

**The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk**

Andrew J. Loveridge<sup>1,\*</sup>, Marion Valeix <sup>1,2,\*</sup>, Nicholas B. Elliot<sup>1</sup>, David W. Macdonald<sup>1</sup>

1. Wildlife Conservation Research Unit, Recanati-Kaplan Centre, Department of Zoology, Oxford University.
2. Laboratoire de Biométrie et Biologie Evolutive, CNRS UMR 5558, Université Claude Bernard Lyon, Villeurbanne, France.

\* authors contributed equally to this work.

Running title: Lions in a landscape of anthropogenic mortality risk

## Summary

1. Demography and conservation status of many wild organisms are increasingly shaped by interactions with humans. This is particularly the case for large, wide ranging carnivores.
2. Using 206 mortality records (1999–2012) of lions in Hwange National Park, Zimbabwe, we calculated mortality rates for each source of anthropogenic mortality, modelled risk of anthropogenic mortality across the landscape accounting for time lions spent in different parts of the landscape, and assessed whether subsets of the population were more at risk.
3. Anthropogenic activities caused 88% of male and 67% of female mortalities; male mortality being dominated by trophy hunting while the sources for female mortality were more varied (snaring, retaliatory killing, hunting).
4. Landscapes of anthropogenic mortality risk revealed that communal subsistence farming areas, characterized by high risk (due to retaliatory killing) but avoided by lions, are population sinks. Trophy hunting areas and areas within protected areas bordering communal farmland, where bush-meat snaring is prevalent, form ‘ecological traps’ (or ‘attractive sinks’).
5. Lions avoided risky areas, suggesting they may make behavioural decisions based on perceptions of risk. Experienced adults used risky areas less and incorporated lower proportions of them in their home ranges than young individuals, suggesting that the latter may either be naïve or forced into peripheral habitats.
6. *Synthesis and applications.* This paper contributes to an understanding of how large carnivore populations are affected by anthropogenic mortality across the conservation landscape. This is critical to designing focussed, appropriate and cost-effective conservation management strategies. Agricultural areas are intuitively identified by conservationists as being risky for carnivores due to retaliatory or pre-emptive killing, with threats largely mitigated against by improving livestock protection. However, parts of protected areas may

also form less easily identified ‘attractive sinks’ for carnivores. In particular, trophy hunting areas adjacent to national parks needs careful management to avoid damaging effects of overhunting. Law enforcement is needed to reduce the effects of bush-meat poaching on predators and other wildlife in protected areas. To be most effective, resource-limited anti-poaching activities should prioritise wildlife rich areas close to human settlement as these tend to be hotspots for bush-meat poaching.

**Key-words:** anthropogenic mortality, African lion, Hwange National Park, ecological traps, *Panthera leo*, attractive sinks, bushmeat snaring, trophy hunting, protected areas, retaliatory killing

## Introduction

Worldwide, human populations are increasing at the edges of protected areas (Wittemyer *et al.* 2008). The associated loss in natural habitat and intensification of human activities and human-wildlife interactions increase the isolation of protected areas and ultimately threaten the wildlife populations living inside them (Woodroffe & Ginsberg 1998). In human populated areas at the edge of protected areas, different sources of wildlife mortality exist; ranging from the legal hunting of animals (Packer *et al.* 2011) to illegal killing (Liberg *et al.* 2012), human-wildlife conflict-related mortality (Treves & Karanth 2003) and vehicle collision (Kramer-Schadt *et al.* 2004). Wide ranging species that roam outside protected areas, as is typical of large predators, are particularly vulnerable to these different sources of anthropogenic mortality.

Predators are often symbolic of the wild ecosystems they inhabit and have immense cultural importance and significant economic value to both consumptive and photographic tourism (Loveridge *et al.* 2010b). Furthermore, there is growing evidence that an intact guild of predators is essential to maintenance of healthy ecosystem functions and the loss of large predators results in profoundly negative effects (Estes *et al.* 2011). Nevertheless, predator populations are particularly extinction prone and are declining worldwide (Ripple *et al.* 2014). Many African lion (*Panthera leo*) populations are declining and geographic range has declined by 75% in the last 500 years (Riggio *et al.* 2013). Anthropogenic edge effects have been shown to be particularly detrimental to lion populations, impacting population density, population structure as well as elevating adult mortality and causing declines in juvenile and dispersing sub-adult survival (Loveridge *et al.* 2010a; Elliot *et al.* 2014b). Projected human population increases of 400% in sub-Saharan Africa over the next Century (United Nations 2015) suggest that lions and other large African species will become increasingly space

81 limited as available habitat becomes converted to agriculture. Simultaneously, it is likely that  
82 detrimental interactions with people will become more frequent and inevitably result in the  
83 demise of many large predator populations across the continent. Understanding the way in  
84 which large predator populations are affected by anthropogenic mortality in the landscapes  
85 they inhabit, particularly on the periphery of protected areas, is critical to designing  
86 conservation management strategies for these species in an African savannah environment  
87 that is far from secure.

88  
89 In the same way that locations of live animals provide information about the process of  
90 habitat selection, mortality events provide spatially-explicit information about the riskiness of  
91 habitats, i.e. where animals die (Nielsen *et al.* 2004; Roever, vanAarde & Chase 2013). This  
92 information is important in identifying population sinks in source-sink systems and ecological  
93 traps where habitat selection of animals is maladaptive, i.e. individuals select areas that  
94 ultimately reduce their fitness (Kristan 2003; Battin 2004). In this paper, we model the  
95 landscape of anthropogenic mortality risk for African lions based on mortality records  
96 collected over thirteen years in and around Hwange National Park, Zimbabwe, and examine  
97 the way in which GPS radio-collared lions utilise this landscape. Our expectation is that  
98 anthropogenic mortality risk and its sources vary across the landscape depending on human  
99 influences, leading to ‘hotspots’ of mortality that will affect different age and sex classes of  
100 lions in different ways. It is likely that animals in different age and sex classes respond in  
101 different ways to these varying risks, either through an acquired perception of risk (in the case  
102 of experienced adult individuals) or through behavioural necessity (in the case of displaced or  
103 young dispersing individuals).

## Materials and methods

### STUDY AREA AND ENVIRONMENTAL DATA

This study was undertaken in the northern section of Hwange National Park (HNP), Zimbabwe (19°00'S, 26°30'E), (Supporting Information 1; Fig. S1). The study area comprised different land use types including protected areas (National Parks in Zimbabwe and Game Reserves in Botswana), trophy hunting areas, communal lands set aside for agro-pastoralism (seasonal crop growing and livestock ownership), and others (including forest reserves, which are primarily set aside for forest products, but have a mandate for conservation, and state, private or community-owned land managed primarily for photographic tourism) (Fig. S1). The boundary of HNP is demarcated by the heavily used Bulawayo-Victoria Falls railway line. Vegetation consists primarily of woodland and bush-land savannah with patches of grassland. In this study, we used the MODIS Vegetation Continuous Fields dataset (Hansen *et al.* 2005), which provides percentage tree cover at a resolution of 500m. The long-term mean annual rainfall is ca. 600 mm (CV = 25%) and generally falls between October and April. Surface water is available from seasonal rivers and waterholes. In the dry season, water is mainly available from artificially supplied waterholes (Fig. S1b). The location of households and number of houses in each household in the communal lands of the study area were digitised from Google Maps using Zonum's tools (<http://www.zonums.com/gmaps/digipoint.php>) and imported into ArcGIS 10.1 (ESRI, Redlands, CA, USA; Fig. S1b).

### LION MORTALITY DATA AND LION GPS DATA

Lion density in the study area is estimated around 3.5 lions/100 km<sup>2</sup> (unpublished data). Between 1999 and 2012, we recorded 206 events of lion mortality due to anthropogenic

causes in the core study area (Table 1, Fig. S1c). Cause of mortality was assessed by the field team when mortalities were found or reported (snaring, natural and conflict) or from official records (trophy hunting, problem animal control). We had mortality records from 85 adult males, 33 sub-adult males, 61 adult females, 14 sub-adult females, 5 sub-adults of unknown sex, and 8 unidentified individuals. Thirty-one natural mortality events were also recorded (Fig. S1c) but were not analysed in this study. Eighty four lions (for which the fate was known) have been monitored with GPS radio-collars in the core study area since 2002. Animals' locations were available hourly from 18h00 to 7h00, plus fixes at 9h00 and 16h00.

#### MORTALITY RATES

Because male and female lions are not effected to the same extent by different sources of anthropogenic mortality (e.g. trophy hunting), we used data from the 84 collared individuals to calculate cause-specific mortality rates separately for each sex between August 1999 and August 2012. These were calculated using the modified Mayfield method (Heisey & Fuller 1985), a method that allows comparison of cause specific mortality rates and which performs well when sample sizes are small and also provides reasonable precision when mortality rates are high (Murray 2006).

#### DETERMINANTS OF LION ANTHROPOGENIC MORTALITY

We pooled the 206 mortality events from both sexes and all age classes, and developed logistic regression models to identify the variables associated with each anthropogenic mortality source: trophy hunting, conflict-related, snaring bycatch, and vehicle-related mortality. The locations of anthropogenic mortality events (n=206, dependent variable = 1) were compared to randomly generated locations in the core study area (n=250, dependent variable = 0). For each observed and randomly generated location, we extracted (in ArcGIS

10.1.) the distance to the closest water source (“distance to water”, km), the distance to the closest household (“distance to a household”, km), the distance to a hunting camp (km), and the distance to the railway (km). We also calculated a proxy of human density for each location as the number of houses in a buffer of 2 km of the location (“number of houses”). We created *a priori* candidate models to test whether the mortality events were a function of land use (protected area, trophy hunting area, communal land, and other), woody cover (extracted from the MODIS image), distance to water, distance to a household, number of houses, distance to a hunting camp, distance to the railway, and combinations and interactions therein. To identify the best model(s), we used model selection based on Akaike Information Criterion corrected for small sample size (AICc). When several models were selected ( $\Delta AICc \leq 2$ ), we performed model-averaging procedure correcting for model weights to provide unconditional estimates and confidence intervals. All statistical analyses were performed in R 2.15.2. (R Core Team). We then used the results provided by the logistic regression models to build landscapes of likelihood of mortality for each mortality source for the larger study area (HNP and the 25km buffer around HNP) using the function ‘Map Algebra’ of ArgGIS 10.1 ‘Spatial Analyst’ extension. Each pixel was attributed a value ranging from 0 (very low likelihood of mortality) to 1 (very high likelihood of mortality).

## MODELLING THE LANDSCAPE OF ANTHROPOGENIC MORTALITY RISK

We developed an approach in 3 steps. We first used the cause specific mortality rates calculated above to weight the landscapes of likelihood of mortality for each mortality source into a combined landscape of likelihood of anthropogenic mortality for each sex (i.e. a map of “where lions are likely to die from anthropogenic causes”). Because lions can only die where they roam, and because for a given area, the risk taken by lions will differ depending on the time they spend in this area, we then built landscapes of use for each sex (see details in



Supporting Information 1) to be able to model the risk of anthropogenic mortality accounting for variation in lion occurrence. To ultimately produce a proxy of such a risk, we weighted the landscape of likelihood of anthropogenic mortality by the landscape of use with the following formula: 
$$\text{[landscape of likelihood of anthropogenic mortality]} / ((\text{[Landscape of use]} + 0.05) * 20)$$
. The term “0.05” was added to avoid the denominator being null, and the division by “20” allowed an index ranging between 0 and 1 to be produced. Using this formula, we created a landscape of anthropogenic mortality risk for each sex (i.e. a map of “where lions are at risk of dying from an anthropogenic cause accounting for variation in their occurrence”) using the function ‘Map Algebra’ of ArgGIS 10.1 ‘Spatial Analyst’ extension. The index used to build this final landscape ranges between 0 (very low risk of anthropogenic mortality) and 1 (very high risk of anthropogenic mortality).

#### SPACE USE IN RELATION TO RISK OF MORTALITY

We asked whether lions dying from anthropogenic causes used the landscape in a way that was different from lions that survived to the end of the study or died of natural causes. For the 84 GPS radio-collared lions monitored throughout the study, we extracted for each location the index of anthropogenic mortality risk from the landscape previously built and calculated the proportion of time spent in the 6 following anthropogenic risk categories: none ( $< 0.01$ ), very low (between 0.01 and 0.03), low (between 0.03 and 0.06), medium (between 0.06 and 0.1), high (between 0.1 and 0.2), and very high risk ( $> 0.2$ ). High risk and very high risk areas were pooled in some subsequent analyses as the risky areas of the landscape (index of risk of anthropogenic mortality  $> 0.1$ ). For individuals that had settled, i.e. for which we were able to calculate a home range ( $n=66$ ), we calculated the proportion of their home range in the 6 categories of anthropogenic mortality risk. We assessed whether individuals that died from an anthropogenic cause spent more time in the risky areas of the landscape and had home ranges

characterized by higher proportions of these risky areas than individuals that died from natural causes or were still alive. The proportion of time spent in risky areas and the proportion of home range encompassing risky areas were arcsine transformed to meet normality requirements. For those individuals with a home range, we then assessed preference using Jacobs' selection index (Jacobs 1974):  $D = (r-p)/(r+p-2rp)$  where  $r$  is the proportion of the total number of locations in a particular category of anthropogenic mortality risk, and  $p$  is the proportional availability of this category in the animal home range. Jacobs index ranges between -1 (highly avoided), 0 (used in proportion to availability), and 1 (highly selected). Of the 206 events of anthropogenic mortality recorded, 19 corresponded to lions that had been GPS radio-collared and for which data on their movement was available for the 2 months preceding the death of the animal. We thus selected GPS-collared individuals that did not die from an anthropogenic cause (natural death or still alive) and whose home range was located at the edge of HNP (i.e. encompassing land use types other than protected areas), and extracted information on their movement for 2 months ( $n=21$ ). We performed general linear models with a binomial error structure where our response variable was survived or died naturally (0) or died from an anthropogenic cause (1), and tested for the effect of the proportion of time spent in risky areas over the 2 study months.

#### WHICH LIONS ARE THE MOST AT RISK IN THIS LANDSCAPE OF ANTHROPOGENIC MORTALITY?

We finally tested for the influence of sex and age class on the proportion of time spent in risky areas and the proportion of the home range encompassing risky areas. For age class, we contrasted experienced adults (> 6 years), young adults (between 4 and 6 years) and sub-adults (between 2 and 4 years). Because of small sample sizes, we pooled young adults and sub-adults in the analyses. The proportions were arcsine transformed to meet normality

requirements. Finally, for each home range, we calculated the barycentre of the home range using the ‘genpointinpoly’ function of Geospatial Modelling Environment and correlated the distance of this barycentre to the park border to the proportion of risky areas in their home range for both sexes and contrasting experienced adults with younger individuals.

## Results

### MORTALITY RATES

Over the study period it was clear that anthropogenic mortality rates were very high for both sexes in the study population but natural mortality rates relatively low (1999-2012, natural mortality rates are  $0.11 \pm 0.002$  and  $0.31 \pm 0.006$  for males and females respectively) and that the relative importance of the different sources of anthropogenic mortality differs between the two sexes (Fig. S2). Cause specific mortality rates for anthropogenic sources of mortality for males were  $0.65 \pm 0.002$  for trophy hunting,  $0.11 \pm 0.002$  for snaring,  $0.11 \pm 0.002$  for conflict, and 0 for vehicles. Those for females were  $0.29 \pm 0.005$  for snaring,  $0.16 \pm 0.003$  for conflict,  $0.16 \pm 0.003$  for trophy hunting, and  $0.03 \pm 0.0001$  for vehicles. These mortality rates were used to build the landscape of anthropogenic mortality risk.

### DETERMINANTS OF LION ANTHROPOGENIC MORTALITY

For trophy hunting mortality, the top model included land use type and distance to a hunting camp. Trophy hunting mortality was highest in trophy hunting areas and negligible in other land-use types, and decreased as the distance to a hunting camp increased (estimate = -0.00008; CI = -0.00013 to -0.00002; Fig. 1a). For conflict-related mortality, there were two top models, and model-averaging revealed that conflict-related mortality was highest in

communal lands, decreased as the distance to a household increased (estimate = - 0.0001; CI = - 0.0002 to 0; Fig. 1b), increased as the number of houses in the vicinity increased (estimate = 0.003; CI = -0.001 to 0.006; Fig. 1c), and increased as the woody cover increased (estimate = 0.05; CI = 0.01 to 0.09; Fig. 1d). For mortality through snaring bycatch, two top models were selected, and model-averaging revealed that snaring bycatch was lower in communal lands than in other land use types, and that it decreased as distance to a household increased (estimate = -0.0001; CI = -0.0002 to -0.00008; Fig. 1e) and as the distance to water increased (estimate = -0.00004; CI = -0.0002 to 0.0001; Fig. 1f). For vehicle-related mortality, the top model included land use type and distance to the railway line with mortality decreasing as the distance to the railway line increased (estimate = -0.0003; CI = -0.0006 to 0; Fig. 1g). Based on these results, we built four landscapes of likelihood of anthropogenic mortality: a landscape of likelihood of trophy hunting mortality (Fig. 2a), a landscape of likelihood of conflict-related mortality (Fig. 2b), a landscape of likelihood of mortality through snaring bycatch (Fig. 2c), and a landscape of likelihood of vehicle-related mortality (Fig. 2d).

## THE LANDSCAPE OF ANTHROPOGENIC MORTALITY RISK

We used the mortality rates calculated above as weightings to combine the four landscapes of likelihood of anthropogenic mortality initially built (Fig. 4) in order to create a combined landscape of likelihood of anthropogenic mortality for each sex. Across the landscape, areas of high likelihood of anthropogenic mortality were located at the periphery of the protected areas (Fig. 3a, b), with areas of high likelihood of anthropogenic mortality located in trophy hunting areas for males (Fig. 3a) and distributed more widely across land-use types for females (Fig. 3b) reflecting the importance of the differing sources of mortality for females (Fig. S2). Regarding lion habitat selection, both sexes avoided communal lands compared to other land use types and selected areas close to waterholes (Supporting Information 2). The

combination of the preceding landscapes of likelihood of anthropogenic mortality (Fig. 3a, b) and landscapes of likelihood of use (Supporting Information 1) resulted in landscapes of risk of anthropogenic mortality (Fig. 3c, d), which confirmed trophy hunting areas as clear mortality risk hotspots for males, while mortality risk was more evenly distributed across land-use types for females.

## SPATIAL AVOIDANCE OF RISK

We tested whether use of risky areas differed between lions dying from anthropogenic causes compared to those dying naturally or surviving. The proportion of locations in areas we predict to be risky was higher for individuals that died from an anthropogenic cause than for individuals that died naturally or that were still alive ( $t = -2.751$ ;  $p = 0.007$ ), with individuals that died from an anthropogenic cause spending on average twice the proportion of time in risky areas than other individuals (mean = 0.09 and 0.04 respectively). The proportion of home range in risky areas was also significantly higher for individuals that died from an anthropogenic cause ( $t = -3.020$ ;  $p = 0.004$ ), which were characterized by home ranges with proportions of risky areas more than twice that of other individuals (mean = 0.12 and 0.05 respectively). Values of Jacobs' indices were low ( $<0.3$ ) revealing no strong preference or avoidance of areas depending on the risk of anthropogenic mortality risk, but all lions tended to avoid areas characterized by medium, high and very high risk of anthropogenic mortality risk (Fig. S3). Information from GPS-collared individuals revealed that the risk of dying from an anthropogenic cause tended to increase as the proportion of time spent in risky areas over the past two months increased (estimate  $\pm$  SE =  $4.72 \pm 2.67$ ;  $Z = 1.764$ ;  $p = 0.077$ ; result close to significance).

## WHICH LIONS ARE THE MOST AT RISK IN THIS LANDSCAPE OF ANTHROPOGENIC MORTALITY RISK?

Sex affected neither the proportion of locations in risky areas ( $t = -1.700$ ;  $p = 0.093$ ) nor the proportion of risky areas in the home range ( $t = -0.852$ ;  $p = 0.397$ ). However, the effect of age class was close to significance for the proportion of locations in risky areas ( $t = 1.827$ ;  $p = 0.071$ ; Fig. 4a), and significantly influenced the proportion of risky areas in the home range ( $t = 2.298$ ;  $p = 0.025$ ) with this proportion being twice as high for younger individuals than for experienced adults (mean = 0.11 and 0.06 respectively; Fig. 4b). Overall, even lions whose home range barycentre was inside the protected area, even up to a distance of 20km inside the park, had sometimes significant proportions of their home range in risky areas, illustrating the extent to which ‘edge effects’ have the potential to impact lions in this population. Younger individuals had the riskiest home ranges for a given distance of the home range barycentre inside the protected area (Fig. 5).

## Discussion

There is growing evidence that anthropogenic mortality of long-lived carnivores (through legal and illegal hunting, retaliatory killing or poaching bycatch) has significant demographic impacts that are additive rather than compensatory to natural mortality (Creel *et al.* 2016). African lions in and around HNP provide a useful model of how anthropogenic activities at the periphery of the protected area influence the populations inside it. Records show that, even in this large and well protected area, 88% of male mortalities and 67% of female mortalities (1999-2012) were caused by humans. This suggests that anthropogenic impacts may have profound impacts, particularly in smaller and less well protected populations, and that, to be successful, conservation of carnivore species requires approaches that actively limit mortality caused by people. Identifying areas where animals may be most at risk allows

conservation managers to prioritise the allocation of scarce conservation and management resources.

### *DEFINING RISK IN CONSERVATION LANDSCAPES*

In most of the existing conservation literature, the level of risk faced by animals is either inferred on the basis that areas with high human density or infrastructure are riskier (e.g. Kerley *et al.* 2002; Oriol-Cotterill *et al.* 2015), or based on the fact that riskiest areas are those where high levels of mortality occur (e.g. Nielsen *et al.* 2004). However, mortality risk (exposure to a threat likely to result in a mortality event) for an individual cannot be understood without information about both the likelihood that mortality will occur at a particular location and the likelihood that the animal will use this particular location (i.e. the level of exposure to that mortality). Thus, a high risk location may either be one that is seldom visited by an animal but where the likelihood of mortality is extremely high (even though because of infrequent use little mortality may actually occur at the location), or one where the likelihood of mortality may be lower but where animals spend significant amounts of time (here records of mortality may be high simply because animals spend more time exposed to risk). We suggest that incorporating the notion of mortality risk (and other measures of fitness) is needed for better habitat-based management policies for wildlife.

### *SOURCES OF RISK IN THE LANDSCAPE*

Within the greater Hwange landscape, the risk of anthropogenic mortality varied markedly between land use types. For male lions, this risk was noticeably higher in the hunting areas to the north of the park. For females, three mortality hotspots could be identified: some sections of the hunting areas, communal areas and the sections of the wildlife areas adjacent to communal areas within ~ 15km of the protected area boundary.

*Trophy hunting areas as ecological traps*

Trophy hunting was the primary cause of mortality in male lions (which are selectively targeted by trophy hunters) in the study population and trophy hunting concessions clearly appear as mortality hotspots in the landscape for both sexes. Our analyses revealed that lions used hunting areas with similar levels of intensity as fully protected areas (Supporting Information 1). This is because these areas contain relatively intact habitat and prey populations and are characterized by low human presence hence there are no obvious cues to trigger avoidance behaviour in lions. Trophy hunting areas are therefore typical ecological traps (or ‘attractive sinks’ *sensu* Delibes, Goana & Ferreras 2001) with both high levels of use and high risk of mortality that may lead large carnivores into maladaptive habitat selection. Trophy hunting areas may act as mortality hotspots in the landscape that may compromise the viability of large carnivore populations (e.g. (Loveridge *et al.* 2010a). However, if sustainably managed (with sustainable hunting quotas and rigorous monitoring), these areas, which ensure the conservation of intact natural habitat important for wildlife, hold the potential to play an important role of buffer areas around protected areas.

*Communal farming areas as sinks*

Communal areas are associated with two main sources of anthropogenic mortality for lions: killing in retaliation for livestock depredation in the communal areas and snaring for bush-meat (poaching is for food or commercial sale and most predator mortalities are unintentional bycatch) in the protected areas adjacent to communal areas. Both are significant threats to the conservation of large carnivores worldwide (Treves & Karanth 2003; Liberg *et al.* 2012). In our study, areas with high human and livestock populations (Hwange and Tsholotsho communal areas) were used little by lions (Supporting Information 1). However, for lions that



occasionally used these areas the chances of dying was high particularly for females. Conflict-related mortality may have been under-estimated since there is both a legal ('problem animal control' by wildlife managers) and illegal (use of snaring, gin trapping or poisoning by villagers) component to this mortality. Snaring is a completely illegal activity and undetected poaching can be more important than the poaching that is recorded ("cryptic poaching" *sensu* Liberg *et al.* 2012). The risk of conflict-related and snaring mortality is likely higher than we have calculated. However, even with the available data, the communal areas have a high level of mortality risk (particularly for females) and thus appear as sinks for the lion population in the Hwange system. The effects of anthropogenic mortality can create population sinks on reserve boundaries and source-sink dynamics often affects large carnivore populations living in protected areas surrounded by people (Novaro, Funes & Walker 2005; Balme, Slotow & Hunter 2010). Snaring, as inferred from the locations lions died in snares, primarily occurs within land use types rich in wildlife. This is because there is little resident wildlife in communal land and high risk of killing or injuring livestock. Because of snaring, areas of HNP close to park boundaries can also be considered 'attractive sinks' in that they encompass intact natural habitat and contain wild prey species that attract lions, but these areas also pose a significant threat of mortality that is not sufficiently predictable to be avoided by lions. Because snaring largely occurs within travelling distance of villages, it mostly occurs within approximately 15km of the park boundary and thus exerts a significant 'edge effect' for wildlife, including large carnivores.

#### *YOUNG LIONS AT RISK*

Carnivores are known to be able to perceive risk in their environment (Oriol-Cotterill *et al.* 2015), either through previous adverse experiences, behavioural patterns learned from conspecifics in response to specific cues or innate caution of human presence (Ordiz *et al.*

2012; Nielsen *et al.* 2013). Lions in all demographic groups selected safe habitats (null risk) and showed a tendency to avoid risky areas. This suggests that even young lions are capable of perceiving risk, but nevertheless choose (or are forced) to use peripheral, risky environments perhaps because they are excluded from prime habitat by competitive interactions with territorial adults. Nevertheless, we found that lions that died at the hands of humans had riskier home ranges and spent more time in risky areas, and it is the young lions (sub-adults (2-4 years) and younger adults (4-6 years) that were more likely to spend time in and incorporate risky areas into their home-ranges than experienced adults. Learned behavioural avoidance of risky areas therefore seems to have been acquired by experienced adult animals (> 6 years) and be less apparent in naive younger individuals. Elliot *et al.* (2014a) showed that young male lions are more risk-prone and likely to move through human dominated landscapes than adults. Sub-adult male lions, perhaps as a consequence of both necessity and inexperience, are significantly more likely to kill livestock than are adults (Patterson *et al.* 2004), which, in turn, may make them more prone to being destroyed as livestock killers. Males did not have a greater tendency to use risky areas than females which contrasts with findings for other Felid species where males were less risk averse and used habitats in proximity to human habitation more frequently than females (Bunnefeld *et al.* 2006).

#### *EDGE EFFECTS*

Previous research has shown that lions with home ranges in close proximity to the protected area boundary experience significantly higher mortality rates than those living in the protected area core, live in smaller, less successful prides and raise fewer cubs to maturity (Loveridge *et al.* 2010a). Furthermore, mortality of territorial individuals at the park boundary creates territorial vacuums that attract animals out of the protected core into areas where they face a

high risk of mortality (Loveridge *et al.* 2007). Edge effects (processes occurring on the boundary of protected habitat fragments that propagate into the protected area) have been demonstrated for a number of vertebrate species (e.g. birds: Wilkin *et al.* 2007; Carnivores: Balme, Slotow & Hunter 2010) and have significant negative impacts on the capacity of protected areas to fully protect large predator populations (Woodroffe & Ginsberg 1998). In this study, lions with home range centres up to 20km from the protected area boundary are still impacted by anthropogenic mortality illustrating a clear edge effect. This results in a reduction of the fully protected core of the park to approximately 5696 km<sup>2</sup> or 38.7% of its total area. This suggests that isolated protected areas smaller than c 1256- 1600 km<sup>2</sup> (depending on the shape of the protected area) are simply not large enough to protect lion populations.

#### *SYNTHESIS AND APPLICATIONS*

Anthropogenic mortality poses a significant risk to carnivore populations, particularly in Africa where human populations are growing and protected areas are under threat. Incorporating the concept of risk into our understanding of the conservation landscape for large carnivores informs prioritisation of conservation management policy. We show that conservation action should focus not only at the protected area- farmland interface but also in areas that are formally protected but might nevertheless represent areas of high mortality risk which may undermine the viability of protected areas.

Areas with high human or domestic livestock populations are intuitively identified by conservation managers as being high risk for wide-ranging predators. Nevertheless our results suggest that, to a large degree, lions (and likely other large carnivores) avoid areas dominated by humans. This is likely to be because cues exist to allow them to identify the risks inherent in these areas. In these locations conservation efforts focus, often successfully, on mitigation

measures that reduce human-predator conflict (Hazzah *et al.* 2014). The necessity to kill carnivores over livestock losses can often be limited through improved livestock protection and strategies that reinforce avoidance behaviours in predators.

Of more concern are parts of a carnivore's range that constitute 'attractive sinks' and where activities such as trophy hunting or illegal bush-meat snaring greatly increase their exposure to anthropogenic mortality. In such areas predators are attracted by available habitat and prey but be unable to discern the risks because cues such as presence of high numbers of people or infrastructure are absent. The potential threat of excessive trophy hunting mortality can be mitigated against by careful management of hunting offtakes (Creel *et al.* 2016). However, snaring for bush-meat is a growing problem and is likely to increase in areas where growing human populations live adjacent to wildlife rich areas (Watson *et al.* 2014). Bush-meat poaching can have a devastating effect on predator populations largely because predators have very little innate ability to discern the risk posed by wire snares and avoid areas where snaring is prevalent. This calls for intensive law enforcement in areas where bush-meat poaching is likely, which this study suggests is likely to occur in wildlife areas within 15km of human settlements.

## **Acknowledgements**

We thank the Director of ZPWMA for permission to undertake this research and the assistance of ZPWMA and Hwange Lion Project field staff for data collection. Research was supported by Darwin Initiative for Biodiversity Grants 162-09-015 and EIDPO002, Mitsubishi Fund for Europe and Africa, R.G. Frankenberg, Boesak and Kruger, Rufford Maurice Laing, SATIB Trust, Eppley, Panthera, Robertson and, Recanati-Kaplan Foundations and Riv and Joan Winant. Funders had no role in study design, data collection, data analysis, manuscript preparation or decision to submit.

## Data accessibility

Data used in analysis in this paper are provided as online supporting information and in DRYAD entry doi:10.5061/dryad.p35r2 (Loveridge *et al.* 2016).

## References

- Balme, G.A. (2009) The conservation of a nominally protected leopard population. PhD, University of Kwazulu-Natal, Westville.
- Balme, G.A., 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**, 315-323.
- Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, **18**, 1482-1491.
- Bunnefeld, N., Linnell, J.D.C., Odden, J., Van Duijn, M.A.J. & Andersen, R. (2006) Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. *Journal of Zoology*, **270**, 31-39.
- Creel, S., M'Soka, J., Droge, E., Rosenblatt, E., Becker, M.S., Matandiko, W. & Simpamba, T. (2016) Assessing the sustainability of lion trophy hunting with recommendations for policy. *Ecological Applications*, doi:10.1002/eap.1377.
- Delibes, M., Goana, P. & Ferreras, P. (2001) Effects of an attractive sink leading into maladaptive habitat selection. *American Naturalist*, **158**, 277-285.
- Elliot, N., Cushman, S.A., Macdonald, D.W. & Loveridge, A.J. (2014a) The devil is in the dispersers. Predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, **51**, 1169-1178.

505 Elliot, N., Valiex, M., Macdonald, D.W. & Loveridge, A.J. (2014b) Social relationships affect  
 506 dispersal timing revealing a delayed infanticide in African lions. *Oikos*, **123**, 1049-  
 507 1056.

508 Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W., Carpenter, S.R.,  
 509 Essington, T.E., Holt, R.D., Jackson, J., Marquis, R.J., Okasen, L., Oksen, T., Paine,  
 510 R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin,  
 511 J.B., Sinclair, A.R.E., Soule, M., Virtanen, R. & Wardle, D.A. (2011) Trophic  
 512 Downgrading of Planet Earth. *Science*, **333**, 301-306.

513 Hansen, M.C., Townshend, J.R., DeFries, R. & Carroll, M. (2005) Estimation of tree cover  
 514 using MODIS data at global, continental and regional/local scales. *International*  
 515 *Journal of Remote Sensing*, **26**, 4359-4380.

516 Hazzah, L., Dolrenry, S., Naughton-Treves, L., Edwards, C., Mwebi, O., Kearny, F. & Frank,  
 517 L. (2014) Efficacy of two lion conservation programs in Maasiland, Kenya.  
 518 *Conservation Biology*, **28**, 851-860.

519 Heisey, D.M. & Fuller, T.K. (1985) Evaluation of survival and cause-specific mortality rates  
 520 using telemetry data. *Journal of Wildlife Management*, **49**, 668-674.

521 Jacobs, J. (1974) Quantitative measurement of food selection. *Oecologia*, **14**, 413-417.

522 Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B. & Hornocker,  
 523 M.G. (2002) Effects of roads and human disturbance on Amur tigers. *Conservation*  
 524 *Biology*, **16**, 97-108.

525 Kramer-Schadt, S., Revilla, E., Wiegand, T. & Breitenmoser, U. (2004) Fragmented  
 526 landscapes, road mortality and patch connectivity: modelling influences on the  
 527 dispersal of Eurasian lynx. *Journal of Applied Ecology*, **41**, 711-723.

528 Kristan, W.B. (2003) The role of habitat selection behaviour in population dynamics: source  
 529 sink systems and ecological traps. *Oikos*, **103**, 457-468.

530 Liberg, O., Chapron, C., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012)  
531 Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in  
532 Europe. *Proceedings of the Royal Society B: Biological Sciences*,  
533 **doi:10.1098/rspb.2011.1275**.

534 Loveridge, A.J., Hemson, G., Davidson, Z. & Macdonald, D.W. (2010a) African lions on the  
535 edge: Reserve boundaries as 'attractive sinks'. *Biology and Conservation of Wild*  
536 *Felids* (eds D.W. Macdonald & A.J. Loveridge), pp. 283- 304. Oxford University  
537 Press, Oxford.

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

541 Loveridge, A.J., Valeix, M., Elliot, N. & Macdonald, D.W. (2016) Data From: The landscape  
542 of anthropogenic mortality: how African lions respond to spatial variation in risk.  
543 *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.p35r2>.

544 Loveridge, A.J., Wang, S.W., Frank, L.G. & Seidensticker, J. (2010b) People and wild felids:  
545 conservation of cats and management of conflicts. *Biology and Conservation of Wild*  
546 *Felids* (eds D.W. Macdonald & A.J. Loveridge), pp. 161-196. Oxford University  
547 Press, Oxford.

548 Murray, D.L. (2006) On improving telemetry-based survival estimation. *J.Wildl.Manage.*, **70**,  
549 1530-1543.

550 Nielsen, A., Shafer, A., Boyce, M.S. & Syenhouse, G. (2013) Does learning or instinct shape  
551 habitat selection. *PLoS ONE*, **8**, e53721.

552 Nielsen, S., Herrero, S., Boyce, M.S., Mace, R., Benn, B., Gibeau, M. & Jevons, S. (2004)  
553 Modelling the spatial distribution of human-caused grizzly bear mortalities in the  
554 Central Rockies ecosystem of Canada. *Biological Conservation*, **120**, 101-113.

555 Novaro, A.J., Funes, M.C. & Walker, R.S. (2005) An empirical test of source-sink dynamics  
556 induced by hunting. *Journal of Applied Ecology*, **42**, 910-920.

557 Ordiz, A., Stoen, O., Saebo, S., Kindberg, J., Delibes, M. & Swenson, J.E. (2012) Do bears  
558 know they are being hunted? *Biological Conservation*, **152**, 21-28.

559 Oriol-Cotterill, A., Macdonald, D.W., Valeix, M., Ekwanga, S. & Frank, L.G. (2015)  
560 Spatiotemporal patterns of lion space use in a human dominated landscape. *Animal*  
561 *Behaviour*, **101**, 27-39.

562 Packer, C., Brink, H., Kissui, B.M., Maliti, H., Kushnir, H. & Caro, T. (2011) Effects of  
563 Trophy Hunting on Lion and Leopard Populations in Tanzania. *Conservation Biology*,  
564 **25**, 142-153.

565 Patterson, B.D., Kasiki, S.M., Selempo, E. & Kays, R.W. (2004) Livestock predation by lions  
566 (*Panthera leo*) and other carnivores on ranches neighbouring Tsavo National Park,  
567 Kenya. *Biological Conservation*, **119**, 507-516.

568 R\_Core\_Team (2012) R: A language and environment for statistical computing. (ed. R.F.f.S.  
569 Computing). ISBN 3-900051-07-0, URL <http://www.R-project.org/>, Vienna, Austria.

570 Revilla, E., Palomares, F. & Delibes, M. (2001) Edge-core effects and the effectiveness of  
571 traditional reserves in conservation: Eurasian badgers in Doñana National Park.  
572 *Conservation Biology*, **15**, 148-158.

573 Riggio, J., Jacobsen, A., Dollar, L., Bauer, H., Becker, M.S., Dickman, A., Funston, P.J.,  
574 Groom, R.J., Henschel, P.P., DeLongh, H., Lichtenfeld, L. & Pimm, S. (2013) The size  
575 of savannah Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation*, **22**,  
576 17-35.

577 Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E., Hebblewhite, M., Berger,  
578 J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O., Smith, D.W., Wallach, A. &



- Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 124-148.
- Roever, C.L., vanAarde, R.J. & Chase, M.J. (2013) Incorporating mortality into habitat selection to identify secure and risky habitats for savannah elephants. *Biological Conservation*, **164**, 98-106.
- Treves, A. & Karanth, K.U. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, **17**, 1491-1499.
- United\_Nations (2015) World Population Prospects: The 2015 Revision, Key Findings and Advance Tables. pp. 66. Department of Economic and Social Affairs, Population Division, New York.
- Watson, F., Becker, M.S., McRobb, R. & Kanyembo, B. (2014) Spatial patterns of wire-snare poaching: Implications for community conservation in buffer zones around National Parks. *Biological Conservation*, **168**, 1-9.
- Watson, J.E.M., Whittaker, R.J. & Dawson, T.P. (2004) Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. *Biological Conservation*, **120**, 315-331.
- Wilkin, T., Garant, D., Gosler, A. & Sheldon, B. (2007) Edge effects in the Great tit: Analyses of long-term data with GIS techniques. *Conservation Biology*, **21**, 1207-1217.
- Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O. & Brashares, J.S. (2008) Accelerated human population growth at protected area edges. *Science*, **321**, 123-126.
- Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126-2128.

604    **Supporting Information S1:** Supporting material, landscape of mortality.

605    Figure S1: Study site map and location of mortality events.

606    Figure S2: Mortality rates for male and female lions in and around HNP.

607    Figure S3: Jacobs' index of habitat preference over the different categories of anthropogenic  
608    mortality risk by lions.

609    Table S1: Sources of anthropogenic (human induced) mortality events for lions in HNP.

610    **Supporting Information S2:** Calculating the 'landscape of use' for lions.

611    Figure S4: Landscapes of likelihood of use for **(a)** male and **(b)** female lions in and around  
612    HNP. The black line represents HNP border.

613

**Figure legends:**

**Figure 1:** Predictors of the different sources of anthropogenic mortality for lions in and around HNP. The relationships presented are from the selected models – see text for details.

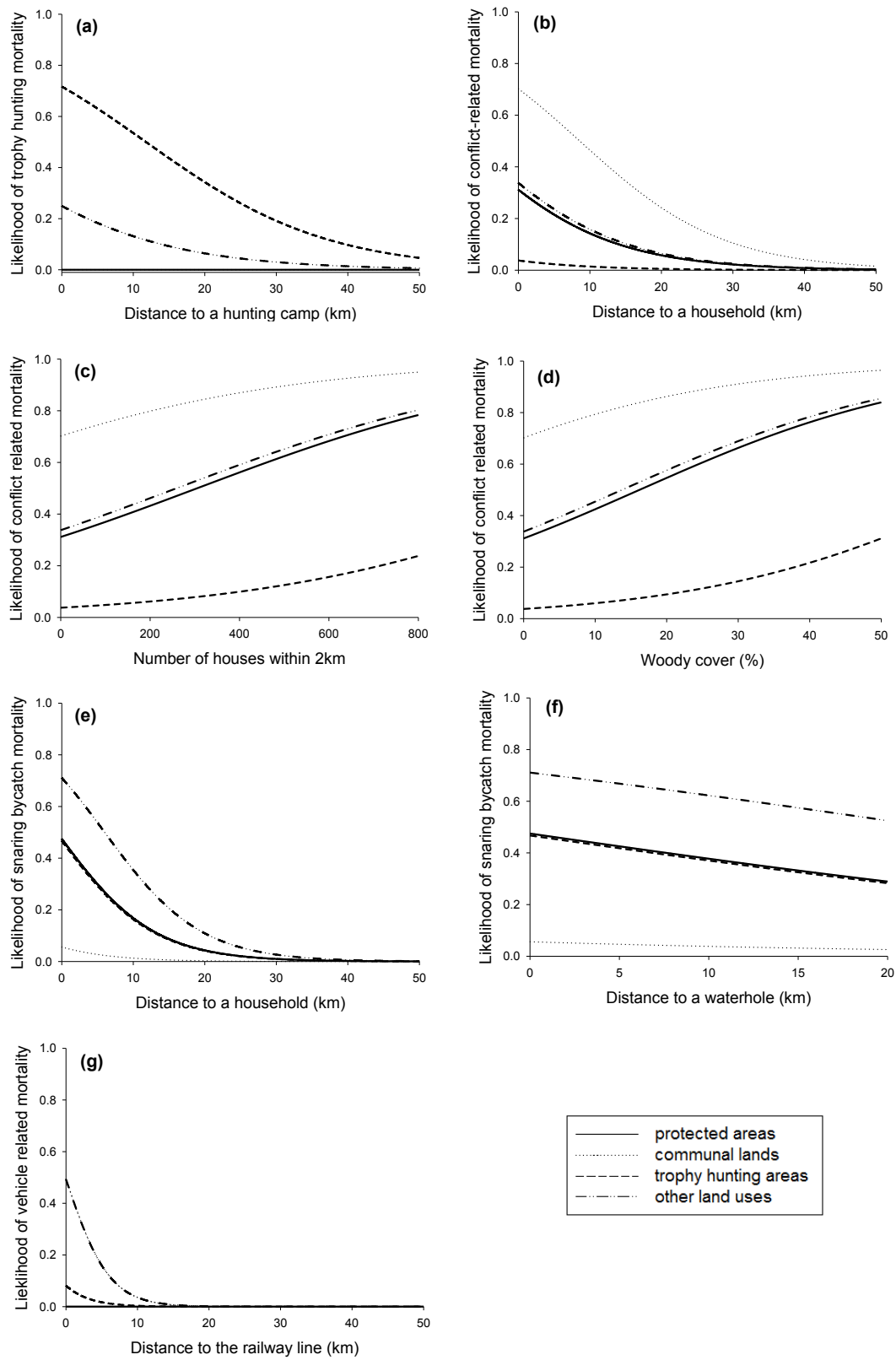
**Figure 2:** Landscapes of likelihood of **(a)** trophy hunting mortality, **(b)** conflict-related mortality, **(c)** mortality through snaring bycatch, and **(d)** vehicle-related mortality for lions in and around HNP. The black line represents HNP border.

**Figure 3:** **(a)** and **(b)** show the combined landscapes of likelihood of anthropogenic mortality for male and female lions respectively in and around HNP. **(c)** and **(d)** show the landscapes of anthropogenic mortality risk (accounting for variation in lion occurrence) for male and female lions respectively in and around HNP. The landscapes of anthropogenic mortality risk weighted the landscapes of likelihood of anthropogenic mortality (a, b) by the landscape of likelihood of use by lions (Supporting Information 1) - see text for details. The black line represents HNP border.

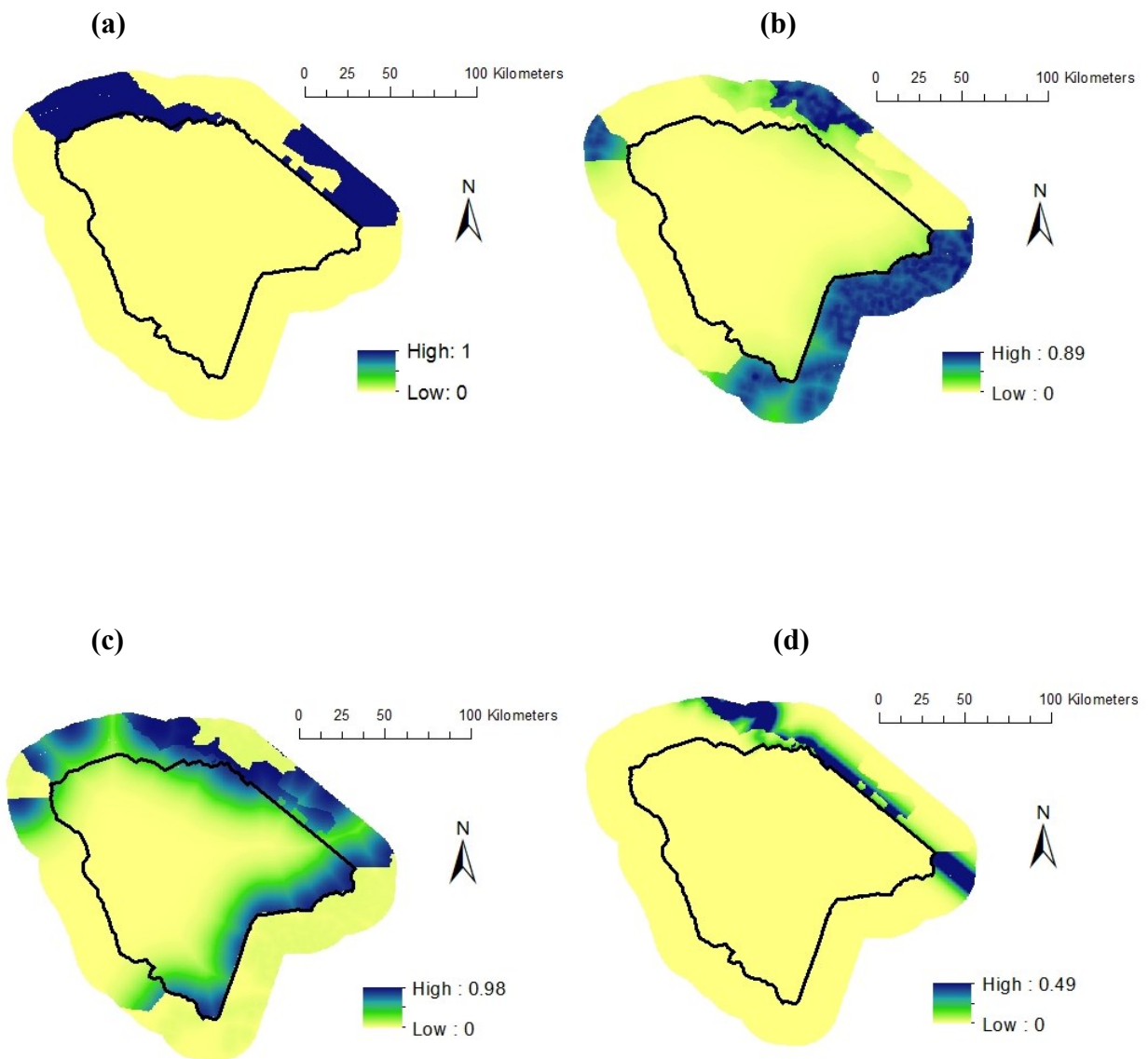
**Figure 4:** **(a)** Proportion of time spent in risky areas of the landscape (anthropogenic mortality risk  $> 0.1$ ), and **(b)** proportion of risky areas encompassed by home ranges of lions in and around HNP. Boxes show median, 25% and 75% quartiles. Bold dashed lines indicate means. Whiskers indicate the range between 10% and 90% percentiles. Dots represent data outside this range. **(c)** and **(d)** Jacobs' index of habitat preference for lions in and around HNP with differences by sex **(c)** and age class **(d)**. Values  $> 0$  indicate preference, values  $< 0$  suggest use but avoidance.

639 **Figure 5:** Relationship between the location of a lion home range and the proportion of the  
640 home range characterized by a high risk of anthropogenic mortality (index  $> 0.1$ ) in and  
641 around HNP.

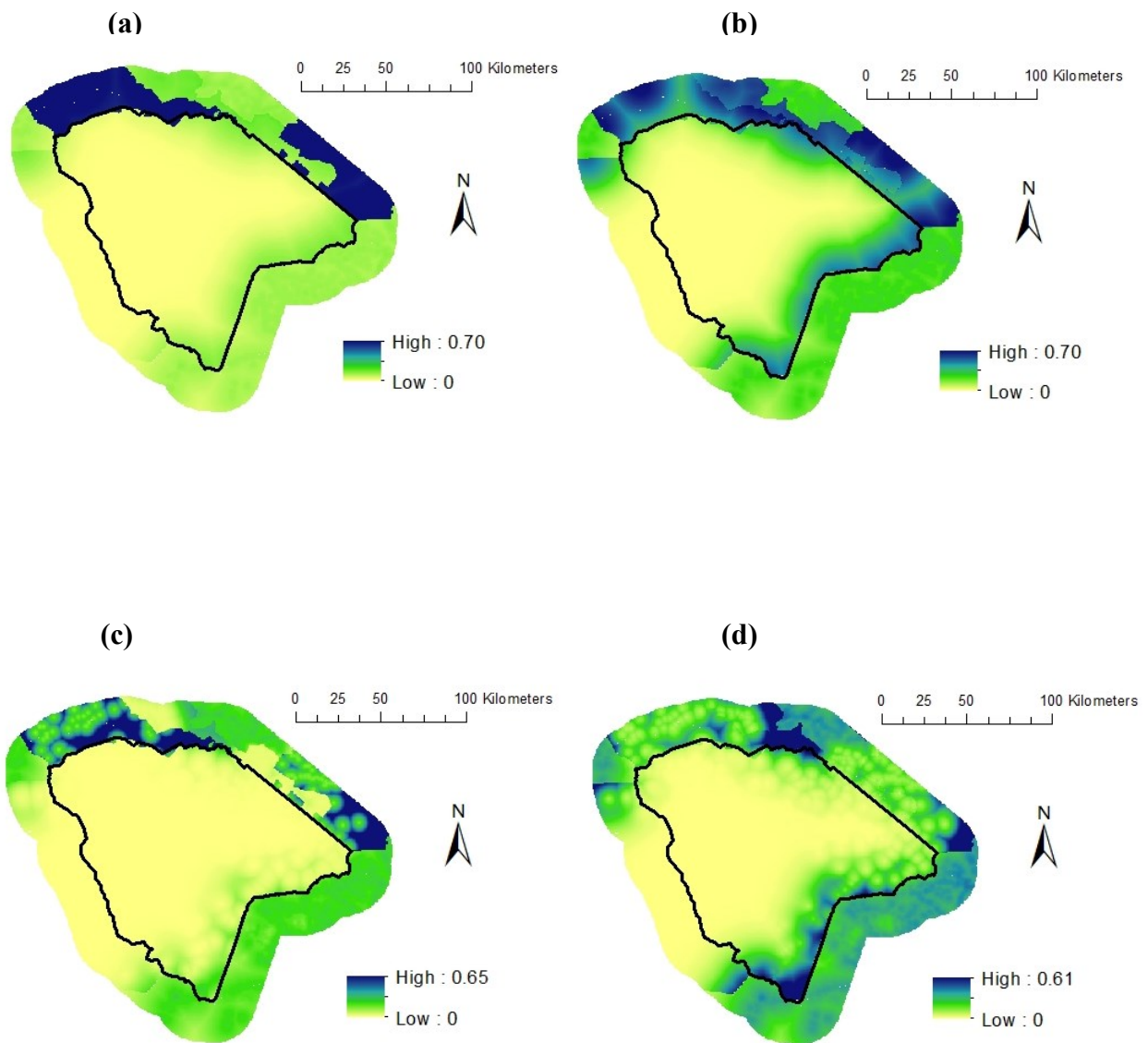
**Figure 1:**



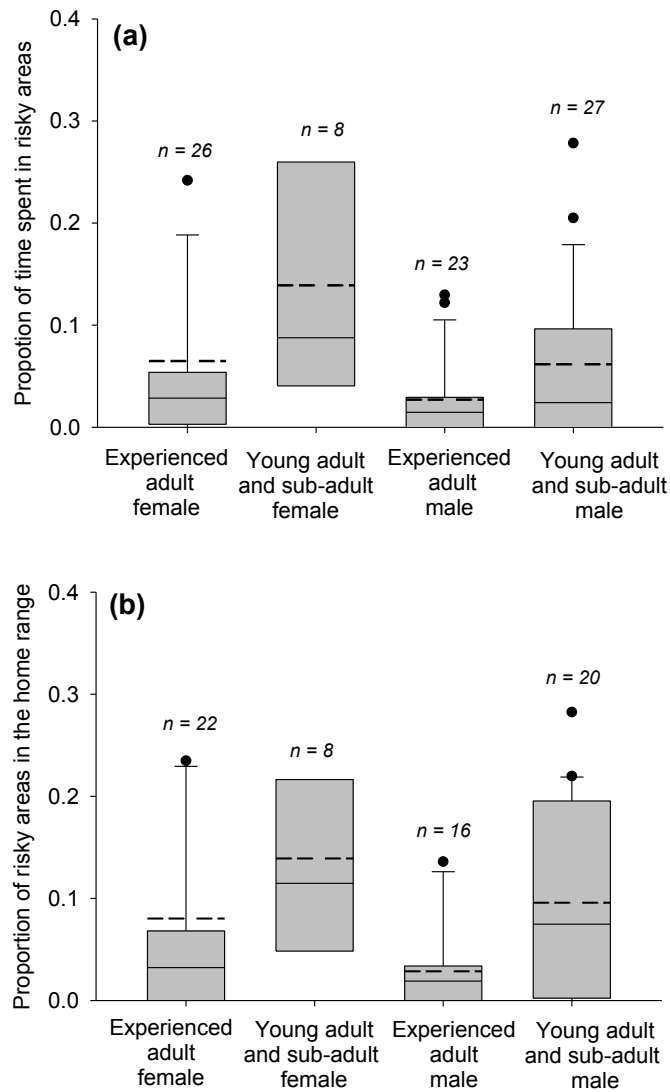
**Figure 2:**



**Figure 3:**



**Figure 4:**





**Figure 5:**

