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Socio-spatial behaviour of an African lion population following perturbation by sport hunting

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ABSTRACT

Hunting of individuals from a population can affect its demography and socio-spatial parameters. This study provided opportunities to assess such effects, and may help to improve the conservation of populations threatened by conflict and over-use. We treated the periods before and after a moratorium on the trophy hunting of lions around Hwange National Park, Zimbabwe, as a quasi-experimental opportunity to examine changes in lion socio-spatial behaviour during and after perturbation. Changes in ranging behaviour coincided with the release from heavy mortality from hunting outside the Park and were likely to be due to changes in the perturbation regime, rather than factors such as prey abundance, which did not change over the study period. Lion home range sizes decreased in both sexes after the moratorium. Overlap between groups decreased in males but increased in females. Variation in home range size reduced both annually and seasonally for both sexes. Home range centres became more closely distributed. Lions increased the use of denser vegetation cover classes (>30%) and decreased the use of open cover classes (10–30%). Lions increased the use of areas within 2–5 km of water, and decreased their use of the >20 km class. Perturbation therefore appeared to influence the socio-spatial behavior of the lion population. Managers considering the use of moratoria as a conservation tool must anticipate changes in the behavior and distribution of the target species.

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1. Introduction

Selective removal of individuals through culling or trophy hunting can affect not only the demographic but also the socio-spatial parameters of the targeted population (Macdonald et al., 2006). For instance, the frequency and intensity of social interactions between the surviving individuals might alter, and so change their spatial organisation (Tuyttens et al., 2000). At high levels of offtake, such socio-spatial perturbations can lead to further population reduction (Loveridge et al., 2007).

Three main indicators are relevant for the socio-spatial perturbation caused by heavy mortality pressures: (1) vacuum effect, where neighbouring individuals disperse towards and to occupy vacated territories, (2) territorial disruption, where the discrete pattern of group territories breaks down and (3) altered movement behaviour, where individuals adjust the nature of their ranging patterns (Carter et al., 2007).

In the case of trophy hunting of African lions (*Panthera leo*) adjacent to Hwange National Park, Zimbabwe (Hwange N.P.), Loveridge et al. (2007) detected a vacuum effect and demonstrated perturbation in the lion population. The lion territories were repeatedly emptied by trophy hunting outside the park boundary and successively re-occupied by new males from the park interior. We investigated the remaining two socio-spatial perturbation processes to determine whether the impact of trophy hunting extended to territorial destabilisation and changes in ranging behaviour.

Sport hunting of lions generally targets adult male trophies. If the number of males decreases in the targeted population, adult sex ratios might become more biased towards females, potentially altering the social structure of the population (Loveridge et al., 2007). One response to the increasing awareness of range-wide decline in lion numbers (Bauer et al., 2005; Chardonnet, 2002), has increasingly been the use of trophy hunting moratoria as an intervention intended to facilitate population recovery. For example, lion hunting was suspended in Botswana between 2001 and 2004 and again since 2007 (DWNP, 2007; MEWT, 2007). In Zimbabwe a temporary suspension on lion hunting was instituted in the Zambezi valley for the year 2000 (Monks, 2001), and in western Zimbabwe between 2005 and 2008 (ZPHAGA, 2004; ZPWMA, 2005). The imposition of a hunting moratorium may facilitate a reversal of processes causing perturbation.

Lions are social felids which display high levels of co-operation and antagonism (McComb et al., 1993). Competition between

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groups is frequently aggressive, and aggression is often precipitated by male take-over or territorial defence (Grinnell et al., 1995; Schaller, 1972). During male take-over infanticide is a regular phenomenon, and small cubs are most at risk from incoming males (Pusey and Packer, 1994; Whitman et al., 2004).

The causes of increased aggression with increased social perturbation are poorly understood (example Delahay et al., 2006). However, this phenomenon has been noted in several species of felid including leopard (*Panthera pardus*), bobcat (*Lynx rufus*) and puma (*Felis concolor*), (Hornocker and Bailey, 1986). We expected that social interactions among lions might also become more antagonistic as social disruption increased under heavy trophy hunting pressure. Lion populations experiencing rapid and regular male replacement probably also experience social conflict as new males establish territories (Schaller, 1972). One example detected in the Hwange population previously was an increased risk of infanticide (Loveridge et al., 2007).

Conversely, with increasing male density following a trophy hunting moratorium, male replacement may decrease as incoming males settle in discrete territories. If male tenure is long enough to allow reproduction and dispersal of cubs, approximately 18–24 months (Pusey and Packer, 1987), perturbation effects may recede. If so, we hypothesize that infanticide will decrease, and home range sizes and ranging behaviour will be affected.

Home range size is limited by, amongst other things, the proximity and perceived threat of neighbouring groups (McComb and Packer, 1994). While a number of factors such a group size, habitat selection and resource use are affected by population density (Packer et al., 2005), it is expected that for territorial animals there is a strong link between territory size and population density (Krebs, 1989). For example, the density of great horned owls (*Bubo virginiaus*) is limited by competition for territories, rather than food abundance (Rohner and Krebs, 1998), and Serengeti lions subdivide territories to accommodate increasing population size when conditions are good (Packer et al., 2005).

When home ranges are large, the probability of encountering a neighbour might decrease. As density increases, the incidence of encounter should increase, limiting the freedom with which lions can travel through the landscape. We propose that the effect of a moratorium in removing perturbation pressures may be detectable in changing home range size, habitat characteristics within home ranges and lion movement parameters.

The number of male lions, and the number and size of their coalitions, increased significantly in Hwange N.P. during the moratorium (Loveridge et al., 2010). Increased group size may influence the effect of increasing density on changes in home range size. However, fine-scale changes should be detected in lion spatial behaviour as the density of competing males' changes. Parameters such as path length, sinuosity and the spacing of home range centroids (see below for details) may provide indicators of socio-spatial adjustment associated with altered levels of social perturbation. The periods before and after the moratorium on hunting thus provide a quasi-experimental opportunity to test predictions developed from the relationship between population density and spatial behaviour:

(1) Since the dispersion and size of carnivore home ranges varies with local population density, home range sizes should decrease over time, in the absence of trophy hunting, as the density of lions increases under stable resource conditions.
(2) If male lion density increases and home range size decreases, all else being equal, home range centres will become more closely packed and there may be a change in overlap between the ranges of neighbouring groups.
(3) If home range size decreases while resource conditions remain stable, fine-scale movement parameters may change in order for the lions to move and hunt within a smaller area. Changes in movement behaviour should be quantifiable in terms of sinuosity (a measure of the winding nature of movement paths), penetration (a measure of the density of movement paths) and the distance travelled per day.
(4) If male lion density increases and home range size decreases then the dispersion of habitat characteristics on which they depend (e.g. vegetative cover and waterholes) within their home ranges may also change, in association with increased competition for scarce resources.

2. Materials and methods

2.1. Study site

Hwange N.P. covers c. 15,000 km^2 of dystrophic savannah (nutrient poor acidic soils) in western Zimbabwe between 18°30′ and 19°50′S, and 25°45′ and 27°30′E. Altitude varies from 800 m to 1100 m. The dominant habitat is woodland and bushland savannah (64%) that opens in places to form short grass vlei lines (open leads) and waterhole clearings (Rogers, 1994). The long-term annual rainfall average is 632 mm but is highly variable (range: 324–1160 mm). There is no perennial water in Hwange N.P., although a few rain-fed pans hold water for much of the year in an average rainfall year (Haynes, 1996). Water is artificially supplied to some waterholes (~50) during the dry season. These are generally only maintained in the northern area of the park. Three seasons are distinguished in this study: wet (November–February), early dry (March–June) and late dry (July–October). The wet season of year *Y* corresponds to the period between November of year *Y* and February of year *Y* + 1.

In 2004 lion hunting was voluntarily suspended on private land in the Gwaai Valley Conservancy adjacent to Hwange N.P. (Fig. 1), eliminating 62.7% of the quota allocation from 10.2% of the area surrounding the park (Loveridge et al., 2007). In 2005 the Zimbabwe Parks and Wildlife Management Authority (ZPWMA) suspended trophy hunting of lion in the entire Matabeleland North Province, in western Zimbabwe, thus eliminating trophy hunting in the Hwange area. Consequently we were able to assess our findings in terms of the periods before (pre: ⩽2003) and after (post: ⩾2005) the period when moratorium came into effect.

Fig. 1. Map showing the location of Hwange N.P. relative to surrounding multiuse wildlife areas. Dates in the legend represent the start of lion hunting suspension in the relevant area.

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