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Sport Hunting, Predator Control and Conservation of Large Carnivores

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Abstract

Sport hunting has provided important economic incentives for conserving large predators since the early 1970's, but wildlife managers also face substantial pressure to reduce depredation. Sport hunting is an inherently risky strategy for controlling predators as carnivore populations are difficult to monitor and some species show a propensity for infanticide that is exacerbated by removing adult males. Simulation models predict population declines from even moderate levels of hunting in infanticidal species, and harvest data suggest that African countries and U.S. states with the highest intensity of sport hunting have shown the steepest population declines in African lions and cougars over the past 25 yrs. Similar effects in African leopards may have been masked by mesopredator release owing to declines in sympatric lion populations, whereas there is no evidence of overhunting in non-infanticidal populations of American black bears. Effective conservation of these animals will require new harvest strategies and improved monitoring to counter demands for predator control by livestock producers and local communities.

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Introduction

Management agencies typically skew harvests toward males in order to protect adult females. However, in species with extensive paternal investment such as African lions (*Panthera leo*), trophy hunting can increase the rate of male replacement (and associated infanticide) to the point of reducing population size unless offtakes are restricted to males old enough to have reared their first cohort of dependent offspring ($\geq$5–6 yrs of age) [1–3]. Solitary felids have none of the "safety nets" provided by the cooperative cub rearing strategies of African lions [4–5], and Fig. 1ab illustrates the greater vulnerability of solitary species by examining the effects of trophy hunting on a hypothetical population of "solitary lions" while leaving other demographic parameters from ref. [1] unchanged (Supporting Information Table S1, also see ref. [6]). Leopards (*Panthera pardus*) may be more sensitive to sport hunting than solitary lions (with a safe minimum age of 6–7 yrs of age, Fig. 1c), whereas cougar (*Felis concolor*) males can be safely harvested as young as 4 yrs of age (Fig. 1d).

We tested whether infanticidal species are vulnerable to over-hunting by focusing on four large carnivore species with sizable markets for sport-hunted trophies, comparing three infanticidal felids (lions, cougars and leopards) to American black bears (*Ursus americanus*). We used black bears as a control case because males do not kill cubs in order to increase mating opportunities (sexually-selected infanticide – SSI), so rates of infanticide are not increased by male-biased trophy hunting; in fact, among ursids, SSI has been documented in only one population of European brown bears (*U. arctos*) [7–9].

We extracted data from the UNEP World Conservation Monitoring Centre (WCMC) CITES trade database (See Materials and Methods). Data on total trophy harvests of lions and leopards are not available, so we used CITES-reported exports, which in cougars and black bears were highly correlated with domestic sport-hunting totals (Supporting Information Fig. S1); likewise CITES-reported trade in Tanzania's lion trophies showed a close match between imports and exports. Given sustained market demand, harvest trends should provide a reasonable proxy of population trends since sport hunters use intensive methods such as baits and hounds to locate these animals, and quotas on annual offtakes are either too high to limit harvests or (for black bears) reflect the management agency's perception of population trend [10].

Results

Fig. 2 shows the annual CITES exports for lions and leopards and US offtakes of cougars and black bears (See Materials and Methods). The reported number of trophies increased rapidly across all four species as markets grew during the 1980's and 1990's [11–12]. Offtakes have continued to increase for black bears, reflecting the sustained growth of bear populations

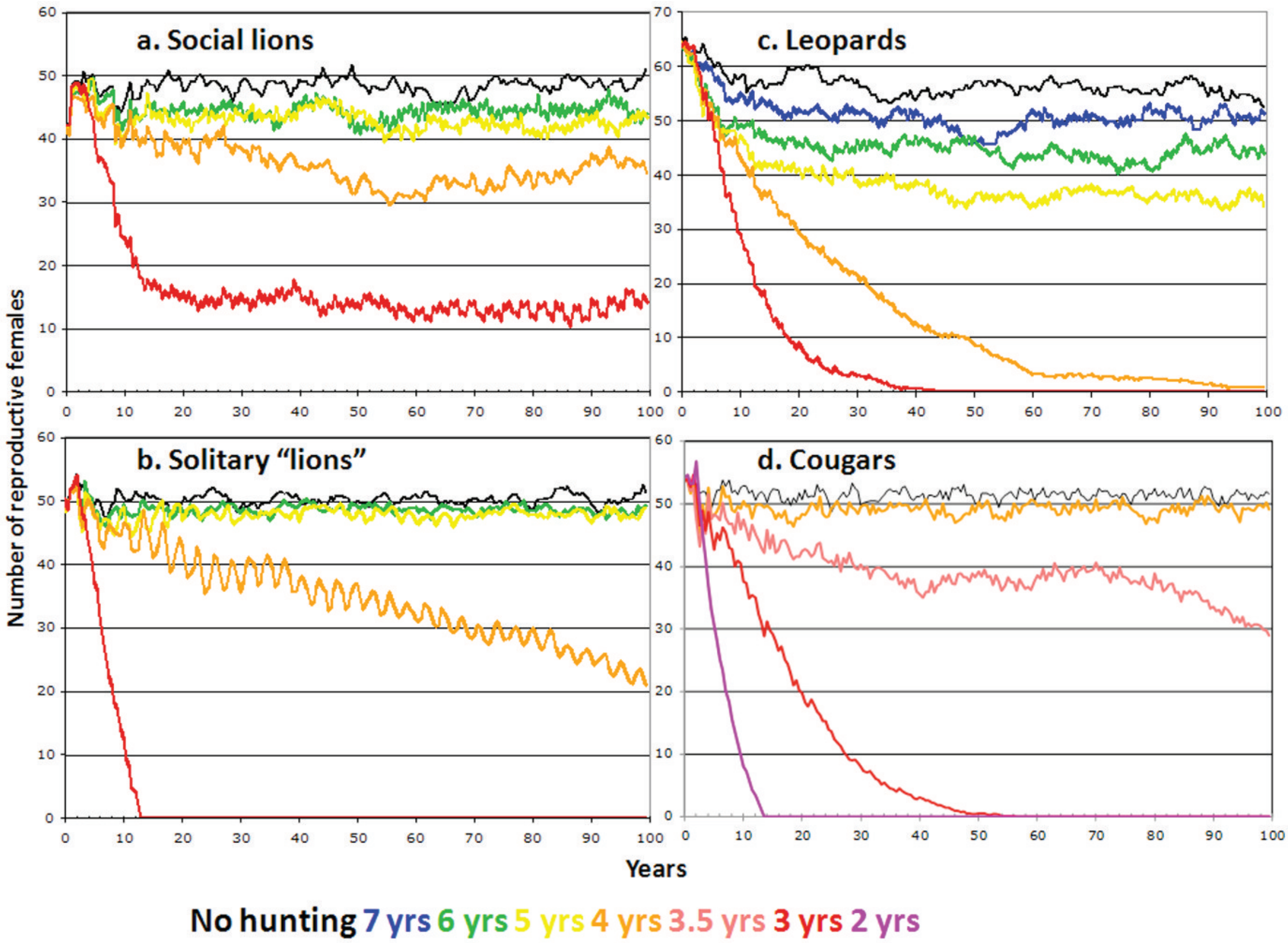

Figure 1. Average number of adult females in population simulations where all eligible males are removed during a 6-mo hunting season each year for 100 yrs. Colors indicate outcomes for different age minima for trophy males; each line indicates average from 20 runs. **A**. Population changes for ''social lions'' follow the assumptions and demographic variables in ref. [1] except to restrict hunting to 6-mo seasons and to incorporate additional details of dispersal, survival and reproduction [44–46]. **B**. Population changes for a hypothetical lion population where males and females are solitary and each territorial male controls one female. **C**. Population changes for leopards based on long-term data from Phinda Private Game Reserve [33,47] and other sources [37,48]. **D**. Population changes for cougars based on demographic data from refs. [27,49–53].
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throughout North America [13]. Leopard offtakes reached an asymptote in most countries, except for declines in Zambia in the 1980's and Zimbabwe in the 1990's and a recent CITES-granted increase to Namibia. In contrast, lion offtakes peaked then fell sharply in the 1980's and 1990's in Botswana, Central African Republic, Namibia, Tanzania, Zambia and Zimbabwe. Cougar offtakes showed similar peaks and declines in the 1990's in Arizona, Colorado, Idaho, Montana and Utah (Fig. 2).

The downward harvest trends for lions and cougars (highlighted in Supporting Information Fig. S2) most likely reflected declining population sizes: success rates (as measured by harvest/quota) have fallen for both cougars and lions (Supporting Information Fig. S3). Demand for lion trophies (as measured by total imports from across Africa) has grown in the US and held stable in the EU since the mid-1990s, sustained in recent years by imports of trophies of captive lions from South Africa [12,14] (Supporting Information Fig. S3). Several countries instituted temporary bans on lion trophy hunting (Botswana in 2001–2004, Zambia in 2000–2001 and western Zimbabwe in 2005–2008) or banned female lions from quota (Zimbabwe, starting in 2005), but these measures were implemented well after the major decline in lion offtake in each country. The harvest trends are also consistent with recent surveys suggesting a 30% continent-wide population decline in African lions [15] and declining cougar populations in several US states [16–17]. Conversely, black bear populations appear to be increasing across their range [13], even in states where cougar populations have declined (Fig. 2). Although not apparent from most hunting offtakes, leopards have undergone an estimated range decline of 35% in Africa [18] and were recently listed as Near Threatened by IUCN due to habitat loss, prey depletion, illegal skin trade and problem animal conflicts [19].

Trophy hunting is likely to have contributed to the declines in lion and cougar populations in many areas. Over the past 25 yrs, the steepest declines in cougar and lion harvests occurred in jurisdictions with the highest harvest intensities (Fig. 3a). Similarly, hunting blocks with the highest lion offtakes per 1000 km^2 in Tanzania's Selous Game Reserve showed the steepest declines between 1996 and 2008 ($r^2 = 0.26$, $n = 45$ blocks, $P = 0.0004$). The Selous is the largest uninhabited hunting area in Africa (55,000 km^2) and has long been the premier destination for lion trophies. Across jurisdictions, declining harvests were unrelated to habitat loss for either lions or cougars (Fig. 3b) or to snow

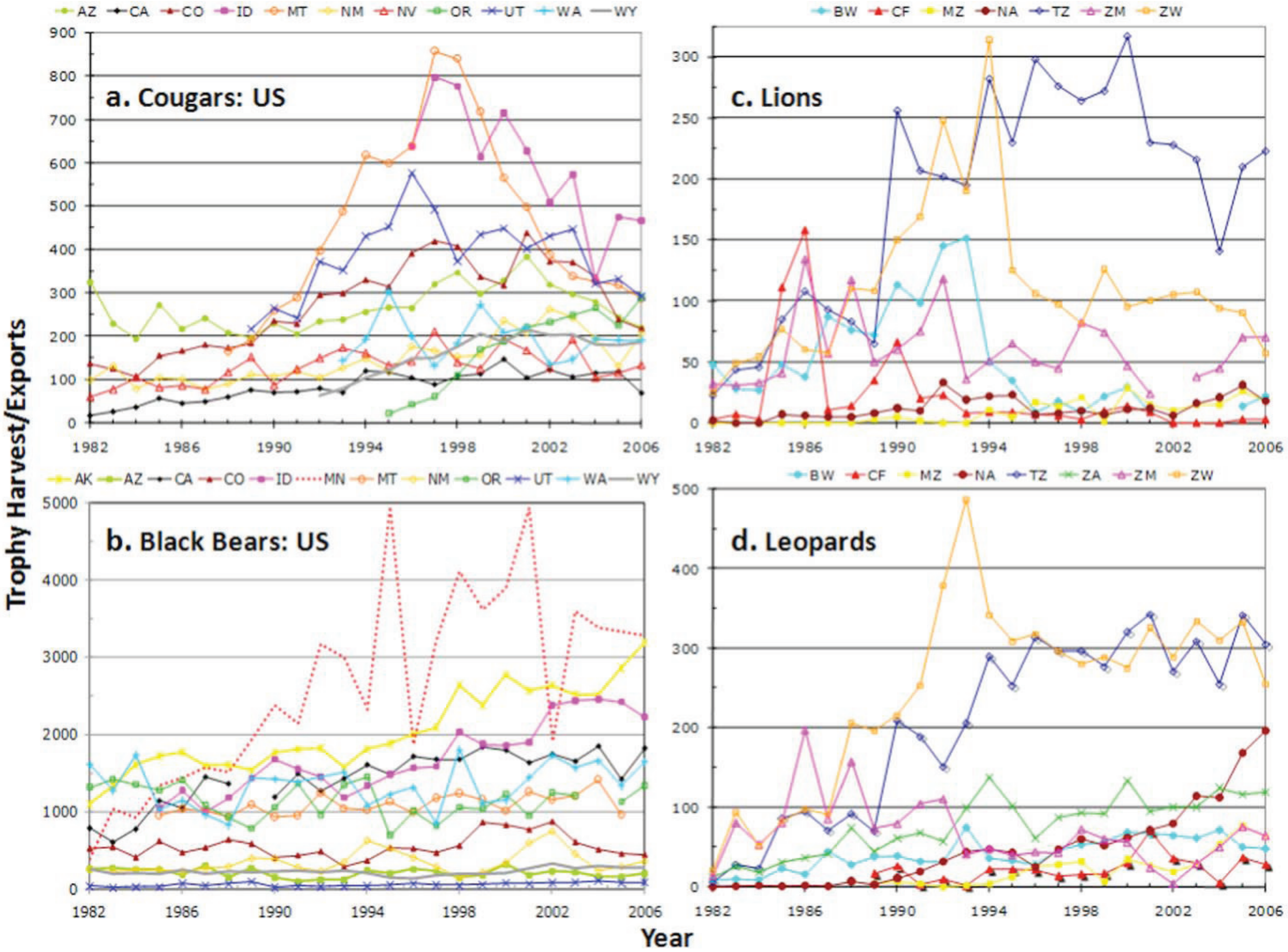

Figure 2. Domestic offtakes of a) cougars and b) black bears and CITES-reported trophy exports of c) lions and d) leopards. For US states: AK = Alaska, AZ = Arizona, CA = California, CO = Colorado, ID = Idaho, MN = Minnesota, MT = Montana, NM = New Mexico, NV = Nevada, OR = Oregon, UT = Utah, WA = Washington, WY = Wyoming. For CITES data: BW = Botswana, CF = Central African Republic, MZ = Mozambique, NA = Namibia, TZ = Tanzania, ZM = Zambia, ZW = Zimbabwe.
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conditions for cougars. We modified our population simulation models to estimate impacts of sport hunting in a changing environment and found that habitat loss only imposes an additive effect on the impact of trophy hunting (Supporting Information Fig. S4). Note that habitat loss in many African nations has been so extensive (Fig. 3b) that lion offtakes have failed to recover for 10–20 yrs following the peak harvest years except in Namibia.

Although trophy hunting of lions and cougars is often portrayed as an economic strategy for increasing support for carnivore conservation, local communities often seek extirpation of problem animals [15,20–22]. Thus, sport hunting quotas may sometimes reflect pressures to control carnivores rather than to conserve them. Across Africa, countries with the highest intensity of lion offtake also had the highest number of livestock units per million hectares of arable land ($P = 0.047$, $n = 7$). In the US, Oregon announced plans in 2006 to reduce its cougar population by 40% to decrease depredation on livestock, pets and game mammals [23], Washington altered its cougar quotas in response to human-wildlife conflicts in the 1990s–2000s, and recent offtakes have exceeded government-sanctioned eradication programs in several states. For example, Utah's sport-hunting cougar harvests averaged 500/yr in 1995-7 compared to peak culls of 150/yr in 1946–1949 [24], and Montana sport hunters harvested 800/yr in 1997–1999 vs. 140/yr in the peak "bounty" years of 1908-11 [25]. Likewise, South Africa exported 120 leopard trophies per year in 2004–2006, similar to the cull of 133 leopards per year in Cape Province (which covered most of the country) during 1920–1922 [26].

Fig. 4 shows the potential consequences of coupling a 40% cull of cougars with intensive sport hunting if the control program only targets males (reflecting traditional trophy hunting), removes males and females in proportion to their abundance, or only removes adult females. Fig. 4adg show population trends for the maximum fixed offtakes that never resulted in population extinctions during 20 simulations, whereas Fig. 4beh show the minimum fixed harvests that caused extinction in all 20 runs (often within 10 yrs of an initial decline). Fig. 4cfi show the consequences of applying the maximum "safe" offtakes if the population were inadvertently culled by 50% because of inaccurate population estimates. Consistent with population viability analyses [27–28], a female-only harvest comes closest to maintaining a persistent population reduction; a mixed male-female strategy allows the largest number of trophies to be harvested; a male-only harvest never maintains a

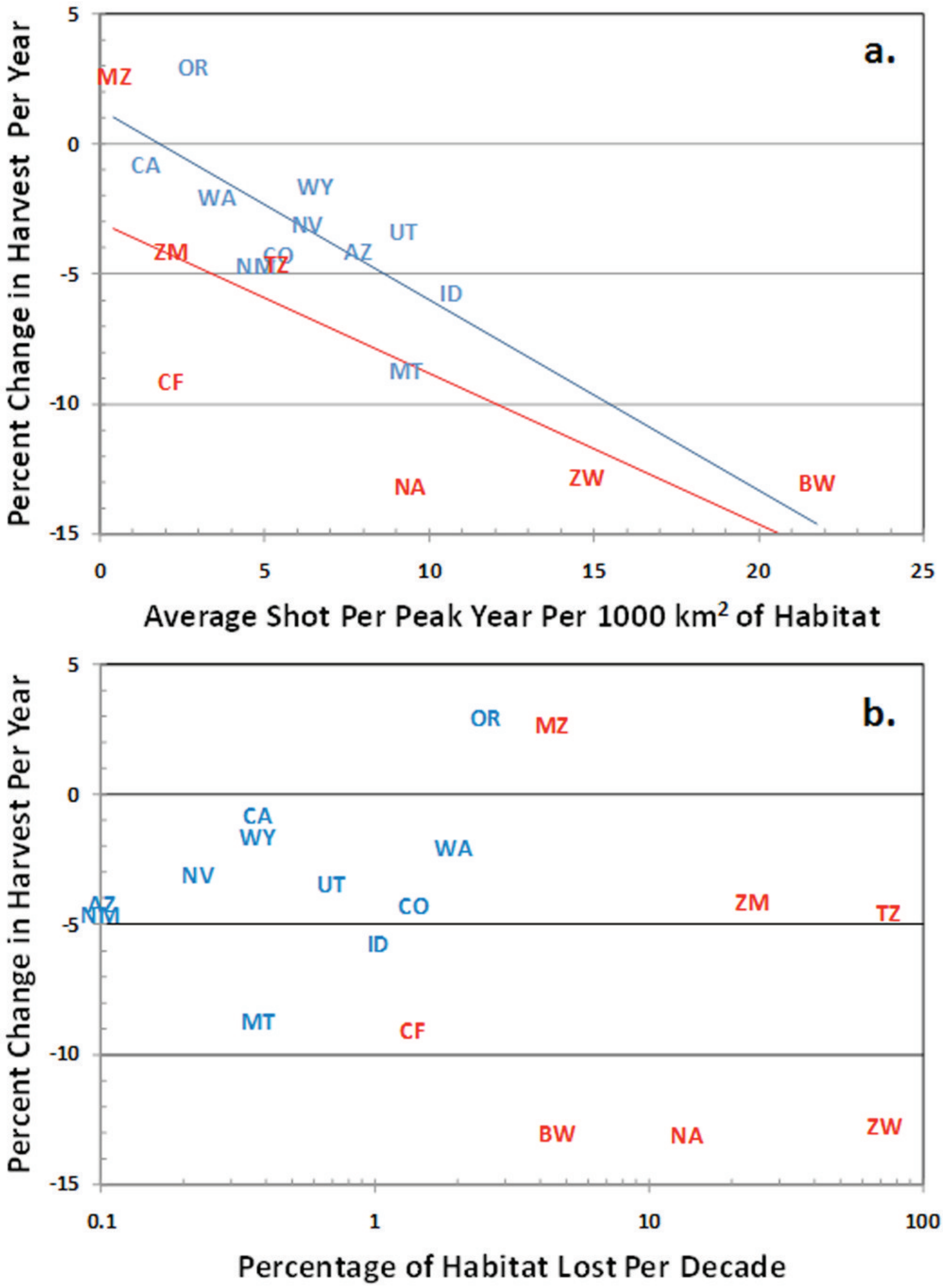

Figure 3. Recent trends in cougar offtakes (blue) and lion offtakes (red) as functions of a) harvest intensity and b) habitat loss. Jurisdictions with the highest harvest intensity showed the greatest decline in cougar offtakes ($r^2 = 0.5151$, $P = 0.0129$) and lion offtakes ($r^2 = 0.5796$, $P = 0.0468$). Habitat loss is plotted on a log scale to allow comparison between the African countries and the US states.
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40% reduction in population size and has the smallest margin of error (male-only harvests can have catastrophic effects even in non-infanticidal species [29]).

These simulations assume a fixed harvest whereas many wildlife agencies reduce their quotas in response to lowered offtakes (Supporting Information Fig. S3 also see ref. [30]). However, offtakes may often be maintained at constant levels through compensatory increases in hunting effort, running the risk of an "anthropogenic Allee effect" [31–32]. Hunters in Zambia, Zimbabwe and Tanzania maintain their lion harvests by shooting males as young as 2 yrs of age (Fig. 5). In Zimbabwe, high lion offtakes were sustained from 1995 until 2005 by allowing females on quota [3], and the duration of lion safaris increased by nearly 18% from 1997 to 2001 (Supporting Information Fig. S3). Similarly, hounds have been used to hunt leopards in Zimbabwe since 2001, potentially masking a continued population decline.

Discussion

Mortality from state-sanctioned and illegal predator control likely contributed to the overall population declines of cougars and lions; while leopards are also killed as pests, the leopard's CITES Appendix I status requires international approval for national export quotas, potentially providing safeguards against overhar-

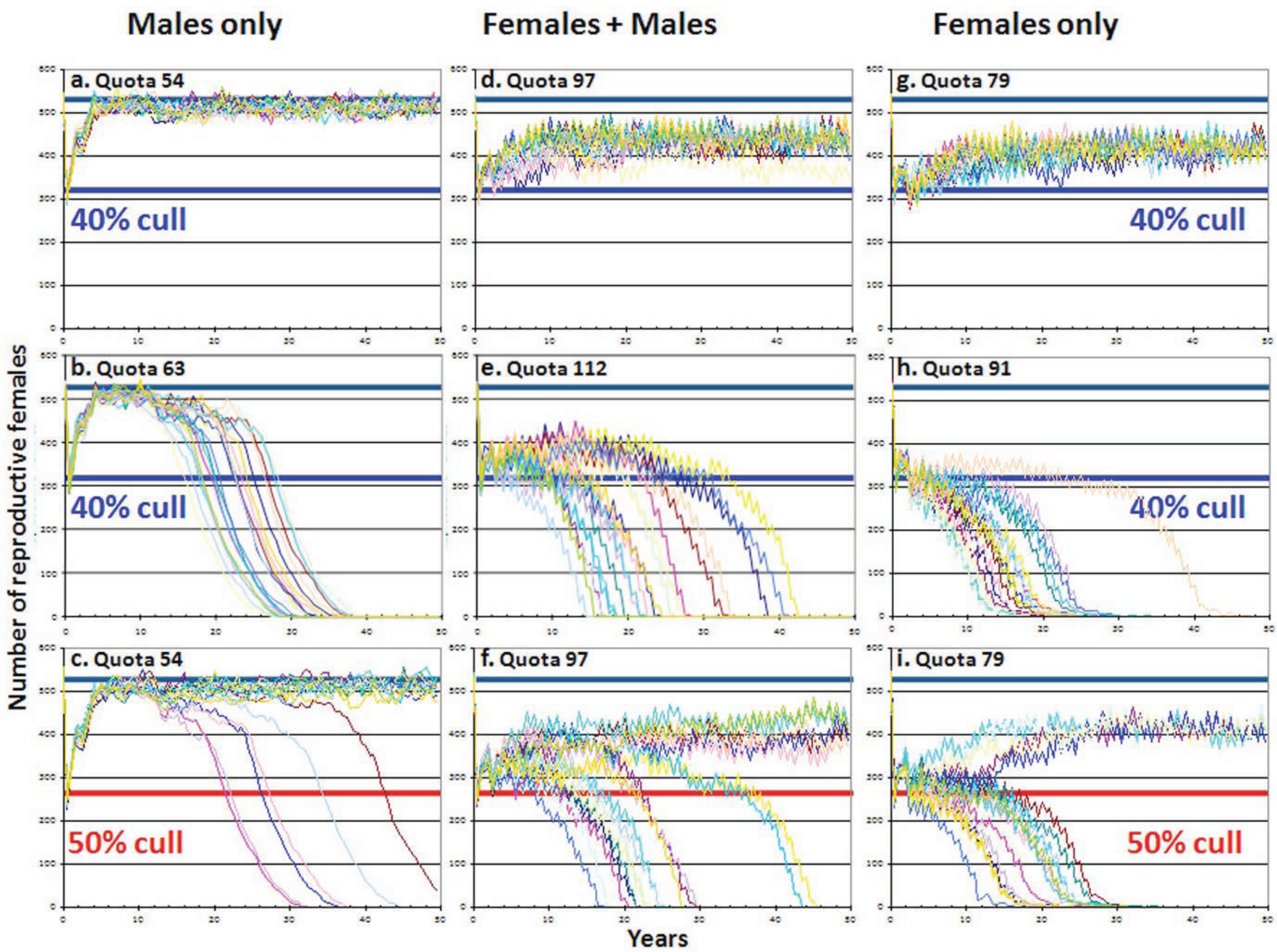

Figure 4. Simulated cougar populations subjected to an initial cull followed by fixed offtakes for 50 yrs. The initial cull is either 40% (top and middle rows) or 50% (bottom row), and the subsequent harvests are either the maximum offtake that incurred no extinctions in 20 runs following a 40% cull (top and bottom rows) or the minimum that produced 20 extinctions in 20 runs following a 40% cull (middle row). In the absence of sport hunting, the stable population size in these simulations is 527 reproductive females (indicated by the heavy black line in each graph); a 40% reduction in population size is indicated by blue lines, a 50% reduction by red lines. Each column represents a different harvest strategy: male only (left column), males and females (middle) and female only (right). Demographic parameters are set as in Fig. 1; quotas allow offtake of animals as young as 2 yrs; each graph shows outputs from 20 runs.
doi:10.1371/journal.pone.0005941.g004

vest. However, leopard exports have declined in some countries, quotas have risen in others, and concerns have been raised over the level of problem animal offtakes and the management of leopard hunting practices [33–35]. Further, leopard populations in many areas may have been "released" [36] by large scale declines in lion numbers: lions inflict considerable mortality on leopards [37]; consequently, hunting blocks in Tanzania's Selous Game Reserve with the highest lion harvest intensities showed the largest *increases* in leopard harvests ($P = 0.0059$ after controlling for declines in lion offtakes, $n = 45$ blocks). Thus the full impact of current trophy hunting practices on leopards may not be fully apparent for several more years.

Harvest policies for infanticidal species such as lions, cougars and leopards that relied on "constant proportion" or "fixed escapement" could help protect populations but require accurate information on population size and recruitment rates, which are virtually impossible to collect; a harvest strategy of "constant effort" can more easily be achieved by measuring catch rates and regulating client days [38–40]. Hunting efficiency could be reduced by banning or limiting the use of baits and hounds, but the absence of direct oversight in remote hunting areas would make enforcement difficult. Alternatively, the age-minimum harvest strategies illustrated in Fig. 1 could be implemented without risk of over-hunting, assuming that ages can be reliably estimated before the animals are shot [41] rather than afterwards [42]. Unsustainable levels of trophy hunting of lions and cougars appear to be driven by conflicts with humans and livestock: the intensity of lion hunting was highest in countries with the most intensive cattle production, and wildlife managers are under similar pressure from US ranchers to raise cougar offtakes. Thus an even more fundamental challenge for carnivore conservation will be to build community tolerance for predators by reducing the need for retaliatory predator control and by improving benefit sharing from well managed trophy hunting [15].

Materials and Methods

We analyzed trophy exports (http://www.unep-wcmc.org/citestrade/) by using the term "trophy" and restricting the analysis to countries that exported at least 25 trophies of a particular

Figure 5. Sample of under-aged male African lions shot by sport hunters in various countries from 2004–2008.
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species for at least 2 yrs from 1982 to 2006 (excluding captive-bred lion trophies from South Africa). Other types of exports (skins) were also analyzed for lions, since non-standard terms are sometimes used by reporting countries [43], but these did not alter overall export trends. Data on Tanzanian hunting quotas were provided by the CITES office at the Division of Wildlife headquarters in Dar es Salaam; data on duration of hunting safaris in Zimbabwe were from the head office of Parks and Wildlife Management Authority in Harare.

Offtake data for black bears and cougars were provided by the Alaska Dept. of Fish & Game, Arizona Game & Fish Dept., California Dept. of Fish & Game, Colorado Division of Wildlife, Idaho Fish & Game, Minnesota Dept. of Natural Resources, Montana Fish, Wildlife & Parks, New Mexico Game & Fish, Nevada Dept. of Wildlife, Oregon Dept. of Fish & Wildlife, Utah Division of Wildlife Resources, Washington Dept. of Fish & Wildlife, and Wyoming Game & Fish. Note that all cougar offtakes in California are due to predator control.

"Harvest intensity" is the average harvest of the three peak offtake years divided by the extent of habitat in that state/country. Regression coefficients were calculated across the time period beginning with the earliest of the three peak harvests and ending in 2006 for cougars or the last of the three lowest subsequent harvest years for lions (Supporting Information Fig. S3); percent change is the regression coefficient divided by the peak harvest. Limited lion and leopard offtake data were available from 1996–2008 in Tanzania's hunting blocks; trends were only calculated for blocks reporting $\geq$5 yrs of activity.

Cougar habitat is forest cover taken from the National Land Cover Database (NLCD) www.mrlc.gov/changeproduct.php; lion habitat is the extent of GLOBCOVER land classification categories 42, 50, 60, 70, 90, 100, 110, 120, 130, 134, 135, 136, 160, 161, 162, 170, 180, 182, 183, 185, 186 and 187 in each country, see http://postel.mediasfrance.org/en/DOWNLOAD/Biogeophysical-Products/. Habitat loss is based on change in forest cover in the US 1990–2000 and in woodland/forest habitat in Africa 1990–2005 from FAO Global Forest Resources Assessment 2005, http://www.fao.org/forestry/32185/en/. Snow conditions for cougars are taken from http://www.wrcc.dri.edu/Climsum.html and African livestock production is taken from http://www.fao.org/es/ess/yearbook/vol_1_1/pdf/b02.pdf, using production levels from years of peak lion offtake in each country.

Supporting Information

Figure S1 The number of CITES-reported exports of a) cougar trophies and b) black bear trophies from the US were highest in years when the most animals were harvested domestically in the western states ($P<0.001$ for each species).
Found at: doi:10.1371/journal.pone.0005941.s001 (0.69 MB EPS)

Figure S2 Trendlines for the population declines of a) cougars and b) lions. Individual states with statistically significant declines in cougar offtakes: MT, ID, AZ, UT and CO; individual countries with significant declines in lion offtakes: BW, TZ and ZW.
Found at: doi:10.1371/journal.pone.0005941.s002 (1.08 MB EPS)

Figure S3 Quotas, offtakes and catch rates each year since the peak harvests for cougars in Colorado, Montana and Utah and lions in Tanzania and Botswana; duration of lion hunts in Zimbabwe. Catch rates are (offtakes/quotas). Catch rates have generally declined because offtakes have fallen more quickly than quotas. Catch rates briefly improved in Utah and Botswana when quotas were adjusted downwards, but subsequently resumed an overall decline; Montana's adjustments in quotas are too recent to evaluate. For Zimbabwe, vertical lines indicate standard errors; numbers are sample sizes; duration of lion hunts became significantly longer between 1997 and 2001 ($P<0.01$). No other data are available on quotas or hunt durations from these or other countries/states. The bottom graphs show that declines in lion trophy exports are unlikely to reflect declining market demand; imports of lion trophies have increased, especially in recent years for captive-bred or "canned" lion trophies for South Africa. The declines in trophy exports are also unlikely to be caused by irregular reporting; adding additional exports of skins from Botswana, Tanzania and Zimbabwe would not significantly change the pattern of decline.
Found at: doi:10.1371/journal.pone.0005941.s003 (1.38 MB EPS)

Figure S4 Simulated impacts of trophy hunting in cougars for varying degrees of habitat loss. Solid lines are the same as in Fig. 1: all available males above the age minimum are harvested each year and available habitat remains unchanged over 100 yrs. Dashed lines show population sizes with the same harvest strategies but with 20% habitat loss in 100 yrs; dotted lines represent outputs with 40% habitat loss.
Found at: doi:10.1371/journal.pone.0005941.s004 (1.49 MB EPS)

Table S1
Found at: doi:10.1371/journal.pone.0005941.s005 (0.03 MB DOC)

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Author Contributions

Conceived and designed the experiments: CP MK KN. Performed the experiments: MK. Analyzed the data: CP MK HB LP KN. Contributed reagents/materials/analysis tools: MK HC HB LP DLG GP MS AS GB LH KN. Wrote the paper: CP DLG KN.

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Contributed Paper

Effects of Trophy Hunting on Lion and Leopard Populations in Tanzania

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Abstract: *Tanzania holds most of the remaining large populations of African lions (*Panthera leo*) and has extensive areas of leopard habitat (*Panthera pardus*), and both species are subjected to sizable harvests by sport hunters. As a first step toward establishing sustainable management strategies, we analyzed harvest trends for lions and leopards across Tanzania's 300,000 km^2 of hunting blocks. We summarize lion population trends in protected areas where lion abundance has been directly measured and data on the frequency of lion attacks on humans in high-conflict agricultural areas. We place these findings in context of the rapidly growing human population in rural Tanzania and the concomitant effects of habitat loss, human-wildlife conflict, and cultural practices. Lion harvests declined by 50% across Tanzania between 1996 and 2008, and hunting areas with the highest initial harvests suffered the steepest declines. Although each part of the country is subject to some form of anthropogenic impact from local people, the intensity of trophy hunting was the only significant factor in a statistical analysis of lion harvest trends. Although leopard harvests were more stable, regions outside the Selous Game Reserve with the highest initial leopard harvests again showed the steepest declines. Our quantitative analyses suggest that annual hunting quotas be limited to 0.5 lions and 1.0 leopard/1000 km^2 of hunting area, except hunting blocks in the Selous Game Reserve, where harvests should be limited to 1.0 lion and 3.0 leopards/1000 km^2.*

Keywords: harvests, *Panthera leo*, *Panthera pardus*, population trends, sport hunting

Efectos de la Cacería Deportiva sobre Poblaciones de Leones y Leopardos en Tanzania

Resumen: *Tanzania mantiene la mayoría de las poblaciones remanentes de leones Africanos (*Panthera leo*) y tiene extensas áreas de hábitat de leopardo (*Panthera pardus*), y ambas especies son sujetas a cosechas considerables por cazadores deportivos. Como un primer paso hacia el establecimiento de estrategias de manejo sustentable, analizamos las tendencias de cosecha de leones y leopardos en los 300,000 km^2 de bloques de cacería de Tanzania. Sintetizamos las tendencias poblacionales de leones en áreas protegidas donde la abundancia de leones ha sido medida directamente, así como datos sobre la frecuencia de ataques de leones sobre humanos en áreas agrícolas altamente conflictivas. Ubicamos estos resultados en el contexto de la población humana en rápido crecimiento en Tanzania rural y los efectos concomitantes de la pérdida de hábitat, el conflicto humanos-vida silvestre y las prácticas culturales. Las cosechas de leones han declinado 50% en Tanzania entre 1996 y 2008, y las áreas de cacería con las cosechas iniciales más altas sufrieron las declinaciones más pronunciadas. Aunque cada parte del país está sujeto a alguna forma de impacto antropogénico por habitantes locales, la intensidad de la cacería deportiva fue el único factor significativo en el análisis estadístico de las tendencias poblacionales de leones. Aunque las cosechas de leopardos fueron más estables, regiones fuera de la Reserva de Caza Selous con las cosechas iniciales de leopardos más altas también mostraron las declinaciones más pronunciadas. Nuestros análisis cuantitativos sugieren que las*

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cuotas anuales de cacería se limiten a 0.5 leones y 1.0 leopardo/1000 km² de área de cacería, excepto los bloques de cacería en la Reserva de Caza Selous, donde las cosechas deben limitarse a 1.0 león y 3.0 leopardos/1000 km².

Palabras Clave: cacería deportiva, *Panthera leo*, *Panthera pardus*, cosechas, tendencias poblacionales

Introduction

Although habitat loss and retaliatory killing are generally considered the primary threats to large felids across Africa (Ray et al. 2005; IUCN 2006; Bauer et al. 2008), hunting can also deplete animal populations (e.g., Milner-Gulland et al. 2003; Fryxell et al. 2010), especially in felids in which sexually selected infanticide is common (e.g.,Whitman et al. 2004; Caro et al. 2009). For example, excessive trophy hunting appears to have caused large-scale declines in African lions (*Panthera leo*), American cougars (*Felis concolor*), and possibly African leopards (*Panthera pardus*) (Packer et al. 2009). Across seven countries (lions) and 11 U.S. states (cougars), jurisdictions with the highest sport-hunting harvests per 1000 km² of habitat subsequently showed the steepest proportional declines in harvests. The growing use of dogs to hunt leopards in Zimbabwe, and declining leopard harvests in Zambia and Zimbabwe (Purchase & Mateke 2008; Balme 2009; Packer et al. 2009; Balme et al. 2010) have also raised concerns about leopard management and trophy hunting.

Tanzania has an extensive network of national parks (38,365 km², including Ngorongoro Conservation Area), game reserves (102,049 km²), and game-controlled areas (202,959 km²), and has more lions than any other country in Africa. Four of the continent's six largest remaining populations of lions occur in Tanzania in the Serengeti, Maasai Steppe, Selous, and western Tanzania (Fig. 1). Leopards are common throughout Tanzania, and the country has been granted one of the highest export quotas for leopard trophies by CITES. In addition, Tanzania is the most popular destination for sport hunting of lions and leopards (http://www.unep-wcmc.org/citestrade/) in the world. An average of 243 wild lion trophies were exported per year between 1996 and 2006. In Zimbabwe and Zambia 96 and 55 trophies/year, respectively, were exported, and no other country exported more than 20 per year (Packer et al. 2009). Tanzania also exported an average of 303 wild leopard trophies/year, whereas Zimbabwe exported 300 per year and no other country exported more than 100 per year.

Lions and leopards throughout Africa are subject to widespread loss of habitat, prey depletion, and human–animal conflicts that are associated with rapid human population growth (e.g., Ray et al. 2005; Woodroffe & Frank 2005; IUCN 2008). In Tanzania, human population growth has been particularly high along the borders of the wildlife areas (Fig. 2a), and deforestation has accelerated in the past 15 years (Packer et al. 2009) with concomitant declines in herbivore populations (Stoner et al. 2007). Thus, there is an urgent need for quantitative analysis to establish sustainable harvest practices, while taking care to disentangle the impacts of trophy hunting from these other anthropogenic factors. Trophy-hunting quotas for lions and leopards have never been based on rigorous quantitative analysis of harvest patterns in any country (Packer et al. 2009).

Data on lion population trends in Tanzania are available from long-term studies conducted in a small number of protected areas where trophy hunting is not permitted (e.g., Kissui & Packer 2004; Packer et al. 2005*a*), but no comparable population data exist for leopards. The population status of both species is unknown in all of the country's hunting blocks. Nevertheless, three factors allow Tanzania's trophy harvests to be used as indirect measures of population trends (Packer et al. 2009). First, hunting companies invest enormous effort into locating lions and leopards, and most animals are shot at baited stations. Male lions frequently scavenge (Schaller 1972) and are thus especially susceptible to baiting. Second, clients must purchase a "21-day safari package" to be granted permission to hunt lions or leopards in Tanzania. Sales have grown by 60% over the past decade, and overall quotas for lions and leopards have also risen (Fig. 2b). Third, a substantial proportion of Tanzania's lion trophies in 2006–2008 consisted of subadult males (see Fig. 5 in Packer et al. 2009), which is a sign of over-exploitation (e.g., Allendorf & Hard 2009). Therefore, any decline in harvest likely reflects declining population size.

We assessed whether trophy hunting has had measureable effects on the abundance of lions and leopards in Tanzania. We tested whether hunting areas with the highest harvest levels subsequently showed signs of overhunting. Additionally, we used data from long-term studies of lions conducted in Tanzania's phototourism areas to examine whether any of these largely unhunted populations have been affected by trophy hunting. We also evaluated the potential effects of other anthropogenic factors, such as conversion of natural vegetation to agriculture, human population density and growth, the presence of ritual and retaliatory killings, and proximity of wildlife habitat to human-occupied areas.

Methods

Continuous, long-term records of individual lions have been collected in 2700 km² of Serengeti National Park since 1966 (Packer et al. 2005*a*), in the 250-km² floor of

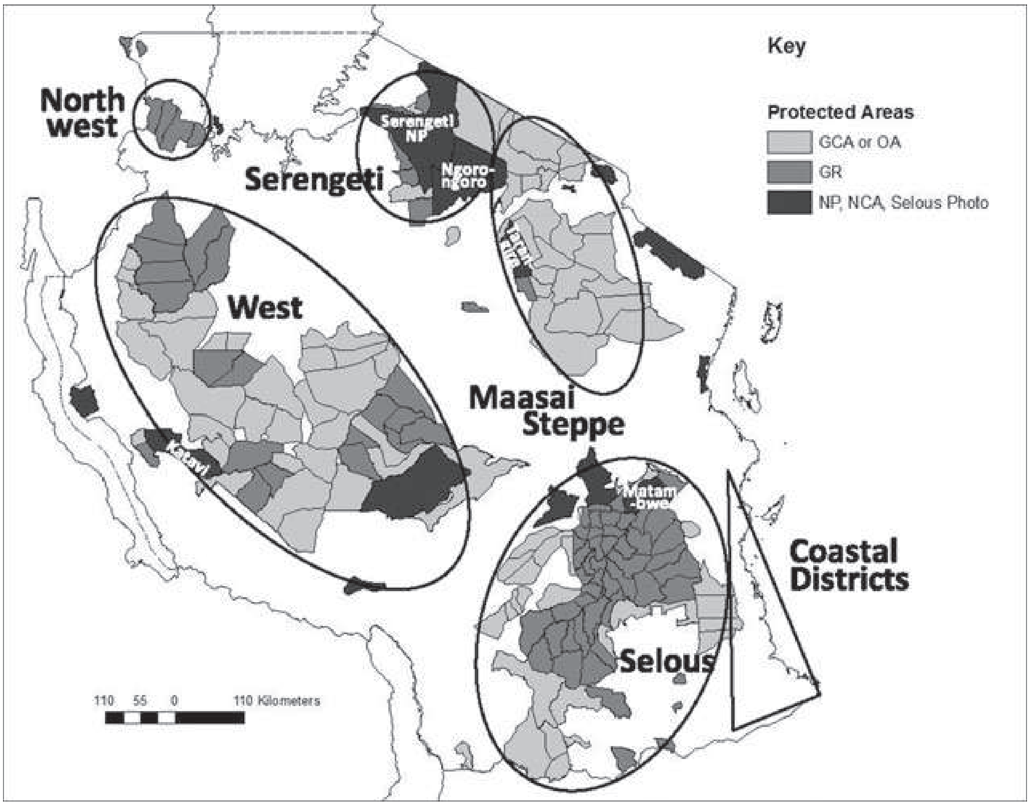

Figure 1. Map of protected areas and hunting areas in Tanzania (ellipses, major ecosystems within the country). No settlements are allowed in game reserves (GR) and national parks (NP); only pastoralist Maasai are allowed to reside in Ngorongoro Conservation Area (NCA); and settlements are permitted in game controlled (GCA) and open areas (OA). Trophy hunting is prohibited inside national parks and the Ngorongoro Conservation Area.

Ngorongoro Crater since 1963 (Kissui & Packer 2004), and in 2000-km^2 of Tarangire National Park since 2003. Comparable short-term studies of individual lions were conducted in 600–850 km^2 areas of the Matambwe Photourism Area of Selous Game Reserve in 1996 and 1999 (Spong 2002) and in 2007–2008. We did not consider data from a 1992 study by Creel and Creel (1997) because of the small size of the area they covered (90 km^2 vs. 725 km^2 in subsequent studies) and because of atypically high lion density in their lakeshore study area.

Female lions in Serengeti, Tarangire, and Matambwe were fitted with radio collars and located and observed two to eight times per month. We used these data to determine the group membership of each pride. Ngorongoro Crater is primarily open grassland; thus, individual lions could be located opportunistically. Our estimates of lion density in Katavi National Park came from Caro (1999), who surveyed 80 km of ground-based transects twice annually since 1995 and controlled for variations in visibility along the width of each transect in his surveys. Cases of lion attacks on humans are reported to District Game Offices throughout the country (Packer et al. 2005*b*). We updated data from districts with the highest number of lion attacks in the country over the past two decades (Lindi, Masasi, Mkuranga, Mtwara, Ruangwa, Rufiji, and Tunduru districts) to extend the analysis to 2008.

The CITES office at the Division of Wildlife Headquarters in Dar es Salaam provided data on quotas and harvests of lions and leopards in each hunting block, as well as the national totals of clients and 21-day safaris. We analyzed the harvest data at two scales: individual hunting blocks and seven geographically discrete regions. Hunting blocks are leased by the Tanzanian government and range in size from 141 to 8440 km^2 (mean [SD] = 1695 km^2 [1339], $n = 168$). We restricted our block-level analysis to the 45 blocks in the Selous Game Reserve because the German Technical Assistance agency, Gesellschaft für Technische Zusammenarbeit (GTZ), had spent considerable development funds on record keeping in the Selous (Baldus & Cauldwell 2004; Caro et al. 2009; Leader-Williams et al. 2009) and because records were available from an average of 87% of the Selous blocks each year (vs. only 69% in the rest of the country). In the regional analysis, we considered seven discrete areas: Maasai steppe (22 blocks), northwestern Tanzania (4 blocks), greater Serengeti (8 blocks bordering Serengeti National Park), western Tanzania (42 contiguous blocks), Selous Game Reserve (45 blocks), a set of blocks near Selous Game Reserve first hunted in 2002 (14 blocks), and a set of

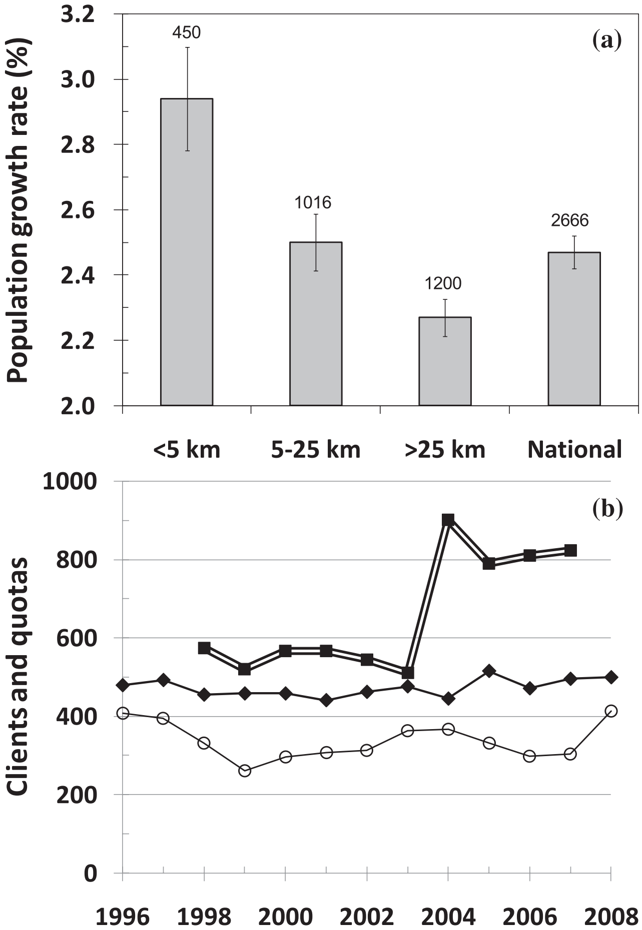

Figure 2. Human population growth and demand for lion and leopard trophies in Tanzania. (a) Annual population growth from 1988 to 2002 in wards located each distance from national parks and game reserves (numbers above bars, number of wards; lines, SE). Wards <5 km from protected areas grew faster than those 5–25 or >25 km away ($p < 0.001$*). (b) Total number of 21-day safaris (double line, solid squares) and total quotas for lions (solid diamonds) and leopards (open circles) across all of Tanzania's hunting blocks.*

blocks near Selous hunted since 1996 (7 blocks). For each hunted area, we defined the initial hunting intensity as the average annual number of animals harvested per 1000 km^2 in 1996–1999. We then calculated the harvest regression coefficient for 1996 through 2008. The annual rate of change in lion harvest was the regression coefficient divided by the initial intensity. Because the rate of change approaches zero at high initial intensities, we log-transformed all data sets where initial intensities exceeded 3 trophies·1000 km^{-2}·year^{-1}.

We estimated potential habitat loss with data from 1997 on land conversion to agriculture within or adjacent to each wildlife area (FAO 2002). We used data from the national census (Tanzanian National Bureau of Statistics 2002) to measure human population density in 2002 and the rate of human population growth in each ward between 1988 and 2002). Ward-level growth rates were calculated from photographs of 1988 ward-boundary maps stored at the National Bureau of Statistics in Dar es Salaam. For most areas, quantitative data were not available for prey loss, extent of retaliatory killing, ritual killing, or disease, so we noted only presence or absence of each factor (Table 1) and whether felids living in phototourism areas were affected by trophy hunting (e.g., Tarangire lions regularly move into hunting blocks from the national park). As a measure of overall exposure to anthropogenic effects of local people, we distinguished between hunting blocks that were completely surrounded by other hunting blocks and blocks that abutted non-wildlife areas and were thus located along an "edge." Proportion of edge is the total area of edge blocks in a particular ecosystem divided by the total hunted area in that ecosystem.

For the analysis of the regional trophy harvests, we constructed a priori candidate models to test the effects of hunting intensity, agriculture, human population density, human population change, and "edge effects" (Table 2). We sought the best model(s) to account for harvest trends in each species. Statistics were run in PROC REG in SAS (version 9.1, SAS Institute 2002). We performed model selection with Kullback–Leibler (K–L) information–theoretic approach with Akaike's information criterion corrected for small sample size (AIC$_c$) (Burnham & Anderson 2002; Anderson & Burnham 2002). For each candidate model, we used the residual sum of squares (RSS) to calculate the values for AIC$_c$: $\Delta\text{AIC}_c = (\text{AIC}i - \text{min AIC})$, where min AIC is the minimum AIC value of all models, ω_i is the Akaike weight (weight of evidence that model i is the best approximating model given the data and the set of candidate models) (Burnham & Anderson 2002).

Mean harvest intensities and harvest trends were tested for normality by regressing the residuals against normal probability curves. We detected no significant deviations or evidence of kurtosis.

Results

Across the five long-term lion studies in nonconsumptive protected areas, lion numbers remained the same in one population (Matambwe), increased in one population (Serengeti), and decreased in three populations (Tarangire, Katavi, and Ngorongoro), and the frequency of lion attacks on humans also declined in the agricultural areas of coastal Tanzania (Fig. 3).

The Serengeti and Ngorongoro lions suffered from severe disease outbreaks (Table 1). Whereas the Serengeti population recovered quickly (Packer et al. 2005*a*), the

Table 1. Summary of threats to Tanzania's lion and leopard populations.

Ecosystem and site	Type of area	Size of ecosystem (km^2)	Survey area (km^2)	Years	Lion population or harvest trend[a] (r^2, p)	Lion harvest/ 1000 km^2/ yr 1996–1999[b]	Leopard harvest trend[a] (r^2, p)	Leopard harvest/ 1000 km^2/ yr 1996–1999	Proportion agriculture in 1997 (%)	Human population density per km^2 in 2002	Human population growth 1988–2002 (%)	Prey loss[b]	Retaliatory lion killing[b]	Ritual lion killing	Disease	Proportion edge
Greater Serengeti																
Ngorongoro Crater	photo tourism	250	250	1989–2009	−0.23 0.027	N			0	9.77	9.53	N	Y	N	Y	N
SE Serengeti National Park	photo tourism	25,000	2,700	1989–2009	+0.74 <0.001	Y			0.67	13.35	3.59	Y	Y	Y	Y	Y
Serengeti blocks (8)	trophy hunting	25,000	11,597	1996–2008	−0.44 0.026	2.06	−0.25 ns	2.30	6.89	11.14	3.72	Y	Y	Y	Y	100%
Maasai Steppe																
Tarangire National Park	photo tourism	52,836	2,000	2003–2009	−0.64 0.031	Y			0	15.52	2.95	Y	Y	N		Y
Maasai Steppe blocks (24)	trophy hunting	52,836	50,036	1996–2008	−0.04 ns.	0.54	−0.15 ns	1.36	16.9	9.04	4.96	Y	Y	N		69%
Greater Selous																
Matambwe Photo-Area	photo tourism	90,089[c]	725	1997–2009	−0.20 ns.	Y			0.02	2.95	1.26	Y	Y	N		Y
Selous game reserve blocks (45)	trophy hunting	90,089	44,244	1996–2008	−0.51 0.006	2.62	+0.05 ns	2.45	2.01	2.51	1.06	Y	Y	N		34%
Selous: old blocks (7)	trophy hunting	90,089	13,774	1996–2008	−0.10 ns.	1.36	+0.13 ns	0.64	17.1	13.05	2.40	Y	Y	Y		100%
Selous: new blocks (16)	trophy hunting	90,089	17,295	2002–2008	−0.41 0.119	2.00	−0.03 ns	1.72	12.5	7.60	1.43	Y	Y	Y		100%
Western Tanzania																
Katavi National Park	photo tourism	143,138	4,300[d]	1995–2009	−0.50 0.016	Y			0.40	4.35	2.97	Y	Y	Y		Y
Western blocks (54)	trophy hunting	143,138	121,551	1996–2008	−0.57 0.004	1.42	−0.10 ns	1.08	5.08	6.61	4.15	Y	Y	Y		76%
Northwest Tanzania																
Northwestern blocks (4)	trophy hunting	4,240	3,995	1996–2008	−0.45 0.034	2.26	−0.11 ns	4.11	2.45	28.43	4.34	Y	Y	N		100%
Southeast Tanzania																
Coastal districts	agriculture	58,704	58,704	1990–2008	±0.24 0.05[e]	Y			42.9	32.62	2.51	Y	Y	N		Y

[a]*Trends are based on annual lion surveys in the photo tourism areas and on lion and leopard harvests in the hunting areas over the years specified in each row.*
[b]*Abbreviations: N, no threat; Y, threat present.*
[c]*Total area of photo tourism areas: 2996 km^2.*
[d]*Area repeatedly surveyed (80 km of ground transects).*
[e]*Number of lion attacks on humans, r^2 and p are for the quadratic term.*

Table 2. Akaike information criterion (AIC) test of the contribution of each variable to lion-harvest trends and leopard-harvest trends in six sport-hunting areas.*

Model	K	AIC_c	ΔAIC_c	ω_i
Lion harvest				
lion trophy hunting	2	−46.64	0.00	0.922
null model	1	−39.31	7.33	0.024
proportion edge	2	−38.02	8.62	0.012
lion trophy hunting + proportion edge	3	−37.65	8.99	0.010
proportion agriculture	2	−37.43	9.21	0.009
Leopard harvest				
log leopard trophy hunting	2	−37.85	0.00	0.637
null model	1	−35.37	2.48	0.184
proportion agriculture	2	−33.29	4.56	0.065
log leopard trophy hunting + proportion edge	3	−31.93	5.92	0.033
Human population change	2	−31.81	6.04	0.031

**The model with the lowest AIC and highest Akaike weight (ω_i) values is the best model, although any model with a ΔAIC value of <2 would be considered a plausible alternative. Models with ΔAIC greater than the null model can be disregarded (Burnham & Anderson 2002) (*K = *df). All the same variables were tested for both species, but only the top five models for each are reported.*

abundance of Ngorongoro Crater lions remained below carrying capacity due to recurrent epizootics (Kissui & Packer 2004). This population also suffered mortality from Maasai herders (Kissui et al. 2009).

The Matambwe and Serengeti study populations were exposed to modest levels of trophy hunting, whereas the Tarangire population spent 4–6 months of the year outside the National Park, where they are subject to high levels of retaliatory killing in response to cattle depredation (Kissui 2008) and to trophy hunting. In contrast, Katavi lions were relatively sedentary, and their numbers were low as a result of high trophy harvests in the surrounding hunting blocks (Kiffner et al. 2009).

Lion harvests declined significantly in four of seven hunting areas across the country: the northwest, the west, around Serengeti National Park, and inside Selous Game Reserve (Fig. 4; Table 1). Record keeping was most thorough inside the Selous Game Reserve and provided the best opportunity for a block-by-block analysis. The "retention scheme" in Selous also provided higher levels of antipoaching and infrastructure development than any other hunting area in the country (Baldus & Cauldwell 2004; Leader-Williams et al. 2009), so we considered hunting trends in this area separate from other areas.

Lion harvests inside the Selous Game Reserve declined most steeply in blocks that experienced the highest legal harvest per 1000 km^2 in 1996–1999 (Fig. 5a). Human settlement is not permitted inside Tanzanian Game Reserves, so none of these blocks suffered any loss of habitat from agriculture or deforestation. Lion harvests did not decline more rapidly in the "edge" blocks of the Selous than in blocks that were completely surrounded by other hunting blocks. In the remaining six hunting areas, regions with the highest initial trophy harvests per 1000 km^2 again showed the steepest proportional declines in harvest (Fig. 5b). No other variable (e.g., agriculture, human population density, etc.) had a statistically significant effect (Table 2).

In contrast to lions, leopard harvests have not shown statistically significant harvest trends in any of the seven hunting areas (Fig. 4). Nevertheless, harvests in the northwest declined by about 10% per year since 1996, and harvests around Serengeti declined 5% per year. Within the Selous Game Reserve, hunting harvests declined more steeply in the blocks with the highest harvest level in 1996–1999, but this trend was not significant (Fig. 5c). Across the rest of the country, the proportional decline in leopard harvest was significantly higher in areas with the highest initial harvests (Fig. 5d), and trophy hunting was the only important variable (Table 2).

Reports by hunting operators and tour guides inside Selous indicate leopard abundance has increased in the past 5 years. Selous hunting blocks with the highest average lion harvests in 1996–2008 showed the largest increases in leopard harvests (Packer et al. 2009).

Discussion

Trophy hunting appears to have been the primary driver of a decline in lion abundance in the country's trophy-hunting areas and is likely affecting lion abundance in Katavi National Park and possibly Tarangire National Park. In contrast, lion abundance was unchanged in two of the three phototourism areas that are only minimally affected by trophy hunting; lion abundance has fallen in Ngorongoro Crater even though the area is protected from hunting. We lacked independent estimates for leopard population trends, but trophy hunting may have similarly driven a decline in leopard abundance in several areas outside Selous. In contrast to the conclusions of IUCN (2006) and Bauer et al. (2008), reports, we were unable to detect any consistent impact from habitat loss or human–carnivore conflict in hunting areas, although retaliatory killing was substantial in several of the protected areas.

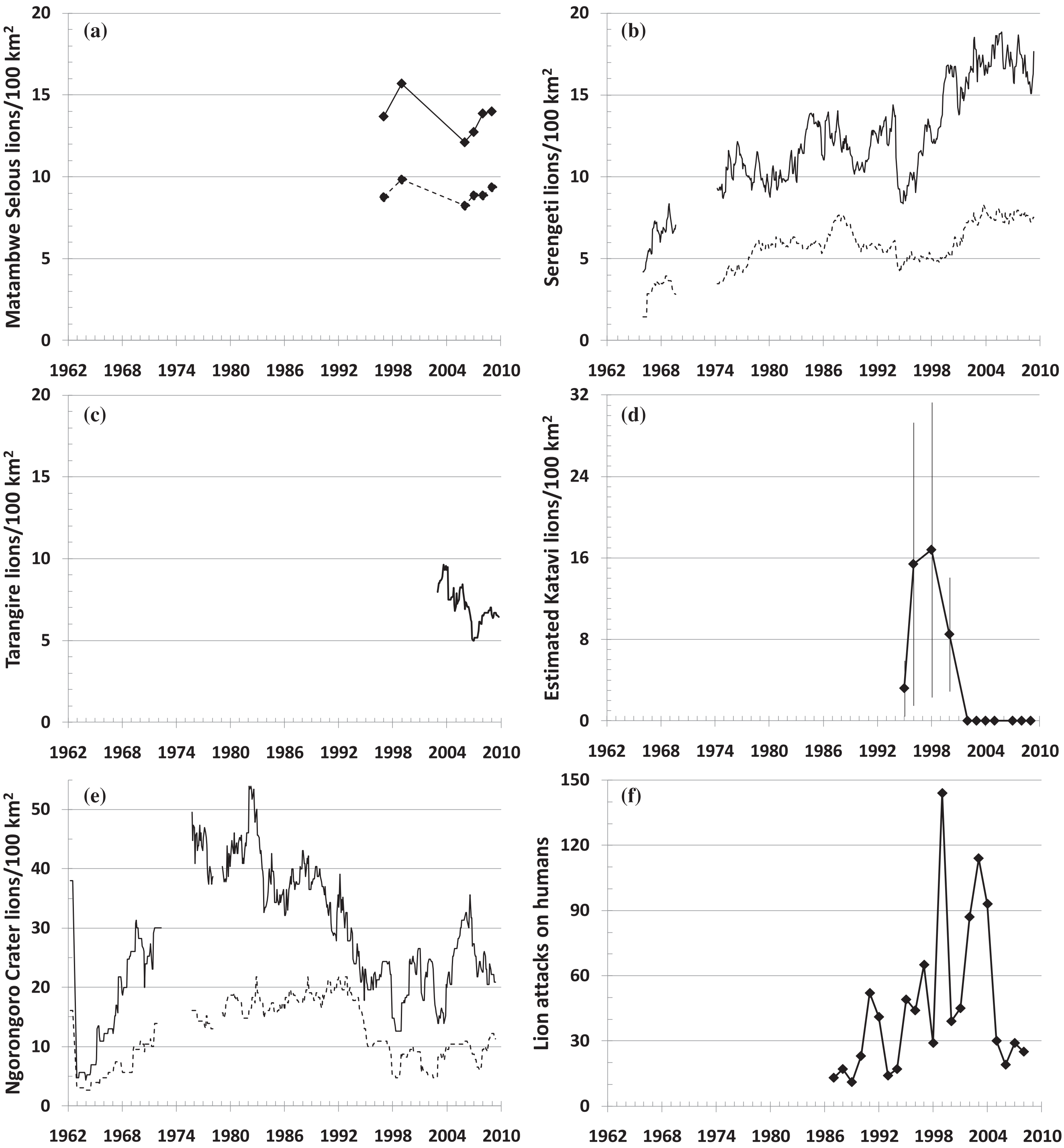

Figure 3. Long-term data on lion population density in (a) Matambwe Phototourism Area, Selous Game Reserve, (b) Serengeti National Park, (c) Tarangire National Park, (d) Katavi National Park (SE), and (e) Ngorongoro Crater and on (f) the number of lion attacks in Lindi, Masasi, Mkuranga, Mtwara, Ruangwa, Rufiji, and Tunduru districts (reported to the Tanzanian Wildlife Authorities) (solid lines, total population density; dotted lines, adult density; diamonds, annual surveys; lines without diamonds, continuous observations).

Trophy Hunting

In Tanzania the Selous Game Reserve is the largest contiguous hunting area uninhabited by humans and is thus the area most exclusively affected by trophy hunting (Caro et al. 2009). The simulation models of Whitman et al. (2004) predicted that removing 10% of ≥4 year-old-male lions each year would cause an eventual 50%

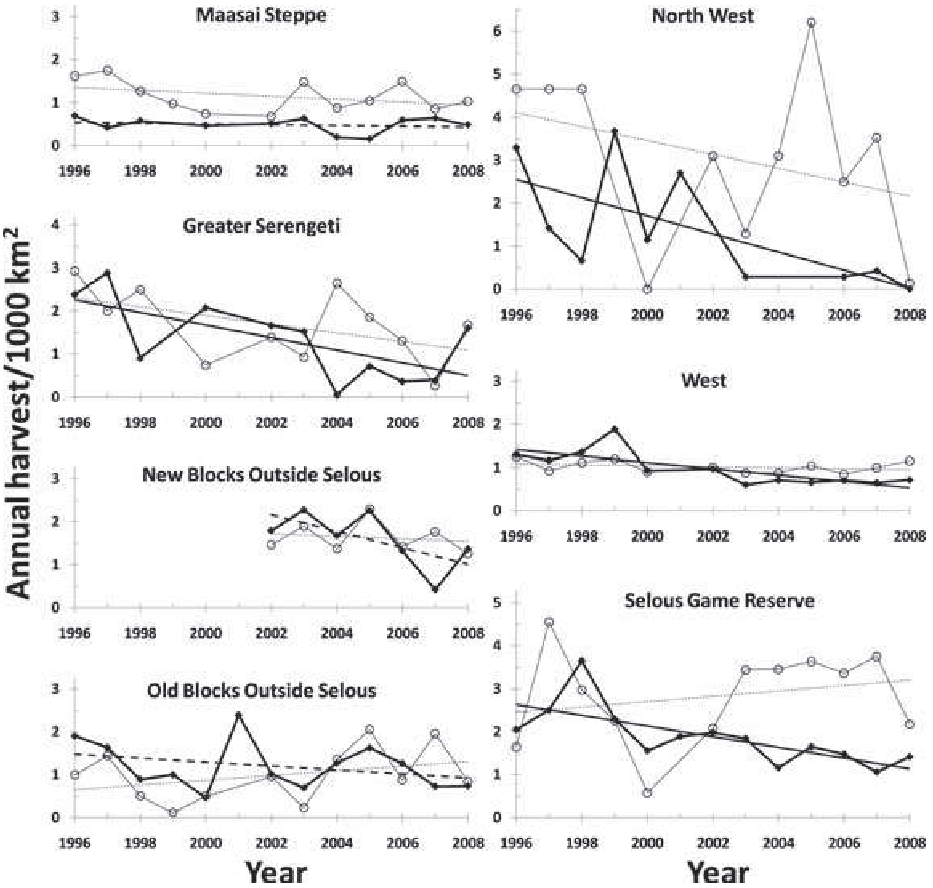

Figure 4. Average number of lions (heavy lines, diamonds) and leopards harvested (thin lines, circles) in major hunting areas (solid regression line, statistically significant declines between 1996 and 2008; dashed regression line, not significant).

decline in the total population. The average annual harvest in Selous was 2.62 males per 1000 km^2 in 1996–1999, which would have comprised 9.4% of 27.9 adult males per 1000 km^2 in the Matambwe phototourism sector. In the Katavi–Rukwa ecosystem, an average of 10.8 males were shot each year between 1996 and 2008, a period when an estimated average of 38 adult males occupied the entire area (Caro 2008; Kiffner et al. 2009), making annual harvests about 28.4% of males. Thus it is plausible that trophy hunting has reduced the lion population inside Katavi National Park, as suggested by Kiffner and colleagues (2009). High lion harvest around Zimbabwe's Hwange National Park has had measureable effects on the population inside the Park (Loveridge et al. 2007, 2009), whereas seasonal movements of lions originating from Tarangire National Park may have helped sustain harvests in nearby hunting blocks—an effect that counters extensive human population growth and habitat loss in the Maasai Steppe.

At least three factors may be responsible for stability of leopard harvests. First, widespread declines in lion abundance could have released leopards from interspecific competition (Crooks & Soulé 1999), and leopards seem to have benefited from declining lion numbers in Selous Game Reserve (Packer et al. 2009), although we have only anecdotal reports that leopards have increased in the Selous. Second, about 30% of Tanzania's documented leopard trophies are female (Spong et al. 2000). Packer et al. (2009) showed that cougar populations can theoretically withstand higher levels of harvest of females than males, and the same pattern should occur in any other polygynous species with sexually selected infanticide. Third, hunting companies might have put more effort into shooting leopards as lions became more difficult to locate in their hunting blocks.

Loss of Habitat and Prey

As seen elsewhere (Wittemyer et al. 2008), human population growth is highest in wards located <5 km from Tanzania's wildlife protected areas (Fig. 2a). Tanzania has lost >37% of woodland and forest habitat since 1990 (Packer et al. 2009), and bushmeat poaching has increased throughout the country (Jambiya et al. 2007), further reducing the prey base for lions and leopards. Bushmeat poachers operate within Katavi National Park (Caro 2008), the western edge of the Serengeti ecosystem (Sinclair et al. 2008), and in most hunting areas around the country (Caro & Andimile 2009). In northern Serengeti National Park, lions were largely extirpated in the 1980s by poachers setting snares for herbivores (Sinclair et al. 2003). Matambwe lions have died after eating poisoned carcasses set out to kill crocodiles in Selous. Conversion of rangeland to agriculture in the Maasai Steppe

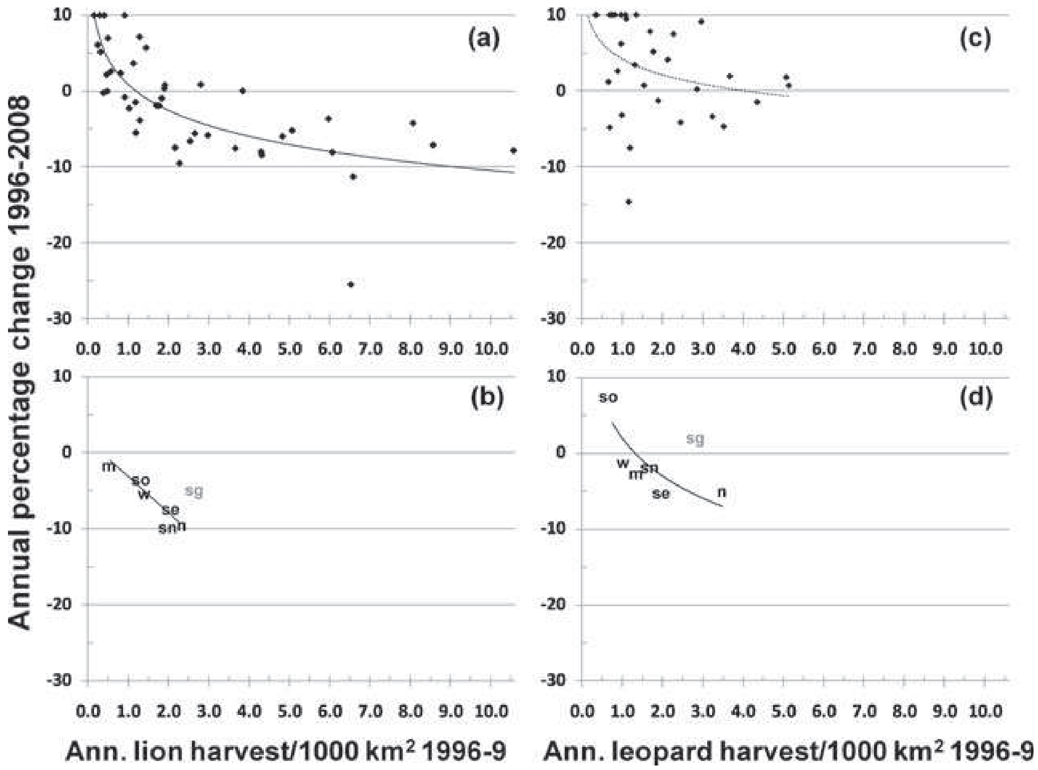

Figure 5. Proportional change in harvest of lions and leopards versus average harvest in 1996–1999: (a) lion harvest patterns in hunting blocks in the Selous Game Reserve ($r^2 = 0.57$, n = 44 blocks, $p < 0.0001$) and (b) lion harvests in the six ecosystems outside of Selous ($r^2 = 0.87$, n = 6 ecosystems, $p = 0.0064$) (M, Maasai Steppe, 24 blocks; n, northwestern Tanzania, 4 blocks; SE, Serengeti, 8 blocks; SN, new blocks outside Selous, 16 blocks; SO, old blocks outside Selous, 7 blocks; W, western Tanzania, 54 blocks; SG, Selous Game Reserve, 45 blocks [plotted for comparison]); (c) leopard harvest patterns in hunting blocks in the Selous Game Reserve ($r^2 = -0.11$, n = 32 blocks, $p = 0.0600$); (d) leopard harvests in the six ecosystems outside Selous ($r^2 = -0.71$, n = 6 ecosystems $p = 0.0345$) (Selous again plotted for comparison).

has blocked several migratory routes of Tarangire's wildebeest and zebra populations, which has likely forced lions to rely more on livestock when outside the park (Kahurananga & Silkiluwasha 1997). Tanzanian districts with the highest number of lion attacks on humans have the lowest abundance of natural prey (Packer et al. 2005*b*), and villages with the most lion attacks on humans have lower richness of prey species than neighboring villages without attacks (Kushnir et al. 2010).

Although rapid human population growth and high human population density in several areas would seem likely to have contributed to declining harvests (Table 1), lion and leopard harvests have been stable in the Maasai Steppe and in the older hunting areas around Selous, despite widespread conversion of land to agriculture and high human population density (Table 1). Thus, losses of habitat and prey do not explain changes in lion and leopard harvests in hunted areas (Table 2). These effects may be obscured, however, by the seasonal influx of lions from nearby National Parks (as for the Maasai Steppe) and by limitations in our data (data on agriculture were from 1997, and the last Tanzanian census was in 2002).

Retaliation

Retaliatory killing mostly affects lions; local communities seldom succeed in retaliating against stock-killing leopards (Kissui 2008). Retaliatory killing likely occurs in every area, but has been prominent in Tarangire, Ngorongoro Crater, and districts along the coast that have high levels of attacks on humans. Around Tarangire and in most of the Ngorongoro Conservation Area, Maasai kill lions in direct proportion to the number of cattle lost to lions (Kissui 2008; Ikanda & Packer 2008). Across the nation, the number of lion attacks on humans increased dramatically in the late 1990s (Packer et al. 2005*b*), possibly as a result of extensive flooding during the El Niño rains of 1998. Retaliatory lion killing in coastal districts intensified in 2004–2005, and few cases of attacks on humans have been reported in the past few years (Fig. 3f). Members of Tanzania's largest ethnic group, the agropastoralist Sukuma, kill lions in response to livestock depredation (Abrahams 1967). The Sukuma have recently settled in wildlife areas (Brandstrom 1985; Paciotti et al. 2005) and may have reduced lion abundance in several hunting areas. Sukuma poisoned 22 lions in 2005–2006 in one block near the Selous (R. Shallom, personal communication). Sukuma have also killed lions in Maswa Reserve (adjacent to the Serengeti) and in the Katavi–Rukwa ecosystem. Nevertheless, the number of lions killed by sport hunters has been stable in the Maasai Steppe, despite intensive retaliatory killing of lions from the Tarangire National Park. Thus, retaliation is unlikely to be the major cause of the overall decline in lion harvests in hunting areas (Table 2).

Ritual Killing

Leopards are not killed in rituals. Maasai kill lions for ritual purposes (*Ala-mayo*), but such incidents are uncommon in the Serengeti-Ngorongoro ecosystem ($\sim$2 per year) relative to retaliatory killing (3–4 per year) (Ikanda & Packer 2008) and trophy harvests (11.5 per year). Ritual killing appears to be rare in Tarangire compared with retaliatory killing (Kissui 2008). The Datoga rituals are similar to those of the Maasai (Wilson 1952; Klima 1965), and, like the Sukuma, they have recently settled in wildlife areas in central and western Tanzania. Lion killings by the Datoga have been documented north of the Selous and in the West, but precise impacts on lions are difficult to evaluate. Sukuma conduct ritual killings in western Tanzania, the extent of which is unknown.

Disease

Diseases of lions have been studied only in Serengeti and Ngorongoro Crater, and no quantitative data are available on diseases of leopards in Tanzania. Severe drought led to fatal infections of canine distemper virus and babesia in Serengeti lions in 1994 and Ngorongoro Crater lions in 2001 (Munson et al. 2008), and the Ngorongoro Crater lions also suffered from two undiagnosed epizootics in 1994 and 1998 (Kissui & Packer 2004) (Figs. 3b & e). The Ngorongoro Crater population appears to be immunocompromised by a high degree of inbreeding (Kissui & Packer 2004); a similar situation in South Africa's Hluhluwe iMfolozi Park was ameliorated by translocating unrelated animals into the park population (Trinkel et al. 2008). Thus, chronic vulnerability to disease largely results from inbreeding in small, isolated lion populations, and disease outbreaks are unlikely to have contributed to the persistent population declines in any of the hunting areas.

Harvest for Body Parts and Edge Effects

Although lion teeth and claws have long been sold in local markets and Sukuma use lion parts as medicine, there are so far no reports of lion bones being exported from Tanzania as substitutes for tiger bones in traditional Chinese medicines.

Hunting areas located adjacent to human-dominated areas did not have larger declines in lions or leopards than hunting areas that were buffered from human-dominated areas, suggesting that the overall effects of local people have been less severe than the effect of sport hunting.

Recommendations

Sport hunters are extremely efficient in locating their quarry, lion and leopard trophy hunting specifically targets adult males, and each male replacement has profound effects on the reproduction of multiple females. Tanzania currently allows about 500 lions and 400 leopards per year to be killed for sport in an area of 300,000 km^2 (1.67 lions and 1.33 leopards/1000 km^2). The proportion of male lions removed by trophy hunters in the mid- to late 1990s was unsustainable (28%/year in some areas).

Lion hunting should not exceed 1.0 lions/1000 km^2 in the Selous Game Reserve (Fig. 5a), whereas an upper limit of 0.5 lions/1000 km^2 should be imposed for the rest of the country (Fig. 5b). Within the Selous, leopard harvests increased 2%/year despite an annual average offtake of 2.9 leopards/1000 km^2 (Fig. 5c); thus, an upper limit of 3.0 leopards/1000 km^2 would be prudent. In the rest of the country, leopard quotas should not exceed 1.0 leopard/1000 km^2 (Fig. 5d). If these recommendations were adopted, national quotas would total about 180 lions and 400 leopards/year. These numbers still exceed current harvest levels, but, if they were adopted, hunting effort would be distributed more evenly across the country.

A strict age minimum would help ensure safe harvest levels despite uncertainties about local population sizes (Whitman et al. 2004, 2007). Restricting harvest to male lions that are $\geq$5 years old may be sufficient to minimize the population impacts of trophy hunting, even if every $\geq$5-year-old male was removed every year (Whitman et al. 2004, 2007). Lion ages can be reliably estimated in field conditions (Whitman & Packer 2007), and Mozambique's Niassa Reserve has successfully implemented a 6-year age minimum for hunted lions (Begg & Begg 2009), and a few Tanzanian hunting companies have voluntarily set a 6-year age minimum. A safe minimum age for leopards may be 7 years (Packer et al. 2009). Age-assessment criteria, however, are not yet available for leopards, and it is unknown whether leopard ages can be estimated reliably in the field.

Lions and leopards are CITES-listed species; thus, every precaution should be taken to prevent harvesting that could cause populations to decline. We therefore recommend, first, that Tanzania reduce quotas to 0.5 lion (or 1.0 in Selous) and 1.0 leopard (or 3.0 in Selous)/1000 km^2. Comparable statistical analysis should be performed in other range states, as sustainable offtake rates are likely to vary between countries. Second, professional hunters and clients in every range state should be educated as to how to estimate ages of lions (Whitman & Packer 2007). Third, the age of each trophy lion should be independently validated by post-mortem photographs illustrating physical features that indicate age (e.g., nose coloration) and tooth x-rays (pulp cavities enclose by year 4 in lions) and physical measurement of tooth wear (Whitman & Packer 2007). Fourth, underage trophy lions should not be exported. Fifth, similar age-assessment criteria and export policies should also be developed for leopards.

Trophy hunting has been considered essential for providing economic incentives to conserve large carnivores (e.g., Baker 1997; Hurt & Ravn 2000; Child 2004; Lindsey et al. 2006; Dickson et al. 2009). Nevertheless, successful conservation clearly requires that hunting harvests not exceed sustainable levels.

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