



Universiteit
Leiden
The Netherlands

Lions of West Africa : ecology of lion (*Panthera leo* Linnaeus 1975) populations and human-lion conflicts in Pendjari Biosphere Reserve, North Benin

Sogbohossou, E.A.

Citation

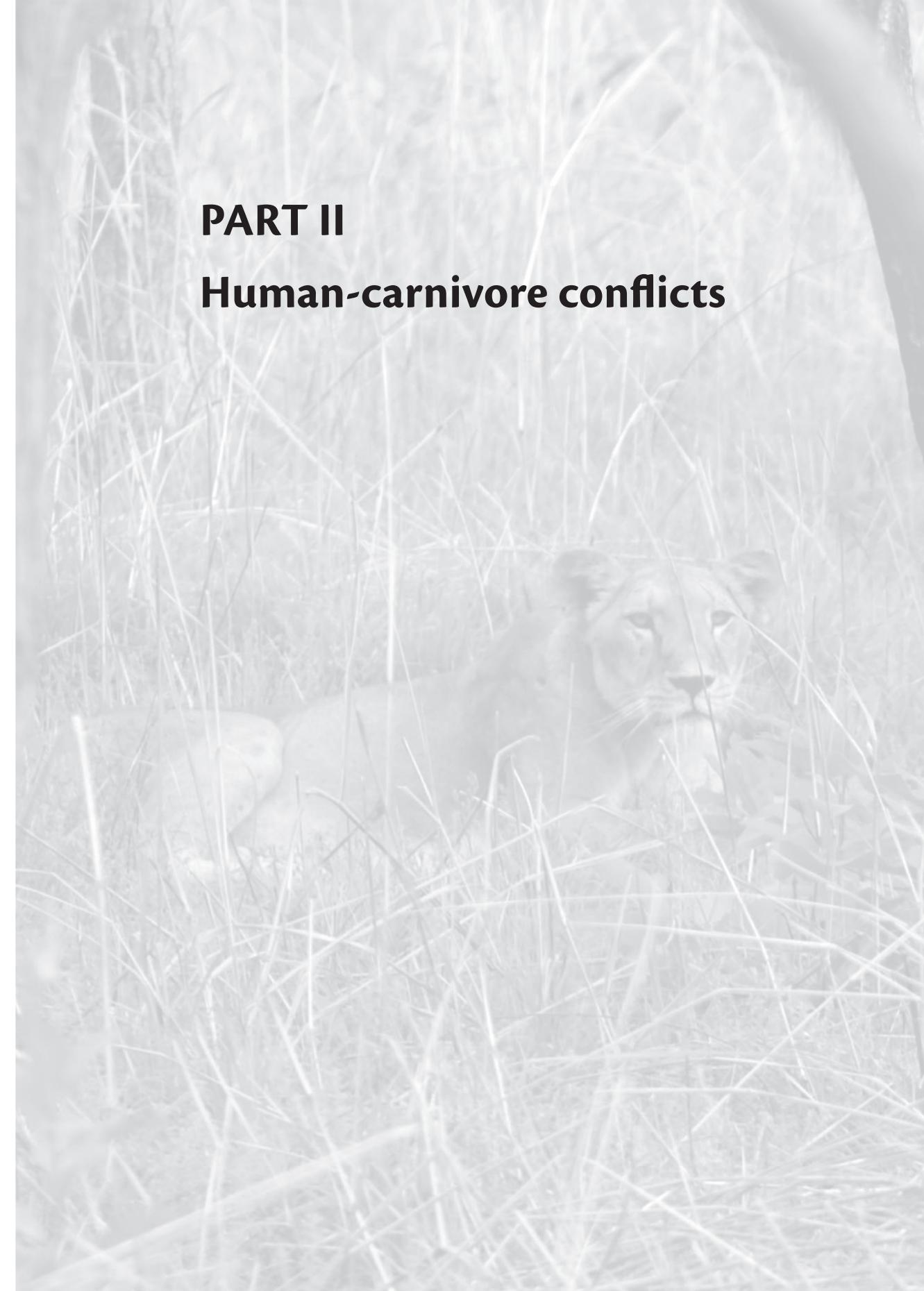
Sogbohossou, E. A. (2011, October 25). *Lions of West Africa : ecology of lion (*Panthera leo* Linnaeus 1975) populations and human-lion conflicts in Pendjari Biosphere Reserve, North Benin*. Retrieved from <https://hdl.handle.net/1887/17988>

Version: Not Applicable (or Unknown)

License: [Licence agreement concerning inclusion of doctoral thesis in the Institutional Repository of the University of Leiden](#)

Downloaded from: <https://hdl.handle.net/1887/17988>

Note: To cite this publication please use the final published version (if applicable).

A black and white photograph of a lioness lying in tall, dense grass. She is positioned in the center-right of the frame, looking slightly to the right. Her face and upper body are visible through the blades of grass. The background is out of focus, creating a sense of depth.

PART II

Human-carnivore conflicts



2

Human-predator conflicts around Pendjari Biosphere Reserve, Northern Benin

Sogbohossou E.A., de longh H.H., Sinsin B., de Snoo G.R. & Funston P.J.

Accepted for publication in Oryx

Abstract

Close proximity between humans and large predators results in high levels of conflict. We investigated the extent of, and factors leading to, this conflict through focal group and individual interviews in all villages around Pendjari Biosphere Reserve, northern Benin. Livestock losses from 2000 to 2007 ($n = 752$) were reported to be mainly caused by spotted hyaena *Crocuta crocuta* (53.6%), baboon *Papio anubis* (24.8%), and lion *Panthera leo* (18.0%). These predators mainly predated sheep and goats (52.1%) and pigs (42.3%), with lions being the main predators of cattle (78.9%). Lion and hyaena diets were more diverse than that of baboons, which killed only small stock. The level of conflict increased during 2000–2007. Predation rate differs between predator species and is significantly influenced by month, rainfall of the month before the predation event, and length of the dry period in a year. The geographical position of the village, the distance of the village to the Park and the number of herbivores legally killed every hunting season also influenced predation intensity. Our findings suggest that improvement of husbandry techniques and education will reduce conflicts and contribute to improved conservation of these threatened predators.

Key words

Benin, livestock–predator conflict, Pendjari Biosphere Reserve, predation, predator conservation, West Africa.

2.1 Introduction

Considerable growth of human populations in the last few decades has had a significant negative impact on biodiversity (Hanski, 2005). The degradation of wildlife habitats has resulted in declines of species, many of which are threatened with extinction (Ginsberg & Macdonald, 1990; Nowell & Jackson, 1996; Mills & Hofer, 1998; Woodroffe, 2000). One of the key factors causing the decline of most large carnivore species is conflict with humans because of predation of livestock (Cozza *et al.*, 1996; Woodroffe, 2000; Treves & Karanth, 2003) and attacks on humans (Kerbis Peterhans & Gnoske, 2002; Packer *et al.*, 2005). Human-predator conflicts cause significant economic losses (Mishra, 1997; Butler, 2000; Patterson *et al.*, 2004; Van Bommel *et al.*, 2007; Palmeira *et al.*, 2008) and can lead to retaliatory killing of predators (Ogada *et al.*, 2003; Holmern *et al.*, 2007), and thus constitute a threat to both wild species and human livelihoods (Woodroffe & Ginsberg, 1998; Hussain, 2003).

Human-wildlife conflicts have intensified in most African countries in recent decades because of exponential human population growth and economic activities (Woodroffe, 2000; Conover, 2002). The highest intensity conflicts tend to occur where humans live adjacent to protected areas (Mishra, 1997; Conforti & de Azevedo, 2003). In Africa there are a number of larger predator species, including the lion *Panthera leo*, leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta*, baboons *Papio* sp., cheetah *Acinonyx jubatus*, African wild dog *Lycaon pictus*, caracal *Caracal caracal* and black-backed jackal *Canis mesomelas* (Butler, 2000; Patterson *et al.*, 2004; Kolowski & Holekamp, 2006; Holmern *et al.*, 2007; Van Bommel *et al.*, 2007).

Livestock predation often follows a seasonal pattern (Butler, 2000; Patterson *et al.*, 2004; Kolowski & Holekamp, 2006) and is influenced by environmental conditions and husbandry practices (Ogada *et al.*, 2003; Kolowski & Holekamp, 2006). Most studies of predation on livestock in Africa have focused on East and Southern Africa, with few studies from West and Central Africa (Boy, 1962; Sogbohossou, 2004; Bauer & de longh, 2005; Van Bommel *et al.*, 2007; Garba & Di Silvestre, 2008).

In contrast to East and Southern Africa, West Africa is characterized by low herbivore biomass (East, 1984; Fritz, 1997) and fragmented wildlife populations mostly confined to small, unfenced protected areas that are surrounded by human settlements. The size of many of these reserves doesn't guarantee the long-term conservation of their wildlife species (Woodroffe & Ginsberg, 1998; Brashares *et al.*, 2001). Thus predation of livestock is inevitable (Binot *et al.*, 2006) and creates a negative attitude to conservation that can lead to the retaliatory killing of carnivores (Kolowski & Holekamp, 2006; Holmern *et al.*, 2007).

The Pendjari Biosphere Reserve in the Republic of Benin is one of the best managed protected areas in the region, with one of the highest wildlife densities in West Africa (Delvingt *et al.*, 1989; Lamarque, 2004). However, the Reserve is located in an important livestock area in one of the poorest parts of the country. Livestock losses thus potentially affect the livelihood of local people. The Reserve is surrounded by a buffer and a hunting zone, intended to minimize human-wildlife conflict. The objectives of this study were to assess: (1) which species are responsible for livestock depredation, (2) any trends and seasonality of predation, (3) patterns of predation, and (4) any other factors that influence the occurrence of predation. We hypothesized that disturbance variables such as presence of safari hunting, poaching and illegal grazing will affect the intensity of livestock depredation.

2.2 Methods

2.2.1 Study area

The study was carried out around the Pendjari Biosphere Reserve in north-west Benin (Fig. 1). The Reserve is part of a complex of four adjoining protected areas (W, Pendjari, Arly and Oti-Mandouri) in four adjacent countries (Benin, Burkina Faso, Niger and Togo). Pendjari Biosphere Reserve was established in 1954, upgraded to National Park status in 1961 and to a UNESCO Man and Biosphere Reserve in 1986. It comprises Pendjari National Park (2,660 km²), Pendjari and Konkombri Hunting Zones (c. 1,600 and 251 km², respectively) and a buffer zone with controlled land-use access for local people (c. 340 km²).

The Reserve is bordered to the north and west by the Pendjari River and to the east by the Atacora Mountain chain. In this Sudanian ecosystem the climate is characterized by a dry season from October to May and a wet season with a total annual rainfall of 800–1,000 mm. Vegetation is a mixture of open grass and tree savannahs interspersed with dry and gallery forests. These habitats harbour a variety of wildlife species including large carnivores (Delvingt *et al.*, 1989). The density of lions in the Reserve is estimated to be between 0.67 (Di Silvestre, 2002) and 1.5 lions per 100 km² (Sogbohossou, 2009) and the spotted hyaena occurs at a minimum density of 1.5 per 100 km² (Sogbohossou, 2009). The cheetah and wild dog populations, which almost disappeared, seem to be recovering, although numbers remain low, and there is no estimate of leopard abundance.

The Reserve is bordered by two main roads, Tanguieta–Porga and Tanguieta–Battia, along which there are 24 villages (Fig. 1). In addition to native farmers most villages are also inhabited by Fulani (with one to eight camps in each village), who are pastoralists. During the dry season migrating herds of cattle led by Fulani

herdsman from neighbouring countries reside within or close to the border of the Park in search of water and fodder.

The Reserve has been financed discontinuously through several programmes, with funding gaps almost abandoning the park to poachers during 1982–1985, 1991–1993 and 1998–2000. Since 2000 the Pendjari Project has managed the Reserve more intensively and illegal activities within the Reserve have largely been curtailed.

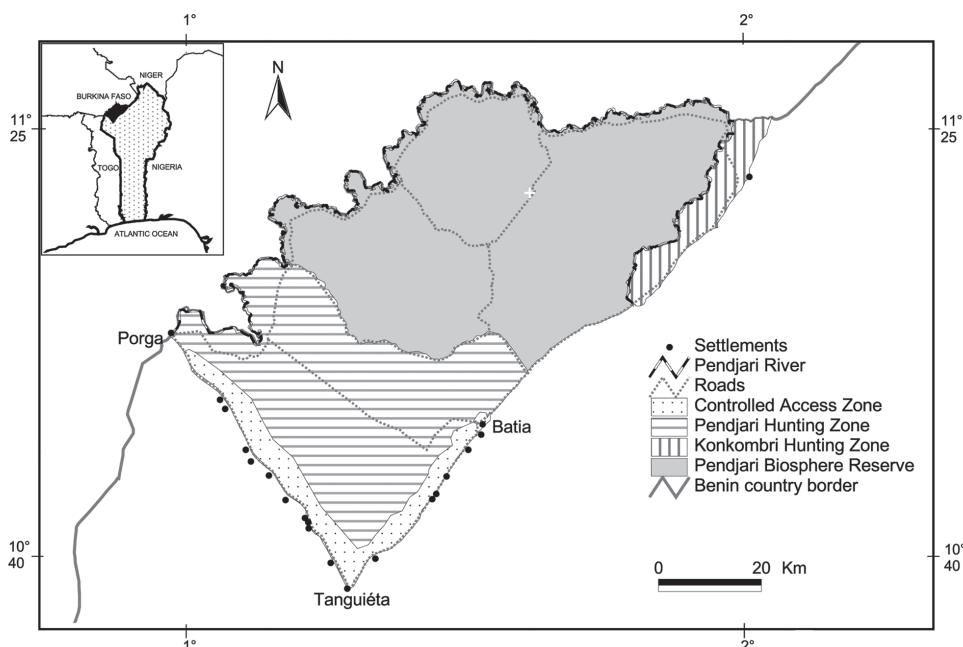


Figure 1 Location of Pendjari Biosphere Reserve in Benin Republic.

2.2.2 Methods

Data on the characteristics of human-wildlife conflict were collected from June to December 2007. All 24 villages surrounding Pendjari Biosphere Reserve were surveyed. We firstly discussed the history and characteristics of predation in group interviews. We then visited farmers' households and Fulani camps, randomly, to ask more detailed questions about the characteristics of livestock depredation. In each household or camp we interviewed the head and if he was absent his elder son or the head's wife. Other people present in a house usually helped in the recall of depredation cases. A total of 387 farmers' households and 78 Fulani camps participated in the study. All predation cases from 2000 to 2007 were recorded. Group interviews allowed crosschecking of the data. Interviews were conducted

by EAS with the help of a local guide. Colour plates of predator species were used during the interviews to ensure correct identification of species and their spoor. Respondents were also asked to describe the characteristics of the species to verify identification.

Data were analysed using SAS v. 9.1 (SAS Institute, Cary, USA). We considered predation by lions, spotted hyaenas and baboons. There were too few records of predation by leopards, cheetahs and wild dogs (< 3 per species) for analysis. Other predators (such as jackals, raptors and snakes), which mainly attack poultry, were not considered. The dependent variable is the intensity of depredation expressed as number of livestock killed. The independent variables used are presented in Table 1.

Table 1 Types of statistical analyses for different used variables. PCA means Principal Component Analysis and GLM is for General Linear Model.

Variables categories	Independent Variables	Type of Analysis
Species involved in predation	Predator species	General Linear Model
	Livestock species	General Linear Model
Trends	Year of predation	General Linear Model
Seasonality	Month of predation	General Linear Model
	Season of predation	General Linear Model
	Rainfall during the month of predation	PCA & Correlation
	Rainfall during the month before the predation	PCA & Correlation
	Rainfall during the year of predation	PCA & Correlation
	Rainfall during the year before the predation	PCA & Correlation
	Duration of the last dry period (month, day)	PCA & Correlation
Geographical distribution	Road axis	General Linear Model
	Village	General Linear Model
	Distance from the village to the hunting zone	PCA & Correlation
	Distance from the village to the park	PCA & Correlation
Other factors	Number of herbivores hunted the previous year	PCA & Correlation
	Number of lions hunted the previous year	PCA & Correlation
	Number of illegal herders arrested last two months	PCA & Correlation
	Number of illegal herders arrested the last six months	PCA & Correlation
	Number of illegal poachers arrested last two months	PCA & Correlation
	Number of illegal poachers arrested the last six months	PCA & Correlation

The distance to the closest protected area border (hunting zone or national park) from each village was determined from coordinates obtained with a global positioning system and *ArcView v. 3.2.* (ESRI, Redlands, USA). χ^2 tests were used to compare the intensity of depredation between predator and livestock species. We checked that the variables were not correlated. For variables with a continuous distribution we used a Principal Component Analysis (PCA) to examine which variables significantly influenced the number of predation events (Table 1). We then tested these relationships using the Pearson non-parametric correlation.

For variables without the problem of co-linearity we used general linear modelling (GLM) to assess the relationship between predation intensity/frequency and the independent variables. The dependent variable was normalized using a log transformation. The minimum level of significance considered was $P < 0.05$. The GLM results are provided as F statistics.

2.3 Results

2.3.1 Cattle husbandry around Pendjari Biosphere Reserve

Agriculture is the main source of rural livelihoods in the villages surveyed, with small-stock (sheep, goats and pigs) husbandry being of secondary importance. Cattle ranching, however, is the principal livelihood of the Fulani herders. Livestock represents savings for both local farmers and Fulani: the sale of small stock provides cash income to compensate for food shortages or to cover other expenses. Other sources of cash income include cotton cultivation, ecotourism and trade of natural resources (wood, straw, fruits) harvested in the Reserve.

Herding characteristics depend on the species and season. At night small stock are usually kept inside compounds or tied to trees. During the rainy season small stock are kept in enclosures, usually made of clay, or tied to trees to prevent them foraging in cultivated fields. In the dry season small stock roam freely in the village.

In the rainy season cattle are left to graze around the villages. During the dry season water and forage close to the villages become scarce and many Fulani herders allow their cattle to graze in the hunting zone. Some (1.2 %) herders move their cattle to more humid areas in a rainy season migration. In this season 3.8% of herders leave the vicinity of the protected area to avoid conflicts with farmers caused by the grazing of farms by cattle.

Fulani camps comprise a circle of several huts or tents. Cattle are usually kept inside the circle of huts but sometimes a whole herd or a group of calves is kept in an enclosure made from thorny branches (*Acacia* spp., *Dichrostachys cinerea* and

Balanites aegyptiaca). Thirteen percent of Fulani herders had received financial support from a project initiated by the Network of West and Central Africa for Lion Conservation to construct clay-brick enclosures to keep calves in at night.

2.3.2 Species involved in livestock predation

Lions (18.0%), spotted hyaenas (53.6%) and baboons (24.8%) were responsible for most livestock mortalities recorded ($n = 752$). Lions and hyaenas mainly attacked livestock during the night, whereas baboon attacks occurred during the day. The mean annual livestock loss per household was 1.8 head.

The majority of livestock killed were sheep and goats (shoats, 52.1%), followed by pigs (42.3%), with cattle (3.7%) and dogs (1.9%) being infrequently taken (Fig. 2). Predation intensity varied between predators ($\chi^2 = 66.28$; $P < 0.0001$) and between livestock species ($\chi^2 = 47.04$; $P < 0.009$; Fig. 2). Cattle were mainly killed by lions, and shoats by baboons and hyaenas. Pigs and dogs were mainly taken by hyaenas and lions.

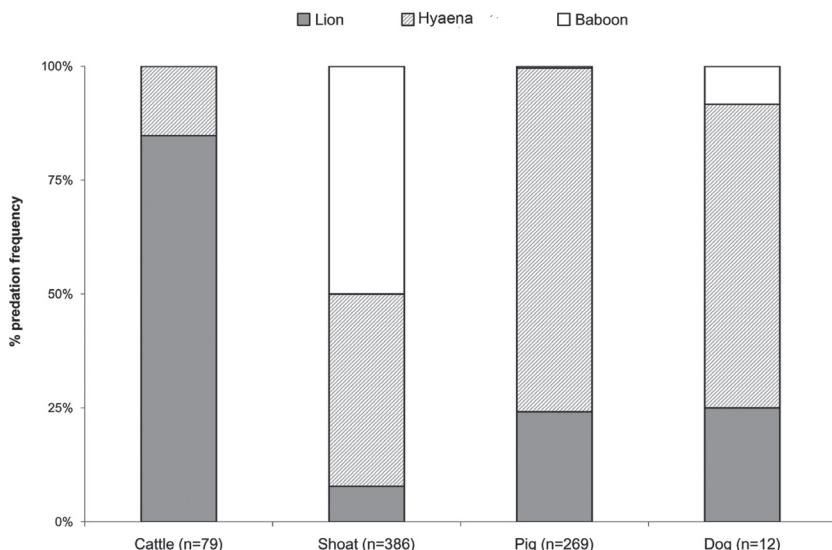


Figure 2 Percentage frequencies of attacks of baboons, hyaenas and lions on cattle, shoats, pigs and dogs from 2000 to 2007 around Pendjari Biosphere Reserve, based on our questionnaire survey.

2.3.3 Trends and seasonal distribution in predation

Predation intensity seemingly increased from five cases in 2000 to 222 cases in 2005 (Fig. 3), followed by a decline. Predation intensity varied by month ($F = 4.43$,

$df = 11, P < 0.0001$) but not by season ($F = 2.40, df = 1, P = 0.12$). There was a peak at the end of the dry season in June–July and another at the end of the wet season in December (Fig. 4). This peak was particularly noticeable in the villages bordering the Atacora mountain along the Tanguieta–Batia road. On the Tanguieta–Porga road a less pronounced peak is evident in the middle of the wet season to the beginning of dry season (Fig. 4). Lions and hyaenas mainly predated livestock from the end of the wet season to the beginning of the dry season, with predation by baboons being most intense at the end of the dry season and from the end of the wet season to the beginning of the dry season.

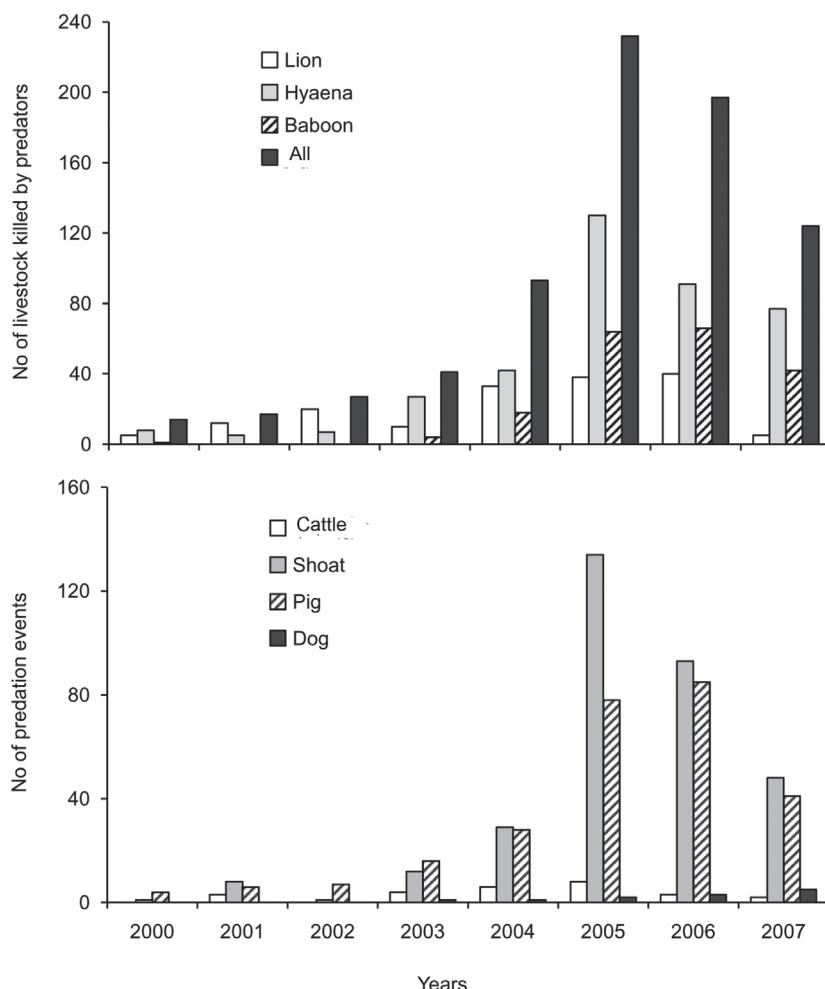


Figure 3 Number of livestock attacks predation frequencies around the Pendjari Biosphere Reserve according to livestock and predator species from 2000 to 2007 based on our questionnaire survey. Shoat represents sheep and goat.

The intensity of predation decreased when the rainfall of the previous month increased ($r = -0.14$, $P = 0.007$). However the rainfall of the current and previous years, and the month of predation, were not significantly correlated with the intensity of predation. The number of dry months in the year was significantly negatively correlated with the intensity of predation ($r = -0.13$; $P = 0.011$).

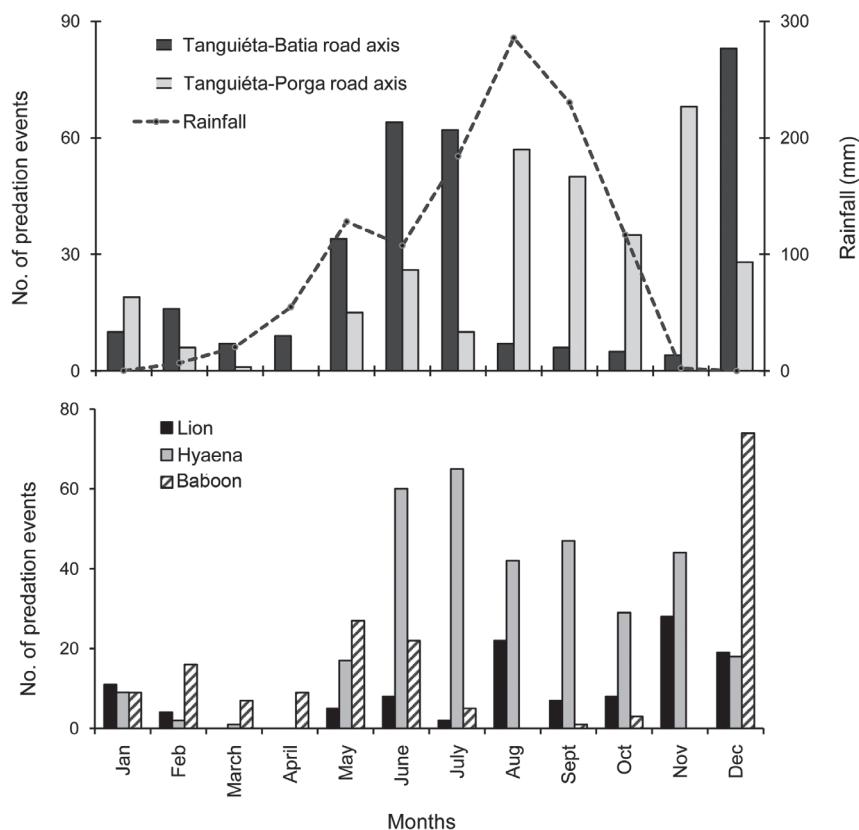


Figure 4 Monthly distribution of depredation events in relation to rainfall based on our questionnaire survey. The data used are from 2000 to 2007.

2.3.4 Geographical distribution of predation

The number of predation events was significantly different between the villages around the hunting zone ($F = 4.26$, $df = 25$, $P < 0.001$; Fig. 5). There was a significant difference between the two road axes in the number of livestock killed ($F = 68.18$, $df = 1$, $P < 0.0001$): 41.3% of the interviewees along the Tanguiéta–Porga road axis and 14.2% of interviewees along the Tanguiéta–Batia road axis had lost at least one animal to predation. Livestock predation intensity increased towards the Na-

tional Park ($r = -0.31$; $P < 0.0001$) but not relative to the distance from a hunting zone ($P > 0.05$).

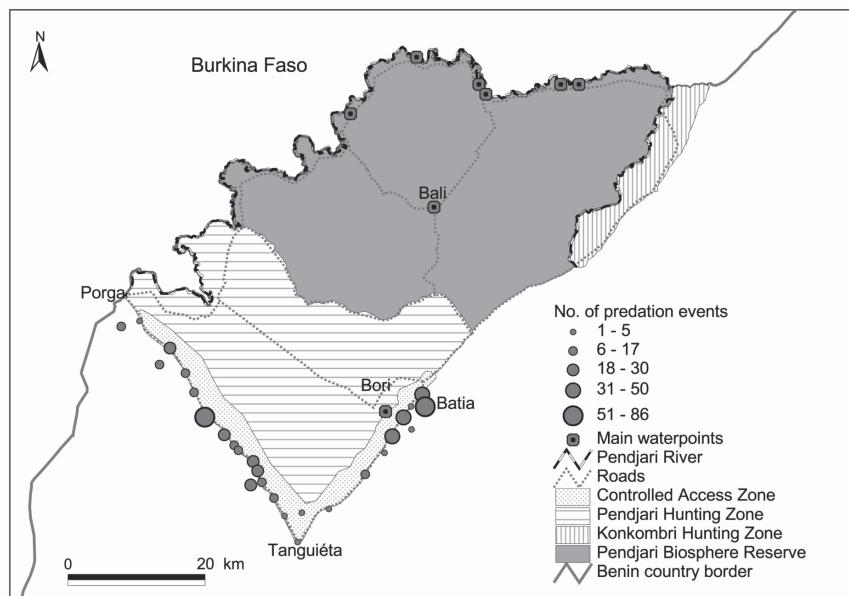


Figure 5 Predation rate in the different localities around the Pendjari Biosphere Reserve (data from 2000 to 2007).

2.3.5 Other factors: illegal herding and hunting

Only the annual number of herbivores killed by safari hunting had a significant impact on predation rate ($r = -0.11$; $P = 0.03$). The PCA and correlation indicated that the number of poachers and the number of herders arrested in the National Park in a year may have affected the intensity of predation in that year but the impact on predation intensity was not significant ($P > 0.05$).

2.4 Discussion

A generic problem with using questionnaires to assess depredation is that people invariably attribute livestock mortality to predators (Wagner, 1988; Hoogesteijn *et al.*, 1993; Rasmussen, 1999). We believe that potential bias was minimal in this study as each interviewee generally reported few cases of depredation, and the low numbers involved may have helped the respondents remember specific cases. In many instances we obtained confirmation of predation events from neighbours.

There are several possible explanations for the recorded increase in predation intensity following the more intensive management of the Pendjari Biosphere Reserve that commenced in 2000. Firstly, the implementation of a management plan may have enhanced predator populations in the Reserve (Oli *et al.*, 1994; Saberwal *et al.*, 1994; Mishra, 1997; Wang & Macdonald, 2006). Survey data suggest that the number of lions in the Reserve increased between 2002 (Di Silvestre, 2002) and 2009 (Sogbohossou, 2009). Alternatively, depredation could have increased because of growth of the human population, with increased encroachment, reduced natural prey populations and unfavourable habitat changes (Thouless & Sakwa, 1995; Cozza *et al.*, 1996; Meriggi & Lovari, 1996; Mladenoff *et al.*, 1997; Dahle *et al.*, 1998; Mizutani, 1999; Woodroffe, 2000; Liu *et al.*, 2001; Naughton-Treves *et al.*, 2003; Treves & Karanth, 2003; Kolowski & Holekamp, 2006). We believe it most likely that the increase in the number of lions explains the increases in predation intensity (Di Silvestre, 2002; Sogbohossou, 2009).

2.4.1 Prey selection

Spotted hyaenas, followed by baboons and then lions, were the predominant predators of livestock. As lions are hunted in the hunting zones it is possible that they occur at lower densities than do spotted hyaenas. This, along with the high plasticity of hyaenas may explain the predominance of hyenas, compared to lions, as livestock raiders (Boydston *et al.*, 2003). In other areas where lions are at high densities they tend to be important livestock predators (Karani, 1994; Kerbis Peterhans & Gnoske, 2002; Patterson *et al.*, 2004). Similarly, when at high densities spotted hyaenas are responsible for a high proportion of attacks (Holmern *et al.*, 2007). Depredation by baboons, which was relatively important around the Reserve, has rarely been reported to be a significant problem elsewhere (Butler, 2000).

Although lions preyed on small livestock they were principally predators of cattle, whereas hyaenas and baboons mainly attacked small stock. This supports the hypothesis that livestock species selection corresponds to the size of the predator (Caro, 1994; Patterson *et al.*, 2004) in accordance with the size of their natural prey (Bodendorfer *et al.*, 2006; Hayward, 2006; Bauer *et al.*, 2008). Lions nevertheless killed a higher proportion of small stock in Pendjari compared to Waza National Park area in Cameroon (Van Bommel *et al.*, 2007), Tsavo ranches in Kenya (Patterson *et al.*, 2004) and around the Serengeti National Park in Tanzania (Holmern *et al.*, 2007).

2.4.2 Seasonality in predation

Livestock predation usually follows seasonal patterns (Oli *et al.*, 1994; Michalski *et al.*, 2006) although there are some exceptions (Holmern *et al.*, 2007). We recorded

a peak in predation by lions and hyaenas in the late wet season, similar to what has been observed in Tsavo (Patterson *et al.*, 2004). This is presumably explained by the variation in prey dispersal with season. During the dry season wild herbivores tend to concentrate near water sources within the Reserve, where it is probably easier for lions and hyaenas to prey on them (Kays & Patterson, 2002). As the wet season progresses and water is more readily available, prey populations disperse widely. In areas with low mean prey density it may be easier for predators to prey upon livestock at these times (Hunter, 1952; Ayeni, 1975; Eltringham *et al.*, 1999). This also probably explains why attacks on livestock were less important in drier years around Pendjari.

However, the pattern of prey movement in relation to the seasonal availability of water may vary from area to area. For example, around Waza National Park lion attacks were only recorded at villages far away from the Park during the wet season, whereas they occurred in all seasons around villages close to the Park (Van Bommel *et al.*, 2007). Thus the season of peak depredation on livestock is seemingly related to prey distribution and availability and distances of villages from a protected area. In regions where attacks peak in the dry season this may be because, subsequent to migration of prey after the rains, livestock become an easy alternative for resident carnivores (Rudnai, 1979; Karani, 1994). Sometimes predation increases during calving as calves are easiest to attack than adult cattle (Polisar *et al.*, 2003; Michalski *et al.*, 2006).

Seasonal predation patterns were different, however, for baboons, which predated livestock mostly during the dry season. This probably explains the difference between the two road axes in the seasonal distribution of predation; baboon attacks are concentrated along the Tanguieta–Batia road because of its proximity of Atacora Mountain. The dry season begins in November–December, the period when local people set fires to burn the bush. At this time even the hills, a prime baboon habitat, are burned. Thus it probably becomes increasingly difficult for baboons to feed in the wild. Livestock in villages bordering the Atacora Mountain thus become an alternate source of food. New forage after the fires draws the baboons away from the villages. Towards the end of the dry season food becomes scarce again, resulting in baboons again preying on livestock. Increased predation by baboons in periods of wild food shortage has also been reported in Uganda (Naughton-Treves *et al.*, 1998) and in Zimbabwe (Butler, 2000).

2.4.3 Husbandry techniques

Husbandry techniques may have a great impact on livestock predation (Robel *et al.*, 1981; Oli *et al.*, 1994; Cozza *et al.*, 1996; Mishra, 1997; Ogada *et al.*, 2003; Patterson *et al.*, 2004; Wang & Macdonald, 2006; Van Bommel *et al.*, 2007; for a different opinion see Graham *et al.*, 2005). In the Pendjari area traditional enclosures,

which are low, with sparse branches, and the absence of enclosures in most cases, probably encourage livestock predation (Butler, 2000; Mazzolli *et al.*, 2002; Wang & Macdonald, 2006). Improved fences and walls are inexpensive and are sustainable methods of deterring predators (Jackson & Wangehuk, 2001; Ogada *et al.*, 2003; Treves & Karanth, 2003); it would be of value to test them around Pendjari. Dogs are relatively inefficient against predators and also served as prey. Similar cases were reported from around Waza (Van Bommel *et al.*, 2007) and Serengeti National Parks, where hyaenas kill dogs (Holmern *et al.*, 2007). However, guarding dogs and other guarding animals have proved to be successful elsewhere (Marker-Kraus *et al.*, 1996; Bangs & Shvik, 2001; Marker, 2002; Ogada *et al.*, 2003; Rigg *et al.*, 2011). The efficiency of guarding animals probably depends on the size and character of the breed and on the size of the predator to be deterred. In Pendjari dogs were reported to be efficient against jackal and baboon attacks but not against lions or hyaenas.

2.4.4 Other factors

Our results suggest that distance to the Reserve was strongly correlated with predation risk. This is similar to results from Waza National Park (Van Bommel *et al.*, 2007), the Serengeti (Holmern *et al.*, 2007) and Brazil (Michalski *et al.*, 2006; Palmeira *et al.*, 2008). The effect of distance could be related to species. Lions usually stay close to their natural habitat whereas hyaenas often move far from protected areas (Kruuk, 1972; Hofer & East, 1993; Mills & Hofer, 1998; Holmern *et al.*, 2007). In Pendjari it was the distance to the Reserve more than the distance to the hunting zone that influenced predation patterns. Thus the Reserve is the main source of wildlife utilized in the hunting zones, which largely function as a sink and thus as a buffer. This pattern has been found in many other areas (Doak, 1995; Noss *et al.*, 1999). However, the low density of competitors in hunting zones may attract wildlife and predators, which may then further disperse into villages, creating conflicts. Thus it is debatable whether hunting zones successfully act as buffers.

We expected that factors affecting the integrity of the vegetation and of natural prey populations, such as poaching, illegal grazing and safari hunting, would influence conflicts. However, only the number of herbivores shot annually significantly affected the predation rate. The non significant impact of illegal grazing and poaching could be related to the relatively low numbers of herders and poachers arrested every year in the Reserve because of the increase in patrolling by the rangers.

2.4.5 Implications for management and conservation

Our findings suggest that conflicts could be significantly reduced by improving husbandry practices. This includes the construction of predator-proof enclosures and a change in herding practices. The park staff, the Wildlife Office and NGOs working in the area should focus on education. As benefits from wildlife can positively affect attitudes (Oli *et al.*, 1994; de Boer & Baquete, 1998; Conforti & de Azevedo, 2003; Mishra *et al.*, 2003), decision makers and conservationists need to ensure that people receive benefits from the Biosphere Reserve. Local people are already involved in reserve management, and receive 30% of the safari hunting revenues. Further studies, however, would facilitate a better assessment of the impact of these revenues and the determinants of people's perceptions and attitudes in this area. Although direct financial compensation is an alternative to the augmentation mitigation measures (Michelle & Smirnov, 1999; Stahl *et al.*, 2001; Wang & Macdonald, 2006) this may not be an appropriate approach for a relatively poor country such as Benin where it is already difficult to secure funds for conservation. Any measures applied need to be based on the knowledge of factors that influence local attitudes (Zimmermann *et al.*, 2005) and not just a replication of what is applied elsewhere (Treves & Karanth, 2003).

Mitigation measures need to be underpinned by a thorough understanding of the socio-ecology and use of space by large predators, which could influence mitigation measures (Stahl *et al.*, 2001). Previous studies, particularly of lions, have shown that conflicts are mostly with problem individuals (Stander, 1990; Woodroffe & Ginsberg, 1998; Patterson *et al.*, 2004; Bauer & de longh, 2005). To limit the territorial expansion of predators into human settlements around Pendjari Biosphere Reserve investigations are required to identify management actions that need to be conducted in the Biosphere Reserve by the Wildlife Office.

Acknowledgements

Financial support for this work was provided to EAS by the Netherlands Organization for International Cooperation in Higher Education and Research (NUFFIC) and a Kaplan Graduate Award from Panthera Foundation. We thank the Wildlife Office (CENAGREF) and the Pendjari Project for allowing us to work in Pendjari Biosphere Reserve. We are grateful to A. Gbangboche, R. Glele Kakai and P. Vos for their help with statistical analyses, and to P. Neuenschwander and two anonymous reviewers for their helpful comments.

References

Ayeni, J.S.O. (1975) Utilization of water holes in Tsavo National Park (East). *East African Wildlife Journal*, **13**, 305–323.

Bangs, E. & Shivik, J. (2001) Managing wolf conflict with livestock in the northwestern United States. *Carnivore Damage Prevention News*, **3**, 2–5.

Bauer, H. & de longh, H.H. (2005) Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology*, **43**, 208–214.

Bauer, H., Vanherle, N., Di Silvestre, I. & De longh, H.H. (2008) Lion–prey relations in West and Central Africa. *Mammalian Biology*, **73**, 70–73.

Bertola, L.D., van Hooft, W.F., Vrielink, K., Uit de Weerd, D.R., York, D.S., Bauer, H., Prins, H.H.T., Funston, P.J., Udo de Haes, H.A., Leirs, H., van Haeringen, W.A., Sogbohossou, E., Tumenta, P.N. & de longh, H.H. 2011. Genetic diversity, evolutionary history and implications for conservation of the lion (*Panthera leo*) in West and Central Africa. *Journal of Biogeography*, **38**. doi: 10.1111/j.1365-2699.2011.02500.x

Binot, A., Castel, V. & Caron, A. (2006) L'interface faune-bétail en Afrique subsaharienne Sécheresse, **17**(1–2), 349–361.

Bodendorfer, T., Hoppe-Dominik, B., Fischer, F. & Linsenmair, K.E. (2006) Prey of leopard (*Panthera pardus*) and the lion (*Panthera leo*) in the Comoé and Marahoué National Parks, Côte d'Ivoire, West Africa. *Mammalia*, **70**, 231–246.

Boer, W.F. de & Baquete, D.S. (1998) Natural resource use, crop damage and attitudes of rural people in the vicinity of the Maputo Elephant Reserve, Mozambique. *Environmental Conservation*, **25**, 208–218.

Boy, A. (1962) Lions des environs du Parc National du W Niger, Haute-Volta. *Bois et Forêts des Tropiques*, **86**, 4–18.

Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M. & Holekamp, K.E. (2003) Altered behaviour in spotted hyenas associated with increased human activity. *Animal Conservation*, **6**, 207–219.

Brashares, J.S., Arcese, P. & Sam, M.K. (2001) Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society of London, Series B*, **268**, 2473–2478.

Butler, J.R.A. (2000) The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. *African Journal of Ecology*, **38**, 23–30.

Caro, T.M. (1994) *Cheetahs of the Serengeti Plains: Group Living in an Asocial Species*. University of Chicago Press, Chicago, USA.

Conforti, V.A. & de Azevedo, F.C.C. (2003) Local perceptions of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in the Iguaçu National Park area, south Brazil. *Biological Conservation*, **111**, 215–221.

Conover, M. (2002) *Resolving Human–Wildlife Conflicts: The Science of Wildlife Damage Management*. Lewis Publishers, Boca Raton, USA.

Cozza, K., Fico, R., Battistini, M-L. & Rogers, E. (1996) The damage-conservation interface illustrated by predation on domestic livestock in Central Italy. *Biological Conservation*, **78**, 329–336.

Dahle, B., Sørensen, O.J., Wedul, H., Swenson, J.E. & Sandegren, F. (1998) The diet of brown bears in central Scandinavia: effect of access to free-ranging domestic sheep. *Wildlife Biology*, **3**, 147–158.

Delvingt, W., Heymans, J.-C. & Sinsin, B. (1989) *Guide du Parc National de la Pendjari*. CECA-CEE-CEEA, DFRNMDR, Cotonou, Bénin.

Di Silvestre, I. (2002) *Dénombrement des grands carnivores au niveau de la Réserve de Biosphère de la Pendjari*. Unpublished Report, Projet Pendjari, Cotonou, Benin.

Doak, D.F. (1995) Source-sink models and the problem of habitat degradation, general models and applications to the Yellowstone grizzly. *Conservation Biology*, **9**, 1370–1379.

East, R. (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, **22**, 245–270.

Eltringham, S.K., Cooksey, I.A., Dixon, W.J.B., Raine, N.E., Sheldrick, C.J., McWilliam, N.C. & Packer, M.J. (1999) Large mammals of Mkomazi. In *Mkomazi: The Ecology, Biodiversity and Conservation of a Tanzanian Savanna* (eds M. Coe, N. McWilliam, G. Stone & M. Packer.), pp. 485–504. Royal Geographical Society, London, UK.

Fritz, H. (1997) Low ungulate biomass in West African savannas: primary production or missing megaherbivores or large predator species. *Ecography*, **20**, 417–421.

Garba, H.M. & Di Silvestre, I. (2008) Conflicts between large carnivores and domestic livestock in the peripheral zone of the Regional Park 'W' in Niger. In *Proceedings of an International Seminar on Management and Conservation of Large Carnivores in West and Central Africa* (eds B. Croes, R. Buij, H.H. de longh & H. Bauer), pp. 133–144. Leiden, The Netherlands.

Ginsberg, J.R. & Macdonald, D.W. (1990). *Foxes, Wolves, Jackals and Dogs: an action plan for the conservation of canids*. IUCN, Gland, Switzerland.

Graham, K., Beckerman, A.P. & Thirgood, S. (2005) Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation*, **122**, 159–171.

Hanski, I. (2005) Landscape fragmentation, biodiversity loss and the societal response. *EMBO Reports*, **6**, 388–392.

Hayward, M.W. (2006) Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology* (London), **270**, 606–614.

Hofer, H. & East, M.L. (1993) The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. I. Social organization. *Animal Behaviour*, **46**, 547–557.

Holmern, T., Nyahongo, J. & Røskaft, E. (2007) Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation*, **135**, 518–526.

Hoogesteijn, R., Hoogesteijn, A. & Mondolfi, E. (1993) Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan Llanos. *Symposium of the Zoological Society of London*, **65**, 391–407.

Hunter, J.A. (1952) *Hunter*. Harper and Brothers Publishers, New York, USA.

Hussain, S. (2003) The status of the snow leopard in Pakistan and its conflict with local farmers. *Oryx*, **37**, 26–33.

Jackson, R. & Wangehuk, R. (2001) Linking snow leopard conservation and people-wildlife conflict resolution: grassroots measures to protect the endangered snow leopard from herder retribution. *Endangered Species Update*, **18**, 138–141.

Karani, I.W. (1994) *An Assessment of Depredation by Lions and Other Predators in the Group Ranches Adjacent to Masai Mara National Reserve*. MSc dissertation, Moi University, Kenya.

Kays, R.W. & Patterson, B.D. (2002) Mane variation in African lions and its social correlates. *Canadian Journal of Zoology*, **80**, 471–478.

Kerbis Peterhans, J.C. & Gnoske, T.P. (2002) The science of man-eating among lions *Panthera leo* with a reconstruction of the natural history of the man-eaters of Tsavo. *Journal of East African Natural History*, **90**, 1–40.

Kolowski, J.M. & Holekamp, K.E. (2006) Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biological Conservation*, **128**(4), 529–541.

Kruuk, H. (1972) *The Spotted Hyena: A Study of Predation and Social Behaviour*. The University of Chicago Press, Chicago, USA.

Lamarque, F. (2004) *Les grands mammifères du complexe WAP*. ECOPAS, Ouagadougou, Burkina Faso.

Liu, J., Linderman, M., Ouyang, Z., An, L., Yang, J. & Zhang, H. (2001) Ecological degradation in protected areas: the case of Woolong Nature Reserve for giant pandas. *Science*, **292**, 98–101.

Marker, L.L. (2002) *Aspects of cheetah (Acinonyx jubatus) biology, ecology and conservation strategies on Namibian farmlands*. PhD thesis, University of Oxford, Oxford, UK.

Marker-Kraus, L., Kraus, D., Barnett, D. & Hurlbut, S. (1996) *Cheetah Survival on Namibian Farmlands*. Cheetah Conservation Fund, Windhoek, Namibia.

Mazzolli, M., Graipel, M.E. & Dunstone, N. (2002) Mountain lion depredation in southern Brasil. *Biological Conservation*, **105**, 43–51.

Meriggi, A. & Lovari, S. (1996) A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock. *Journal of Applied Ecology*, **33**, 1561–1571.

Michalski, F., Boulhosa, R.L.P., Faria, A. & Peres, C.A. (2006) Human–wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. *Animal Conservation*, **9**, 179–188.

Michelle, D.G. & Smirnov, E.N. (1999) People and tigers in the Russian Far East: searching for the 'co-existence receipt'. In *Riding the Tiger-Tiger Conservation Efforts in Human-Dominated Landscapes* (eds J. Seidensticker, S. Christie & P. Jackson), pp. 273–295. The Zoological Society of London and Cambridge University Press, Cambridge, UK.

Mills, G. & Hofer, H. (1998) *Hyenas: Status Survey and Conservation Action Plan*. World Conservation Union, Gland, Switzerland.

Mishra, C. (1997) Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation*, **24**, 338–343.

Mishra, C., Allen, P., McCarthy, T., Madhusudan, M.D., Bayarjargal, A. & Prins, H.H.T. (2003) The role of incentive programs in conserving the snow leopard. *Conservation Biology*, **17**, 1512–1520.

Mizutani, F. (1999) Impacts of leopards on a working ranch in Laikipia, Kenya. *African Journal of Zoology (London)*, **37**, 211–225.

Mladenoff, D.J., Haight, R.G., Sickley, T.A. & Wydeven, A.P. (1997) Causes and implications of species restoration in altered ecosystems. *BioScience*, **47**, 21–31.

Naughton-Treves, L., Grossberg, R. & Treves, A. (2003) Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*, **17**, 1500–1511.

Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. (1998) Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, **35**, 596–606.

Noss, R.F., Dinerstein, E., Gilbert, B., Gilpin, M., Miller, B.J., Terborgh, J. & Trombulak, S. (1999) Core areas: where nature reigns. In: *Continental Conservation: Scientific Foundations of Regional Reserve Networks* (eds M.E. Soulé & J. Terborgh), pp. 99–128. The Wildlands Project, Island Press, Washington, DC, USA.

Nowell, K. & Jackson, P. (1996) *Wild Cats: Status Survey and Conservation Action Plan*. IUCN/SSC Cat Specialist Group, Gland, Switzerland.

Ogada, M.O., Woodroffe, R., Oguge, N.O. & Frank, L.G. (2003) Limiting depredation by African carnivores: the role of livestock husbandry. *Conservation Biology*, **17**, 1521–1530.

Oli, M.K., Taylor, I.R. & Rogers, M.T. (1994) Snow leopard (*Panthera uncia*) predation on livestock: an assessment of local perceptions in the Annapurna Conservation Area, Nepal. *Biological Conservation*, **68**, 63–68.

Packer, C., Ikanda, D., Kissui, B. & Kushnir, H. (2005) Lion attacks on humans in Tanzania. *Nature*, **436**, 927–928.

Palmeira, F.B.L., Crawshaw, Jr, P.G., Haddad, C.M., Ferraz, K.M.P.M.B. & Verdade, L.M. (2008) Cattle depredation by puma (*Puma concolor*) and jaguar (*Panthera onca*) in central-western Brazil. *Biological Conservation*, **141**, 118–125.

Patterson, B.D., Kasiki, S.M., Selempo, E. & Kays, R.W. (2004) Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Park, Kenya. *Biological Conservation*, **119**, 507–516.

Polisar, J., Matix, I., Scognamillo, D., Farrell, L., Sunquist, M.E. & Eisenberg, J.F. (2003) Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biological Conservation*, **109**, 297–310.

Rasmussen, G.S.A. (1999) Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. *Biological Conservation*, **88**, 133–139.

Rigg, R., Findo, S., Wechselberger, M., Gorman, M.L., Sillero-Zubiri, C. & Macdonald, D.W. (2011) Mitigating carnivore–livestock conflict in Europe: lessons from Slovakia. *Oryx*, **45**, 272–280.

Robel, R.J., Dayton, A.D., Henderson, R.R., Meduna, R.L. & Spaeth, C.W. (1981) Relationships between husbandry methods and sheep losses to canine predators. *Journal of Wildlife Management*, **45**, 894–911.

Rudnai, J. (1979) Ecology of lions in Nairobi National Park and the adjoining Kitengela Conservation Unit in Kenya. *African Journal of Ecology*, **17**, 85–95.

Saberwal, V.K., Gibbs, J.P., Chellam, R. & Johnsingh, A.J.T. (1994) Lion human conflicts in the Gir Forest, India. *Conservation Biology*, **8**, 501–507.

Sogbohossou, E.A. (2004) *Etude des conflits entre les grands carnivores et les populations riveraines de la Réserve de Biosphère de la Pendjari, Nord Bénin*. Unpublished Report to MAB UNESCO. Cotonou, Bénin.

Sogbohossou, E.A. (2009) *Dénombrement des lions dans la Réserve de Biosphère de la Pendjari. Rapport Technique*. Unpublished Report, Projet Pendjari, Cotonou, Benin.

Stahl, P., Vandel, J.M., Herrenschmidt, V. & Migot, P. (2001) Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability. *Journal of Applied Ecology*, **38**, 674–687.

Stander, P.E. (1990) A suggested management strategy for stockraiding lions in Namibia. *South African Journal of Wildlife Resources*, **20**, 37–43.

Thouless, C.R. & Sakwa, J. (1995) Shocking elephants: fences and crop raiders in Laikipia District, Kenya. *Biological Conservation*, **72**, 99–107.

Treves, A. & Karanth, U.K. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, **17**(6), 1491–1499.

Van Bommel, L., Bij de Vaate, M.D., Boer, W.F. de & longh, H.H. de (2007) Factors affecting livestock predation by lions in Cameroon. *African Journal of Ecology*, **45**(4), 490–498.

Wagner, F.H. (1988) *Predator Control and the Sheep Industry: The Role of Science in Policy Formation*. Regina Books, Claremont, USA.

Wang, S.W. & Macdonald, D.W. (2006) Livestock predation by carnivores in Jigme Singye Wangchuk National Park, Bhutan. *Biological Conservation*, **129**, 558–565.

Woodroffe, R. (2000) Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*, **3**, 165–173.

Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126–2128.

Zimmermann, A., Walpole, M.J. & Leader-Williams, N. (2005) Cattle ranchers' attitudes to conflicts with jaguar *Panthera onca* in the Pantanal of Brazil. *Oryx*, **39**(4), 406–412.

