Biological Conservation 144 (2011) 3064–3072

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

The impact of trophy hunting on lions (*Panthera leo*) and other large carnivores in the Bénoué Complex, northern Cameroon

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ARTICLE INFO

Article history:
Received 30 June 2011
Received in revised form 23 September 2011
Accepted 25 September 2011
Available online 3 November 2011

Keywords:
Trophy hunting
Lion
Large carnivores
West/Central Africa
Moratorium

ABSTRACT

In West and Central Africa large carnivores have become increasingly rare as a consequence of rapid habitat destruction and lack of resources for protected area management. The Bénoué Complex (23,394 km^2) in northern Cameroon is a regionally critical area for large mammal conservation. In the complex lions (*Panthera leo*), leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) are formally protected in three national parks and 28 hunting zones. Over-hunting may be having a strong additive effect precipitating declines in large carnivore numbers across the complex. We used a coarse level track index method to estimate the relative abundance of these three species both in hunting zones and national parks. The results were interpreted with respect to ungulate abundance, and hunting impact. There was no significant difference between the densities of medium to larger species of ungulates in the hunting zones and the national parks, and no difference in leopard and spotted hyena densities in the respective areas. However, lions occurred at significantly lower densities in the hunting zones, and even in the national parks occurred at significantly lower densities than prey biomass would predict.

1. Introduction

Compared to other regions on the continent the impact of human population pressure around protected areas has been severe in western Africa, resulting in strong declines of large mammal populations since the 1970s (Craigie et al., 2010). Habitat destruction and poaching are the main direct causes for this decline, aggravated by the lack of financial resources and human capacity for the effective protection of parks (Brashares et al., 2011). Fragmentation and the relatively small size of protected areas (<1% of the total area; Sournia et al., 1998) in this densely populated region add to the vulnerability of large mammals (Brashares et al., 2011; Woodroffe and Ginsberg, 1998). Large carnivore populations reflect the general tendency of decline in mammal populations (Fuller and Sievert, 2001; Woodroffe, 2001). While information on the status of large carnivores in West and Central Africa is extremely limited (Bauer et al., 2003; Bauer and van der Merwe, 2004; Burton et al., 2011; Di Silvestre, 2002; Henschel et al., 2010), a decline in lion (*Panthera leo*), leopard (*Panthera pardus*) and spotted hyena (*Crocuta crocuta*) populations over the past decades has become evident (Bauer and van der Merwe, 2004; Bauer et al., 2008, Mills and Hofer, 1998, Nowell and Jackson, 1996). African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*), particularly dependent on the protection of vast stretches of natural habitat, have disappeared from the majority of protected areas in the region (McNutt et al., 2008, Nowell and Jackson, 1996, Ray et al., 2005; Woodroffe et al., 1997).

Estimates of the numbers of lions in West and Central Africa vary quite widely, but less than a decade ago were thought to comprise 1200–2700 individuals (Bauer et al., 2003). The IUCN (2006) identified four key lion conservation units (LCU's) across the two subregions, with the Chad–Central Africa Republic and the Bénoué Gashaka Gumti complex in Cameroon–Nigeria being the key zone for lion conservation in Central Africa.

The importance of the Bénoué Complex as a regional stronghold for lions was supported by survey results of Henschel et al. (2010). Although lion population estimates for individual LCU's are largely lacking, recent foot and camera trapping surveys in 15 of 27 identified LCU's revealed that many of previously identified lion populations elsewhere no longer exist with a probable extirpation of lions from 13 of 15 surveyed LCU's in West- and Central Africa

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doi:10.1016/j.biocon.2011.09.013

(Henschel et al., 2010). Despite a lack of reliable population estimates for the Bénoué Complex, large carnivores likely followed the general decline of their preferred prey populations as from the 1970s (e.g. Planton et al., 1995). Results from 109 interviews conducted in the Central Bénoué Complex in 2006 indicated that villagers perceived a marked decline in both large carnivores and large herbivores between 1990 and 2005 (Croes et al., 2008).

Studies on lions in Pendjari national park in Benin and Waza national park and the Bénoué national park in Cameroon suggest that group sizes were generally smaller, while body weights were lower for West- and Central African lions when compared to lions in East and Southern Africa (Bauer, 2003; de Iongh et al., 2005). Recent findings further suggest that West and Central African lions are relatively genetically distinct from other African lion populations (Bertola et al., 2011). The latter especially highlights the importance of protecting remaining lion populations in this region.

Studies of leopards in rainforest habitat of the Congo Basin (Henschel, 2008) and in savanna regions of East and Southern Africa (Marker and Dickman, 2005; Ray et al., 2005) show that leopards are generally better adapted to habitat changes than other carnivore species. Leopards are, however, sensitive to changes in prey biomass (Hayward et al., 2007; Henschel et al., 2008) and are negatively affected by roads and associated poaching (Henschel, 2008; Laurance et al., 2006).

Similar to other parts of their distributional range, spotted hyenas in West and Central Africa have become increasingly threatened. Fragmented populations are affected by general habitat degradation and prey loss, but also by poisoning and snaring, often in retaliation for livestock predation (Mills and Hofer, 1998, Honer et al., 2008).

In northern Cameroon, lions only occur in the Bénoué Complex and in Waza national park in the far north. The Waza population is severely imperiled (de Iongh et al., 2009; Tumenta et al., 2009) and unless drastic action is taken it is possible that lions may be extirpated in this park within the next 5 years. Due to its contiguous land-use the massive Bénoué Complex (23,394 km^2), comprising three national parks (Bénoué NP, Boubandjida NP and Faro NP, combined 7580 km^2) and surrounding hunting zones, is potentially the key conservation area for lions in the Central African region. Similar to other protected area complexes in West and Central Africa hunting concessions comprise a significant part of the protected area, in this case covering about 70% of the area (Kwabong, 2008). Hunting quotas for 25 mammal species are allocated annually by the Ministry of Forest and Wildlife (MINFOF) to each hunting concession. Quota setting is not based on scientifically obtained data, but typically the managers of hunting concessions could obtain a quota of up to three lions or five spotted hyena, based on their own wildlife monitoring figures and mainly depending on the size of the hunting zone (Adam Saleh, pers. comm.). Trophy hunted lions comprise 60% of the number of large carnivores hunted in the complex.

While studies show that stable populations of lions can sustain certain levels of hunting provided that strict rules are implemented (Whitman et al., 2004), uncontrolled hunting of lions and other large carnivores has proven to greatly impact population structure and size especially if populations are small and fragmented (Brashares et al., 2011; Loveridge et al., 2007; Packer et al., 2011). Lion hunting inside hunting concessions often directly impacts populations in surrounding national parks, as hunted male lions are generally replaced by younger individuals from bordering territories (Loveridge et al., 2007). This 'vacuum effect' in boundary areas draws lions from deep inside the parks to peripheral areas, where if shot, they affect reproduction and survival deep into the park (Davidson et al., 2011; Loveridge et al., 2007). In these areas estimating lion densities with prey-biomass regression models (Hayward et al., 2007) overestimates densities even inside protected areas when they are subject to natural and anthropogenic edge effects (Kiffner et al., 2009; Loveridge and Canney, 2009).

Considering the importance of hunting concessions in West and Central Africa, particularly in terms of proportional contribution of surface area to protected areas but also in terms of potential income generated through professional hunting (Lindsey, 2008), we investigated the effects of long-term trophy hunting on lion populations in the Bénoué Complex. The study further offers important insights into population status of leopard and spotted hyena in relation to different management regimes. The results could serve as a model to understand some of the factors contributing to the regional dramatic decline in large carnivore numbers.

2. Methods

2.1. Study area

The Bénoué Complex is located in the Sudanian wooded savanna region of northern Cameroon and comprises three national Parks (Bénoué NP, Boubandjida NP and Faro NP) covering an area of approximately 7580 km^2, as well as 28 sport-hunting zones or blocks. The surface area of the hunting blocks is 15,814 km^2, resulting in a total protected area of 23,394 km^2. Annual rainfall ranges from 1200 to 1500 mm allowing for predominantly densely wooded savanna, comprising *Isoberlinia doka* dominated woodland savanna and *Anogeissus leiocarpus* dominated riparian forests along watercourses (Stark and Hudson, 1985). The terrain is generally undulating with some scattered rocky outcrops which vary in height but are generally up to 500 m in altitude. The major rivers are the Bénoué River and the Faro River, which hold water year-round. The 17 species of ungulates include elephant (*Loxodonta africana*), buffalo (*Cyncerus caffer*), giraffe (*Giraffa camelopardalis peralta*), hippopothamus (*Hippopotamus amphibius*), common warthog (*Phacochoerus africanus*), red river hog (*Potamochoerus porcus*) and 12 species of antelope (Mayaka, 2002). Local communities historically depend on resources from the complex, such as fuelwood, thatch, fish, gold, medicinal plants, pasture for livestock and bushmeat (Weladji and Tchamba, 2003). Bushmeat represents ca. 24% of the animal protein intake for the region (Njiforti, 1996). With a human growth rate of 5.1% for the North Province (Mayaka, 2002), the Bénoué Complex is thus extremely prone to over-exploitation and encroachment. Villages in the complex are mainly located along the main North–South road. Permanent villages are absent inside national park boundaries but villages are typically concentrated along major roads, directly bordering both national parks and hunting zones. A total of 26 villages in the Bénoué Complex provide permanent residence to ca. 25,000 inhabitants, who typically live in small settlements (a congregation of 2–6 households on average). Inhabitants are mostly migrant Cameroonians (80%) who moved from the overpopulated Far North Province over the past four decades. Part of the hunting concessions' revenues are paid to the villages inhabiting the hunting concession, resulting in an annual revenue of around 0.25 euro per inhabitant (Adam Saleh, pers. comm.).

2.2. Herbivore abundance

We used the total counts of all large mammals from an aerial survey over an area of 14,141 km^2, of the Bénoué Complex, which was conducted in 2008 (Omondi et al., 2008). Although few hunting zones in the Northwest and Southeast of the Complex were not included in the aerial survey, the survey area had an overlap of 100% with our study area. To cover all the areas within the available time, transects were spaced at 3 km intervals in national parks, and 5 km intervals in hunting blocks. These data were

processed to derive density and population abundance estimates using survey technique standards for the monitoring of illegal killing of elephant program as detailed in Craig (2004), Douglas-Hamilton (1996) and Omondi et al. (2002). We compared the relative difference of the density of all medium- to large-sized herbivores counted in both national parks and hunting zones using the student's *t*-test.

2.3. Large carnivore abundance

To estimate relative large carnivore abundance we used track index surveys using a generalized model for relatively hard clay soils (Funston et al., 2010). Tracks of lion, leopard and spotted hyena were sampled by repeat sampling on 25 km stretches of road transect. Transects were surveyed in each national park (Bénoué NP, Boubandjida NP and Faro NP) and a corresponding similar area in hunting zones adjacent to each national park (Fig. 1), thus arriving at three pairs of 25-km transects for the entire study area (Table 1). The road stretches were considered representative for lion densities under the respective management regimes, even where they were located near the edge of the park (Faro NP). Surveys were conducted in the late dry season until early wet season (February–May) of 2007 (Bénoué), 2008 (Boubandjida) and 2010 (Faro). The hunting zones were chosen based on accessibility, mainly for the status of the road network, covering a wide geographical range and management regimes largely representative for the area, thereby reducing the effect of local confounding variables, such as management regimes. Following Funston et al. (2010) the ratio between the kilometers covered and the size of each study site (*Ai*) provided an index of 'sampling effort' (Es;i ¼ $Ai \cdot Pn\ j$¼1 $di;j$) where di,j was the distance covered on a transect j of a total of n transects in area i. The repeated nature of our survey design, thus, includes both spatial (how many transects) and temporal (how many repeats) components of effort. This survey was most constrained by the former, as only one suitable sampling transect could be identified for each study site. Although the repeat sampling of each transect imperiled assumptions of independence of samples, this was justified by the separation of repeats for each of the six sites into two repeat clusters: one cluster period of 3 weeks in the late dry season and one cluster period of 3 weeks in the early wet season. Mean sampling interval during each repeat cluster was 3 days (2–5). Repeatedly sampling the same transect allows the recording of track incidences that were less influenced by random short-term effects of other factors on the encounter rate of tracks.

In effect, transects were repeat sampled 16 times, except for Boubandjida and the adjacent hunting zones (n = 6 repeat surveys) where logistical constraints prevented such thorough sampling. The track frequency of large carnivores km^{-1} as a measure of relative abundance, in national parks and hunting zones, was compared using the student *t*-test. As there was only one transect per park, and per adjacent hunting zone, we lumped the repeat transect data to derive average abundance and density estimates for national parks and hunting zones, and then computed estimates for specific areas based on these averages. Confidence intervals for track densities, and hence carnivore densities, were derived from the mean spoor frequencies expressed per 100 km.

Linear regression analyses were conducted to investigate the relationship of distance to the nearest village on track frequency. Transects were divided into 25 1-km segments for which distance to nearest village was determined at 0–17 km with GIS Arcview. Track frequencies were combined for each segment and then

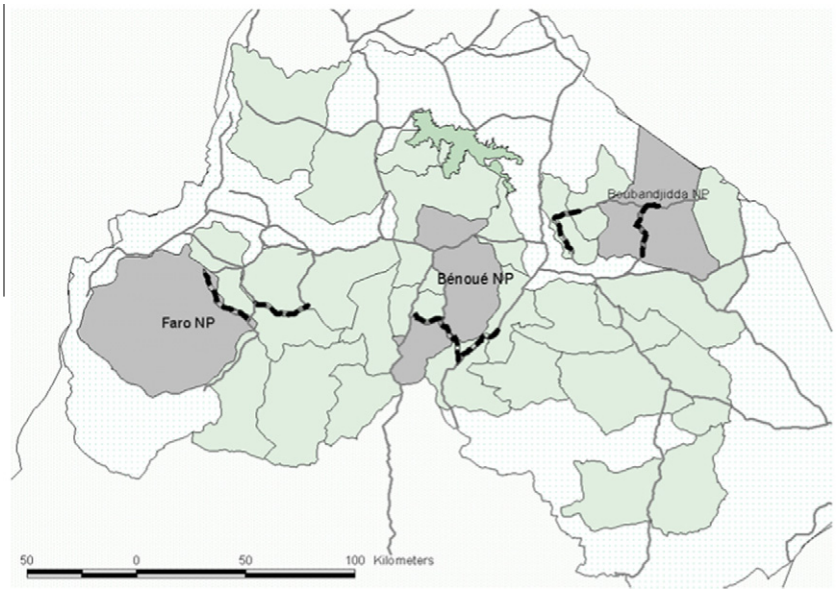

Fig. 1. Map showing the position of the Bénoué Complex in northern Cameroon highlighting the three national parks, surrounding hunting zones and the location of our transects.

Table 1
The size of the six study areas surveyed in the Bénoué Complex including the details of sampling effort.

	Bénoué		Boubandjida		Faro	
	National park	Hunting zones	National park	Hunting zones	National park	Hunting zones
Size of the area (km^2)	1980	3826	2114	2065	3486	671
Number of transect repeats	16	16	6	6	16	16
Sampling effort	0.24	0.13	0.09	0.08	0.14	0.71

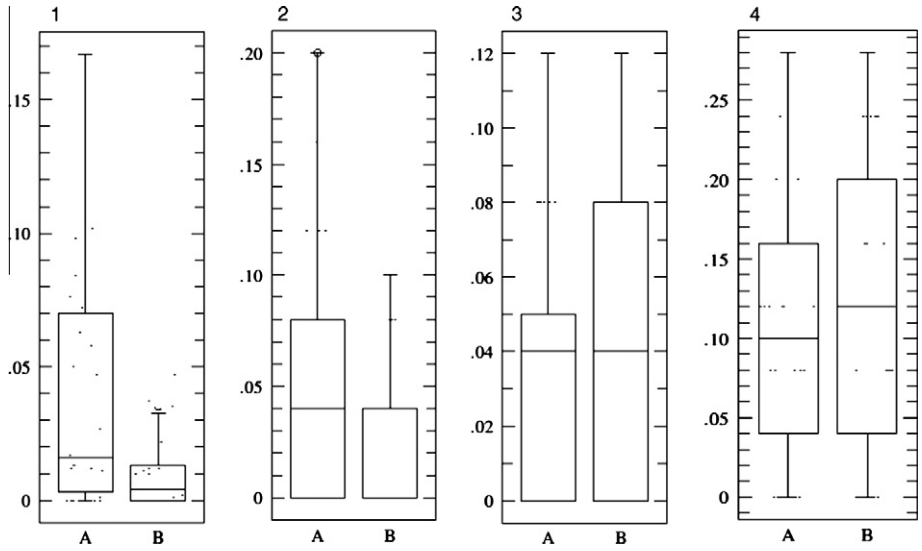

Fig. 2. Box plots showing the relative differences in (1) the densities (/km^2) of medium- to large-sized ungulates in 2008 (data from Ormondi et al. (2008)), and (2–4) track densities (/100 km) of lions, leopards and spotted hyenas in 2007–2010 in (A) national parks and (B) hunting zones in the Bénoué Complex.

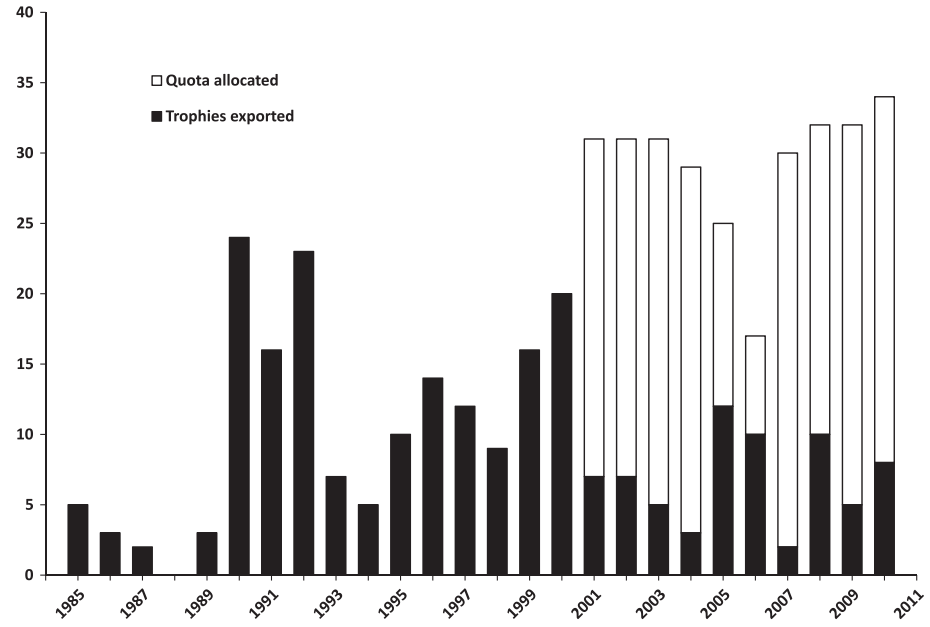

Fig. 3. The number of exported lion trophies from hunting zones in the Bénoué Complex between 1985 and 2010 (solid bars), with the relative quotas that were allocated from 2001 to 2010 (open bars). Quota allocations were not available for 1985–2000.

averaged for repeat surveys. Data were tested for normality using Shapiro–Wilk tests. We used the generalized model of Hayward et al. (2007) to estimate predicted large carnivore abundances in national parks and hunting zones, with ungulate prey population estimates from Omondi et al. (2008). The predicted abundances were then compared against estimates of the three large carnivores based on the spoor frequency estimates.

2.4. Hunting data

Records of the numbers of exported lion trophies hunted in the Bénoué Complex from 1985 to 2010 were collated from CITES (2011). Data on lion hunting quota and actual numbers of lions hunted in the Complex were available for the period 2001–2010 (Fig. 4, MINFOF, 2011).

3. Results

3.1. Abundance estimates

Aerial count data were converted into density estimates for each of the six study areas (Table 2). Across all three national parks and hunting zones there was no significant difference in the density of medium- to large-sized ungulates ($t = 2.00$, $df = 5$, $P = 0.051$; Table 2). This result was, however, close to significant with a wider data range for national parks (Fig. 2.1). This was because there was a tendency for certain ungulate species to occur at higher densities in the national parks than in hunting zones, especially buffalo and hartebeest (Table 1).

There was a highly significant difference between the frequency of lion tracks counted on transects in the national parks compared

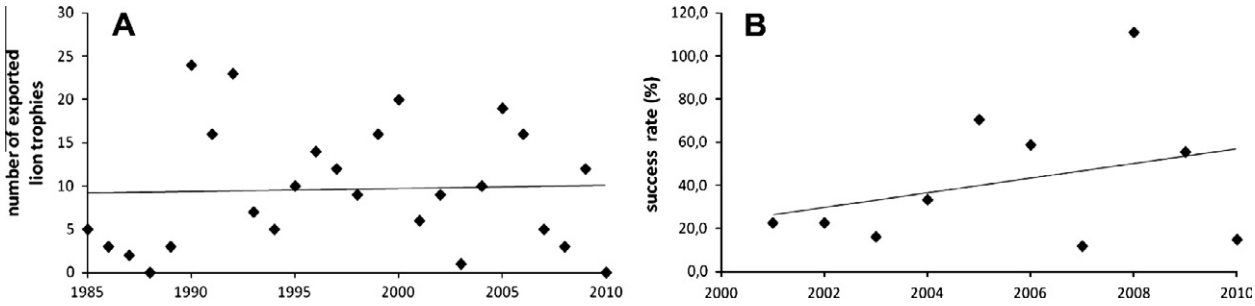

Fig. 4. Scatter plot of (A) numbers of lion trophies exported per year in the hunting zones between 1985 and 2010, and (B) the percentage of lion quota hunted, in the Bénoué Complex from 2001 to 2010.

Table 2
Total counts and density estimates (per km^2) of important large carnivore prey species in each of the six study areas conducted in 2008 (from Omondi et al., 2008).

	Bénoué				Boubandjida				Faro			
	National park		Hunting zones		National park		Hunting zones		National park		Hunting zones	
	Count	Density	Count	Density	Count	Density	Count	Density	Count	Density	Count	Density
Medium to large herbivores												
Buffalo	125	0.063	45	0.012	160	0.076	26	0.013	41	0.012	0	0.000
Eland	0	0.000	9	0.002	178	0.084	0	0.000	9	0.003	0	0.000
Giraffe	6	0.003	0	0.000	27	0.013	2	0.001	0	0.000	0	0.000
Hartebeest	143	0.072	0	0.000	352	0.167	97	0.047	94	0.027	7	0.010
Kob	115	0.058	141	0.037	100	0.047	21	0.010	245	0.070	107	0.160
Roan	202	0.102	134	0.035	207	0.098	46	0.022	173	0.050	45	0.067
Topi	0	0.000	0	0.000	28	0.013	0	0.000	2	0.001	0	0.000
Waterbuck	24	0.012	15	0.004	35	0.017	26	0.013	1	0.000	0	0.000
Small herbivores												
Bushbuck	7	0.004	7	0.002	6	0.003	8	0.004	10	0.003	1	0.001
Duiker	28	0.014	42	0.011	20	0.010	9	0.004	20	0.006	3	0.004
Oribi	87	0.044	56	0.015	164	0.083	36	0.017	52	0.015	3	0.004
Warthog	0	0.000	47	0.012	33	0.016	23	0.011	38	0.011	0	0.000

with the hunting zones ($t = 3.12$, sdev = 0.0456, $df = 74$, $P = 0.0026$) (Table 2). There was, however, no difference between the track frequencies of leopards and spotted hyenas in the national parks or hunting zones (Fig. 2b–d). The average density of lions in the three national parks was estimated to be 1.81 (CL: 1.17–2.45) lions/100 km^2 as compared to 0.56 (CL: 0.12–1.00) lions/100 km^2 in the hunting zones. Of concern was that there was also significant difference between the estimated number of lions in national parks and what would have been expected from prey biomass relationships ($t = -3.648$, $df = 4$, $P = 0.022$) (Table 3). This was not the case for leopards and spotted hyenas ($t = 1.804$, $df = 6$, $P = 0.121$), which occurred in higher numbers in both national parks and hunting zones, compared to prey biomass relations, although this difference was not significant.

A linear regression showed track frequency and distance to nearest village were related for lion (r^2 (1,17) = 0.435, $p = 0.003$ – Fig. 5) and spotted hyena (r^2 (1,17) = 0.504, $p = 0.001$ – Fig. 6). No effect of distance to village was noted for leopard track frequency.

3.2. Hunting data

From 1985 to 2010 an average of 9.2 (CL: 6.7–11.6) lion trophies were exported from the Bénoué Complex per year (Fig. 3). Despite peaks in 1990–1992, and 1999–2000 (Fig. 3), there was no significant trend in the number of lion trophies exported per year ($R^2 < 0.01$, power of performed test with alpha = 0.050: 0.029, which is below the desired power of 0.800; Fig. 4a). The average success rate of annual hunts from 2001 to 2010, expressed as a percentage that was hunted of the quota allocated, was 25.6% (CL: 15.4-35.7). There was also no trend in this data from 2001 to 2010 ($R^2 < 0.01$, power of performed test with alpha = 0.050: 0.035, which is below the desired power of 0.800) (Fig. 4b).

4. Discussion

The results presented here raise several important conservation dilemmas that need to be addressed by government as to improve protected area management in the North Province of Cameroon. Firstly, despite the vast range of relatively intact habitat present in the Bénoué Complex, our results show that lion populations are currently below carrying capacity in both the hunting zones and the national parks, occurring at ca. 50% of potential population density, as low as ca. 30% in the hunting zones. As elsewhere in Africa, a combination of high poaching pressure and excessively high lion trophy off-takes appear to have led to the lion population demise (Caro et al., 2009; Packer et al., 2011, Whitman et al., 2004). The low lion densities compared to potential capacity in the hunting zones as compared to the national parks indicates that lions in the hunting zones are strongly impacted through excessive trophy off-takes. Although counts of carnivore tracks on roads may be influenced by road conditions and habitat structure (Stander, 1998; Funston et al., 2010), the similar road surface and environmental characteristics, as well as long distances covered by our road surveys probably limited the effects of such confounding factors on our abundance estimates. This conclusion is supported by the fact that our lion population estimates are comparable to calling station surveys conducted recently in Bénoué NP (35 lions; de Iongh et al., Unpublished results) and Boubandjida NP (60 lions; Bauer, 2007). Furthermore, our estimates were derived from hunting zones directly adjacent to national parks, which probably

Table 3
Density and abundance estimates of large carnivores in national parks and hunting zones in the Bénoué Complex between 2007 and 2010 based on track frequency counts and estimates based on prey biomass relationships (Hayward et al., 2007).

	Large carnivore density (/100 km^2)		Population estimates from track counts	Potential populations based on prey biomass
Lions				
National parks	1.81 (1.17–2.45)			
		Bénoué	36 (23–49)	74
		Boubandjida	63 (46–81)	97
		Faro	38 (25–42)	86
		Total	137 (94–172)	257
Hunting zones	0.56 (0.12–100)			
		Bénoué HZ1,2,3,4,7,8,9	21 (5–38)	78
		Boubandjida HZ10,11,23	12 (2–21)	44
		Faro	4 (1–7)	14
		Total (6562 km^2)	37 (8–66)	136
	Total in all hunting zones (15,814 km^2)		81 (17–145)	300
Leopards				
National parks	1.28 (0.77–1.80)		97 (58–136)	53
Hunting zones	1.46 (0.85–2.07)		212 (123–301)	73
Spotted hyenas				
National parks	2.43 (1.23 – 3.13)		184 (131–237)	139
Hunting zones	2.75 (2.07 – 3.43)		400 (301–499)	140
Cheetahs				
National parks	0		0	30
Hunting zones	0		0	42
Wild dogs				
National parks	0		0	23
Hunting zones	0		0	29

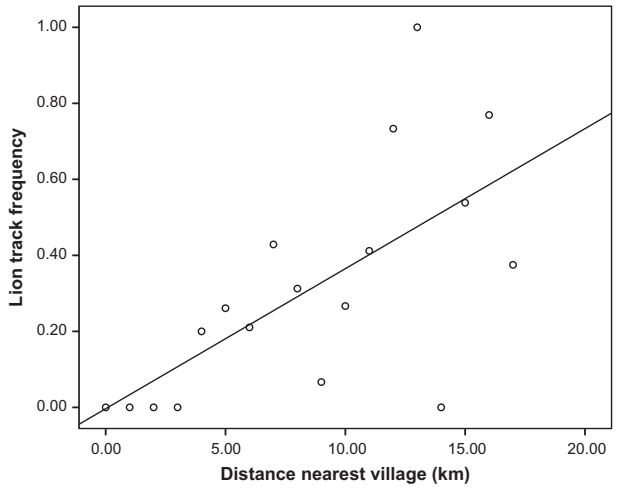

Fig. 5. Lion track frequency along a gradient of distance to the nearest village (r^2 (1,17) = 0.435, p = 0.003). The trendline shown is a linear regression for mean track frequency at 1-km transect sections to the nearest village.

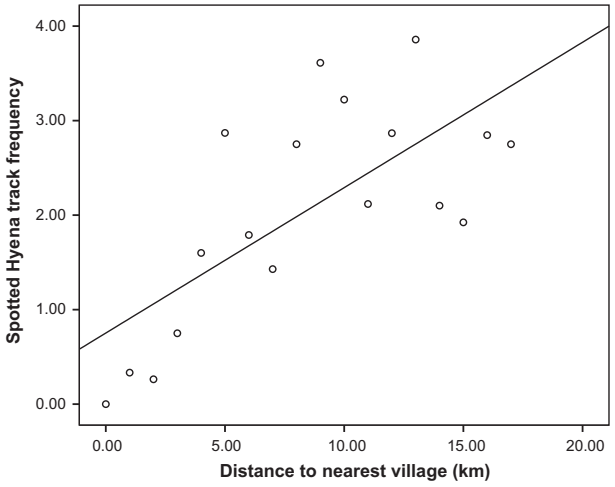

Fig. 6. Spotted hyena track frequency along a gradient of distance to the nearest village (r^2 (1,17) = 0.504, p = 0.001). The trendline shown is a linear regression for mean track frequency at 1-km transect sections to the nearest village.

underestimated differences in abundance, given the better status of lion populations inside the parks compared to hunting zones.

The recorded difference in occupied capacity between the parks and hunting zones might also have been caused by a higher poaching level in the hunting zones compared to the parks. Although we do not have data on lions indiscriminately killed and hunted, based on our observations during 2005–2010, includ-

ing assessments by four wardens in the parks and numerous exchanges with hunting zone managers, we believe that anti-poaching effort is higher in the hunting zones compared to the parks. In general, national parks in Cameroon are notoriously understaffed and underfunded, mostly due to a general lack of government funds which constrains regular anti-poaching efforts (e.g. de Iongh et al., Unpublished results). Conversely, economic incentive maximizes anti-poaching efforts in hunting zones, and anti-poaching units operate at regular intervals. More importantly, our data illustrate that rather than being a local effect, the discrepancies in potential population capacity occupied are consistently observed in all three regions of the ecosystem. The positive correlation between distance to village and both lion and spotted hyena presence suggests that lions and spotted hyena respond to higher poaching levels in the vicinity of human settlements. Spotted hyena are perceived to often take livestock from villages in the Bénoué Ecosystem and are thus prone to conflict with humans (Croes et al., 2008). Although lions were reported to hardly ever take livestock from resident livestock owners, they are sensitive to indiscriminate killing methods such as poisoning which does occur in the complex. A steady increase of nomadic pastoralists, who are often leading their large herds of cattle and sheep off the predefined livestock corridors into pristine habitat, is further causing an increased risk of large carnivores coming into conflict with nomadic herdsmen (Croes et al., 2008). As numbers of nomadic pastoralists who are moving through the complex are increasing and herds are expanding (Adam Saleh, Personal communication), retaliatory killing of lions, spotted hyena and leopard as well as accidental poisoning of large carnivores and other predatory animals could become a major threat to such wildlife populations. The increased frequency of reported targeted hunting of lion and leopard for the trade in body parts, most probably by organized poachers from Chad and Nigeria (Anonymous, 2011) further calls for urgent actions.

We estimate that in the hunting zones generally there might only be about eighty lions from which currently an annual harvest of about nine lions is being taken. All three national parks together harbor approximately 120 lions, thus arriving at an estimated total of 200 lions for the complex. Creel and Creel (1997) found that a sustainable off-take of lions is about 3% of the population, with Whitman et al. (2004) suggesting that sustainable lion harvests depend on hunting males older than 5 years of age. Thus, in the Bénoué Complex a sustainable harvest in the hunting zones would be two lions per year at current abundance estimates. Nevertheless, such estimates of sustainable lion off-take are based on the assumption that the lion population occurs at a level which is close to its potential carrying capacity. This being clearly not the case for the Bénoué Complex, we suggest that there should be an immediate moratorium of at least 5 years on the hunting of lions in Cameroon, during which lions are allowed to recover and a management plan for lion hunting is established. Provided that professional hunting of lions is ceased immediately, retaliatory killing of lions by nomadic pastoralists is controlled and anti-poaching efforts are increased to allow for the recovery of prey populations, we foresee a recovery of the lion population up to a level which is closer to potential carrying capacity, as observed elsewhere (e.g. Zimbabwe; Loveridge et al., 2010).

Only a drastic change in management practices would allow for the sustainable off-take of lions after this 5-year moratorium. Ideally, such management strategies should include hunting quota settings based on scientific survey work conducted by independent organizations. Alternatively, in case scientific quota setting turns out to be unrealistic, a restricted lion quota could be implemented based on a maximum off-take (e.g. 0.5–1.0/1000 km^2), with a minimum 6 year age limit for hunted lions (Whitman et al., 2004). Hunting indices such as catch effort, success rates and trophy quality could subsequently be monitored and used to adaptively manage hunting lion in response; e.g. if there is a consistent decline in success rates, quotas should be cut. If such requirements are met, the moratorium can be viewed as a window period rather than an ongoing restriction.

Leopard and spotted hyena appeared to occur at over equilibrium densities throughout the Bénoué Complex, but this was not significant. Since prey biomass estimates used to determine these densities were probably strongly biased towards larger, and thus more suitable, lion prey, leopard and spotted hyena densities were rather as expected. Nevertheless, as top-predators in a fragile ecosystem, both leopards and spotted hyenas are potentially sensitive to excessive off-take either through poaching or trophy hunting in a similar manner as was shown for lions (Johnson et al., 2001, Packer et al., 2011, Ray et al., 2005). The ban on leopard trophy hunting in 1996 may have contributed to current population levels. It is possible, however, that meso-predator release, due to lower lion densities, may be favoring leopards and spotted hyenas (Caro and Stoner, 2003; Creel et al., 2001; Durant, 1998). Our results further reveal that human-related factors did impact distribution patterns of spotted hyena: their presence was positively correlated with distance to human settlements. This suggests that, although leopard and spotted hyena in the Bénoué Complex are not yet suffering from human induced threats in the same way as lions do, they are prone to ecosystem disturbances and direct persecution which should be taken into account in future implementation of management strategies.

During our surveys no tracks of cheetah or African wild dog were observed, suggesting that both species are 'functionally extirpated' in the Bénoué Complex (Croes et al., in press; de Iongh et al., in press). Both species were estimated to potentially occur at the lowest abundances of the five large carnivores based on prey biomass, with respectively only 72 and 62 individuals of each species being estimated. Thus at such low potential numbers both species would have been vulnerable to anthropogenic mortality of any type, which seemingly led to their demise. It is interesting to note that hunting zone managers have a generally negative attitude towards wild dog and cheetah, both integrally protected in Cameroon (Croes et al., in press; de Iongh et al., in press).

In conclusion, we recommend that immediate ministerial intervention is enacted to halt the trophy hunting of lions in the Bénoué Complex, and that steps are taken that would allow a window period of recovery for this regionally critical lion population. We further recommend an intensification of local projects to sensitize local communities to the plight of all species of large carnivores occurring in the area, and ensure they benefit from trophy hunting revenues. Ideally, a system is required whereby communities are involved in, and benefit from hunting (e.g. Namibia; Weaver and Petersen, 2008), but given the growing human population in the area (which stands now at ca. 25,000 for the complex) it is going to be difficult to generate significant revenues on a per person basis and certainly not enough to offset potential personal gains through bushmeat hunting. However, if benefits were channeled such that the communities could use the funds for whatever they most need (e.g. building wells, improve road maintenance), then the incentives created could be particularly effective. Raising current lion trophy fees to increase revenues should be seriously considered, particularly in view of the low trophy fees compared to other parts of Africa, and is justified given the potential genetic uniqueness of lions in West and Central Africa (Bertola et al., 2011). Other administrative issues that limit current earnings from hunting in Cameroon (e.g. the leopard hunting ban, and the lack of a CITES quota for elephant trophies) should probably be addressed for the full value of wildlife in the hunting blocks to be harnessed. Given the high population growth rate, such efforts should go hand in hand with landuse planning, limiting human populations to certain areas, whereas other areas are retained with a wildlife focus only.

Without these measures, carnivore populations will not likely be able to persist in the area in the long term.

Acknowledgements

We would like to thank the Minister and staff of the Ministry of Fauna and Forests (MINFOF) for their support during the full duration of the study. We thank Monique de Jager, Iris Kirsten, André Ndjidda, Ahononga Fiacre Codjo, N'sera Parfait, Aboudou Mensa, Saskia Klumpers and Sofia Sanders for their contribution to data collection. In addition, we acknowledge Dr. Jean Pierre Mvondo, Coordinator of the Centre for Environment and Development studies (CEDC), and Mr. Francis Tarla, director of the Garoua Wildlife College for their advice and logistical support. Comments by Hans Bauer and an anonymous referee greatly improved a first draft. Finally we are grateful to WWF-NL, Prins Bernhard Fund for Nature, Mohamed bin Zayed Species Fund and the Rufford Small Grants Programme for funding this three year project. PJF thanks the Tshwane University of Technology for funding and permission to travel to Cameroon.

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