



Conservation of large predator populations: Demographic and spatial responses of African lions to the intensity of trophy hunting



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ABSTRACT

Large predators are in decline globally with growing concerns over the impacts of human activity on conservation status and range of many populations. The role of trophy hunting in the conservation or decline of predators is hotly debated, though opposing views are often poorly supported by empirical evidence. Nevertheless an understanding of effects of trophy hunting on populations and behaviour is critical to the conservation of large carnivore populations. The impacts of trophy hunting on African lion population demographics, social structure and spatial behaviour were investigated in Hwange National Park, Zimbabwe, from 1999 to 2012, a period characterized by different trophy hunting intensities. Adult males were primarily targeted by trophy hunters, but survival of all age and sex classes were lowest when male lion off-takes were highest. Reduction in hunting quotas over the study period resulted in a 62% increase in the total population and a 200% increase in adult male density. Adult sex ratios were highly skewed towards females when hunting was intense. Intensity of hunting affected male and female home-range size, which declined in periods of low hunting corresponding to increases in adult males and male coalitions. Trophy hunting on the park boundary exerted a measurable edge effect with lower survival for animals of all age and sex classes living on the park boundary compared to those distant from it. This study provides evidence for negative impacts of uncontrolled trophy hunting on lion population and behaviour. However, limited, well regulated quotas may be compatible with large carnivore conservation.

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1. Introduction

Loss of apex predators has profound effects on terrestrial ecosystems potentially resulting in destabilisation of herbivore-plant interactions, reduction of diversity, and loss of resilience within ecosystems (Ripple et al., 2014). Globally, large carnivore populations are in decline due to habitat loss, conflict with people over livestock depredation and over-exploitation (Loveridge et al., 2010b). Trophy hunting is a potential cause of over-exploitation and decline of carnivore populations, and has thus been highlighted as a cause of conservation concern (Becker et al., 2013; Cooley et al., 2009; Packer et al., 2009). Indeed, hunting may cause social perturbation in territorial species and amplify mortality through sexually selected infanticide (Swenson et al., 1997). Removal of males further creates vacua within the territorial structure which are filled by new males, often from protected source populations (Loveridge et al., 2007) exerting a measurable edge effect on protected populations (Kiffner et al., 2009; Loveridge et al., in press).

Indiscriminate harvest of males has been shown to hamper recruitment and cause population declines both theoretically (Caro et al., 2009) and in practice, with areas most heavily hunted showing the most significant population declines (Packer et al., 2011; Packer et al., 2009). However, limiting harvests to older males has been shown to be sustainable (Creel et al., 2016; Whitman et al., 2004) and there is evidence that trophy hunting incentivises conservation of wild habitats and provides revenues for conservation (Lindsey et al., 2012). Potential for over-exploitation juxtaposed with the benefits of sustainable use in conserving ecosystems underlines the need for clear, science-based evidence to demonstrate the sustainability of trophy hunting and mitigate against adverse effects on the conservation status of hunted populations. Sparked by several high profile and publically debated incidents (Creel et al., 2015; Macdonald et al., 2016a), there is global concern over the extent to which wild animal populations are exposed to trophy hunting and the potential impacts this has on the conservation status and population viability of wild species, many of which are already under threat. Despite widespread trophy hunting of carnivores, there is little empirical evidence to quantify the impact of hunting, particularly on African carnivores. To date much of the evidence supporting sustainable trophy

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hunting of large carnivores is derived from population simulation models (Caro et al., 2009; Taylor et al., 2008; Whitman et al., 2004), the results of which have yet to be tested under field conditions.

Both lion populations and their geographic range have declined rapidly over the last few decades (Bauer et al., 2015), and recently global concern over the impacts of hunting on this species has prompted several governments, including Australia, the European Union and USA, to take direct steps to control or ban imports of lion trophies (USFWS, 2015; Vaughan, 2015). However, significant regional populations remain, many being protected within lands set aside for trophy hunting (DiMinin et al., 2016) and lion hunts command amongst the highest prices and contribute between 5 and 17% of hunting revenue (Lindsey et al., 2012), which may provide significant incentives to conserve both lions and lion habitat. There is therefore an urgent need to better understand the link between trophy hunting and the conservation of lion populations, and large carnivore populations in general.

Here, we present long-term data on the impact of trophy hunting on the conservation status of a protected African lion *Panthera leo* population, in Hwange National Park, Zimbabwe, one of ten remaining lion strongholds in Africa (Bauer et al., 2015). This population is subjected to trophy hunting in surrounding hunting concessions and evolving management of lion trophy hunting regimes over a thirteen year period (1999–2012) has provided a unique opportunity to assess the impact of hunting on population demographics, social structure, spatial ecology and their influence on the conservation status of this population.

2. Methods

2.1. Study site

Hwange National Park (HNP), (14600 km², 19° 00' S, 26°30' E) is an arid, dystrophic savannah ecosystem (Rogers, 1993). Mean annual rainfall is 600 mm and highly variable and water is artificially supplied at water-points in the dry season. Trophy hunting occurs on all lands, including communal land, adjacent to the HNP boundary, but not within the park (Fig. A1, Online Appendix).

2.2. Lion management data

Annual hunting quota and off-take data were collated from Zimbabwe Parks and Wildlife Management Authority (ZPWMA) and project records (Fig. 1; Table A1, Online Appendix). The system of quota allocation is described in Loveridge et al. (2009a). We recognise three distinct management periods. From 2000 to 2004, trophy hunting of both males and females was intense and largely indiscriminate with a high proportion (c. 30%) of males being sub-adult (<4 years) (Loveridge et al., 2007), we term this the 'pre-intervention' period. From 2005 to 2008, based on the initial findings of this research (Loveridge et al., 2009a; Loveridge et al., 2007), a hunting moratorium was imposed by ZPWMA for the entire province (Matabeleland North), we term this the 'intervention period'. Finally, based on evidence of population recovery (Davidson et al., 2011; Loveridge et al., 2010a), limited, male only hunting quotas were introduced in 2009. We use the term 'post-intervention' to describe this management period, corresponding to the years 2009–2012. The three varying intensities of hunting off-take provide the basis for comparison of survival rates, demographic structure and space use between periods.

2.3. Lion population monitoring

From 2000 to 2012, we intensively monitored a core study area of 2769 km², where road access was extremely good (Fig. A1 Online Appendix) within a more extensive study area (c 7000 km²) where we monitored 33 prides and 29 male coalitions or singletons and developed a database of 626 lions, individually identified by whisker patterns (Pennycuik and Rudnai, 1970) and other natural physical

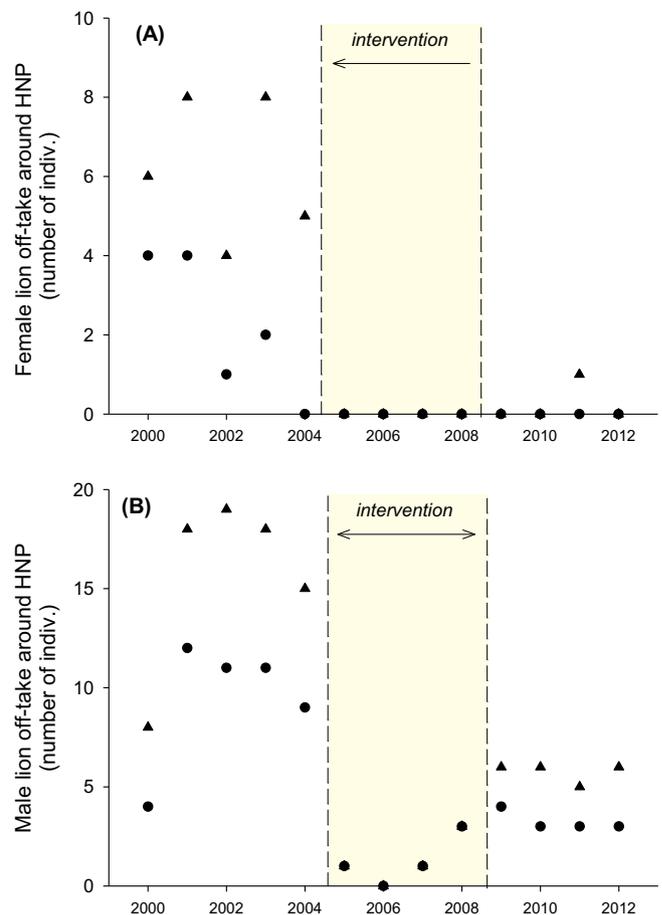


Fig. 1. Hunting off-takes of A) female and B) male lions in hunting concessions adjacent to HNP for the period 2000–2012. Circles denote off-takes from directly adjacent to the core study area and triangles total off-take from all hunting areas adjacent to Hwange National Park.

characteristics to record births, deaths, immigration and emigration (Barthold et al., 2016). Within the core study area 53 ± 22 (range 22–94) % of males, 81 ± 18 (range 50–100) % of coalitions, 35 ± 8 (range 29–48) of females and 67 ± 13 (range 40–78) % of prides were instrumented for telemetry. We radio-collared 140 lions (62 adult males, 19 sub-adult males, 59 females) with VHF radio-collars (Sirtrack Ltd, Havelock North, New Zealand; 600 g) or global positioning system (GPS) collars with either UHF or satellite remote downloads (Televilt Positioning, Lindsberg, Sweden, 950 g; Sirtrack, 1460 g; Africa Wildlife Tracking, Pretoria, South Africa, 1400 g). Lions were immobilised for handling by qualified field staff using standard protocols for the species (Fahlman et al., 2005). Study animals were located weekly to bimonthly from a 4×4 vehicle or microlight aircraft. Positional data from the GPS radio-collars were downloaded (one location hourly from 18 h00 to 7 h00), and observations made of group composition.

We estimated annual population size in the core study area following the approach of Rosenblatt et al. (2014) for the South Luangwa lion population in Zambia. We used MARK (White and Burnham, 1999) to fit Huggins closed-capture models (White, 2008), selecting the best models with Akaike's Information Criteria and estimating annual population size for the total population, adult males, adult females and sub-adults (24–48 months). All prides and coalitions in the intensive study area were known.

2.4. Analysis of survival in response to hunting intensity

Survival and cause specific mortality rates of adult lions were calculated from telemetry data using the modified Mayfield method (Heisey

and Fuller, 1985), which performs well when sample sizes are small (most studies of large carnivores), provides reasonable precision when mortality rates are high (Murray, 2006) and allows comparison of cause specific mortality rates (Heisey and Patterson, 2006). Annual survival and cause-specific mortality rates for trophy hunting, human lion conflict (problem animal control and retaliatory killing), poaching and other causes of mortality were calculated and averaged for each management period. Survival and mortality rates were compared using the statistical procedure of Hines and Sauer (1989).

The Kaplan-Meier survival estimator (PASW Statistics v18.0, 2012) was used to compare survival times for adults and cubs between management periods. This procedure allows for staggered entry of animals typical of a radio-telemetry study and can cope with censored data where the fate of some individuals cannot be confidently assigned (Pollock et al., 1989). For radio-tagged adults we calculated the number of radio-days (collar fitted to one individual for one day) from the date the radio-collar was fitted until the date the animal died, was censored or survived to the end of the study period. Previous analyses have shown that survival differs between sexes so male and female data were analysed separately. For cubs, survival times were recorded as cub age in months. Cubs surviving to 24 months or which had not reached this age but had not died by the end of the study were right censored from the analysis. As edge effects are known to have significant impacts on lion populations (Loveridge et al., 2010a), we stratified the analysis by whether cubs came from prides whose ranges straddled or were directly adjacent to the park boundary or within the core of the park (mean of 17.8 ± 8.5 km, range 3.8–36.2 km from the park boundary). A total of 284 (131 male and 153 female) cubs were sexed. Pilot analysis showed there was no evidence for an effect of sex on survival times between male and female cubs in either core or edge areas (Log-Rank Test (Mantel Cox): Edge $X^2 = 0.566$, d.f. = 1, $p = 0.452$; Core: $X^2 = 0.422$, d.f. = 1, $p = 0.516$). We did not, therefore, differentiate between the sex of cubs in subsequent analyses.

We used a Cox Proportional Hazard Regression model (PASW Statistics v18.0, 2012) to examine covariates that influenced survival of adult males, adult females and cubs. In the hazard model an event was defined as mortality of the individual and for each event we recorded the age in months (cubs) or number of radio days (adults) at which the individual died. For adults covariate predictors in the hazard model were location of the home-range in relation to the park boundary (whether on the edge or within the core), group size (number of adult females in pride and males in coalition) and the management period. For cubs covariate predictors were number of adult females in the pride, number of cubs in the age-set (cubs born into the same pride within 6 months of each other), the location of the pride range in the park and management period. For all analysis variables were entered simultaneously into an adjusted model (there was no effect of the order of entry into the model).

2.5. Analysis of population estimates and structure in response to hunting intensity

We explored how the estimates of the different lion demographic groups (total population, male adults, female adults, sub-adults), group size and the adult sex ratio changed over management periods using linear models. Management period and year were included as explanatory variables and the interaction management period*year tested to assess change in slope. Annual rainfall was included as a co-variable to account for potential seasonal changes in herbivore abundance and availability. Statistical analyses were performed with R software (R Core Team 2012 v2.15.2, 'lm' function).

2.6. Analysis of space use in response to hunting intensity

We used data from 36 female and 45 male adults fitted with GPS radio-collars to calculate seasonal 4-month home ranges (home ranges

hereafter) for resident individuals whose GPS receiver was operational during an entire 4-month season. Three seasons are distinguished in this study: wet season (November–February), early dry season (March–June), and late dry season (July–October). The wet season of year Y corresponded to the period between November of year Y-1 and February of year Y. We defined home ranges as the 90% probability contour of location distribution using the fixed kernel density estimator and reference smoothing factor h_{ref} (Börger et al., 2006). Home ranges were calculated using "adehabitat" for R software (Calenge, 2006).

Because pride biomass and annual rainfall are likely to influence the size of a lion home range (Loveridge et al., 2009b), we included these factors in the analyses. Pride biomass was calculated from the composition of each pride and field data for adult weight; mean weight (\pm SD) was 199 ± 10 kg for adult males ($N = 4$) and 143 ± 11 kg for adult females ($N = 6$). These weights are consistent with those published for southern African populations (Smuts et al., 1980). For cubs and sub-adults, we used growth equations from Smuts et al. (1980) to calculate weights. Annual rainfall was calculated from daily records (ZPWMA, Main Camp station) and defined as the rainfall that fell between October and September the following year.

118 female seasonal home ranges (from 30 females) and 94 male seasonal home ranges (from 25 males) were analysed. We fitted a mixed linear model with restricted maximum likelihood estimation, using home range size as the dependent variable and individual identity as a random factor. Since several home ranges were calculated for a single individual, we performed repeated measures procedure for lion identity. As temporal serial autocorrelation often affects time series data, we accounted for it using a first-order autoregressive covariance structure. Management period and year were included as explanatory variables and the interaction management period*year tested to assess changes in slopes. Other co-variables were lion group biomass, season, and annual rainfall. The expected underlying mechanism influencing temporal variation in home range size is a consequence of changes in lion density due to the effects of management intervention (an increase in lion density is expected to lead to a decrease in home range size), we therefore performed a similar model but instead of investigating temporal changes, we examined the influence of the population size (number of adult females, prides, adult males, coalitions and adults) on home range size (SAS Institute Inc., 1999, version 8.2, MIXED procedure).

3. Results

3.1. Survival and cause specific mortality rates

For both sexes the lowest survival rates occurred in the pre-intervention period and were highest during the intervention period (Table A1). Female survival rates differed between management periods ($X^2 = 325.3$, d.f. = 2, $p \leq 0.001$). For males, survival rates in the intervention and post-intervention period differed from those in the pre-intervention period ($X^2 = 4.39$, d.f. = 1, $p = 0.04$). For both sexes mortality to trophy hunting differed between management periods (females: $X^2 = 8.56$, d.f. = 2, $p = 0.01$; males: $X^2 = 10.98$, d.f. = 2, $p = 0.004$) with the highest mortality occurring in the pre-intervention period. Mortality rates for snaring and human-lion conflict did not differ between periods for either females or males. Natural mortality (as a result of intra-specific fights, hunting accidents or old age) did not differ between periods for females, but increased for males with slightly higher rates in the intervention and post-intervention periods (Table A1).

3.2. Adult male survival

Of 62 radio-collared adult males, 40 died during the study; 13 of 19 (68.4%) in the pre-intervention period, 12 of 27 (44.4%) in the intervention period and 15 of 33 (45.5%) in the post-intervention period. Survival times of adult males differed between management periods (Kaplan-

Meier estimator, Mean \pm SE (95% CI) days: pre-intervention: 493.3 \pm 79.1 (338.2–648.4); intervention: 914.6 \pm 108.8 (701.3–1127.9); post-intervention: 914.9 \pm 94.8 (729.1–1100.7), Log Rank (Mantel-Cox) Test, $X^2 = 10.057$, d.f. = 2, $p = 0.007$). The hazard rate for adult male mortality was most influenced by location (Cox-Proportional Hazard model: $B = 1.57 \pm 0.456$, Wald = 11.862, d.f. = 1, $p = 0.001$, $\text{Exp}(B) = 4.808$ (95% CI = 1.967–11.751), suggesting the chances of mortality were 4.8 times higher for males on the edge compared to the core of the protected area. Overall, management period had a significant influence on the hazard rate (Wald = 6.018, d.f. = 2, $p = 0.049$); the effect of the management period did not differ significantly from that of the pre-intervention period (Wald = 2.585, d.f. = 1, $p = 0.11$), however influence of the post-intervention period differed significantly from the pre-intervention period ($B = -0.849 \pm 0.357$, Wald = 5.655, d.f. = 1, $p = 0.017$). Coalition size had no effect on the hazard rate (Wald = 2.323, d.f. = 1, $p = 0.128$).

3.3. Adult female survival

Of 59 radio-collared females, 41 died during the study; 16 of 34 (47.0%) died in the pre-intervention period, 11 of 32 (34.4%) in the intervention period and 14 of 29 (48.3%) died in the post-intervention period. Survival times of females did not differ between management periods (Kaplan-Meier estimator, Mean \pm SE (95%CI) days: pre-intervention: 901.7 \pm 121.4 (663.8–1139.7); intervention: 1025.5 \pm 96.5 (836.4–1214.6); post-intervention: 830.0 \pm 122.4 (590.1–1069.9), Log Rank (Mantel-Cox), $X^2 = 2.97$, d.f. = 2, $p = 0.227$). The hazard rate for female mortality was influenced only by location of the pride in relation to the protected area edge (Cox-Proportional Hazard model: $B = 0.872 \pm 0.368$, Wald = 5.605, d.f. = 1, $p = 0.018$, $\text{Exp}(B) = 2.392$ (95%CI, 1.162–4.925)). The potential for mortality to occur was almost two and a half times higher on the park edge than in the core. Neither management period nor pride size had an effect on the hazard rate in the model.

3.4. Cub survival

Records of survival were available for 411 cubs in 25 prides. 145 cubs were born during the pre-intervention period, 118 during the intervention period and 148 were born during the post-intervention period. 230 cubs were born in 18 'edge' prides, 181 cubs were born in 14 'core' prides. Overall, 198 cub mortalities were recorded between 2000 and 2012. Survival of cubs in 'core' prides was not influenced by management period (Kaplan-Meier estimator: Log Rank (Mantel Cox) test, $X^2 = 3.84$, d.f. = 2, $p = 0.15$, overall mean survival time 20.2 \pm 0.58 (SE) months; 95% CI = 19.1–21.3). However, management period influenced survival of cubs in 'edge' prides ($X^2 = 14.12$, d.f. = 2, $p = 0.001$; mean survival times [months \pm SE, 95% CI]: pre-intervention: 13.4 \pm 0.88 months, 11.7–15.2; intervention period 13.4 \pm 1.28 months, 10.9–15.9; post-intervention period 15.8 \pm 1.03 months, 13.9–17.8).

Location (edge or core) was highly influential in determining the survival of cubs. Mortality of cubs in prides living in 'edge' areas was three times more likely to occur than for cubs in core areas (Cox Proportional Hazard model $B = 1.114 \pm 0.049$ (SE), Wald = 37.756, d.f. = 1, $p = 0.00$; $\text{Exp}(B) = 3.046$, 95% CI = 2.135–4.345). Size of a cub's age set also had a significant influence on survival. Mortality was 6.7% less likely for every additional cub in an age set ($B = -0.069 \pm 0.033$, Wald = 4.364, d.f. = 1, $p = 0.037$; $\text{Exp}(B) = 0.933$, 95% CI = 0.874–0.996). Overall, management period had a significant effect on the potential for cub mortality to occur (Wald = 9.466, d.f. = 1, $p = 0.009$). Mortality did not differ between the 'intervention' period compared to the 'pre-intervention' period ($B = -0.292 \pm 0.189$, Wald = 2.385, d.f. = 1, $p = 0.123$), but was 44.2% lower in the 'post-intervention' period compared to the 'pre-intervention' period ($B = -0.584 \pm 0.190$, Wald = 9.464, d.f. = 1, $p = 0.002$; $\text{Exp}(B) = 0.558$, 95% CI = 0.385–0.809). There was no evidence for an effect of the number of adult

females in the pride on survival (Wald = 0.392, d.f. = 1, $p = 0.531$), likely because pride size is highly correlated to size of age sets and location of the pride in relation to the park boundary.

3.5. Population estimates and structure

Population estimates obtained by capture-mark-recapture analysis had very narrow confidence intervals suggesting that most lions in the study area were observed (Fig. 2C–F).

The slopes of relationships between year and estimates of adult female, adult male, and coalition number differed between the different management periods (female: $F_{2,7} = 12.56$; $p = 0.0048$; male: $F_{2,6} = 13.57$; $p = 0.0059$; coalition: $F_{2,6} = 6.56$; $p = 0.0309$) with significant increases during the intervention period (Table A2 Online Appendix, Fig. 2B, C, and D). The number of prides did not significantly change during the study. However, for pride size and coalition size, the management period*year interaction was significant at the p-level of 0.1 ($F_{2,7} = 3.63$; $p = 0.083$ and $F_{2,7} = 4.27$; $p = 0.061$ respectively), showing a relative stability in the period before the intervention, an increase in slope after it, and a decrease after the intervention period (Table A2 Online Appendix, Fig. 3A, B). The number of sub-adults was not influenced by the interaction management period*year, but was influenced by the management period ($F_{2,10} = 12.26$; $p = 0.002$): sub-adult numbers were higher during the post-intervention period than during the intervention period ($t_{1,10} = 4.55$; $p = 0.001$), which was not significantly different from the pre-intervention period ($t_{1,10} = 0.74$; $p = 0.47$; Fig. 2E). For overall lion number, the management period*year interaction was not significant ($F_{2,7} = 3.12$; $p = 0.107$; relationship close to significance at the p-level 0.1), but there was a significant effect of management period ($F_{2,10} = 6.33$; $p = 0.017$) with the estimated total number of lions during the intervention period significantly higher than before the intervention ($t_{1,10} = -2.38$; $p = 0.039$) but not significantly different than after the intervention ($t_{1,10} = 0.99$; $p = 0.34$; Fig. 2F).

There were strong negative correlations between levels of hunting off-take and estimated number of males and coalitions, with obvious implications for total lion numbers and the adult male: adult female sex-ratio (Table A3 Online Appendix). The relationship between pride size and female hunting off-takes was significant at the p-level 0.1 (Table A3).

The sex ratio of the adult population (females/males) was influenced by management period ($F_{2,10} = 15.59$; $p = 0.0008$) with the sex ratio being higher before the intervention period ($t_{1,10} = 4.29$; $p = 0.0016$; Fig. 3C). Males comprised 35 \pm 4% of the adult population during and after the intervention period whereas they comprised only 22 \pm 4% before. The sex ratio increased in favour of females as hunting off-takes increased (Table A3).

3.6. Space use

For females, the interaction year*management period had a significant effect on female home range size with a negative slope estimate during the intervention period (estimate \pm SE = -55 ± 23), which was significantly different from the positive slope estimate pre-intervention (estimate \pm SE = 170 ± 53 ; $t_{96,64} = 4.21$; $p < 0.0001$); it was also different after the intervention period but the result only approached significance (estimate \pm SE = 14 ± 36 ; $t_{98,10} = 1.90$; $p = 0.061$; Fig. A2a, Online Appendix). No other significant effect (rainfall, season, pride biomass) was detected. Female home range size decreased as the number of coalitions increased (estimate \pm SE = -21.43 ± 10.37 ; $F_{1,47} = 4.27$; $p = 0.044$; Fig. A2, Online Appendix), as the number of males increased (estimate \pm SE = -10.74 ± 4.57 ; $F_{1,92} = 5.53$; $p = 0.021$), and as the number of females increased (estimate \pm SE = -7.27 ± 3.21 ; $F_{1,99} = 5.13$; $p = 0.025$). Female home range size was not affected by the number of prides.

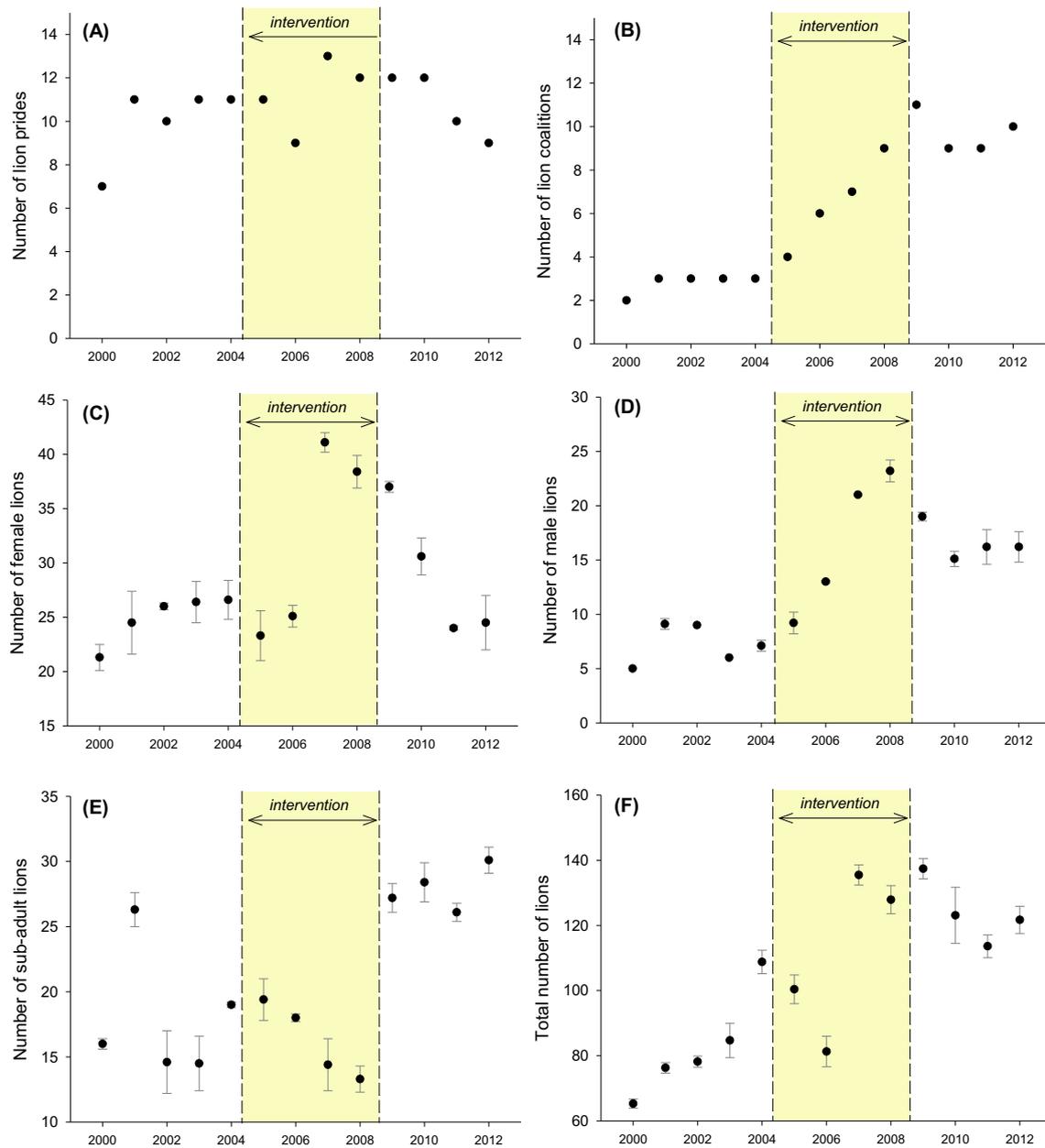


Fig. 2. The number of A) female prides, B) male coalitions, C) adult females, D) adult males, E) sub-adults, and F) total population in the intensively monitored core study area in Hwange National Park from 2000 to 2012. Error bars denote Standard Deviation.

For males, there was no effect of the interaction year*management period ($F_{2,52} = 1.09$; $p = 0.34$). However, a long-term decreasing trend in home-range size was detected ($F_{1,17} = 6.70$; $p = 0.0185$; Fig. A2b) as well as an influence of season ($F_{2,64} = 13.56$; $p < 0.0001$) with home ranges in the wet and early dry seasons larger than in the late dry season. Male home range size was not affected by any demographic group number but there was a negative relationship with the number of males significant at the p-level 0.1 (estimate \pm SE = -12.4 ± 6.39 ; $F_{1,13} = 3.77$; $p = 0.072$).

4. Discussion

Large mammalian predators are in decline globally and their management and conservation have come under increasing scrutiny. There is significant societal concern, and in some cases outrage, over the often widespread use of trophy hunting as a tool to manage and

conserve wild animals and the practice is increasingly questioned (Macdonald et al., 2016a; Macdonald et al., 2016b; Nelson et al., 2016). Many large felid (e.g. African leopard *Panthera pardus*: Balme et al., 2010; cougar *Puma concolor*: Cooley et al., 2009, Maletzke et al., 2014), ursid (e.g. polar bear *Ursus maritimus*: Taylor et al., 2008) and canid populations (e.g. wolves *Canis lupus*: Creel et al., 2015) are trophy hunted. While there are widely held ethical objections to hunting predators and other wild animals for sport, many concerns stem from the suggestion that over-hunting may be responsible for predator population declines. Despite heated debate, there is frequently a paucity of empirical data, particularly for ecosystems outside North America, to demonstrate either sustainability or damaging effects. Consequently, wildlife management and conservation policy is frequently the result of the divergent objectives of managers and different stakeholder groups and less frequently the result of explicit tests of ecological hypotheses. Our long-term study of a lion population spanning three

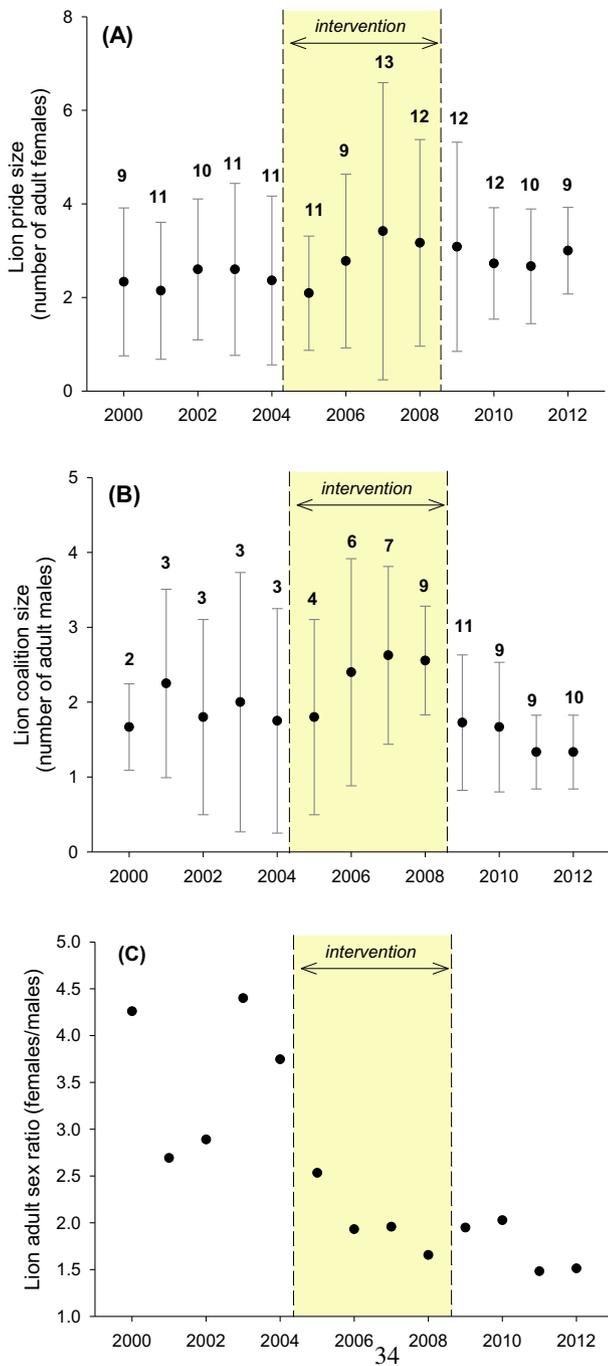


Fig. 3. Graphs showing the a) mean lion pride size b) mean lion coalition size and c) adult sex ratio (number of females per male) in the core study area in Hwange National Park from 2000 and 2012. Yearly numbers of prides or coalitions are shown in parentheses. Error bars denote Standard Deviation.

contrasting periods of trophy hunting intensity provides a unique opportunity to test explicitly the impacts of different trophy hunting regimes on population dynamics, population structure and spatial behaviour of a large carnivore population, and ultimately the impact of trophy hunting on conservation of this species. Prior to 2005 trophy hunting of lions in hunting concessions bordering HNP was intense vastly exceeding the conservative off-take of 0.5 lions/1000 km², recommended for higher density Tanzanian populations (Packer et al., 2011). Management of hunting quotas was revised in 2005 with imposition of a four year hunting moratorium, followed by the introduction of relatively conservative quotas.

4.1. Impacts of trophy hunting on survival and population demographics

The moratorium on trophy hunting followed by relatively conservative quotas resulted in a 62% increase in the number of lions and an increase in all demographic groups within the study population, most notably a trebling of adult males and male coalitions. Natural and anthropogenic mortality other than trophy hunting (as a result of conflict with pastoralists or illegal snaring) remained relatively stable throughout the study (Table A1). Prey populations in HNP have been stable for the last decade (Chamaillé-Jammes et al., 2009) and there was no evidence for disease epizootics in carnivores, so we rule out a numerical response to increases in prey or recovery from disease outbreaks as the explanation for changes in lion abundance. This suggests that the observed recovery of the lion population is most likely to be explained by reduced levels of trophy hunting after 2005.

In large, long-lived mammals, such as large carnivores, high mortality of adult age classes has large impacts on population viability and persistence (Crooks et al., 1998; Gaillard et al., 2000) and compensatory population responses (such as sexually selected infanticide) are common in large carnivores exposed to high levels of adult mortality (Swenson et al., 1997; Wielgus et al., 2013). The primary and most direct impact of lion trophy hunting is removal of adult males (less frequently females) from the population. Consequently, density of adult males and male coalitions increased markedly in response to reduced levels of trophy hunting resulting in a cascade of indirect effects on juvenile and sub-adult survival. Frequent removal of territorial males elevates levels of infanticide of dependant cubs (Whitman et al., 2004) resulting in low juvenile and sub-adult survival when hunting is most intense and also premature eviction of sub-adults resulting in higher disperser mortality (Elliot et al., 2014). At light hunting intensities, adult male survival increased and more cubs survived to be recruited into the sub-adult demographic group ultimately resulting in an increase in population size. The effect of hunting on females was less pronounced; female survival rates were lower in the period when hunting pressure was high but there was no effect of either hunting off-take or management period. However, female density increased over the study probably as a result of higher survival and increased recruitment of juvenile females into the population. The slight increase in natural mortality for males in the intervention and post-intervention periods (two mortalities of collared adults due to intra-specific fights in the intervention period and three in the post-intervention period) was potentially a result of an increase in territorial conflict perhaps precipitated by a higher density of adult males in the population.

Edge effects, such as trophy hunting and other forms of anthropogenic mortality (Woodroffe and Ginsberg, 1998) have been shown to have significant impacts on persistence and viability of wide ranging large carnivore populations inside protected areas (e.g. wolves: Creel et al., 2015; African wild dogs *Lycaon pictus*: Woodroffe et al., 2007; leopards: Balme et al., 2010; spotted hyaena *Crocuta crocuta*: Hofer et al., 1993). In our analysis, proximity to the protected area boundary, and thus exposure to 'edge effects' was highly influential in determining survival in adult males, adult females and cubs. Adult males faced high risk of being trophy hunted when their home ranges were on the park boundary and adult females were more likely to be exposed to other sources of anthropogenic mortality in these areas (Loveridge et al., 2010a).

4.2. Impacts of trophy hunting on social structure

Trophy hunted lion populations often have adult sex ratios heavily skewed towards females, ranging between 3 and 6 females per male (Becker et al., 2013; Loveridge et al., 2007), while unexploited populations have less heavily biased sex ratios, usually around 1 male to 2 females (Ogutu and Dublin, 2002; Smuts et al., 1978). In HNP, when hunting off-takes were high, adult sex ratios (~1 male: 3 to 4 females), were characteristic of a heavily hunted population but with declining

off-takes halved to ~1 male: 2 females; similar to that of unexploited populations. Skewed sex ratios have been linked to reduced reproductive success and declining population viability in ungulates (e.g. Saiga Antelope *Saiga tatarica*, Milner-Gulland et al., 2003) and there is evidence that they may impact conception rates in brown bears *Ursus arctos* (Miller, 1993). It is still unclear whether skewed sex ratios have an important effect on breeding success in polygynous carnivores, such as lions, where males routinely mate with multiple females.

In social carnivores living in undisturbed environments, the size of social groups is determined by the richness of resource patches within the home range and the distribution and number of social groups by the distribution of resource patches (Carr and Macdonald, 1986; Valeix et al., 2012). Thus, population increases due to environmental change or recovery from perturbation occur through formation of new social groups rather than increases of existing ones (e.g. lions, Packer et al., 2005; wolves, Hayes and Harestad, 2000, Wabakken et al., 2001). This is the case in this study where coalition sizes did not increase as adult male survival and density increased, instead, the overall number of these social groups increased.

Behaviours that define social carnivores, such as group territoriality and co-operative breeding, mean that reproductive success is highly dependent on the size, stability and social cohesion of groups (e.g. wild dogs, Creel et al., 2004; Ethiopian wolves *Canis simensis* Sillero-Zubiri et al., 2004). In this study, size of the age-set of cubs contributed significantly to reduction of the hazard rate with cubs in large age-sets advantaged, in terms of survival, over those in small ones. This is because large age-sets are inevitably only born into large prides that breed synchronously. Females in large prides are able to defend cubs co-operatively in a crèche and this increases success in raising offspring, with larger prides achieving higher reproductive success (Packer et al., 1988). Synchronous breeding is more likely in socially stable prides, associated with a stable coalition of males, while avoidance of new males by females with young cubs can lead to asynchrony in births.

4.3. Impact of trophy hunting on space use

In social, territorial species, removal of territory holders (by trophy hunters, wildlife management or accidental mortality) causes spatial perturbation, which can increase disease transmission (e.g. European badgers, *Meles meles*, Carter et al., 2007), vulnerability to edge effects (Loveridge et al., in press) and exposure to conflict with people (e.g. cougars, Peebles et al., 2013).

In large felids, male ranges are largely determined by access to mates and male to male competition (Macdonald et al., 2010). As in cougars (Maletzke et al., 2014), male lion range sizes increased when hunting pressure was high and male density correspondingly low. Males moved extensive distances and consorted with multiple prides, unconstrained by territorial competitors (Loveridge et al., 2007). Large fluid ranges increased the likelihood male lions would leave the protected area and made them exceptionally vulnerable to edge effects, particularly trophy hunting. When, hunting pressure was low and male density was high, male-male competition restricted male movements and space was consequently more closely partitioned as evidenced by smaller home ranges. Increased mortality due to male territorial fights as male population density increased provides additional evidence of increased territorial competition between males for more limited space.

In large felids, female ranges are largely determined by resources (Loveridge et al., 2009b; Valeix et al., 2012) but their spatial behaviour can also be driven by the need for sexual segregation to avoid infanticidal males (e.g. brown bears, Steyaert et al., 2013; cougars, Keehner et al., 2015). We recorded the smallest mean range sizes in the period when the number of adult males and density of male ranges peaked. It seems likely that, in situations of high social stability and high male density, female movements were curtailed by avoidance of potentially infanticidal males in surrounding territories and confined their movements to areas controlled by pride males. Conversely, in times of

high pride male turn-over, female ranges may be inflated as females with dependent cubs attempt to avoid new males.

5. Conclusions

There is increasing acknowledgement of the impact of trophy hunting on social behaviour, space use and population status of hunted species. Furthermore, due to the significant spatial disturbance caused by high levels of trophy hunting, our findings point to the possibility that, at the ecosystem level, management of large apex carnivores may also potentially have an, as yet poorly understood, cascade of fine-scale effects on predator – prey interactions and hence possibly wider ecosystem processes.

This study provides quantitative evidence that uncontrolled trophy hunting of African lions was a cause of population decline and significant social and spatial perturbation. It also supports, empirically, population models predicting that harvest of adult males causes indirect mortality of cubs and sub adults through increased levels of infanticide (Creel et al., 2016; Whitman et al., 2004). However, the recovery of the population following improved regulation of trophy hunting in terms of abundance, social structure and ranging behaviour suggests that lions and other large felids (Newby et al., 2013) are relatively resilient in the face of low levels of hunting mortality. This points to the need for limited, well monitored and responsibly managed hunting quotas to be imposed where large predator populations are exploited.

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Appendix A. Supplementary data

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