risk

According to the MaxEnt habitat model, Limpopo comprised 36 % low-quality habitat, 45 % medium-quality habitat, 15 % high-quality habitat, 1 % very high-quality habitat, and 3 % undefined habitat (due to missing data; Swanepoel et al. 2013). Leopard offtake rates were significantly affected by habitat quality at the catchment-scale (zero-inflated GLM: trophy hunting scenario: $z = -3.60$, $P < 0.001$; trophy hunting and problem leopard scenario: $z = -3.98$, $P < 0.001$) and municipal-scale (zero-inflated GLM: trophy hunting scenario: $z = -4.17$, $P < 0.001$; trophy hunting and problem leopard scenario: $z = -3.78$, $P < 0.001$), but not at the district-scale (zero-inflated GLM: trophy hunting scenario: $z = -0.01$, $P > 0.5$; trophy hunting and problem leopard scenario: $z = -0.01$, $P > 0.5$).

De facto refugia and ecological traps

When determining refugia and ecological traps using trophy hunting permits alone, the total area of refugia at a catchment (74,556 km^2, $N = 145$) and a municipal (70,847 km^2, $N = 19$) scale exceeded that of ecological traps (catchment = 41,519 km^2, $N = 48$; mu-nicipality = 45,210 km^2, $N = 6$) by 44 and 36 %, respectively (Online Resource 1; Fig. 2b). In contrast, the total area of ecological traps (80,773 km^2, $N = 3$) at the district-scale exceeded refugia (35,282 km^2, $N = 2$) by 56 % (Online Resource 1; Fig. 2b). Refugia (catchment = 514 km^2; municipality = 3729 km^2, district = 17,641 km^2) were significantly smaller than ecological traps (catchment = 865 km^2; mu-nicipality = 7535 km^2, district = 26,924 km^2; ANOVA: $F_{2,217} = 5.96$, $P = 0.003$) at all scales. Mean annual offtake rates within ecological traps were 94 % (catchment-scale), 83 % (municipal-scale) and 66 % (district-scale) greater than in refugia (Fig. 2c). A total of 73 (50 %), 12 (63 %), and 2 (100 %) refugia abutted an ecological trap from a catchment-, municipal- and district-scale, respectively (Fig. 3a–c). The distances between the remaining 'spatially aggregated' refugia and their closest ecological trap were sig-nificantly different (ANOVA: $F_{1,77} = 6.79$, $P < 0.05$) at the catchment- (21 ± 0.82 km) and municipal-scale (41 ± 3.36 km; Fig. 3a–c). A district-scale approach to management would misclassify (i.e., classify an area as a refuge when it should be classified as an ecological trap; and vice versa) 5531 km^2 of refugia and 44,797 km^2 of ecological traps when measured against the catchment-scale; similarly, a municipal-scale approach to management would misclassify 12,606 km^2 of refugia and 16,306 km^2

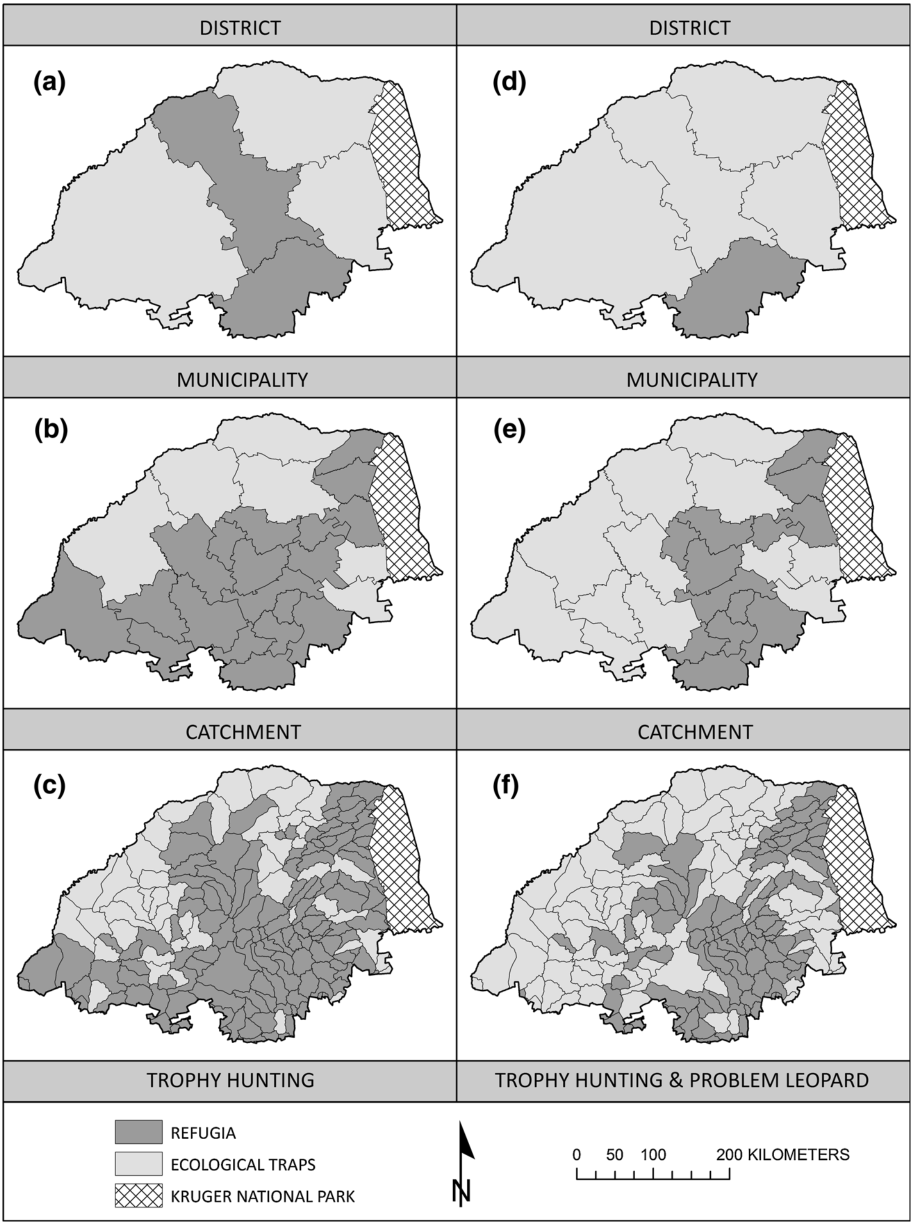

Fig. 3 Distribution of de facto refugia and ecological traps under two offtake scenarios (trophy hunting **a**–**c** and trophy hunting and problem leopard **d**–**f**) at the catchment- (**c** and **f**), municipal- (**b** and **e**), and district-scale (**a** and **d**) across Limpopo Province, South Africa

of ecological traps when measured against the catchment-scale. Using trophy hunting permits alone, offtake within ecological traps exceeded what is considered sustainable (Caro et al. 2009) by up to 19.07 % (offtake range per annum: 3.63–22.67 %), 7.32 % (offtake range per annum:

3.71–10.92 %), and 2.32 % (offtake range per annum: 3.63–5.92 %) from a catchment-, municipal-, and district-scale, respectively (Online Resource 1).

When determining refugia and ecological traps using a combination of trophy hunting and problem leopard permits, the total area of ecological traps (catchment = 71,212 km^2, N = 84; municipality = 79,588 km^2, N = 12; district = 102,504 km^2, N = 4; Online Resource 1) exceeded that of refugia (catchment = 44,863 km^2, N = 109; mu-nicipality = 36,469 km^2, N = 13; district = 13,551 km^2, N = 1; Online Resource 1) from a catchment-, municipal- and district-scale by 37, 54 and 87 %, respectively (Fig. 2b). Refugia (catchment = 412 km^2; municipality = 2805 km^2, dis-trict = 13,551 km^2) were significantly smaller than ecological traps (catch-ment = 848 km^2; municipality = 6632 km^2, district = 25,626 km^2; ANOVA: $F_{2,217} = 10.07$, $P < 0.001$) at all scales. Mean annual offtake rates within ecological traps were 96 % (catchment-scale), 86 % (municipal-scale) and 80 % (district-scale) greater than in refugia (Fig. 2c). A total of 68 (62 %), 10 (77 %), and 1 (100 %) refugia abutted an ecological trap from a catchment-, municipal- and district-scale, respectively (Fig. 3d–f). There was no significant difference (ANOVA: $F_{1,42} = 0.01$, P = 0.9) in the distances between the remaining ‘spatially aggregated’ refugia and their closest ecological trap at the catchment- (14 ± 0.76 km) and municipal-scale (12 ± 2.27 km; Fig. 3d–f). A district-scale approach to management would misclassify 2539 km^2 of refugia and 33,847 km^2 of ecological traps when measured against the catchment-scale; similarly, a municipal-scale approach to management would misclassify 8325 km^2 of refugia and 16,713 km^2 of ecological traps when measured against the catchment-scale. Using trophy hunting and problem leopard permits, offtake within ecological traps exceeded what is considered sustainable (Caro et al. 2009) by up to 61.87 % (offtake range per annum: 3.63–65.47 %), 10.82 % (offtake range per annum: 4.51–14.42 %), and 6.80 % (offtake range per annum: 6.22–10.40 %) from a catchment-, municipal-, and district-scale, respectively (Online Resource 1).

Discussion

In many developing countries, conservation authorities lack the human and financial re-sources to accurately and consistently monitor wildlife populations (Rodrıguez et al. 2005), particularly cryptic species such as leopard that range widely, and occur mainly outside of formally protected areas (Swanepoel et al. 2013). As a result, carnivore management is rarely underpinned by strong science (Ray et al. 2005). Here, we demonstrate a rigorous approach for identifying de facto refugia and ecological traps among leopard populations at multiple scales, which can be readily incorporated in a management framework without requiring detailed knowledge of local animal numbers or movements. Such an approach enables authorities to quantitatively evaluate the impact of human-mediated mortality and implement management interventions by using data that are easily and cheaply sourced. A similar model was previously proposed to manage cougar harvest in North America (Stoner et al. 2013), and it appears equally suitable for regulating the hunting of leopard in Limpopo. In Limpopo, human-mediated leopard mortality was greatest in prime leopard habitat. Leopard are capable of distinguishing and selecting high-quality habitats (Balme et al. 2007; Pitman et al. 2013), a trait which is likely maladaptive in Limpopo due to the fitness costs associated with such habitat (Delibes et al. 2001). African wild dogs (*Lycoan pictus*) in Hwange National Park, Zimbabwe, similarly selected high-quality habitat within the buffer zone of the protected area, thereby increasing their risk of human-induced mortality (van der Meer et al. 2014). Localized population densities may be maintained in ecological traps by immigration from adjacent suboptimal habitat (Gilroy and Sutherland 2007), even as the broader metapopulation declines (Battin 2004). For example, closed population models predicted a precipitous decline of a heavily hunted cougar population within prime cougar habitat, whilst the population actually remained stable due to increased immigration from nearby refugia (Robinson et al. 2008). Such compensatory immigration may erro-neously suggest wider population stability or even growth, often leading to increased public pressure to maintain or raise harvest levels (Cooley et al. 2009). These scenarios are difficult to detect in situ and may ultimately cause the local extirpation of animal populations (Cooley 2008; Robinson et al. 2008).

Compensatory immigration is partly dependent on the distribution of refugia in relation to ecological traps. The majority of Limpopo's refugia abut an ecological trap, which puts supposedly safe leopard populations in close proximity to elevated sources of human-mediated mortality. The negative consequences of this were demonstrated in KwaZulu-Natal Province, South Africa, where leopard within a protected area experienced higher levels of human-mediated mortality the closer they ventured to the reserve boundary (Balme et al. 2010b). Although 'spatially aggregated' refugia have a reduced risk of mortality (Sanchez-Mercado et al. 2014), in Limpopo, these areas are still within dispersal distance (catchment: 14–21 km; municipality: 12–41 km) of ecological traps for leopard (Fattebert et al. 2013). Fattebert (2014) demonstrated that dispersing subadult leopard favour suitable habitat. Given that habitat selection by leopard in Limpopo is likely maladaptive, further concern is raised regarding the success of dispersal from, and within, refugia and ecological traps. Increased connectivity is typically beneficial for population persistence (Rabinowitz and Zeller 2010), but it may be detrimental in the context of managing the wider impacts of ecological traps. These negative consequences are further exacerbated when we consider that refugia across Limpopo are significantly smaller, with lower habitat suitability, lower leopard densities, and greater human population densities, than ecological traps. Although this may suggest that refugia offer little conservation value, research on cougar suggest that, in the event of widespread human-mediated mortality, refugia are likely to harbor carnivore populations and may therefore have greater conservation value than previously assumed (Stoner et al. 2013).

The relative size and distribution of refugia to ecological traps suggest that leopard management practices in Limpopo may not be sustainable when based on a maximum sustainable offtake rate of $\leq$3.6 % (Caro et al. 2009; see Stoner et al. 2013). Historically, the LEDET has not quantified and included problem leopard offtake when administering trophy hunting permits. Similar to research on gray wolf (Creel and Rotella 2010), our study emphasizes the importance of considering the compounding effects of other forms of human-mediated mortality when evaluating the impact of harvesting. Limpopo currently issues three-times more problem leopard permits per year than any other province in South Africa (Lindsey et al. 2011). Problem leopard complaints are almost exclusively attributed to livestock and game depredation (LEDET unpublished data). To appropriately deal with the issue of problem animal control, conservation authorities require official guidelines on how to manage problem animals (see Balme et al. 2009). Furthermore, landowners can be encouraged to implement a variety of traditional and modern non-lethal techniques to reduce the risk of stock depredation (Marker et al. 2005; Ogada et al. 2003; Stahl et al. 2002). By our estimates, Limpopo's current offtake is well beyond what Caro et al. (2009) would indicate is sustainable. However, a better understanding of population demographics within the local context is needed in order to define sustainable offtake in Limpopo. This will require more detailed population information, as well as demographic modelling for defining sustainability under the local context—similar to research on elephant (*Loxodonta africana*) subject to hunting and problem animal control in north-western Limpopo (Selier et al. 2014). Illegal offtake of carnivores in South Africa's Northern provinces are greater than levels of legal offtake (St John et al. 2012; Thorn et al. 2013) indicating that our results are conservative since we could not account for illegal killing of leopard. Conservation authorities should either attempt to include some estimate of annual illegal offtake (perhaps through innovative questionnaire-based methods; see St John et al. 2012), or apply conservative annual quotas since mortality rates are likely underestimated.

Scaling issues are beginning to feature prominently in conservation planning, for instance, Delsink et al. (2013) demonstrated how current management zones for African elephant in Kruger National Park are not biologically relevant or appropriate for elephant management. In Limpopo, leopard trophy hunting is currently managed at the district-scale; however, this level of management is too coarse and unable to detect the maladaptive relationship between leopard mortality and habitat quality. A district-scale approach to management consistently misclassifies large areas of refugia and ecological traps, regardless of whether problem leopard control is taken into account. Allocating leopard trophy hunting permits across a finer-scaled management unit will (1) facilitate a more evenly distributed harvest, (2) allow conservation authorities to pinpoint potential areas of over-utilization, (3) benefit landowners that have previously not had an opportunity to host a leopard hunt, and (4) preserve or restore the integrity of leopard population structure by the creation of fewer ecological traps. Even though a municipal-scale approach to management would misclassify a smaller area of refugia and ecological traps when compared to the district-scale, a catchment-scale approach to management remains the most precise at identifying areas of potentially unsustainable offtake.

Our study highlights the importance of identifying de facto refugia and ecological traps, management scale mismatching, and the worrying relationship between disproportionately high human-mediated leopard mortality in prime habitat when devising leopard management policies. To counter these challenges, we recommend an adaptive, science-based approach to leopard management; specifically: (1) shift leopard management to a smaller scale, (2) account for problem leopard offtake in the determination of annual hunting quotas, (3) undertake a local context specific modelling exercise on an annual basis to better define the level of sustainable offtake, and (4) use this sustainable offtake rate to identify and reduce the number of ecological traps. These recommendations fall within the capacity South African conservation authorities and potentially more widely. A similar management approach that accounts for refugia and ecological traps could readily be applied to other wide-ranging species that undergo harvest or population control.

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Supplementary material

	Management Zone	Problem Leopard Control[A]	Trophy Hunting[A]	Area (km^2)	Human Population Density (km^2)[B]	Habitat Quality	Trophy Hunting			Trophy Hunting & Problem Leopard Control		
							Category	Offtake Rate Per Annum (%)	Leopards[C]	Category	Offtake Rate Per Annum (%)	Leopards[C]
Catchments	A24E	2	0	195	20	Low	Refuge	0.00	0.0	Ecological Trap	29.13	-0.35
	A61G	1	0	928	98	Low	Refuge	0.00	0.4	Refuge	1.73	0.22
	B31J	1	1	1 352	40	Low	Refuge	1.28	0.4	Refuge	2.56	0.16
	B41B	0	0	95	19	Low	Refuge	0.00	0.0	Refuge	0.00	0.02
	A23C	0	0	403	10	Low	Refuge	0.00	0.2	Refuge	0.00	0.16
	A71B	0	0	884	191	Low	Refuge	0.00	0.2	Refuge	0.00	0.19
	B41C	0	0	285	18	Low	Refuge	0.00	0.1	Refuge	0.00	0.11
	B81H	0	0	670	68	Low	Refuge	0.00	0.1	Refuge	0.00	0.14
	A23G	0	0	767	63	Low	Refuge	0.00	0.3	Refuge	0.00	0.28
	A71E	0	1	894	92	Low	Refuge	3.09	0.0	Refuge	3.09	0.03
	A71A	0	0	1 146	199	Low	Refuge	0.00	0.3	Refuge	0.00	0.34
	B51E	9	1	2 930	22	Low	Refuge	0.66	0.9	Ecological Trap	6.56	-0.90

A72A	2	1	1 910	48	Low	Refuge	0.84	0.7	Refuge	2.53	0.25
B51C	1	0	639	61	Low	Refuge	0.00	0.2	Ecological Trap	4.30	-0.03
B31E	1	1	974	10	Low	Refuge	3.08	0.0	Ecological Trap	6.15	-0.17
A24D	0	0	86	15	Low	Refuge	0.00	0.0	Refuge	0.00	0.02
B31F	0	0	33	65	Low	Refuge	0.00	0.0	Refuge	0.00	0.00
B32E	0	0	195	8	Low	Refuge	0.00	0.1	Refuge	0.00	0.07
B51A	0	0	312	147	Low	Refuge	0.00	0.1	Refuge	0.00	0.06
B52C	0	0	201	23	Low	Refuge	0.00	0.1	Refuge	0.00	0.05
B52D	0	0	342	176	Low	Refuge	0.00	0.1	Refuge	0.00	0.08
B52F	0	0	119	72	Low	Refuge	0.00	0.1	Refuge	0.00	0.07
B72G	0	0	48	50	Low	Refuge	0.00	0.0	Refuge	0.00	0.03
B90C	0	0	246	121	Low	Refuge	0.00	0.1	Refuge	0.00	0.05
A62E	0	0	621	75	Low	Refuge	0.00	0.1	Refuge	0.00	0.14
A91G	0	0	407	271	Low	Refuge	0.00	0.2	Refuge	0.00	0.17
A92A	0	0	330	145	Low	Refuge	0.00	0.1	Refuge	0.00	0.14
A92C	0	0	456	54	Low	Refuge	0.00	0.1	Refuge	0.00	0.13
B31H	0	0	402	103	Low	Refuge	0.00	0.1	Refuge	0.00	0.11
B32J	0	0	323	174	Low	Refuge	0.00	0.1	Refuge	0.00	0.14
B51G	0	0	592	111	Low	Refuge	0.00	0.2	Refuge	0.00	0.17
B51H	0	0	719	168	Low	Refuge	0.00	0.2	Refuge	0.00	0.15
B52B	0	0	634	134	Low	Refuge	0.00	0.2	Refuge	0.00	0.18
B81G	0	0	514	198	Low	Refuge	0.00	0.1	Refuge	0.00	0.13
B82H	0	0	746	91	Low	Refuge	0.00	0.2	Refuge	0.00	0.18
B90B	0	0	358	109	Low	Refuge	0.00	0.1	Refuge	0.00	0.11
B90F	0	0	425	102	Low	Refuge	0.00	0.1	Refuge	0.00	0.10
A62F	0	0	620	51	Low	Refuge	0.00	0.3	Refuge	0.00	0.29
A62H	0	0	872	52	Low	Refuge	0.00	0.2	Refuge	0.00	0.23
A91F	0	0	582	213	Low	Refuge	0.00	0.2	Refuge	0.00	0.20
B52H	0	0	564	127	Low	Refuge	0.00	0.2	Refuge	0.00	0.20
B71E	0	0	784	122	Low	Refuge	0.00	0.3	Refuge	0.00	0.29
A71F	1	1	684	86	Low	Refuge	3.51	0.0	Ecological Trap	7.03	-0.20
B51B	1	0	592	77	Low	Refuge	0.00	0.3	Refuge	2.87	0.05

A91E	0	0	224	566	Low	Refuge	0.00	0.1	Refuge	0.00	0.08
B90G	0	0	15	9	Low	Refuge	0.00	0.0	Refuge	0.00	0.00
B52A	0	0	567	76	Low	Refuge	0.00	0.1	Refuge	0.00	0.13
B32G	0	0	100	306	Low	Refuge	0.00	0.0	Refuge	0.00	0.02
B82F	0	1	762	176	Low	Refuge	3.22	0.0	Refuge	3.22	0.02
B82D	2	2	633	134	Low	Ecological Trap	8.08	-0.2	Ecological Trap	16.16	-0.62
B60F	1	1	159	11	Low	Ecological Trap	11.42	-0.1	Ecological Trap	22.85	-0.34
A41D	17	5	1 911	1	Low	Ecological Trap	6.25	-0.4	Ecological Trap	27.49	-3.82
A63E	1	17	1 990	3	Low	Ecological Trap	17.24	-2.7	Ecological Trap	18.26	-2.89
B81A	0	1	169	26	Low	Ecological Trap	16.16	-0.2	Ecological Trap	16.16	-0.16
B82G	0	1	923	112	Low	Ecological Trap	3.63	0.0	Ecological Trap	3.63	0.00
A71C	0	3	1 333	59	Low	Ecological Trap	4.15	-0.1	Ecological Trap	4.15	-0.08
A24J	21	6	2 417	3	Medium	Refuge	2.95	0.3	Ecological Trap	13.30	-3.94
A80E	6	0	248	54	Medium	Refuge	0.00	0.2	Ecological Trap	18.55	-0.97
A61F	6	1	790	128	Medium	Refuge	1.89	0.2	Ecological Trap	13.26	-1.02
B72H	4	1	387	19	Medium	Refuge	2.17	0.1	Ecological Trap	10.85	-0.67
B81J	4	0	569	28	Medium	Refuge	0.00	0.3	Ecological Trap	8.52	-0.46
A42D	2	1	497	2	Medium	Refuge	1.61	0.2	Ecological Trap	4.83	-0.15
B60J	2	1	617	11	Medium	Refuge	1.52	0.3	Ecological Trap	4.57	-0.13
A61A	1	0	382	81	Medium	Refuge	0.00	0.3	Refuge	2.53	0.08
B82E	1	1	424	47	Medium	Refuge	3.15	0.0	Ecological Trap	6.29	-0.17
B83A	1	0	227	37	Medium	Refuge	0.00	0.2	Refuge	3.41	0.01
A62J	1	3	930	18	Medium	Refuge	3.23	0.1	Ecological Trap	4.30	-0.13
B32B	0	0	12	8	Medium	Refuge	0.00	0.0	Refuge	0.00	0.01
B41F	0	0	96	9	Medium	Refuge	0.00	0.1	Refuge	0.00	0.06
A80A	0	0	288	153	Medium	Refuge	0.00	0.2	Refuge	0.00	0.19

B72E	0	0	321	109	Medium	Refuge	0.00	0.2	Refuge	0.00	0.19
A62C	0	0	385	32	Medium	Refuge	0.00	0.2	Refuge	0.00	0.23
A91B	0	0	275	46	Medium	Refuge	0.00	0.2	Refuge	0.00	0.22
B41H	0	0	400	104	Medium	Refuge	0.00	0.2	Refuge	0.00	0.21
B52G	0	0	291	73	Medium	Refuge	0.00	0.2	Refuge	0.00	0.21
B71A	0	0	298	17	Medium	Refuge	0.00	0.2	Refuge	0.00	0.23
B71B	0	0	275	37	Medium	Refuge	0.00	0.2	Refuge	0.00	0.23
B71H	0	0	331	48	Medium	Refuge	0.00	0.2	Refuge	0.00	0.22
A92B	0	0	567	77	Medium	Refuge	0.00	0.3	Refuge	0.00	0.32
B72A	0	1	536	97	Medium	Refuge	2.18	0.1	Refuge	2.18	0.13
B81D	0	0	480	267	Medium	Refuge	0.00	0.3	Refuge	0.00	0.30
A24H	14	4	1 338	24	Medium	Refuge	2.84	0.2	Ecological Trap	12.80	-2.59
A23H	8	0	805	6	Medium	Refuge	0.00	0.4	Ecological Trap	13.14	-1.16
A80D	7	0	128	7	Medium	Refuge	0.00	0.1	Ecological Trap	53.84	-1.31
A32E	7	6	2 374	1	Medium	Refuge	2.84	0.3	Ecological Trap	6.15	-1.08
B72K	5	3	970	114	Medium	Refuge	3.03	0.1	Ecological Trap	8.08	-0.89
A63B	5	2	1 506	18	Medium	Refuge	1.61	0.5	Ecological Trap	5.64	-0.51
B82B	4	0	407	31	Medium	Refuge	0.00	0.3	Ecological Trap	10.38	-0.52
B60G	4	0	372	12	Medium	Refuge	0.00	0.3	Ecological Trap	9.57	-0.50
A71G	4	2	876	32	Medium	Refuge	2.83	0.1	Ecological Trap	8.50	-0.69
B81F	3	0	1 204	73	Medium	Refuge	0.00	0.6	Ecological Trap	3.69	-0.01
A42E	3	0	1 008	11	Medium	Refuge	0.00	0.8	Refuge	2.70	0.20
A72B	3	5	1 557	6	Medium	Refuge	2.76	0.3	Ecological Trap	4.41	-0.29
B32F	2	0	668	42	Medium	Refuge	0.00	0.3	Ecological Trap	4.87	-0.10
A24B	2	0	564	8	Medium	Refuge	0.00	0.3	Ecological Trap	4.31	-0.07
A24F	2	1	591	34	Medium	Refuge	2.34	0.1	Ecological Trap	7.01	-0.29
A61C	2	0	587	13	Medium	Refuge	0.00	0.3	Ecological Trap	4.21	-0.06
A42B	2	2	522	3	Medium	Refuge	3.18	0.1	Ecological Trap	6.35	-0.35
A62B	2	0	711	39	Medium	Refuge	0.00	0.5	Refuge	2.87	0.10
A80J	2	1	869	22	Medium	Refuge	1.25	0.4	Ecological Trap	3.75	-0.02
B73A	1	0	37	9	Medium	Refuge	0.00	0.0	Ecological Trap	65.47	-0.19
A61D	1	1	456	31	Medium	Refuge	2.93	0.0	Ecological Trap	5.86	-0.15

A62G	1	1	627	28	Medium	Refuge	1.88	0.2	Ecological Trap	3.76	-0.02
B42H	1	0	392	18	Medium	Refuge	0.00	0.3	Refuge	2.27	0.12
B41J	1	0	688	126	Medium	Refuge	0.00	0.5	Refuge	1.48	0.29
A63A	1	4	1 929	11	Medium	Refuge	2.07	0.6	Refuge	2.59	0.39
A91D	0	0	133	173	Medium	Refuge	0.00	0.1	Refuge	0.00	0.08
B42G	0	0	45	9	Medium	Refuge	0.00	0.0	Refuge	0.00	0.03
B73C	0	0	32	75	Medium	Refuge	0.00	0.0	Refuge	0.00	0.02
B81C	0	0	209	194	Medium	Refuge	0.00	0.1	Refuge	0.00	0.10
B90A	0	0	30	137	Medium	Refuge	0.00	0.0	Refuge	0.00	0.03
A80H	0	0	266	40	Medium	Refuge	0.00	0.1	Refuge	0.00	0.13
A91C	0	0	250	137	Medium	Refuge	0.00	0.2	Refuge	0.00	0.15
B31D	0	0	168	8	Medium	Refuge	0.00	0.1	Refuge	0.00	0.12
B41E	0	0	238	66	Medium	Refuge	0.00	0.1	Refuge	0.00	0.13
B41G	0	0	238	9	Medium	Refuge	0.00	0.2	Refuge	0.00	0.18
B51F	0	0	395	10	Medium	Refuge	0.00	0.2	Refuge	0.00	0.19
B52E	0	0	452	87	Medium	Refuge	0.00	0.2	Refuge	0.00	0.19
B82C	0	0	300	85	Medium	Refuge	0.00	0.2	Refuge	0.00	0.19
B72B	0	1	333	11	Medium	Refuge	2.59	0.1	Refuge	2.59	0.08
B81B	0	0	482	32	Medium	Refuge	0.00	0.3	Refuge	0.00	0.27
A41B	0	1	357	1	Medium	Refuge	2.22	0.1	Refuge	2.22	0.12
A92D	0	0	781	21	Medium	Refuge	0.00	0.3	Refuge	0.00	0.33
B32D	0	0	522	20	Medium	Refuge	0.00	0.4	Refuge	0.00	0.37
B52J	0	0	396	61	Medium	Refuge	0.00	0.3	Refuge	0.00	0.31
B41K	0	0	637	92	Medium	Refuge	0.00	0.4	Refuge	0.00	0.44
B82A	1	0	468	73	Medium	Refuge	0.00	0.3	Refuge	2.08	0.15
B31C	0	0	116	8	Medium	Refuge	0.00	0.1	Refuge	0.00	0.10
B71J	0	0	79	34	Medium	Refuge	0.00	0.1	Refuge	0.00	0.06
B32C	0	0	192	8	Medium	Refuge	0.00	0.1	Refuge	0.00	0.12
B82J	0	0	247	23	Medium	Refuge	0.00	0.1	Refuge	0.00	0.12
A91H	0	0	429	134	Medium	Refuge	0.00	0.3	Refuge	0.00	0.27
B60H	0	0	307	41	Medium	Refuge	0.00	0.2	Refuge	0.00	NA
A61E	0	0	548	9	Medium	Refuge	0.00	0.3	Refuge	0.00	0.31

B32H	0	0	599	70	Medium	Refuge	0.00	0.3	Refuge	0.00	0.32
A61H	0	1	586	5	Medium	Refuge	1.61	0.2	Refuge	1.61	0.25
A63D	6	7	1 320	11	Medium	Ecological Trap	6.38	-0.6	Ecological Trap	11.85	-1.81
A50A	4	2	298	6	Medium	Ecological Trap	5.64	-0.1	Ecological Trap	16.93	-0.94
A24C	3	4	765	15	Medium	Ecological Trap	7.84	-0.4	Ecological Trap	13.72	-1.03
A71J	3	12	1 164	7	Medium	Ecological Trap	8.45	-1.4	Ecological Trap	10.57	-1.98
A61B	2	3	363	24	Medium	Ecological Trap	9.60	-0.4	Ecological Trap	15.99	-0.77
B81E	2	2	667	116	Medium	Ecological Trap	4.08	0.0	Ecological Trap	8.16	-0.45
A42C	2	5	699	8	Medium	Ecological Trap	7.95	-0.5	Ecological Trap	11.13	-0.95
A50G	2	9	821	25	Medium	Ecological Trap	13.88	-1.3	Ecological Trap	16.97	-1.73
B72J	2	10	539	13	Medium	Ecological Trap	16.17	-1.6	Ecological Trap	19.40	-1.95
A41A	2	4	692	2	Medium	Ecological Trap	4.87	-0.2	Ecological Trap	7.31	-0.61
B73B	1	2	316	6	Medium	Ecological Trap	5.90	-0.2	Ecological Trap	8.86	-0.36
A80C	0	2	294	68	Medium	Ecological Trap	5.59	-0.1	Ecological Trap	5.59	-0.14
A63C	21	20	1 318	2	Medium	Ecological Trap	22.67	-3.4	Ecological Trap	46.47	-7.56
A41E	17	9	1 927	4	Medium	Ecological Trap	7.54	-0.9	Ecological Trap	21.80	-4.34
A42J	13	9	1 811	16	Medium	Ecological Trap	4.99	-0.5	Ecological Trap	12.19	-3.10
A50J	12	4	1 254	4	Medium	Ecological Trap	3.74	0.0	Ecological Trap	14.97	-2.43
A71L	11	14	1 762	2	Medium	Ecological	14.44	-2.1	Ecological Trap	25.78	-4.30

						Trap					
A62A	10	2	428	20	Medium	Ecological Trap	4.42	-0.1	Ecological Trap	26.54	-2.07
A41C	10	8	1 111	1	Medium	Ecological Trap	6.68	-0.7	Ecological Trap	15.02	-2.74
A50E	9	6	629	3	Medium	Ecological Trap	7.50	-0.6	Ecological Trap	18.76	-2.42
A50H	9	5	1 943	15	Medium	Ecological Trap	4.06	-0.1	Ecological Trap	11.37	-1.91
A91A	3	1	233	47	Medium	Ecological Trap	4.42	0.0	Ecological Trap	17.66	-0.64
A80F	3	4	631	9	Medium	Ecological Trap	5.27	-0.3	Ecological Trap	9.23	-0.85
A61J	3	4	818	17	Medium	Ecological Trap	4.62	-0.2	Ecological Trap	8.09	-0.78
A71K	3	8	1 672	20	Medium	Ecological Trap	4.18	-0.2	Ecological Trap	5.75	-0.82
A71D	2	3	893	11	Medium	Ecological Trap	3.99	-0.1	Ecological Trap	6.65	-0.46
B72D	2	12	856	8	Medium	Ecological Trap	11.01	-1.6	Ecological Trap	12.84	-2.02
A80G	2	21	1 230	8	Medium	Ecological Trap	15.71	-3.2	Ecological Trap	17.20	-3.64
B72C	1	5	336	23	Medium	Ecological Trap	16.34	-0.8	Ecological Trap	19.61	-0.98
A62D	1	4	603	15	Medium	Ecological Trap	6.36	-0.3	Ecological Trap	7.95	-0.55
B73E	0	1	107	6	Medium	Ecological Trap	9.93	-0.1	Ecological Trap	9.93	-0.13
A80B	0	1	252	195	Medium	Ecological Trap	4.16	0.0	Ecological Trap	4.16	-0.03
B41D	0	1	404	42	Medium	Ecological Trap	3.66	0.0	Ecological Trap	3.66	0.00
A71H	0	8	1 014	70	Medium	Ecological Trap	8.34	-0.9	Ecological Trap	8.34	-0.91

A42A	1	4	574	9	Medium	Ecological Trap	6.89	-0.4	Ecological Trap	8.61	-0.58
A91J	0	0	162	38	High	Refuge	0.00	0.2	Refuge	0.00	0.17
B71D	0	0	228	24	High	Refuge	0.00	0.2	Refuge	0.00	0.23
A24G	8	2	735	5	High	Refuge	2.06	0.3	Ecological Trap	10.31	-1.30
A32D	1	0	199	1	High	Refuge	0.00	0.2	Ecological Trap	3.74	-0.01
A50B	1	1	407	4	High	Refuge	1.54	0.3	Refuge	3.09	0.07
B71F	1	0	542	40	High	Refuge	0.00	0.6	Refuge	1.14	0.43
B42E	0	0	42	9	High	Refuge	0.00	0.0	Refuge	0.00	0.03
B71C	0	0	263	8	High	Refuge	0.00	0.2	Refuge	0.00	0.24
B71G	0	0	246	40	High	Refuge	0.00	0.3	Refuge	0.00	0.25
B72F	0	0	81	8	High	Refuge	0.00	0.1	Refuge	0.00	0.10
A42H	12	14	1 057	8	High	Ecological Trap	9.86	-1.8	Ecological Trap	18.32	-4.18
A50D	3	7	638	2	High	Ecological Trap	7.38	-0.7	Ecological Trap	10.54	-1.32
A50C	0	3	362	2	High	Ecological Trap	4.88	-0.2	Ecological Trap	4.88	-0.16
A42G	19	13	1 206	6	High	Ecological Trap	7.01	-1.3	Ecological Trap	17.25	-5.06
A50F	5	5	372	2	High	Ecological Trap	10.02	-0.6	Ecological Trap	20.05	-1.64
A42F	14	6	1 022	1	High	Ecological Trap	4.12	-0.2	Ecological Trap	13.74	-2.95
B73D	0	0	14	6	Very High	Refuge	0.00	0.0	Refuge	0.00	0.01
A23B	0	0	6	8	Very High	Refuge	0.00	0.0	Refuge	0.00	0.00
A23L	0	0	2	7	Very High	Refuge	0.00	0.0	Refuge	0.00	0.00
A24A	0	0	14	7	Very High	Refuge	0.00	0.0	Refuge	0.00	0.00
B32A	0	0	1	8	Very High	Refuge	0.00	0.0	Refuge	0.00	0.00

	A23F	0	0	3	8	Very High	Refuge	0.00	0.0	Refuge	0.00	0.00
	A32B	0	0	0	1	Very High	NA	NA	NA	NA	NA	NA
Municipality	Greater Giyani	1	1	2994	79	Low	Refuge	0.90	0.60	Refuge	1.80	0.40
	Greater Letaba	3	0	1896	112	Low	Refuge	0.00	0.83	Refuge	2.61	0.23
	Thulamela	0	0	2910	197	Low	Refuge	0.00	1.15	Refuge	0.00	1.15
	Aganang	0	1	1883	71	Low	Refuge	1.57	0.26	Refuge	1.57	0.26
	Molemole	1	4	3353	33	Low	Refuge	2.23	0.49	Refuge	2.79	0.29
	Polokwane	1	0	3772	165	Low	Refuge	0.00	1.17	Refuge	0.61	0.97
	Ephraim Mogale	2	0	2014	67	Low	Refuge	0.00	0.79	Refuge	1.82	0.39
	Makhuduthamaga	1	0	2101	132	Low	Refuge	0.00	0.53	Refuge	1.36	0.33
	Fetakgomo	0	0	1107	85	Low	Refuge	0.00	0.48	Refuge	0.00	0.48
	Mutale	0	0	2640	46	Medium	Refuge	0.00	1.28	Refuge	0.00	1.28
	Lepele Nkumpi	2	1	3470	69	Medium	Refuge	0.34	1.94	Refuge	1.01	1.54
	Elias Motsoaledi	2	1	3716	67	Medium	Refuge	0.41	1.57	Refuge	1.22	1.17
	Greater Tubatse	8	1	4613	70	Medium	Refuge	0.22	3.06	Refuge	1.99	1.46
	Greater Tzaneen	6	5	3252	120	Medium	Refuge	2.05	0.76	Ecological Trap	4.51	-0.44
	Thabazimbi	72	28	11176	8	Medium	Refuge	3.16	0.78	Ecological Trap	11.28	-13.62
	Mookgopong	16	11	5694	7	Medium	Refuge	2.62	0.83	Ecological Trap	6.42	-2.37
	Modimolle	15	16	4680	15	Medium	Refuge	3.08	0.54	Ecological Trap	5.96	-2.46
	Bela Bela	14	4	3405	20	Medium	Refuge	1.84	0.77	Ecological Trap	8.26	-2.03
	Mogalakwena	25	10	6171	46	Medium	Refuge	1.84	1.91	Ecological Trap	6.44	-3.09
	Phalaborwa	17	12	3019	47	Medium	Ecological Trap	3.71	-0.07	Ecological Trap	8.97	-3.47
	Maruleng	7	23	3256	29	Medium	Ecological Trap	6.84	-2.18	Ecological Trap	8.92	-3.58
	Musina	19	69	7585	7	Medium	Ecological Trap	10.92	-9.25	Ecological Trap	13.93	-13.05
	Makhado	32	36	8317	62	Medium	Ecological Trap	4.47	-1.40	Ecological Trap	8.44	-7.80
	Blouberg	45	36	9253	18	Medium	Ecological Trap	4.74	-1.73	Ecological Trap	10.66	-10.73

	Lephalale	114	95	13780	8	Medium	Ecological Trap	6.56	-8.57	Ecological Trap	14.42	-31.37
	Sekhukhune	13	2	13551	80	Medium	Refuge	0.21	6.43	Refuge	1.58	3.83
	Capricorn	49	42	21731	58	Medium	Refuge	2.87	2.13	Ecological Trap	6.22	-7.67
District	Mopani	34	41	14417	75	Medium	Ecological Trap	3.63	-0.07	Ecological Trap	6.64	-6.87
	Vhembe	51	105	21451	59	Medium	Ecological Trap	5.92	-8.23	Ecological Trap	8.80	-18.43
	Waterberg	256	164	44905	15	Medium	Ecological Trap	4.06	-3.73	Ecological Trap	10.40	-54.93

A number of mortality events attributed to that particular source of offtake

B human census data were obtained from Statistics South Africa (2011) and defined as the number of people per km^2

C the difference required in the number of leopards killed per annum to meet the 3.6% sustainability threshold

7