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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 measureable 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 km^2, 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 km^2, where road access was extremely good (Fig. A1 Online Appendix) within a more extensive study area (c 7000 km^2) where we monitored 33 prides and 29 male coalitions or singletons and developed a database of 626 lions, individually identified by whisker patterns (Pennycuick and Rudnai, 1970) and other natural physical

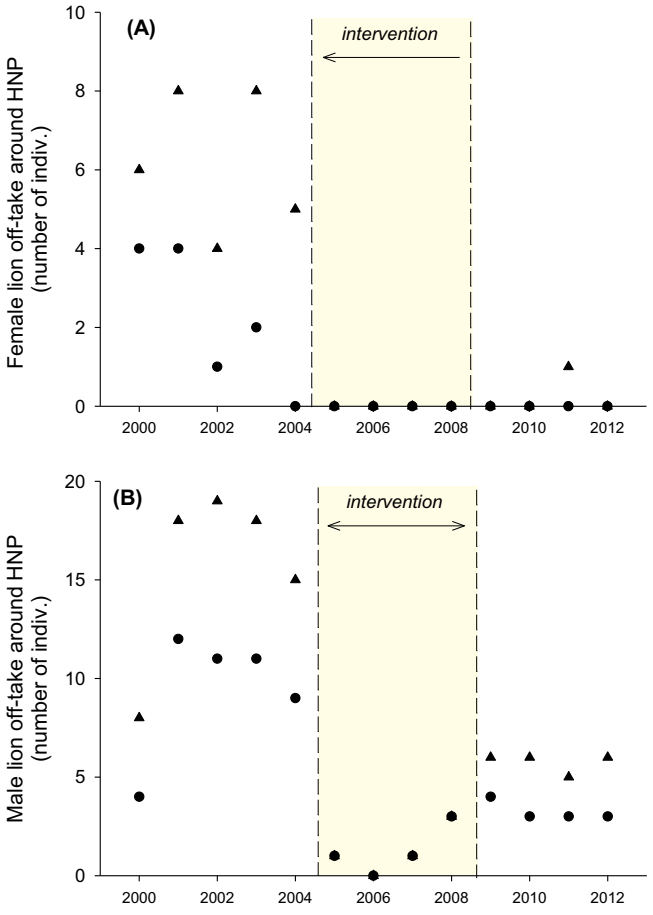

Fig. 1. Hunting off-takes of A) female and B) male lions in hunting concessions adjacent to HNP for the period 2000–2012. Circles denote offtakes from directly adjacent to the core study area and triangles total offtake from all hunting areas adjacent to Hwange National Park.

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, Lindesberg, 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

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