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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 perturba-

tion 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

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 sociospatial 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.

2.2. Lion data

The lion population of the northern region of Hwange N.P. (c. 7000 km^2), was monitored using 18 radio-collared adult females (14 prides) and 14 radio-collared adult males (10 coalitions) between 2003 and 2007 (Table 1). Lions were instrumented with GPS radio-collars (see Loveridge et al., 2007 for details). Where two collars were used for a particular group, these were temporally consecutive so data from only one collar was used per group at any time. Positional data were recorded hourly during the night and downloaded at regular intervals. Because statistical results are reliable only if sampling regimens are standardised for the estimation of home range size, and the minimum number of locations required for accurate estimation is ten per month (Börger et al., 2006), we excluded any month with less than 20 days of location data, and considered annual home range size to be represented by a minimum of 100 days of data in each year. During the estimation of home range size, we found a strong correlation between the estimates based on all available lion locations per day ($n = 15$) and those using only one location per day ($n = 1$) ($F_{1,53} = 679.1$; $R^2 = 0.93$; $p < 0.001$). Consequently, in all home range size and overlap analyses, we arbitrarily used the location taken at, or closest to, 00h00 in order to limit the effects of autocorrelation in our data. For the analysis of movement metrics all available lion locations were included.

2.3. Home range size and use

All home range areas were calculated as the 90% density distribution (isopleth) of locations (Börger et al., 2006) using the bivariate normal Kernel method (Worton, 1989) and smoothing factor h_{ref} (Hemson et al., 2005) with Ranges 7 software (South and Kenward, 2006). We calculated the size of mean monthly and seasonal home range size for each individual, as well as their annual home range size. Lions are sexually dimorphic and detailed studies in the Serengeti ecosystem reveal that they occupy territories that are inherited by daughters from mothers, while males compete for succession (Schaller, 1972). Data gathered on male and female lions were therefore analysed separately (Table 2).

In order to assess change in home range size between pre- and post-moratorium periods, we compared home range area data annually using ANOVA to test the significance of home range size change and the change in variance of mean home range size over time. Overlap of annual home range areas was calculated using overlap analysis in Ranges 7 (South and Kenward, 2006) and is expressed as the proportion of the annual home range. Home range centre spacing was calculated by generating a distance matrix between home range centroid locations using Arc Map 9.2 (ESRI, 2004), and assessing changes in distribution using the Donnelly modification of the Clarke and Evans aggregation index (Krebs, 1989).

2.4. Movement

Lion movement was assessed using three home range metrics: (1) by combining the step length between each recorded location from an individual's daily movement path ($n \geqslant 10$ steps) and obtaining the mean daily distance moved, (2) by calculating the sinuosity (degree of convolution of path) of each daily movement path: sinuosity $= L_t/L_{se}$; where L_t is the total path length and L_{se} the distance between the start and end points of the path. Larger scores of sinuosity represent increased sinuosity. (3) By calculating a proxy of the proportion of the home range visited and measure of effort (termed penetration in this analysis): penetration $= A/L_t$; where A is the area (km^2) of a monthly home range. Larger scores for penetration represent a lower proportion of home range visited, i.e. a lower effort. Movement metrics were calculated using the movement parameters tool in Hawths Tools for Arc Map 9.2 (Beyer, 2007; ESRI, 2004).

2.5. Habitat Characteristics

For each home range we calculated: (1) the proportional area represented by five classes of woody vegetation cover (0–10%, 10–20%, 20–30%, 30–40% and >40% cover), from the MODUS Vegetation Continuous Fields satellite image (Hansen et al., 2003), using ArcView 3.2 software (ESRI, 2004); (2) the number of waterholes and the proportional area situated in five distance classes from the nearest waterhole (0–1 km, 1–2 km, 2–5 km, 5–20 km and >20 km) to represent water availability.

2.6. Prey abundance

We have monitored the abundance of herbivores in the study area since December 2002 using road counts following the line-transect method (Buckland et al., 2001). We calculated the kilometric prey biomass per lion home range following the methods of Loveridge et al. (2009). We tested the abundance of prey within home ranges annually using ANOVA, to measure any change in prey abundance over the study period.

3. Results

Male annual home range size decreased after the moratorium, by a mean of 421 km^2 between 2005 and 2007 (ANOVA:

Table 1
Sample size indicating number of lions monitored and the period within which the data was available for individual collared lions in Hwange N.P.

n	Female ID	Name	Telemetry From	To	Pride
1	1	Balabala	February-03	October-07	1
2	20	Balabala	February-03	October-07	
3	2	Nyamandhlovu	March-03	November-07	2
4	14	Nyamandhlovu	March-03	November-07	
5	3	Mbuyamabena	March-03	September-03	3
6	4	Linkwasha	February-03	June-04	4
7	5	Mastiff	May-03	March-05	5
8	6	Biva	April-03	June-04	6
9	7	Spice	May-03	September-07	7
10	21	Spice	May-03	September-07	
11	8	Nehimba	April-03	October-05	8
12	9	Shumba	August-03	November-04	9
13	10	Shumba	August-03	November-04	
14	19	Bak Pans	December-05	November-07	10
15	15	Scott's Pan	October-04	September-07	11
16	22	Guvalala	September-03	August-07	12
17	24	Kennedy	March-04	September-06	13
18	28	Secheche	October-07	December-07	14

n	Male ID	Name	Telemetry From	To	Coalition
1	1	Mpofu	January-03	December-07	1
2	2	Mpofu			
3	3	Mpofu			
4	5	Shumba	January-03	August-03	2
5	4	Kataza	February-03	May-03	3
6	6	Shapi	August-03	January-04	4
7	7	Pamwe	May-03	October-04	5
8	8	Vuka	May-04	December-04	6
9	9	Ngamo	December-04	January-07	7
10	13	Ngamo			
11	11	Nehimba	October-05	January-07	8
12	12	Dynamite	October-05	November-07	9
13	14	Dynamite			
14	10	Makalolo	March-05	September-05	10

Table 2

Sample Size for telemetry data used in the estimation of home range size and overlap statistics for male and female lion in Hwange N.P. Numbers represent the number of individuals per season with 20 days of location data available for analysis, using one fix per day. Bold rows provide seasonal totals from which mean home range size was calculated.

Year	2003		2004		2005		2006		2007	
Sex	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Jan	0	4	9	3	5	1	7	2	2	2
Feb	0	3	8	3	6	2	7	2	3	0
Nov	9	3	9	2	7	2	3	2	3	2
Dec	9	3	8	2	5	2	2	2	1	0
Wet Season	**18**	**13**	**34**	**10**	**23**	**7**	**19**	**8**	**9**	**4**
Mar	3	4	9	3	5	2	7	1	2	1
Apr	5	4	8	2	5	3	6	3	4	4
May	6	3	8	3	5	3	6	3	5	4
Jun	8	3	8	3	5	3	6	3	5	3
Early dry season	**22**	**14**	**33**	**11**	**20**	**11**	**25**	**10**	**16**	**12**
Jul	7	2	9	4	6	3	6	3	5	3
Aug	8	2	10	4	6	3	5	3	6	3
Sep	7	2	9	4	5	2	5	3	5	3
Oct	8	2	10	4	5	2	4	2	4	3
Late dry season	**30**	**8**	**38**	**16**	**22**	**10**	**20**	**11**	**20**	**12**
Annual _n_ individuals (100 days of data)	**9**	**5**	**10**	**4**	**7**	**3**	**6**	**3**	**5**	**3**

$F_{1,1} = 245.8$; $p < 0.001$, Fig. 2a), and female annual home range size also decreased, by a mean of 200 km^2 between 2003 and 2007 (ANOVA: $F_{1,1} = 1177.9$; $p < 0.001$, Fig. 2b). Variations in home range size decreased at both the seasonal (Fig. 3), and annual levels (Fig. 4) when compared to the pre-moratorium period for both sexes. Male average annual home range size remained larger than that of females both before (647 ± 274 km^2 and 447 ± 267 km^2 respectively) and after (324 ± 190 km^2 and 293 ± 210 km^2 respectively) the moratorium.

Over the moratorium period, the average annual home range overlap between groups decreased for males from $60.9 \pm 2.4\%$ in 2003 to $5.6 \pm 3.9\%$ in 2007 ($F_{1,4} = 8.11$; $R^2 = 0.43$; $p = 0.029$) and increased for females from $10.6 \pm 14.3\%$ in 2003 to $32.3 \pm 32.4\%$ in 2007 ($F_{1,4} = 6.01$; $R^2 = 0.09$; $p = 0.017$). There was a decreasing trend in the average nearest neighbour distances between monthly home range centroids for both males and females (ANOVA: $F_{1,1} = 139.94$; $P < 0.0001$; $F_{1,1} = 41.59$; $P < 0.001$ respectively; Fig. 5.1). Home range centroid distribution coalesced over the study period with aggregation index scores changing from 3.5 ± 1.8 ($Z = 14.6$; $p = 0.01$) to 1.5 ± 0.3 ($Z = 2.7$; $p = 0.01$) between 2005 and 2007. Within the sexes the change in overlap of home ranges was thus different as home range size decreased, however, all ranges became more tightly packed and their centroids more closely located.

Mean daily path length did not change significantly over the moratorium period for either males or females (ANOVA: $F_{1,1} = 0.16$, $P < 0.71$; $F_{1,1} = 0.35$, $P = 0.59$ respectively, Fig 5.2b). Daily path length was poorly correlated with home range size in males but significantly correlated in females (Pearson correlation: $p_{\male} = 0.15$ and $p_{\female} = 0.049$).

Sinuosity and penetration of male and female movement paths did not vary significantly over the moratorium period ($S_{\male}$: $F_{1,4} = -2.98$; $R^2 = 0.88$; $p = 0.58$ and $S_{\female}$: $F_{1,4} = 5.10$; $R^2 = 0.72$; $p = 0.15$; and $P_{\male}$: $F_{1,4} = 6.34$, $R^2 = 0.086$; $p = 0.136$ and $P_{\female}$: $F_{1,4} = 9.98$; $R^2 = 0.82$; $p = 0.09$ respectively). All trends were decreasing, with the difference between both parameters approaching significance for male lions, and penetration approaching significance for female lions, indicating increasing penetration and decreasing sinuosity.

The proportion of vegetation classes characterised by >30% cover increased and the proportion of vegetation classes characterized by a woody cover between 10% and 30% decreased in home ranges of both sexes (Fig. 6). There was no significant change in the proportion of vegetation represented by the 0–10% class for either sex (Fig. 6).

Nearest neighbour analysis revealed no significant difference in distance to the nearest waterhole between years or between the sexes themselves (Equal variances assumed; $t_{1,21} = -1.36$; $p = 0.19$).
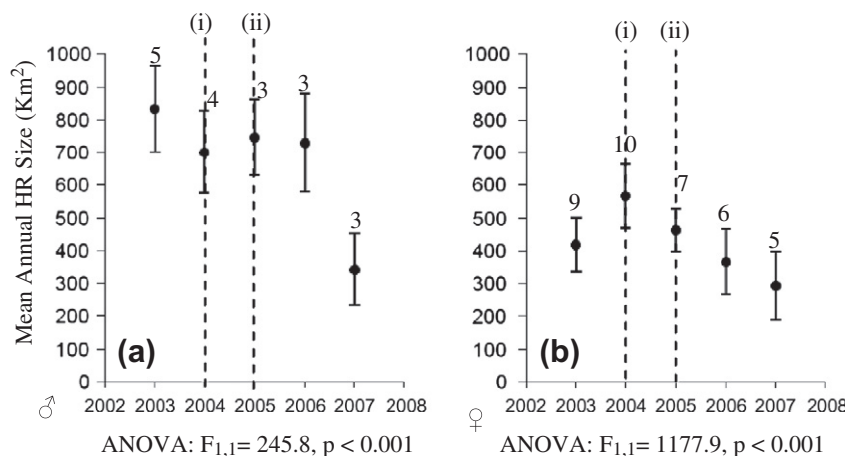
Fig. 2. Mean annual home range size (km^2) for (a) male and (b) female lions in Hwange N.P. Line (i) represents the start of voluntary suspension of lion hunting on private land and line (ii) represents the start of the full hunting moratorium.
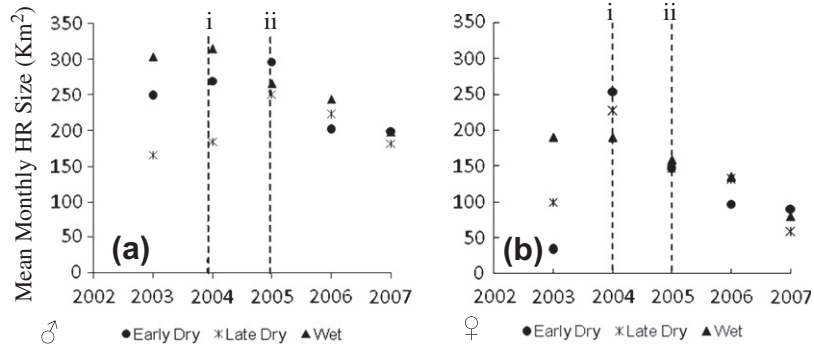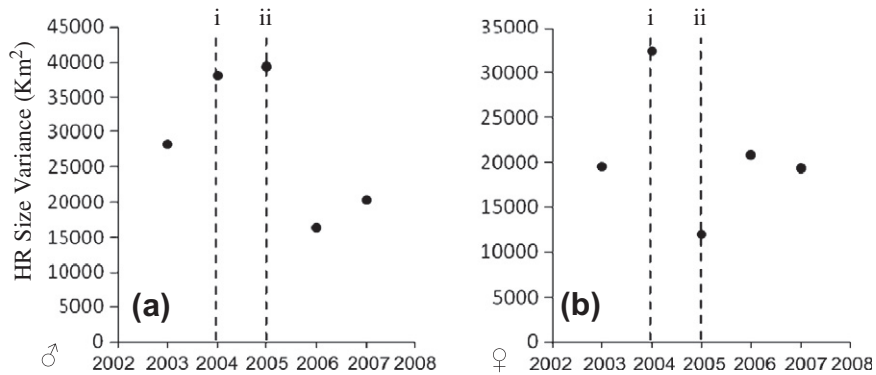
Fig. 3. Mean seasonal home range size variation (km^2) for (a) male and (b) female lions in Hwange N.P. Line (i) represents the start of voluntary suspension of lion hunting on private land and line (ii) represents the start of the full hunting moratorium.

Fig. 4. Mean annual home range size variation (km^2) for (a) male and (b) female lions in Hwange N.P. Lines (i) and (ii) are defined as per Fig. 3.
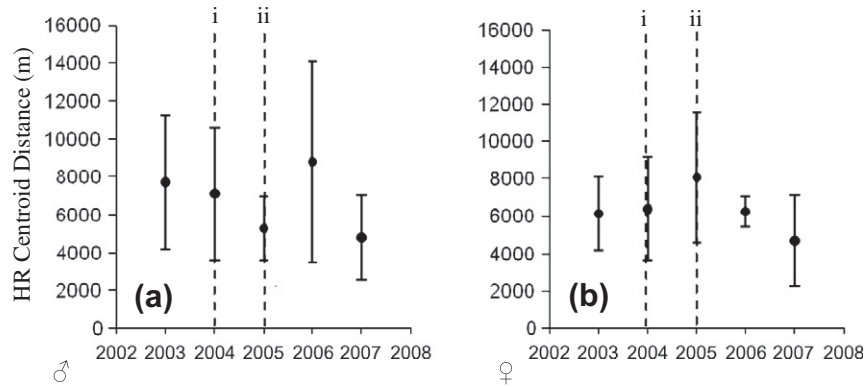

Fig. 5.1. Mean annual monthly home range centre spacing (km).

The 2–5 km distance class to the nearest waterhole comprised the dominant proportion of both male and female home ranges (Fig. 7). The proportion of the 2–5 km distance class increased ($F_{1,4} = 9.11$; $R^2 = 0.13$; $p = 0.004$) and the >20 km distance class decreased ($F_{1,4} = 5.51$; $R^2 = 0.08$; $p = 0.023$) in male home ranges between pre- and post-moratorium periods, while all other classes were unaffected. In female home ranges the proportion of the 5–20 km distance class decreased ($F_{1,4} = 5.949$; $R^2 = 0.1$; $p = 0.01$) between pre- and post-moratorium periods while all other classes remained unaffected. This means that males adopted more similar distances within the 2–5 km distance class as females did. Lions therefore were more likely to avoid areas further away from waterholes.

The number of waterholes per annual home range remained unchanged for both males and females over the study period ($F_{1,4} = 1.27$; $R^2 = 0.009$; $p = 0.263$ and $F_{1,4} = 0.225$; $R^2 = 0.001$; $p = 0.635$ respectively). Finally, mean prey abundance per male and female home range was not significantly different between pre and post-moratorium periods (ANOVA: $_{\male}F_{1,1} = 0.48$; $p < 0.54$ and $_{\female}F_{1,1} = 0.67$; $p < 0.81$) (see Fig. 8).

4. Discussion

This study focused on the socio-spatial implications of the suspension of trophy hunting in a lion population. Whereas home range size is known to be influenced by prey abundance in Hwange N.P. (Loveridge et al., 2009), the overall abundance of prey did not change significantly during the study period (Valeix et al., 2008). Furthermore, we found that prey abundance in lion home ranges
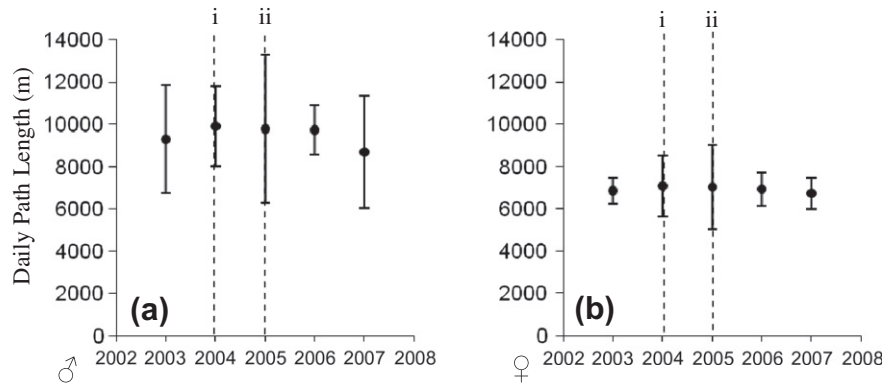
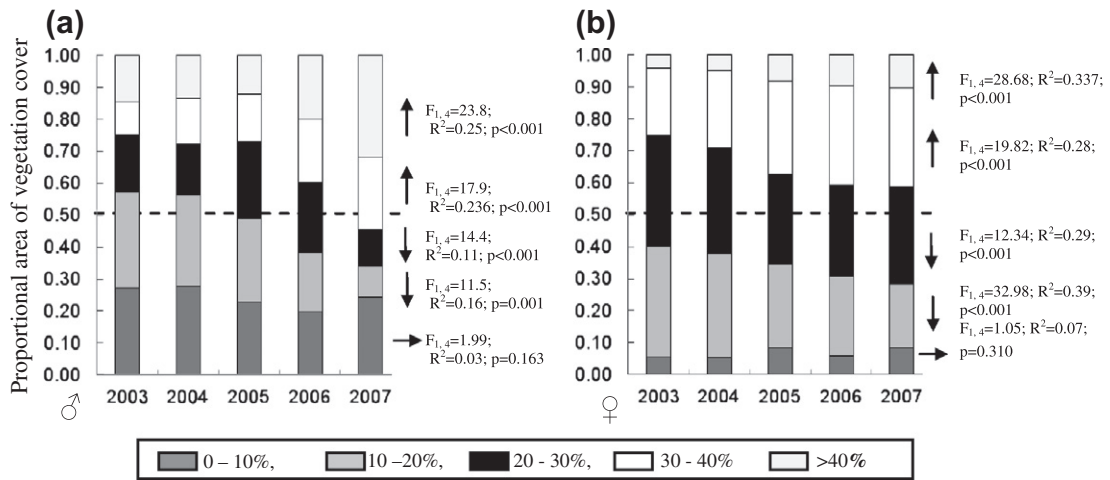**Fig. 5.2.** Mean annual monthly path length per day (km).

Fig. 6. Proportional composition of vegetation types in monthly home range areas for (a) male and (b) female lions in Hwange N.P. Dotted line represents the 50% proportion and arrows indicate direction of change in trend. Inferetial statistics for each vegetation cover class are given adjacent.
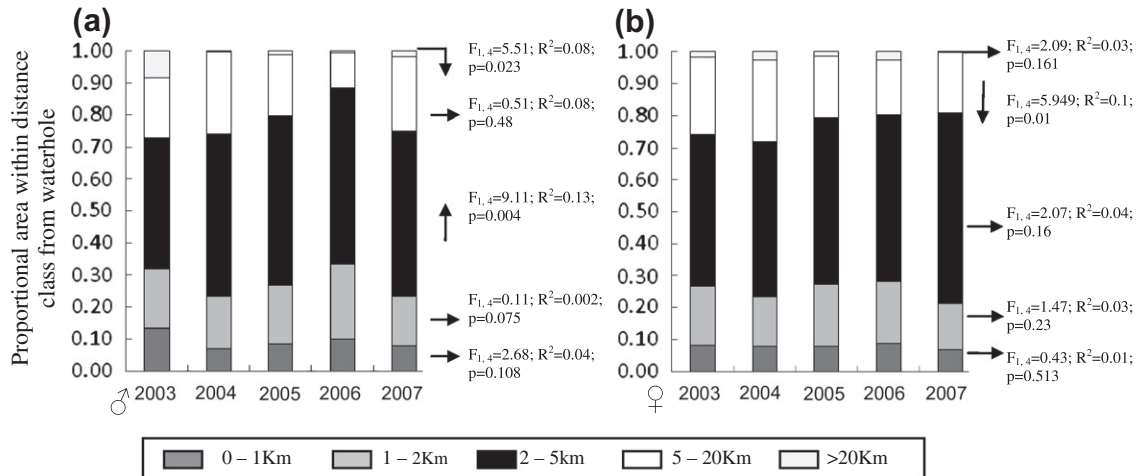

Fig. 7. Proportional composition of distance to waterhole classes in monthly home range areas for (a) male and (b) female lions in Hwange N.P.

was unaffected by their decreased size, supporting the assumption that food resource abundance did not limit home range size during the study.

It is generally accepted that male and female lions differ in the resources that are most important to them. Females are influenced by food dispersion patterns, males by access to female lions (Sch-

aller, 1972). Female reproductive fitness is linked to habitat quality and access to food (Mosser and Packer, 2009), and habitat quality influences hunting success (Hopcraft et al., 2005). Cub survival also increased in the post-moratorium period (Loveridge et al., 2010), indicating that habitat quality was satisfactory for reproductive success, despite diminished territory sizes. Thus alternative expla-
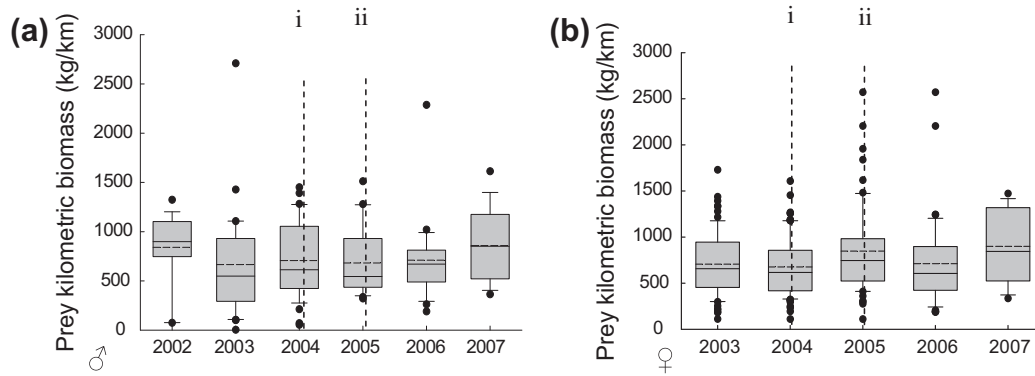
Fig. 8. Mean prey abundance in male and female lion home ranges over the moratorium period.

nations based on a decrease in the number of female territories available per male territory, or the reproductive condition of pride females, were assumed unlikely proximal causes of changing home range size.

Accurate lion density measurements were not available owing to the difficulty of locating un-collared groups of lions and performing censuses in the densely wooded Hwange environment. We believe that the decrease in lion home range size is the direct result of an increase in the abundance of male lions as suggested by the increased number and size of coalitions in the study area after the moratorium (Loveridge et al., 2010). Increased male lion abundance thus caused increased competition for home range area, as suggested by the reduced overlap of male home ranges, adjustments in ranging behaviour and movement dynamics.

The overlap between the ranges of resident female groups then increased as they were more tightly bounded by resident males' territories. The size differential between male and female home ranges decreased from 50% to 14% over the moratorium period. Very few females were harvested on trophy hunting quota (Loveridge et al., 2007) and we did not anticipate changes in adult female density after the moratorium. We suggest that socio-spatial changes observed for territorial females were due to their adjusting to the changes in male home range settlement.

Many bird and mammal species evidence an inverse relationship between home range size and population density (Makarieva et al., 2005). Krebs's (1971) work on great tits (Parus major) supported the hypothesis that population size is limited by, and predicated upon, territorial competition. The so-called Wynne-Edward's, 1962 view, which has recently been confirmed in lions, where population size has been found to be limited by territoriality (Packer et al., 2005). Similarly, home range size does appear to scale inversely with population density in the Hwange lion population (Loveridge et al., 2009; Macdonald et al., 2010).

The compression of home ranges is also shown by diminishing distances between annual home range centroids as the moratorium progressed. Lions were more closely packed in a configuration of smaller home ranges for both sexes. Home ranges thus shrunk toward their centres providing space in the interstices to accommodate new groups of lions.

While there was no significant change in the sinuosity, penetration or daily length of lion paths with a change in home range size, female home ranges contracted around waterhole resources where cover was least available (0–10%) and prey abundance was highest (Valeix et al., 2009). The proportional inclusion of the 0–10% vegetation cover class, typically found around waterhole areas in lion home ranges, was unaltered by the moratorium period. This emphasised the importance of habitat type and waterholes in the configuration of lion home ranges. Similar relationships have been shown for the distribution of Serengeti lions with regard to river confluences (Mosser and Packer, 2009). Coupled with this, reduced annual and seasonal variation in home range size suggest a stabilisation of territory configuration which allowed for less spatial drift of home range areas over the landscape.

Predictions 1 and 2, respectively that home range sizes would decrease and become more tightly packed in the absence of trophy hunting, were therefore upheld. Perturbation effects on the size and spatial relationship of home ranges in the Hwange lion population were thus shown to have occurred in the period before the moratorium. The moratorium period therefore evidenced a reversal in the disruption associated previously with hunting, and a transition to smaller, more discrete ranges within a more stable socio-spatial structure in the post-moratorium period.

Predictions 3 and 4 were supported by the habitat composition of decreasing home range sizes, relative to waterhole and vegetation cover resources. Lions make use of denser cover in an effort to remain undetected by prey and increase the probability hunting success (Hopcraft et al., 2005). An intensifying landscape of fear brought about by the increasing number, and more densely packed dispersion, of lions within the landscape (Valeix et al., 2009), should cause prey to become more vigilant (Abramsky et al., 2002; Ripple and Beschta, 2004). Hunting would thus require more effort and result in the inclusion of denser habitat in home ranges in order to maintain hunting success. Maintaining access to dense habitat would allow them to gain the advantage in, or avoid, potentially violent encounters. We suggest that areas located between 2 and 5 km from a waterhole may provide a good trade-off between prey abundance, (with herbivores selecting habitats close to waterholes (Valeix et al., 2009)), prey catchability and concealment. (With herbivores being easier to catch in denser vegetation (Hopcraft et al., 2005).) Changes detected in the vegetation composition of home ranges may reflect changes in prey distribution and habitat selection, however no such important change has been reported yet.

We surmise that rather than include new resources in their home ranges, lions retain the essential resources around which they are configured, retreating into their minimum necessary range as competition increases.

In summary, studying lion spatial organisation before and after a moratorium on lion trophy hunting has revealed that high levels of male mortality had caused several perturbation effects, in addition to the edge effects observed by Loveridge et al. (2007). These perturbations affected the socio-spatial ecology of the survivors, and were consistent with previous demographic findings, suggesting that the lion population has been increasing (Loveridge et al., 2010). Hence, both demographic and socio-spatial effects indicate that with the moratorium, the perturbation effects were largely reversed. The potential usefulness of such an intervention in restor-

ing lion populations and their functioning in hunted areas is strongly suggested.

References

Abramsky, Z., Rosenzweig, M.L., Subach, A., 2002. The costs of apprehensive foraging. Ecology 83, 1330–1340.

Bauer, H., Chardonnet, P., Nowell, K., 2005. Status and Distribution of the lion (*Panthera leo*) in east and southern Africa. In East and Southern African Lion Conservation Workshop South Africa.

Beyer, H.L., 2007. Hawths Analysis Tools, p. Spatial Modelling Tools for GIS.

Börger, L., Franconi, N., De Michelle, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., Coulson, T., 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75, 1393–1405.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford.

Carter, S.P., Delahay, R.J., Smith, G.C., MacDonald, D.W., Riordan, P., Etherington, T.R., Pimley, E.P., Walker, N.J., Cheesman, C.L., 2007. Culling-induced social perturbation in Eurasian badgers, *Meles meles*, and the management of TB in cattle: an analysis of a critical problem in applied ecology. Proceedings of the Royal Society of London. Series B 274, 2769–2777.

Chardonnet, P., 2002. Conservation of the African lion: contribution to a status survey. In: Chardonet, P., (Eds.), Conservation of the African Lion: Contribution to a Status Survey. International Foundation for the Conservation of Wildlife, France & Conservation Force, USA.

Delahay, R.J., Walker, N.J., Forrester, G.J., Harmsen, B., Riordan, P., Macdonald, D.W.M., Newman, C., Cheesman, C.L., 2006. Demographic correlates in bite wounding in Eurasian Badgers, *Meles meles* L., in stable and perturbed populations. Animal Behaviour 71, 1047–1055.

DWNP, 2007. Department of Wildlife and National Parks, Gaborone.

ESRI, 2004. ArcGis 9, In Build, p. 535.

Grinnell, J., Packer, C., Pusey, A.E., 1995. Cooperation in male lions: kinship, reciprocity or mutualism? Animal Behaviour 49, 95–105.

Hansen, M.C., De Fries, R.S., Townshend, J.R.G., Caroll, M., Dimiceli, C., Sohlberg, R.A., 2003. Global percent tree cover at a spatial resolution of 500m: first results of the MODIS vegetation continuous fields algorhythm. Earth Interactions 7, 1–15.

Haynes, G., 1996. Quaternary climates and environmental changes in Hwange National Park, Zimbabwe. University of Zimbabwe Publications, Harare.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R., Macdonald, D.W., 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home range analyses with least-squares-cross-validation. Journal of Animal Ecology 74, 455–463.

Hopcraft, J., Grant, C., Sinclair, A.R.E., Packer, C., 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74, 559–566.

Hornocker, M.G., Bailey, T.N., 1986. Natural Regulation in Three Species of Felids. National Wildlife Federation, Washington, DC.

Krebs, J.R., 1971. Territory and breeding density in the great tit (*Parus major L.*). Ecology 52, 3–22.

Krebs, C.J., 1989. Ecological Methodology. R.R. Donnely and Sons Company, New York.

Loveridge, A.J., Searle, A.W., Murindagomo, F., Macdonald, D.W., 2007. The impact of sport-hunting on the lion population in a protected area. Biological Conservation 134, 548–558.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., Macdonald, D.W., 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. Ecography, 32 (online early).

Loveridge, A.J., Hemson, G., Davidson, Z., Macdonald, D.W., 2010. African lions on the edge: reserve boundaries as 'attractive sinks'. In: Macdonald, D.W., Loveridge, A.J. (Eds.), The Biology and Conservation of Wild Felids. Oxford University Press, Oxford.

Macdonald, D.W.M., Riordan, P., Mathews, F., 2006. Biological hurdles to the control of TB in cattle: a test of two hypotheses concerning wildlife to explain the failure of control. Biological Conservation 131, 268–286.

Macdonald, D.W., Mosser, A., Gittleman, J.L., 2010. Felid society. In: Macdonald, D.W., Loveridge, A. (Eds.), Biology and Conservation of Wild Felids. Oxford University Press, Oxford.

Makarieva, A.M., Gorshkov, V.G., Li, B., 2005. Why do population density and inverse home range scale differently with body size? Implications for ecosystem stability. Ecological Complexity 2, 259–271.

McComb, K.E., Packer, C., 1994. Roaring and numerical assessment in contests between groups of female lions (*Panthera leo*). Animal Behaviour 47, 379–387.

McComb, K.E., Pusey, A.E., Packer, C., Grinnell, J., 1993. Female lions can identify potentially infanticidal males from their roars. Proceedings of the Royal Society of London. Series B 252, 59–64.

MEWT, 2007. Ministry of Environment and Wildlife Tourism, Gaberone.

Monks, N., 2001. The lion on the Mana Pools floodplain – are they decreasing? African Hunter 9, 22–24.

Mosser, A., Packer, C., 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Animal Behaviour 78, 359–370.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Boner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., Sinclair, A.R.E., 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. Science 307, 390–393.

Pusey, A.E., Packer, C., 1994. Infanticide in Lions: consequences and counter-strategies. Harwood Academic Publishers, Chur, Switzerland.

Ripple, W.J., Beschta, R.L., 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? BioScience 54, 755–766.

Rogers, C.M.L., 1994. The woody vegetation of Hwange National Park. Transactions of the Zimbabwe Scientific Association 68, 15–24.

Rohner, C., Krebs, J.R., 1998. Response of great horned owls to experimental "hot spots" of snowshoe hare density. The Auk 115, 694–705.

Schaller, G.B., 1972. The Serengeti Lion. University of Chicago Press, Chicago.

South, A.B., Kenward, R.E., 2006. Ranges 7, Software for the Analysis of Tracking and Location Data. Antrack Ltd., Wareham, UK.

Tuyttens, F.A.M., Delahay, R.J., Macdonald, D.W., Cheeseman, C.L., Long, B., Donnelly, C.A., 2000. Spatial Perturbation caused by badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). Journal of Animal Ecology 69, 815–828.

Valeix, M., Fritz, H., Chamaillé-Jammes, S., Bourgarel, M., Murindagomo, F., 2008. Fluctuations in abundance of large herbivore populations: insights into the influence of dry season rainfall and elephant numbers from long-term data. Animal Conservation 11, 391–400.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., Macdonald, D.W., 2009. Behavioural adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90, 23–30.

Whitman, K., Starfield, A.M., Qadling, H.S., Packer, C., 2004. Sustainable trophy hunting of African lions. Nature 428, 175–178.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168.

Wynne-Edwards, V.C., 1962. Animal Dispersion in Relation to Social Behaviour. Oliver & Boyd, Edinburgh.

ZPHAGA, 2004. Zimbabwe Professional Hunters and Guides Association.

ZPWMA, 2005. Zimbabwe Parks and Wildife Management Authority, Harare.