

# Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: what is driving the population collapse?

ROSEMARY J. GROOM, PAUL J. FUNSTON and ROSELINE MANDISODZA

**Abstract** The African lion *Panthera leo* is an iconic species but it has faced dramatic range reductions and possibly as few as 30,000 individuals remain in the wild. In the absence of detailed ground-based surveys, lion populations may be estimated using regression models based on prey biomass availability but these often overestimate lion densities as a result of a variety of compounding factors. Anthropogenic factors can be key drivers of lion population dynamics and in areas with high human impact lion numbers may be significantly lower than those predicted by prey biomass models. This was investigated in two protected areas in Zimbabwe, where lion population densities were found to be significantly lower than would have been predicted by prey-availability models. High hunting quotas either within or around the protected areas are the most likely cause of the low lion numbers, with quotas in some areas being as high as seven lions per 1,000 km<sup>2</sup> in some years. Other factors, including persecution, poisoning and problem animal control, as well as disease and competition with spotted hyaenas *Crocuta crocuta*, are also discussed.

**Keywords** African lion, call-up survey, edge effects, *Panthera leo*, prey-biomass models, snaring, trophy hunting, Zimbabwe

## Introduction

African lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* are two of the most iconic of Africa's large carnivores. Whereas spotted hyaenas are widely distributed throughout Africa, lions are now believed to number only 32,000–35,000 individuals, with only ten areas qualifying as lion strongholds (Riggio et al., 2013). The low number

of lions is already cause for concern but the reality may be even more serious given that most estimates are based on educated guesses, often related to prey availability (Chardonnet, 2002; Bauer & van der Merwe, 2004; IUCN SSC Cat Specialist Group, 2006).

As the potential density of large carnivores is scaled with biomass of prey (Carbone & Gittleman, 2002), carnivore density can be estimated indirectly using regression models based on available prey biomass (Gros et al., 1996; Hayward et al., 2007). However, this rarely relates to real densities in many natural systems because of a number of largely anthropogenic factors. Thus using indirect methods has the potential to overestimate the number of large carnivores in an area (Kiffner et al., 2009; Croes et al., 2011). Relying on such models in the face of the financial, logistical and time constraints of conducting direct population surveys may result in unreliable estimates of population size (Ferreira & Funston, 2010).

For lion populations a variety of limiting factors have been identified (Kiffner et al., 2009), including habitat fragmentation, epizootic diseases (Kissui & Packer, 2004) and, most importantly, increasing human–lion conflict and associated persecution of lions (Woodroffe & Frank, 2005). Deaths in wire snares, illegal hunting, use of lethal means for problem animals, and prey losses as a result of the bushmeat trade can also affect populations (Lindsey et al., 2011), causing decline or local extinction of lions, even within protected areas (Woodroffe & Ginsberg, 1998). Trophy hunting can also contribute to declining lion numbers in protected areas, as has been illustrated in Hwange National Park, Zimbabwe (Loveridge et al., 2007). Conversely, trophy hunting can create incentives for the retention of land for wildlife and thus benefit conservation of lions (Lindsey et al., 2012).

Here we examine the situation in two protected areas in Zimbabwe, Gonarezhou National Park and the Tuli Safari Area. We used call-up surveys to obtain direct estimates of lion populations and compared actual lion densities with potential density estimates. Call-up stations are a popular technique for surveying lions and hyaenas (Smuts et al., 1977; Ogutu & Dublin, 1998; Mills et al., 2001; Ferreira & Funston, 2010). The calibrated technique described by Ferreira & Funston (2010) was used to estimate lion populations in both protected areas. We also present data on trophy hunting for lions for both areas and discuss to what extent hunting may have affected lion populations.

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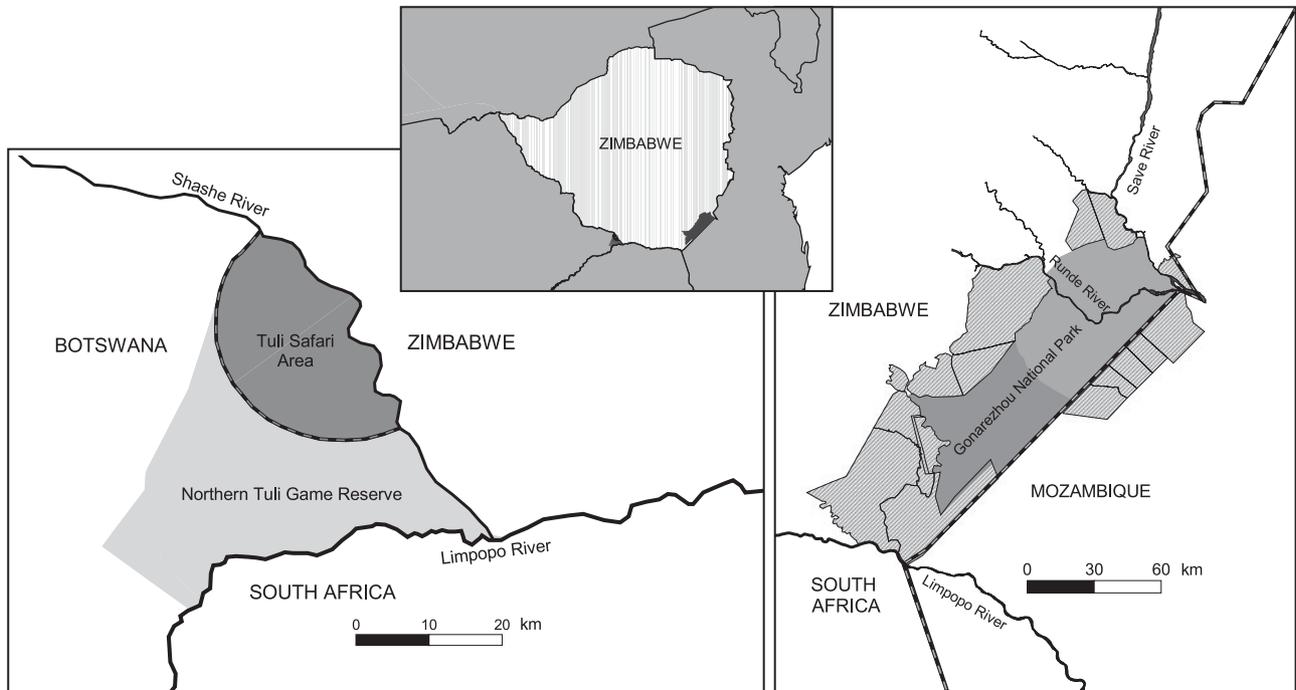


FIG. 1 Tuli Safari Area and Northern Tuli Game Reserve (left), and Gonarezhou National Park (right) showing surrounding hunting concessions (hatched areas). The black areas on the inset indicate the location of the two areas in Zimbabwe.

## Study areas

Gonarezhou National Park (hereafter Gonarezhou) in south-east Zimbabwe comprises 4,963 km<sup>2</sup> and was gazetted as a national park in 1975. It borders Mozambique along its eastern edge and Kruger National Park in South Africa lies <50 km to the south-west. The biomass density of key herbivore species in Gonarezhou is only slightly lower than that in the similarly vegetated north-western part of Kruger (Ferreira & Funston, 2010: Fig. 1). Consumptive wildlife utilization is not allowed in the Park but is allowed in the surrounding hunting concessions (Fig. 1).

The 416 km<sup>2</sup> Tuli Safari Area (hereafter Tuli) is situated in the relatively low-lying savannahs of south-western Zimbabwe along the Shashe River. It borders the Northern Tuli Game Reserve in Botswana to the south (Fig. 1). Since 1958 Tuli has been a controlled hunting area, designated as a Safari Area in 1975 under the governance of the Zimbabwe Parks and Wildlife Management Authority. Consumptive use of wildlife is allowed in the Tuli Safari Area through trophy hunting regulated by the Management Authority.

## Methods

### Call-up survey

Call-up surveys were used to estimate lion and spotted hyaena populations in Tuli and Gonarezhou. Both surveys

were conducted during the dark phase of the lunar cycle, in the winter months, during 11–14 July 2009 in Tuli and 3–18 August 2010 in Gonarezhou. We followed the methods used in Kruger by Ferreira & Funston (2010), using a minimum density of eight call-up stations per 1,000 km<sup>2</sup> to ensure sufficient sampling intensity. Thirty-nine completed stations sampled an area of 2,262 km<sup>2</sup> (45%) in Gonarezhou and eight stations sampled 100% of the area in Tuli. To ensure independence, stations were placed along roads, a minimum of 8 km apart in Tuli and 10 km apart in Gonarezhou (see Ferreira & Funston, 2010).

At each station the sound of an African buffalo *Syncerus caffer* calf in distress was broadcast continuously for 1 hour, using a 12 volt, 60 watt amplifier connected to two 4-ohm horn speakers, each with a 40 watt driver unit. The speakers were connected in series and placed c. 2.5 m above the ground (in Gonarezhou on the roof of the vehicle and in Tuli on a steel tripod), facing 180° from each other. The vocalizations were broadcast at full volume, with speakers rotated 180° every 15 minutes to get an all-round sound distribution. No bait was provided. Two observers sat in the back of the vehicle and one in the front seat. When any animal was heard approaching, a torch and/or a red-filtered spotlight were used to determine the number of individuals, group composition (age and sex) and time of arrival at the station. A minimum of two and a maximum of four stations were completed each night, starting just after dark and finishing no later than 2.00.

## Ungulate surveys

Ungulate surveys were conducted using aerial counts, following the well-established procedures for aerial surveys of large African herbivores (Norton-Griffiths, 1978). No counts were available for Tuli and therefore we used estimates from a survey of the adjacent and contiguous Northern Tuli Game Reserve, Botswana (Fig. 1). This survey was flown in September 2008 and was a total count of the 720 km<sup>2</sup> Game Reserve using a fixed-wing aircraft (Selier, 2008). It was considered reasonable to extrapolate these results to the Tuli Safari Area because of its immediate proximity, similar vegetation and lack of any physical barrier between the two areas. The reliability of this extrapolation is considered further in the discussion, below. In Gonarezhou the aerial survey was a sample count, with a 20% sampling intensity, conducted in September 2009 using a fixed-wing aircraft. Full details are available in Dunham et al. (2010). Estimates were adjusted for undercounting according to Bothma et al. (1990).

## Data on hunting of lions

There are 12 hunting concessions directly adjacent to Gonarezhou in Zimbabwe and five more on the Mozambican side (Fig. 1). In Zimbabwe nine of the concessions are state land: eight communal areas where the predominant activity is subsistence agriculture and where wildlife is utilized under the Communal Areas Management Plan for Indigenous Resources (CAMPFIRE), and one safari area (National Parks Estate). The remaining three concessions are classified as alienated land and include one private conservancy and two cooperative areas. Tuli itself is also Parks Estate, where hunting is permitted. Quota data for hunting of lions in Zimbabwe were provided by the Zimbabwe Parks and Wildlife Management Authority. Additional information was gathered from Rural District Council representatives and hunters.

## Data analysis

Data from both surveys were analysed as per Ferreira & Funston (2010), taking into account survey effort, variability of response likelihoods, and probability of sampling the same individual more than once. Briefly, a fitted inverse sigmoid model on response data from Kruger predicts that lions respond up to  $4.3 \pm \text{SE } 0.9$  km away from call-up stations, thus each station samples 57.7 km<sup>2</sup>. Response probabilities suggest that the number of lions observed at a call-up station needs correction by a factor of 1.51 and 3.66 for groups with and without cubs, respectively (Ferreira & Funston, 2010).

Estimates of abundance of key ungulate species were calculated from the aerial surveys. Following Hayward et al. (2007) we converted these abundance estimates to biomass per km<sup>2</sup>, using 75% of adult female body mass estimates from Stuart & Stuart (2000). Use of 75% of adult female body mass (following Schaller, 1972) is to account for subadults and young in the population. We considered African buffalo, eland *Taurotragus oryx*, giraffe *Giraffa camelopardalis*, wildebeest *Connochaetes taurinus*, zebra *Equus burchelli*, kudu *Tragelaphus strepsiceros* and impala *Aepyceros melampus* to be preferred lion prey species, following Radloff & du Toit (2004), Hayward & Kerley (2005) and Mbizah (2009) and based on our field observations. We then used the following equations to convert prey biomass into an estimate of lion density at carrying capacity

$$y = 10^{(-2.158+0.377x)} \quad \text{Hayward et al. (2007)}$$

where  $y$  is lion density (km<sup>-2</sup>) and  $x$  is log<sub>10</sub>(prey biomass in kg km<sup>-2</sup>)

$$y = 0.010x^{0.878} \quad \text{Loveridge & Canney (2009)}$$

where  $y$  is lion density (per 100 km<sup>2</sup>) and  $x$  is prey biomass.

Resulting density estimates were multiplied by area to estimate the number of lions in each protected area that could theoretically be supported by the available prey biomass. For comparison, similar calculations were made for spotted hyaenas, following Hayward et al. (2007).

## Results

### Direct estimates of carnivore populations from surveys

In Gonarezhou lions were seen at only two (5%) of the 39 calling stations; one group of two females and one of eight individuals (total  $n = 10$ ). This equates to a total population estimate of 33 lions (95% CI 28–39), which is consistent with the results of a spoor survey conducted in Gonarezhou in June 2010, which estimated 34 lions south of the Runde River, extrapolated to 44 in the whole Park (Groom, 2010). In Tuli, no lions responded physically or vocally to the calling stations, and no lion tracks were observed on the roads during 4 days of searching.

For spotted hyaenas the call-up survey in Gonarezhou estimated 400 individuals (95% CI 312–487), with 491 estimated from the spoor survey (Groom, 2010). In Tuli the call-up survey estimated 45 spotted hyaenas (95% CI 35–59).

### Indirect lion population estimates from prey biomass availability

Using the calculations of Hayward et al. (2007), biomass density of preferred lion prey in Gonarezhou was calculated

TABLE 1 Summary of estimates of lion *Panthera leo* and spotted hyaena *Crocuta crocuta* populations for Gonarezhou National Park and the Tuli Safari Area (Fig. 1), using various methods.

	Survey estimates		Predictions from prey biomass		Comparison
	Spoor survey <sup>1</sup>	Call-up survey	Hayward et al. (2007)	Loveridge & Canney (2009)	Using densities from north-west Kruger <sup>2</sup>
<b>Gonarezhou National Park</b>					
Lions	44	33	357	115	248
Spotted hyaenas	491	400	354		
<b>Tuli Safari Area</b>					
Lions		0	40	21	31
Spotted hyaenas		45	66		

<sup>1</sup>Extrapolated from Groom (2010); spoor survey conducted May 2010 in Gonarezhou National Park

<sup>2</sup>Assuming a population density equivalent to that of a habitat with comparable prey biomass in Kruger National Park (Ferreira & Funston, 2010)

to be 494 kg km<sup>-2</sup>, which could support 357 lions (7.2 per 100 km<sup>2</sup>). Using the model of Loveridge & Canney (2009) this biomass could support 2.3 lions per 100 km<sup>2</sup> (115 lions). In the ecologically similar north-west section of Kruger National Park, where lion prey biomass is 643 kg km<sup>-2</sup>, lion density was 5.0 per 100 km<sup>2</sup> (Ferreira & Funston, 2010). A similar prey density in Gonarezhou would result in 248 lions in the Park (Table 1).

In Tuli biomass density of preferred lion prey was estimated to be 1,217 kg km<sup>-2</sup> (through extrapolation from neighbouring Northern Tuli Game Reserve), suggesting the area could support a density of 10.1 lions per 100 km<sup>2</sup> (a total of 42 lions), using the Hayward et al. (2007) model. The Loveridge & Canney (2009) model estimates 21 lions in Tuli, and should the density of lions in Tuli be similar to those areas with similar prey biomass in Kruger (as per Ferreira & Funston, 2010) we would expect 31 lions (Table 1).

Our findings suggest that in Gonarezhou the lion population was at 16% of the mean predicted ecological carrying capacity (range 11–33%). As no lions were seen or heard in Tuli the estimated lion population was 0% of predicted ecological carrying capacity. For spotted hyaenas the Hayward et al. (2007) model predicts 354 individuals in Gonarezhou and 66 in Tuli, relatively similar figures to those estimated by the surveys (Table 1).

### Trophy hunt quotas for lions

Hunting quotas in the early 2000s were high in both areas although there has been a significant decrease in quota allocation in recent years (Table 2). In Tuli, from 2005 to 2010, 11 lions were on quota, but only six were actually shot. Success rate in 2008 and 2009 was 0%, after which no lions were on quota. Historical figures for successful hunts for lions around Gonarezhou are not available but, since 2007, despite 29 lions on quota, only two were actually utilized (one as a problem animal control issue) and none have been taken since 2009.

The hunting concessions in Mozambique adjacent to Gonarezhou total 980 km<sup>2</sup>. We do not have access to all long-term hunting quota figures but in 2009 there were at least seven male lions on quota in the reserves immediately bordering the eastern boundary of Gonarezhou (H. van der Westhuizen, pers. comm.).

### Discussion

In both Gonarezhou and Tuli direct lion density estimates were considerably lower than the theoretical estimates, a finding not repeated for spotted hyaenas. Similar findings are presented by Croes et al. (2011) for northern Cameroon. Before discussing this it is important to evaluate potential biases, some of which could be inherent in the survey design. However, given their similar climatic and vegetation characteristics we see no reasons why the method used in Kruger (Ferreira & Funston, 2010) should not be applicable to the Zimbabwe study sites. The fact that lions were actively hunted in Tuli could also bias the lion response to call-up there. However, lions were not hunted in Tuli using sound recordings or from a vehicle, thus limiting the potential for negative association. Moreover, the complete lack of lion spoor in Tuli, and infrequent reports by rangers of a total of no more than four lions suggest that these results are credible. In Gonarezhou our call-up results correlated closely with spoor survey results (Groom, 2010) and other, anecdotal, evidence. Thus we are reasonably confident that our estimates of lion and spotted hyaena abundance are accurate.

It could be argued that the extrapolation of ungulate estimates from the Northern Tuli Game Reserve may have overestimated ungulate biomass in the Tuli Safari Area. This could be a result of trophy hunting and possibly higher poaching levels in Tuli. However, spotted hyaena numbers were close to the predicted density, and although they forage widely and predate livestock, it is unlikely that the recorded numbers could be sustained without sufficient natural prey.

TABLE 2 Lion quota figures, including both male and female lions, for the twelve hunting concessions in Zimbabwe adjacent to Gonarezhou National Park, and in Tuli Safari Area (where only male lions were on quota) for 2001 to 2011 (data from Roseline Chikerema-Mandisodza, Zimbabwe Parks and Wildlife Management Authority sport hunting quotas, 2000–2011 records).

Name of property	Area type*	01	02	03	04	05	06	07	08	09	10	11	Total
<b>Gonarezhou National Park (males)</b>													
Malipati Safari Area	SA	1	1	1	1	1	1	1	1	1	0	0	9
Sengwe Area 1	CF	1	1	1	1	1	1	1	1	1	0	0	9
Sengwe Area 2	CF					0	0	0	1	1	0	0	2
Malipati Communal	CF							0	0	0	0	0	0
Naivasha	CF	3	3	2	2	0	0	0	1	1	0	0	12
Chibwedziva	CF	1	1	1	1	0	0	0	1	1	1	1	8
Chizvirizvi	CF	0	0	0	0	0	0	0	0	0	0	0	0
Chitsa	CF	2	2	2	2	0	0	0	0	1	1	1	11
Mahenya/Mutandahwe	CF	1	1	1	1	1	1	1	1	1	0	0	9
Gonakudzingwa Area 1	CO				0	0	0	0	0	1	0	0	1
Gonakudzingwa Area 2	CO						1	1	0	1	0	0	3
Malilangwe Reserve	PR	0	0	0	0	2	2	2	1	1	1	1	10
<i>Total</i>		9	9	8	8	5	6	6	7	10	3	3	74
<b>Gonarezhou National Park (females)</b>													
Naivasha	CF	1	1	1	1	1	0	0	0	0	0	0	5
Chibwedziva	CF	1	1	1	1	0	0	0	0	0	0	0	4
<i>Total</i>		2	2	2	2	1	0	0	0	0	0	0	9
<b>Tuli Safari Area</b>	SA	1	1	1	2	2	3	3	2	1	0	0	16

\*SA, safari area; CF, CAMPFIRE area; CO, cooperative; PR, private conservancy

Hunting records for Tuli for 2005–2010 indicate a consistently high trophy quota and hunt success rate for key lion prey species. Thus we are confident that the ungulate abundance estimates were relatively accurate.

Another consideration is that potential predator densities based solely on prey biomass data are not always realistic, especially in areas with highly skewed prey distributions. For example, in Gonarezhou permanent water is restricted to the major river systems and a few perennial pans, which are where the majority of ungulates are concentrated in winter (see maps in Dunham et al., 2010). Thus, while there may be sufficient numbers of prey it is possible that their seasonal distribution may restrict the potential number of lion territories (Packer et al., 2005). However, even in more arid systems lions occupy territories that are seemingly little influenced by water distribution (Funston, 2011).

Thus, even if our lion estimates were biased by any of these factors, the differences between the predicted and estimated lion numbers are so extreme that we are confident that lions are currently well below their potential densities in both areas, having experienced a population collapse at some time in the past. This, combined with spotted hyaena densities approximating potential densities, suggests that prey biomass was not the driver of low lion abundance in these areas. This is further supported by the fact that estimates of densities of other carnivore species in Gonarezhou (R. Groom, unpubl. data) were similar to

predicted densities; e.g. for leopards *Panthera pardus* (159 leopards from the spoor survey, using the equation of Funston et al. (2010), compared with 121 predicted from the Hayward et al. (2007) model) and for African wild dogs *Lycaon pictus* (c. 80 wild dogs from direct monitoring compared with 72 predicted by the model).

After reviewing the literature for other potential drivers of low lion abundance we conclude that these could include intra-guild competition with spotted hyaenas, diseases or anthropogenic influences. Both areas had a relatively high density of spotted hyaenas (8.1–10.8 per 100 km<sup>2</sup>). However, there is no firm evidence suggesting that hyaenas affect lion populations (Hayward & Kerley, 2008), although they may compete with them for carcasses (Cooper, 1991).

Disease can severely affect lion populations (Kissui & Packer, 2004; Cleaveland et al., 2005) but there was no evidence of any disease in the lions in either reserve and there were no reports of sick, thin or weak lions and no unexplained carcasses. Although bovine tuberculosis has been noted in lions in nearby Kruger (De Vos et al., 2001; Michel et al., 2006; Keet et al., 2010), it is mainly restricted to southern Kruger (Rodwell et al., 2000) and at present there is no evidence of it affecting either African buffalo (Cross et al., 2009) or lion populations (Ferreira & Funston, 2010) there.

Thus we do not ascribe the suppression of lion numbers to disease and conclude that the population collapse was most likely driven by anthropogenic influences.

We surmised that these could include unsustainably high trophy hunting quotas within Tuli and in the concessions around Gonarezhou, illegal killing of lions (including shooting, poisoning and snaring) both in and outside these areas, and high levels of lethal problem animal control.

In assessing the impact of trophy hunting we consider that although Gonarezhou is a protected area with no legal utilization of lions, hunting of lions is allowed in all concessions areas adjacent to the Park. The majority of these are CAMPFIRE areas and most of the lions hunted originate from the Park (RJG, pers. obs.). Quotas are generally proposed by the landowners or CAMPFIRE or council representatives and approved by the Parks and Wildlife Management Authority, which has typically based the allocation at least partly on estimates of the number of lions in the Park. Prior to our recent population surveys these were considerably overestimated. Between 2001 and 2011 a total of 74 male and nine female lions were on quota in the Zimbabwe hunting concessions adjacent to Gonarezhou. However, there have been no females on quota since 2006, and only six males since 2009, after recognition of the low lion numbers in the Park and decreasing trophy size. No lions have been hunted in these concessions since 2009. In the 980 km<sup>2</sup> of hunting area adjacent to Gonarezhou in Mozambique the 2009 quota of seven male lions was 14 times higher than the general recommendation of 0.5 lions per 1,000 km<sup>2</sup> (Packer et al., 2011).

Similarly high quotas were set for the much smaller Tuli Safari Area, with a total of 16 male lions on quota between 2000 and 2009, with three on quota in each of 2006 and 2007. This is a high number for an area of only 416 km<sup>2</sup> and would no doubt have had a major impact on the lion population, despite no females being hunted. A moratorium on hunting of lions in Tuli was imposed in 2010 and 2011 because of this.

Significant edge effects in Gonarezhou may have been induced by hunters drawing lions out of the Park with carcass baits placed near the Park boundaries, as has been reported elsewhere (Loveridge et al., 2007). The primary problem with this is the concomitant territorial vacuum that draws lions from further inside protected areas, which increases their vulnerability to hunting and increases infanticide rates in boundary prides (Loveridge et al., 2007). The extent of these effects depends on the size and shape of the protected area and the home range dynamics of its lions. Gonarezhou, although relatively large, is long and thin, greatly increasing its boundary length to surface area ratio and thus its vulnerability to edge effects (Woodroffe & Ginsberg, 1998). Furthermore, given the relatively low prey density in the Park, lion home ranges are likely to be large. Even in Hwange National Park Loveridge et al. (2009) found that lion home ranges there typically covered several hundred km<sup>2</sup>. It is thus likely that in Gonarezhou almost all lion prides would have home ranges that include boundary

areas of the Park, exposing them to the risks outlined above. Although not the only factor, excessive trophy hunting combined with significant edge effects suggests that hunting has probably had a strong negative effect on lion abundance in both reserves.

These effects are also potentially exacerbated by both illegal killing and problem animal control. Within and outside both reserves lions were illegally killed for skins, caught in snares and also probably affected by the poisoning events recorded for other species (H. van der Westhuizen, pers. comm.; Snyman, 2011). Lions are often accidentally caught in wire snares set for other species (Lindsey et al., 2011) and are especially vulnerable because they are attracted to carcasses in snare-lines. In Hwange National Park 11.8% of recorded lion mortality was because of snaring (Loveridge et al., 2007). Generally, however, these sources of mortality are difficult to measure accurately as evidence of illegal killing is often concealed (Loveridge et al., 2007) but anecdotal evidence suggests they may be considerable.

Another important cause of lion mortality in Gonarezhou was the destruction of lions considered to be problem animals. Problem animal control incidences are poorly recorded and the responsibility is often handed over to hunting operators, with apparently little record-keeping (RJG, pers. obs.). However, we acquired records of at least 18 lions being shot as problem animals between 1993 and 2009 around the southern half of Gonarezhou. In many cases the sex of the lion killed was not recorded but at least five of them were females and one was a cub. This is likely to affect the population negatively, as regular removal of even small numbers of reproductive females can expose a population to decline (Van Vuuren et al., 2005). Moreover, as reproductive success is closely related to pride size, and prides of three or more adult females are significantly more successful at rearing cubs than smaller prides (Packer et al., 1988), removal of adult females may result in lower cub survival. Since 2009 there has been virtually no lethal problem animal control for lions around Gonarezhou, although lions are still reported to be killing livestock and there is evidence that communities poison them. Exact figures are unknown but presumed to be higher than recorded.

There is a growing recognition that efforts must be made to reduce conflict between carnivores and local communities. These include education and outreach efforts, training in predator-friendly livestock management practices, and increasing community benefits from wildlife resources. Additionally, effective law enforcement is critical, and appropriate penalties for illegal killing of carnivores need to be enforced. Effective anti-poaching efforts to reduce deaths in snares, reduction of unnecessary lethal problem animal control, and enhanced cooperation with relevant authorities in neighbouring countries for effective cross-border law enforcement are also crucial.

There are also several interventions that could be considered to reduce the edge effects of hunting, including banning the use of baits on park boundaries, monitoring trophy ages, with appropriate penalties for harvesting underage animals (Whitman et al., 2004), establishing buffer zones where lion hunting is excluded along park boundaries (Loveridge et al., 2007), and ensuring quotas are realistic and based on robust population estimates and/or limiting quotas based on the area of the hunting concession (Packer et al., 2011). If the guideline of 0.5 lions per 1,000 km<sup>2</sup> (Packer et al., 2011) were enforced this would preclude lion hunting in Tuli and probably reduce the hunting around Gonarezhou to sustainable levels, as long as this guideline was followed in Mozambique as well as in Zimbabwe.

Our results suggest that where carnivore populations are subject to anthropogenic influences, densities derived from prey biomass equations tend to be overestimated and should be treated with caution, even for protected areas. The low lion populations in both of the studied protected areas in Zimbabwe are largely attributable to the net effect of various anthropogenic influences, primarily previously excessive trophy hunting and indiscriminate problem animal control, with additional influences of poaching and persecution. Given the widespread and strikingly similar problems in many other areas (Ogutu et al., 2005; Woodroffe & Frank, 2005; Kiffner et al., 2009; Packer et al., 2009; Tumenta et al., 2010) and for other species (Balme et al., 2010), it is critical that effective strategies are designed and implemented to reduce these negative impacts. Trophy hunting for lions is a valuable management and conservation tool but needs much stricter regulation, especially in and around relatively small and/or isolated protected areas.

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## Biographical sketches

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