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The impact of sport-hunting on the population dynamics of an African lion population in a protected area

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ABSTRACT

Between 1999 and 2004 we undertook an ecological study of African lions (Panthera leo) in Hwange National Park, western Zimbabwe to measure the impact of sport-hunting beyond the park on the lion population within the park, using radio-telemetry and direct observation. 34 of 62 tagged lions died during the study (of which 24 were shot by sport hunters: 13 adult males, 5 adult females, 6 sub-adult males). Sport hunters in the safari areas surrounding the park killed 72% of tagged adult males from the study area. Over 30% of all males shot were sub-adult (<4 years). Hunting off-take of male lions doubled during 2001–2003 compared to levels in the three preceding years, which caused a decline in numbers of adult males in the population (from an adult sex ratio of 1:3 to 1:6 in favour of adult females). Home ranges made vacant by removal of adult males were filled by immigration of males from the park core. Infanticide was observed when new males entered prides. The proportion of male cubs increased between 1999 and 2004, which may have occurred to compensate for high adult male mortality.

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1. Introduction

Lions have been hunted both for sport and as livestock raiders for millennia. Due to persecution and loss of suitable habitat and prey species, the geographic range of this species has been vastly reduced. Sizeable populations of lions only occur in East and southern Africa (Chardonnet, 2002; Bauer and van der Merwe, 2004) and are usually only abundant in protected areas (Kingdon, 1997).

Sport or safari hunting of wildlife is often considered a necessary part of wildlife conservation and management and has been a driving force in conservation since the early 20th Century (Adams, 2004). It can be a conservation tool that brings revenue to biodiversity rich states, provides justification for protection of wildlife habitats (Loveridge et al., 2006) and has been responsible for many species recoveries. However, poorly defined or mixed objectives, institutional failure, lack of management capacity and corruption may limit the benefits to conservation (Murombedzi, 1999; Smith, 2003). Hunting may also extirpate populations (Frank and Woodroffe, 2001) or cause perturbation within animal populations, e.g., badgers, Meles meles (Tuyttens and Macdonald, 2000); lynx, Lynx canadensis (Bailey et al., 1986). Increased rates of male infanticide in some carnivore species (Swenson et al., 1997; Greene et al., 1998; Whitman et al., 2004) and long-term genetic change in phenotypic traits, especially those that are sexually selected (Harris et al., 2002; Coltman et al., 2003) have also been demonstrated.

Lions are often the most valuable species sold in safari hunting concessions, they fetch the highest price of any single species at auctions (Booth, 2004), and lion hunts sell out ahead of all other species on a hunting operator's quota (Grobbelaar and Masulani, 2003). Safari operators in Botswana charged

US$ 130,000 per lion hunt in 2005 (Loveridge unpublished data). There has been considerable debate as to whether hunting of this species is carried out on a sustainable basis in some areas (Pain, 2003). Creel and Creel (1997) suggest that hunting in Selous Game Reserve, Tanzania is sustainable with an off-take of 4% of adult males while Greene et al. (1998) modelled the effects of male infanticide and suggest that removal of 10% of adult male lions will result in a stable harvest. These off-take levels are similar to levels considered sustainable for other large carnivores, e.g., brown bears, *Ursus arctos* (Swenson et al., 1994). Whitman et al. (2004), in an alternative model, parameterised with data from the Serengeti, Tanzania, suggest that removal of males of 6 years and older will not affect the persistence of a lion population and furthermore, if age limits were used quotas would be unnecessary. However, some field research indicates a wider reaching influence of removing male lions. Yamazaki (1996) found that social behaviour may be disrupted by removal of pride males by sport-hunters and Cooper (1991) found that, in male de-populated areas, spotted hyenas (*Crocuta crocuta*) kleptoparasitise kills from those prides without a territorial male present, impacting the ability of females to retain kills. Clearly an understanding of the impacts of hunting on populations of this species around large national parks is crucial for implementation of conservation management. This study was undertaken around Hwange National Park, in western Zimbabwe and focuses on the anthropogenic processes, including sport hunting, that impact this and probably many other populations of African lions.

2. Methods

2.1. Study area

Hwange National Park (HNP) is 14 900 km^2, situated in North-western Zimbabwe (between latitudes 18° 30′ and 19° 50′ and longitudes 25° 45′ and 27° 30′). Park vegetation was largely woodland and scrubland (predominantly *Baikiaea plurijuga*, *Terminalia sericea*, *Combretum* spp. and *Coleospermum mopane*) and less than 10% of the entire area comprised open grassland or bushed grassland (Rogers, 1993). Mean monthly temperatures range from 17.2 to 30.4 °C. The region receives an average of 650 mm of rainfall from November to April. Our study site was in the northern area of the park and parts of the surrounding land and covered 7129 km^2, of which 5884 km^2 was situated in HNP. HNP is surrounded by safari areas and hunting concessions (Fig. 1), no sport hunting occurs within HNP. Concession areas either formed buffers between the park and areas of human settlement (Forestry land, Deka and Matetsi Safari Areas and Gwaai Intensive Conservation Area – ICA), or were communal areas (Tsholotsho Communal Land) where subsistence agriculture is the predominant activity and wildlife is utilised under the Communal Areas Management Plan for Indigenous Resources (CAMPFIRE) and had generally lower densities of wildlife (Dunham, 2002). The southern boundary of the Park is formed by the Zimbabwe–Botswana border. On National Park Estate (i.e., Safari Areas) lion hunting quotas are set by the Parks and Wildlife Management Authority (PWMA), on all other land hunting quotas are proposed by landowners or the local

Management Authority (e.g., CAMPFIRE areas) and agreed by PWMA (WWF, 1997; Taylor, 2001). Population censuses, community estimates and trophy quality are used as the basis for setting quotas (Taylor, 2001; Chardonnet, 2002). However, because lions are difficult to census (Loveridge et al., 2001) and trophy quality data are often unavailable it is difficult to set realistic quotas for this species. Since the 1970s, lion sport hunting harvests in Zimbabwe have been some of the highest in relation to population size in Africa (Packer et al., 2006) with annual off-takes of between 90 and 141 lions between 1992 and 2002 (Grobbelaar and Masulani, 2003). The lion population of north-western Zimbabwe (including our study area) is the most heavily utilised for sport hunting in the country, usually making up around 41% of the country's entire lion quota (Grobbelaar and Masulani, 2003).

2.2. Capture of study animals

We immobilised study animals in order to instrument them. We initially used a cocktail of 5.0 ± 0.79 (range 3.48–6.22) mg/kg Ketamine hydrochloride (Kyron laboratories (Pvt.) Ltd, Benrose, RSA) and 2.23 ± 0.44 (range 1.39–2.82) mg/kg Xylazine (Rompun; Bayer, Leverkusen, Germany), reversed with 0.12 ± 0.10 (range 0.01–0.28) mg/kg Atipamezole (Antisedan, Farmos, Orion Corp., Finland). Later we used 1.76 ± 0.64 (range 0.67–3.72) mg/kg Tiletamine hydrocloride/Zolazepam hydrochloride (Zoletil; Virbac RSA, Halfway house, RSA) and 0.95 ± 0.43 (range 0.48–2.0) mg/kg Xylazine, reversed with 0.1 ± 0.03 (range 0.05–0.17) mg/kg Atipamezole or 0.83 ± 0.32 (range 1.38–0.53) mg/kg Zoletil and 0.05 ± 0.01 (range 0.04–0.06 mg/kg Medatomidine (Zalopine, Wildlife Pharmaceuticals, Karino, RSA), reversed with 0.18 ± 0.07 (range 0.01–0.28)mg/kg Atipamezole (Fahlman et al., 2005). We used a Dan-inject JM Special, CO_2 dart rifle (Dan-inject RSA, Skukuza, South Africa) to deliver the dart from a range of 10–40 m. Recumbency occurred 12 ± 7 min after darting and animals were immobilised for a mean of 172 ± 64 min. From 1999 to 2002 we fitted lions with VHF radio-collars (600 g; Sirtrack Ltd. Havelock North, New Zealand) and from 2002 either a VHF radio-collar or a GPS Simplex radio-collar (female: 900 g; male: 950 g; Televilt Positioning AB, Lindesberg, Sweden). We also fitted lions with an ear tag (Dalton Rototag, Henley, UK). We took morphometric measurements including measurement of the length of the mane at four standard points (crest of skull at the distal end of the sagittal crest, the middle of the chest, between the shoulder blades and at the distal curve of the mandibular bone). Scores were added together to give an overall measure of mane size. Testicle length was measured along the longest side of the testicle. We estimated the age of lions based on tooth wear after Smuts et al. (1978a). We weighed lions using a canvas stretcher attached to a scale, suspended from poles attached to the front of a 4 × 4 vehicle.

2.3. Demographic and movement data

We attempted to radio-collar all adult (>4 years old) males within the study-site and at least one adult female from each pride. As far as is known only four adult males in the study area were not collared, but in three cases at least one of their coalition were collared. From 2000 we also caught sub-adult
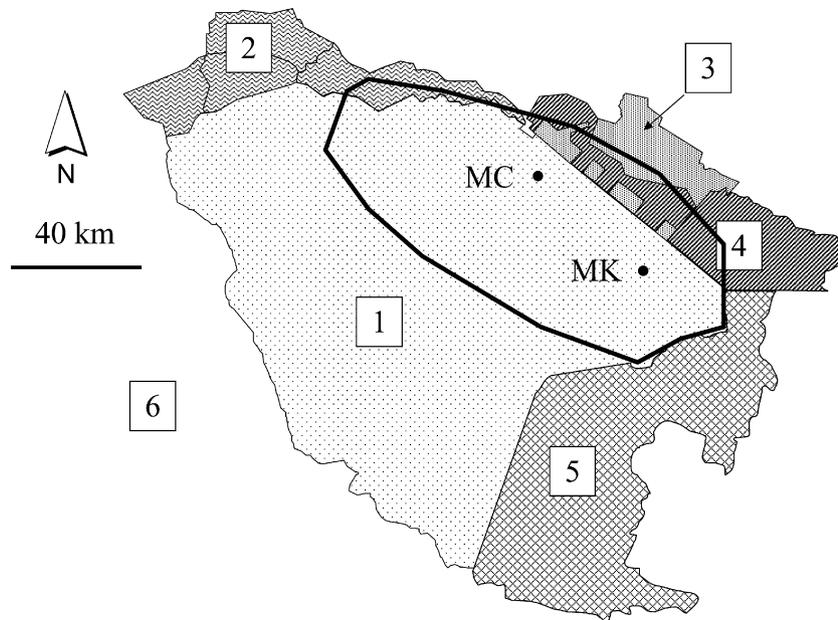
Fig. 1 – Map of study site showing Hwange National Park and adjacent hunting concessions. Study site shown within broad black line. MC, Main Camp; MK, Makalolo Camp. 1, Hwange National Park; 2, Southern part of Matetsi Safari Area (Units 3, 4 and 5) and Deka Safari Area; 3, Southern part of Gwaai Valley Conservancy (Gwaai ICA), South of main Victoria Falls to Bulawayo road; 4, Sikumi and Ngamo State Forest Land; 5, Tsholotsho Communal Land (CAMPFIRE Area); 6, Botswana (CT 3 and CT5 wildlife management areas border HNP).

males (3–4 years old) and where practicable radio-collared them. We radio-tracked from a vehicle, using a four-element yagi antenna (Sirtrack Ltd.) and either a Telonics TR4 or TR5 (Telonics Inc. Mesa, Arizona) or Televilt RX900 telemetry receiver (Televilt Positioning AB). From mid 2001 we used an ultra-light aircraft (Fulcrum 912; Ultra-light Aviation, Zimbabwe), fitted with an 'H' antennae on either wing, to locate radio-collared lions. GPS Simplex collars were programmed to download data remotely (Hemson, 2002). We relocated lions as often as possible (every day – once per month) by radio-telemetry. In addition to our own sightings, we used detailed records of lion sightings recorded by safari guides in two photographic safari concessions in the East of the park.

2.4. Sport hunting data

We obtained data on numbers of lion on quota and numbers shot each year during the study from PWMA records. However, because hunting records were not always complete (especially for Gwaai ICA), we augmented these where possible with field data (study animals shot, reports of lions hunted). We encouraged hunting operators to report lions shot and return collars and ear tags of study animals. In addition photographic safari operators, hunters and PWMA staff reported incidences of lion mortality in the study area. Where these reports could be confirmed, they were included in our records. For the purposes of calculating quota and off-take levels we included in analysis only those areas directly adjacent to HNP. These included Matetsi Safari Area hunting units 3, 4 and 5, Deka Safari Area (1708 km^2), Gwaai ICA South of the Bulawayo to Victoria Falls road (881 km^2), Sikumi and

Ngamo forest lands (1542 km^2) and Tsholotsho CAMPFIRE area (the five wildlife management areas closest to HNP; 4536 km^2). During 2004, hunting of lions was suspended on private land (making up 10.2% of land surrounding the park) due to concerns raised by early results of this study. A moratorium banned lion hunting in Botswana from 2001 to 2004.

2.5. Data analysis

We conducted statistical tests using SPSS for Windows (version 10.0.5, SPSS Inc.). Changes in mane and testicle length with age were tested using a regression ANOVA as was cub sex ratio over the study period. For males caught more than once we used only the most recent measurements. Male ranges were defined using the Minimum Convex Polygons (MCP) method. We used one location per day in calculating ranges for males equipped with GPS collars. The relationship between the proportion of adult males in the population and the harvest of males in the hunting areas surrounding the park was tested using Spearman's correlation.

3. Results

From 1999 to 2004 we captured and marked a total of 62 lions (radio-collared: 17 males, 33 females, 7 sub-adult males; ear-tagged only: 1 adult male, 1 adult female, 3 sub-adult males). Females were from 26 distinct prides known to exist in the study area. Adult males in the study included 8 singletons, 5 coalitions of 2 males and one coalition of 4 males. Not all prides or male groups were extant for the whole six year study period and there was a high attrition of study animals throughout the study. Mean pride size (number of adult

females) was 2.7 ± 0.43 ($n = 26$, range = 1–10). Mean male group size (including singletons) was 1.7 ± 0.39 ($n = 14$, range 1–4). All adult males had established home-ranges and associated with at least two and sometimes more prides (Loveridge and Macdonald, 2002). Home range and demographic data suggest that the density of the population in HNP was around 2.7 lions/100 km^2.

We were able to sex 142 cubs in 32 cohorts. The sex ratio of cubs increased from 1 male: 2.6 females in 1999 to 1.5 males to 1 female in 2004 ($r^2 = 0.72$, $F_{1,4} = 10.48$, $n = 6$, $P = 0.03$). Although the number of cubs per female in the population declined from 1999 to 2002, cub numbers increased in 2003/4, overall there was no trend in the number of cubs per female in the population over the entire study period ($r^2 = 0.01$, $F_{1,4} = 0.05$, $n = 6$, $P = 0.9$).

3.1. Mortality of tagged study animals

Of the 62 (18 adult male, 10 sub-adult male, 34 female) marked individuals 38 died or disappeared during the study. The majority of lion mortality was due to sport hunting (24 individuals; 13 male, 5 female and 6 sub-adult male). The mean distance from the park boundary that tagged study animals were shot was 1.7 ± 3.5 km ($n = 17$ adult and sub-adult males, 2 females; range 0–15 km, exact locations for the remaining 5 animals shot could not be ascertained). 82% of sport-hunted lions were shot within 1 km of the park boundary. Other sources of mortality of marked animals were due to human conflict (4 females killed by illegal wire snares or gin-traps; 1 female hit by a train). In addition, two sub adult males and one adult female (all unmarked) were rescued from snares and all survived. At least one adult male, three adult females and three sub-adults (all unmarked) were also known to have been killed in snares during the study. Five marked females died of natural causes; none within one year of capture. Four individuals (1 adult male, 1 sub-adult male and 2 females) disappeared during the study and despite intensive searches, could not be found. We could not discount radio-collar failure or long range dispersal in these cases. The only adult male to disappear was displaced from his territory by a younger coalition and there was circumstantial evidence that he was then shot by hunters. The over riding feature of lion mortality in this population was that at least 72% of adult males we tagged in the study area were shot by sport-hunters outside HNP. In addition 60% of the 10 sub-adult males we tagged were also shot by sport-hunters.

3.2. Maturity of hunted male lions

Mane length was correlated with age ($r^2 = 0.82$, $n = 30$, $F_{1,28} = 133.25$; $P = 0.00$) and appears to continue to increase until at least 6–7 years of age. Testicle length was also correlated with age ($r^2 = 0.52$, $n = 31$, $F_{1,29} = 31.6$; $P = 0.00$), but less tightly and increased with age until at least 6–7 years of age (Fig. 2). It is clear that males in this population become physically and sexually mature (*sensu* Smuts et al., 1978b) between the ages of 6–7 years. The estimated mean age of tagged males (including adults and sub adults) when shot was 5.2 ± 1.7 years ($n = 15$). Mean age of adult males alone was 6.2 ± 1.0 years
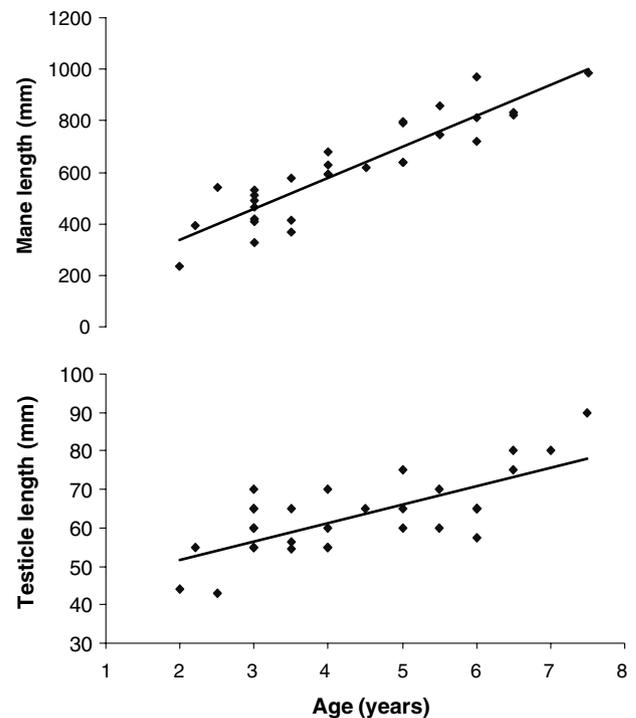
Fig. 2 Mane length plotted against estimated age of male lions captured in Hwange National Park 2000–2004 ($n = 30$; top figure). Testicle length plotted against estimated age of male lions captured in Hwange National Park 2000–2004 ($n = 31$; bottom figure).

($n = 10$). More than 30% of the males that sport-hunters shot were sub-adult (mean age 3.2 ± 0.9 years; $n = 5$).

3.3. Adult male to adult female ratio and sport-hunting off-take

Mean quotas for males in the hunting concessions around HNP between 1998 and 2004 were 0.9 ± 0.2/100 km^2 (range: 0.5–1.2/100 km^2; Fig. 3). The highest quota per unit area was allocated to the Gwaai ICA (1998–2003: 2.5 ± 0.7/100 km^2; range: 1.8–3.2/100 km^2; no quota in 2004). The lowest quota per unit area was allocated to the Tsholotsho Communal Land (1998-2004: 0.2 ± 0.02/100 km^2; range 0.16–0.2/100 km^2). Hunting quotas increased in 2001–2002, but were reduced in 2004, with much of the reduction due to reduced numbers of lion available for hunting on private land in Gwaai ICA, where a disproportionate quota had previously been allocated. Females were also hunted for sport in the areas around HNP. Mean female quotas between 1998 and 2004 were 0.3 ± 0.1/100 km^2 (range 0.2–0.5/100 km^2). Mean female off-take was 0.08 ± 0.02/100 km^2 (range 0.05–0.1/100 km^2). Overall quotas for both males and females greatly exceeded off-take in all years. The mean percentage of quota harvested was 25.8% (range 14.8–41.3%) for males and 30.6% (range 9.7–57%) for females.

During the study the proportion of males in the adult population declined from 26.3% (1 male to 2.8 females) in 1999 to 13.7% (1 male to 6.3 females) in 2003, recovering to 16.9% in 2004; Fig. 4), coinciding with suspension of hunting in the
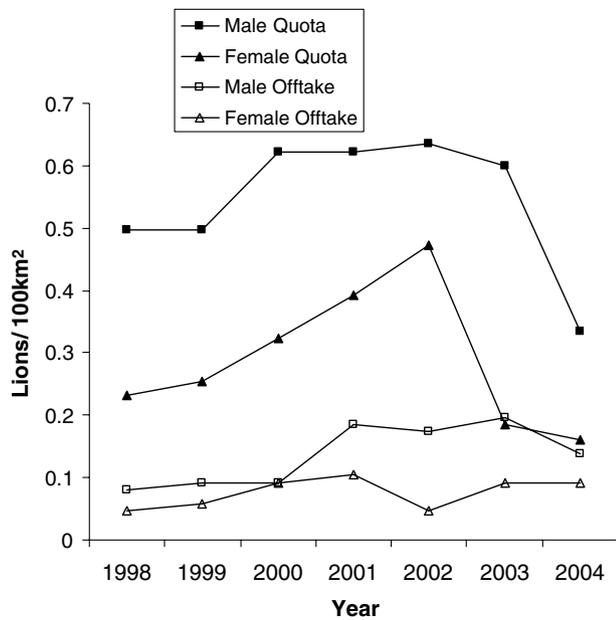
Fig. 3 – Lion hunting quota and actual off-take in the hunting concessions adjacent to Hwange National Park, 1998–2004. Far more animals were given on quota than could be harvested.

Gwaai ICA. Over the same period, off-take of males in the hunting areas surrounding the park almost doubled from a mean of 7.6 ± 0.06 (0.09 ± 0.02 males/100 km²) males in 1998–2000 to 16.0 ± 1.0 males (0.18 ± 0.01/100 km²) from 2001 to 2003. Percentage of males in the park population each year was negatively correlated with off-take of males in hunting concessions (Spearman's correlation -0.812; $n = 6$; $P = 0.05$). An example indicating that males were relatively rare in the population is that after the Airfield coalition were shot by hunters in 2000 their former range (Fig. 5b and c) was not claimed by new males for 16 months (December 2000 to April
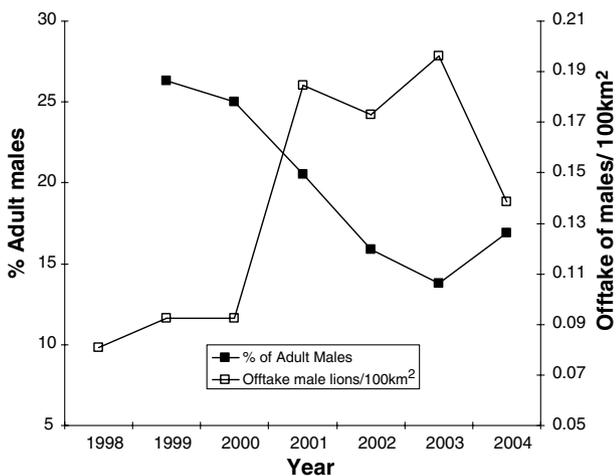
Fig. 4 – The ratio of adult males to adult females in Hwange National Park 1998–2004 (solid squares) compared to the off-take of adult males in the hunting concessions directly adjacent to the park (open squares).

2002), despite being prime habitat and the presence of three prides (two prides of 4 females and one of 2 females) in the area.

3.4. Removal of lions by sport-hunters and the vacuum effect

Throughout the study adult males were removed from the HNP population by sport-hunters on the border of the park. Each removal of a male or coalition left gaps within the territorial structure. These territorial vacuums were filled by males from territories closer to the core of the park (Fig. 5a–e). In most cases the new male groups were themselves shot and in turn replaced. One home range, around Hwange Main Camp was successively filled four times during the study as its occupants were, one after another, removed by sport hunters. Another home-range centred around Makalolo Camp was occupied by four different male groups. One of the consequences of replacement of the territorial male or coalition by a new male or coalition was infanticide by the incoming male or males. We observed or received reports of five incidences of infanticide. Ulaka (UL) killed at least one and probably three cubs in the Dete pride sired by Black-mane (BM) coalition. Mpofu (MP) coalition killed a total of three 1-year-old cubs in the Nyamandlovu pride sired by UL on two separate occasions. This coalition probably killed most of this cohort of twelve cubs since all disappeared, although we only observed three incidences on two occasions. The last remaining MP male (single male after three coalition members shot in 2003) killed a male cub from the Guvalala pride, and probably killed three cubs in the Ballaballa pride, cubs that were sired by his former coalition partners before they were shot. In all five cases infanticide occurred during the period subsequent to territorial males being removed by sport hunters.

4. Discussion

Hunting mortality within the HNP population was male biased as sport-hunters preferentially select male lions and hunting quotas were higher for males than females. Sport hunters shot 72% of marked, territorial adult males with most shot close to the park boundary. This may be because of the practice of using carcass baits to lure lions. Baits placed on or close to the park boundary were likely to attract lions whose home ranges fall within the park.

Off-takes of males in the concessions around HNP varied from 0.09/100 km² (1998–2000) to 0.18/100 km² (2001–2003). In comparison, off-takes in Selous Game Reserve, Tanzania were of a similar magnitude (0.13/100 km², based on average off-take and size of hunting units, Creel and Creel, 1997). These off-takes were considered sustainable, however, the population density of lions in Selous GR is between 8 and 13 lions/100 km² (Creel and Creel, 1997), around 3–5 times higher than the density of lions in HNP. So despite comparable off-takes, removal of male lions in relation to population density was considerably higher around HNP. Similarly, quotas in Tanzanian hunting concessions were on average 0.38 males/100 km², (Whitman et al., 2004) while quotas in concessions around HNP were 2.5 times higher (0.9/100 km²) and up to

6.6 times higher (2.5/100 km^2) in the Gwaai ICA, despite generally lower population densities.

Measures of maturity of males in HNP (mane size, testicle size) suggest that lions in this population reach physical maturity at around 6–7 years old. These data accord with those from Kruger National Park, South Africa, showing that testicle weight, seminiferous tubule diameter, body weight and size peak between 5 and 9 years (Smuts et al., 1978b) and mean age of pride males was 6.5 (range 5–9) years (Smuts, 1978). It appears that male lions in southern Africa mature later than conspecifics in East Africa (Tanzania), where male lions reach maturity at 4 years (West and Packer, 2002; Whitman et al., 2004). If an age threshold is used to determine harvests of male lions then the 6 year minimum that Whitman et al. (2004) suggest may need to be reviewed and adjusted to take into account what is apparently later maturation of males in southern Africa. Off-take of males aged between 7 and 8 years might be more appropriate.

Notwithstanding this, males from HNP were killed below even Whitman et al's minimum age threshold of 6 years with over 30% being sub-adult animals (<4 years). Apart from the fact that sub-adults have had few opportunities to reproduce, these animals make poor trophies. Although there are no long term data available for HNP to determine if population decline is in fact occurring due to over-harvesting of males, the cautionary principle should be applied and sport-hunting quotas limited to conservative levels to ensure sustainable off-takes.

Male lions achieve maximum reproductive success between 7 and 8 years of age, being 50% more successful in terms of surviving offspring than were younger or older males (Packer et al., 1988). Spermatogenesis peaks at 5–9 years (Smuts et al., 1978b) and young adult males have more sperm abnormalities and lower sperm motility than do animals over 6 years of age (Brown et al., 1991). At the population level there is no evidence to suggest that a population composed of younger breeding males is less viable or has lower breeding success *per se*, nevertheless lower reproductive performance in males below the age of 6 years could potentially contribute to reduced breeding success within a population where all mature males have been selectively removed. In addition to size and maturity, the size of the group to which a male belongs has strong influences on reproductive success (Bygott et al., 1979; Packer and Pusey, 1982). Shooting a male from a coalition weakens the coalition's competitive ability and may shorten any remaining males' tenure in a pride. We observed a case when one male of a coalition of two was shot (Fig. 5c). The remaining lion was quickly displaced from the coalition's original home-range by a stronger coalition.

Female lion off-takes around HNP were much smaller than for males, however, regular removal of even small numbers (>3%) of reproductive females has been shown to expose a population to decline (Hermann et al., 2002; Van Vuuren et al., 2005). Reproductive success is closely related to pride size and prides of three or more adult females are significantly more successful at rearing cubs than smaller or much larger prides (Packer et al., 1988) Apart from overall population reduction, one of the consequences of killing adult females is the reduction of the size and success of breeding units in the population. Populations of long lived species have been shown to be relatively resilient to population disturbance if the reproductive female life-stage remains intact, e.g., cheetah, *Acinonyx jubatus* (Crooks et al., 1998) and loggerhead turtles, *Caretta caretta* (Crouse et al., 1987) and this is also likely to be true of lions.

The potential of selective trophy hunting to drive contemporary evolution has been shown in a number species. Competition for access to females is an important process in lion social behaviour, one that shapes social groupings and is of clear evolutionary significance. Males compete strongly for access to females and larger bodied, socially experienced males are likely to be favoured over immature animals in competitive struggles (Smuts et al., 1978b; Funston et al., 2003). West et al. (2006) show that mane colour and size signals physical condition in male lions, with dark maned males having higher levels of testosterone, longer lifespan, producing more surviving cubs and preferentially selected by females (West and Packer, 2002). However, sport-hunters select the same phenotypic characteristics in their trophy (large size with dark, mature mane; (Grobbelaar and Masulani, 2003) as those that appear to signal competitive ability and reproductive advantage. While there is no evidence that selective removal alters the genetic composition of lion populations the occurrence and potential dangers of this form of contemporary evolution have been shown in other hunted mammalian species. For example increasing incidence of tusklessness in heavily hunted populations of African elephants (*Loxodonta africana*) has been attributed to selection of animals with large tusks by poachers (Jachmann et al., 1995). Coltman et al. (2003) show that reproductive success in a big-horn sheep (*Ovis canadensis*) declined because features considered desirable by trophy hunters (large horns) are linked to characteristics conferring reproductive advantage (large body size). Disturbance of these processes could have long-term consequences (Harris et al., 2002), and in a management context this perturbation may alter reproductive rates and ultimately be damaging.

We found that the sex ratio of adult males to adult females declined between 1999 and 2003 most likely as a response to increased levels of male mortality caused by sport hunting during the later part of the study. Almost all lion populations show a bias towards females and have an adult population sex ratio of 1:2 (i.e., around 30% male, e.g., (Schaller, 1972; Mills et al., 1978; Packer et al., 1988; Stander, 1991; Creel and Creel, 1997). In some cases adult sex ratios have been more heavily biased towards females, usually when males are hunted. For example Yamazaki (1996) found that a population exposed to heavy hunting in Zambia had reduced numbers of males (cf. 1 male: 4 females) and altered social behaviour. Cooper (1991) found reduced numbers of mature males (1 male: 5.7 females) in a Botswana population impacted upon by sport hunting. Similar skewed sex ratios have been reported from the peripheral areas of the Serengeti, on the border of Maswa and Loliondo hunting areas; selective hunting of male lions in these areas being implicated (Sinclair and Arcese, 1995).

Bias in sex ratio because of removal of males from a population can have adverse effects in some species (Ginsburg and Milner-Gulland, 1994; Solberg et al., 2002), although skewed sex ratios need to be extreme for reproductive col-

(a) March 1999 – June 2000

(b) June 2000 – February 2002

(c) February 2002 – November 2002

(d) November 2002 – October 2003

(e) October 2003 – October 2004
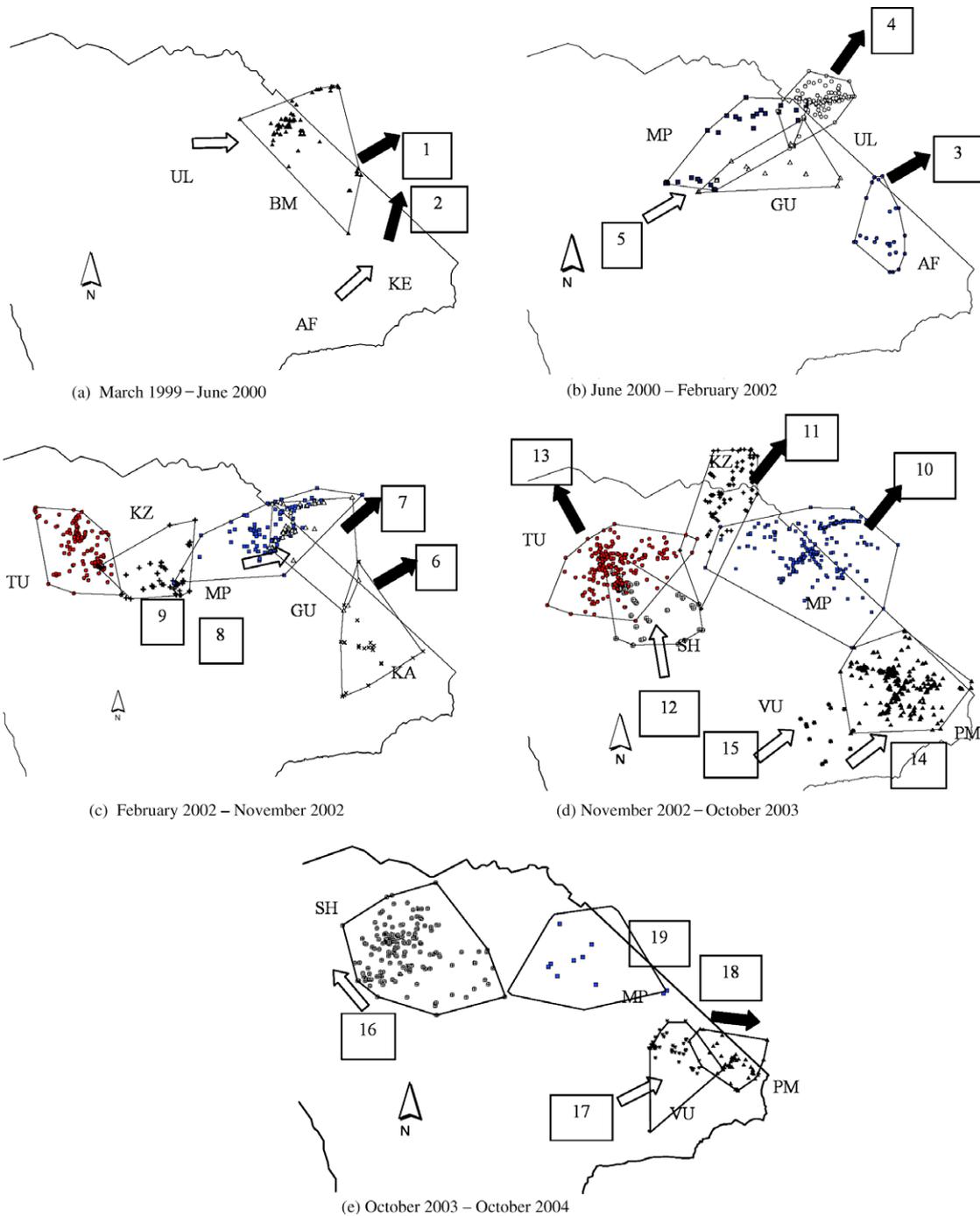
lapse to occur (Milner-Gulland et al., 2003). In HNP it was unclear whether decreasing male: female ratio had any effect on breeding biology in that it did not appear to have any impact on the number of cubs per female in the population. Nevertheless, the decline in male numbers coincided with an increase in the proportion of male cubs observed in cohorts of cubs we were able to sex. Packer and Pusey (1987) show that litters of cubs born within 300 days of a pride takeover tend to be male biased. Creel and Creel (1997), Whitman and Packer (1997) and Woodroffe and Frank (2005) observed biases in cub sex ratio towards males in populations where male mortality was high. This suggests that high sport hunting mortality simultaneously reduced the density of adult males and

increased turnover of territorial males. Increased frequency of territorial male turnover had the consequence of producing a high proportion of male biased litters in the population. While compensation for high adult male mortality by increased recruitment of males into the population may seem to be advantageous for sustainable harvest of males from the population in the long-term, the concomitant reduction in recruitment of females may ultimately result in population decline (Whitman and Packer, 1997).

Removal of territorial individuals and resulting gaps in the territorial structure of populations may cause individuals from surrounding home-ranges to be attracted to the depopulated area by reduced competition for resources. In the case of

male lions that resource may be access to mating opportunities within unattended prides. This 'vacuum effect' is also evident in other mammalian species. For example badger (*Meles meles*) groups removed in bovine Tuberculosis control operations (Cheeseman et al., 1993), lynx populations depleted by fur trapping (Bailey et al., 1986) and experimentally depopulated brush-tailed possum (*Trichosurus vulpecula*) home-ranges (Efford et al., 2000; Ji et al., 2001) were all recolonised through immigration by immediate neighbours. Removal of male lions on the boundary of HNP created vacancies within the territorial structure close to the border of the park. Male groups from nearer the core of the park successively filled these territorial 'vacuums' (as there were no mature males living outside the park). In a similar way, experimental removal of selected lion prides in Kruger National Park resulted in territorial vacancies being filled by infiltration (predominantly by young males) from the surrounding area within about 15 months. The social perturbation created by disturbance to the territorial structure suppressing the birth rate and reducing cub survival (Smuts et al., 1978b). For lions, creation of territorial vacuums on the boundaries of protected areas, such as HNP, has the effect of drawing males from further inside the protected area into boundary areas. This may ultimately expose males even well within the core of a protected area to sport-hunting mortality. As is true with other wide ranging predators, e.g., Iberian lynx, *Lynx pardinus* (Ferreras et al., 1992); kites, *Milvus migrans*, *M. milvus*, (Sergio et al., 2005), high mortality in boundary areas may weaken the potential of even very large protected areas to guard populations.

In addition to mortality from sport hunting, the HNP population also experienced mortality from other anthropogenic sources, including illegal snaring and killing. Lions are often inadvertently caught in snares set for other wildlife. While this only accounted for 11.8% of all mortality of marked animals, we know of at least seven additional unmarked lions killed in snares during the study. It is possible that this source of mortality is under-represented as this is difficult to measure because evidence of illegal killing is often concealed. Conflict mortality needs to be taken into account when setting hunting quotas, as this mortality is additive and it is possible that even conservative hunting off-takes coupled with high levels of illegal killing could make a population vulnerable to decline.

Lions are the dominant predator in most intact African savannah ecosystems. Their ecological position at the apex of the food chain and their relationship to other members of the large carnivore guild are important components of ecosystem function. Decline of keystone predators can impact ecosystems, disrupt food webs and lead to cascades of linked extinctions (Mills, 1991; Crooks and Soulé, 1999; Laurance, 2000). Disruption of lion population numbers and demographics in protected areas could have far reaching consequences, not only on lion numbers, but also on prey species and competing carnivore species (Mills, 1991). The demand

Fig. 5 – (a–e) The 'vacuum effect'. When male lions are shot on the border of the National Park a territorial vacuum is created, which is successively filled by lions from further inside the protected area as each subsequent male group is removed. Each figure shows the border of Hwange National Park and minimum convex polygons and positions for male lions over the period 1999–2004. Although based on positional data, polygons are intended to be illustrative of position and movement of lion home-ranges rather than being quantitative. VHF radio-tracking data was used from 1999 to 2004, GPS telemetry data was used from 2002 to 2004. For lions with GPS collars, one GPS position per day was used to define the home-ranges shown. Use of VHF or GPS data is shown where applicable below. Filled arrows indicate removal of lions by sport-hunters, unfilled arrows indicate shifts in home-range of male groups. Details are given in numbered boxes and relate to numbered explanatory notes below. Symbol key: Light filled triangles, Black-mane coalition (BM – two males); unfilled circles, Ulaka (UL; singleton male); light filled circles, airfield coalition (AF – two males); light filled squares, Mpofu coalition (MP – four males, reduced to one in 2003); unfilled triangles, Guvalala coalition (GU – two males); dark filled circles Tula (TU – singleton male); upright crosses, Kataza (KZ – singleton male); crosses, Kangela (KA – singleton male); crossed circles, Shapi coalition (SH – two males); dark filled triangles, Pamwe (PA – singleton male); stars, Vuka (VU – singleton male). (a) 1, Black-mane (BM) coalition (two adult males) shot in Gwaai ICA on border of HNP, May 2000, Single male, Ulaka (UL) fills territorial vacuum in May 2000 (VHF data). 2, Kennedy (KE) male shot in 1999, replaced by Airfield (AF) Coalition in mid 2000 (no positional data available). (b) 3, Airfield (AF) coalition shot May 2001 on border of HNP (VHF and sighting data), no male fills territory for 16 months. 4, Singleton Ulaka (UL), after replacing Black-mane (BM) coalition shot in Gwaai ICA Feb 2002 (VHF data). 5, Mpofu (MP) coalition (four young males) and Guvalala (GU) coalition (two older males) encroach on UL's territory (VHF data). (c) 6, Single male Kangela (KA) shot July 2002, after filling former AF coalition territory (GPS data). 7, GU coalition shot in September and October 2002. 8, MP coalition move into vacated territory, after one Guvalala male shot, this coalition encroach on former GU territory and displace remaining GU male South East where he is eventually shot. 9, Kataza (KZ) singleton (young adult male) fills vacancy left by movement of MP coalition. (d) 10, MP coalition range widely in home-range vacated by hunted GU coalition. Three of MP coalition of four are themselves shot during 2003. 11, KZ displaced by older male, Tula (TU), to West, MP coalition to East and Shapi (SH) coalition (two mature males) to South. Moves to border area of HNP and is shot May 2003 (GPS data). 12, SH coalition move into area in Feb 2003, in late 2003 invade TU's home-range, displacing him North (GPS data). 13, There is evidence TU may have been shot in Matetsi safari area, late 2003. 14, Pamwe (PM) (single male) fills vacuum left by KA in July 02 (VHF and GPS data). 15, Large single male, Vuka (VU), moves in from Southern areas of HNP, (no MCP shown as VHF data sparse). (e) 16, Shapi (SH) coalition fill vacancy left by displaced single male TU. 17, Single male Vuka (VU) moves North-east mid 2004 and partially displaces PM (GPS data). 18, PM displaced eastwards by incoming male, Vuka (VU) and shot by hunters (GPS data). 19, Last remaining member of MP coalition remains in original territory (GPS data).

for safari hunting is growing in southern Africa (Bond et al., 2004), and lions are an important and valuable species in the safari hunting industry (Grobbelaar and Masulani, 2003; Booth, 2004). Furthermore they are a robust species, with great potential to breed rapidly and recover quickly from harvests (Smuts, 1978), with limited hunting mimicking natural levels of mortality and male turnover. Because of the large contribution of sport hunting to the economies of relatively impoverished countries the utilisation of this species is deemed acceptable by some conservation managers. However, the extent to which exploitation impacts populations in putatively fully protected areas such as National Parks requires careful monitoring. Increasingly, in the face of expanding human populations in Africa, protected areas are the last sanctuary of the African lion. Management of populations of this species in and around large protected areas is crucial for the long-term future of Africa's iconic carnivore.

5. Recommendations

Sport hunting has clear impacts on the demography of the HNP population. While abnormal demographics may not necessarily reduce the viability of a population, social and genetic perturbation leading to reduced reproductive rates need to be guarded against, particularly in a protected area. Reduction of quotas to realistic levels (no more than 10% of adult males) based on robust population estimates would ease excessive off-takes of male lions. Furthermore, monitoring the age of trophies, with appropriate penalties for harvesting animals below a threshold age, could ensure that hunted individuals are primarily post-reproductive and knock-on effects on breeding success therefore minimised. Use of baits on the park boundary to lure lions out of the protected area should be banned (as is the case in Botswana; Chardonnet, 2002), and buffer zones along park boundaries where lion hunting is excluded could also be considered.

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