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

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Lions of West Africa

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Lions of West Africa

Ecology of lion (*Panthera leo* Linnaeus 1975) populations and human-lion conflicts in Pendjari Biosphere Reserve, North Benin

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	Dr. P.J. Funston (Tshwane University of Technology, South Africa)

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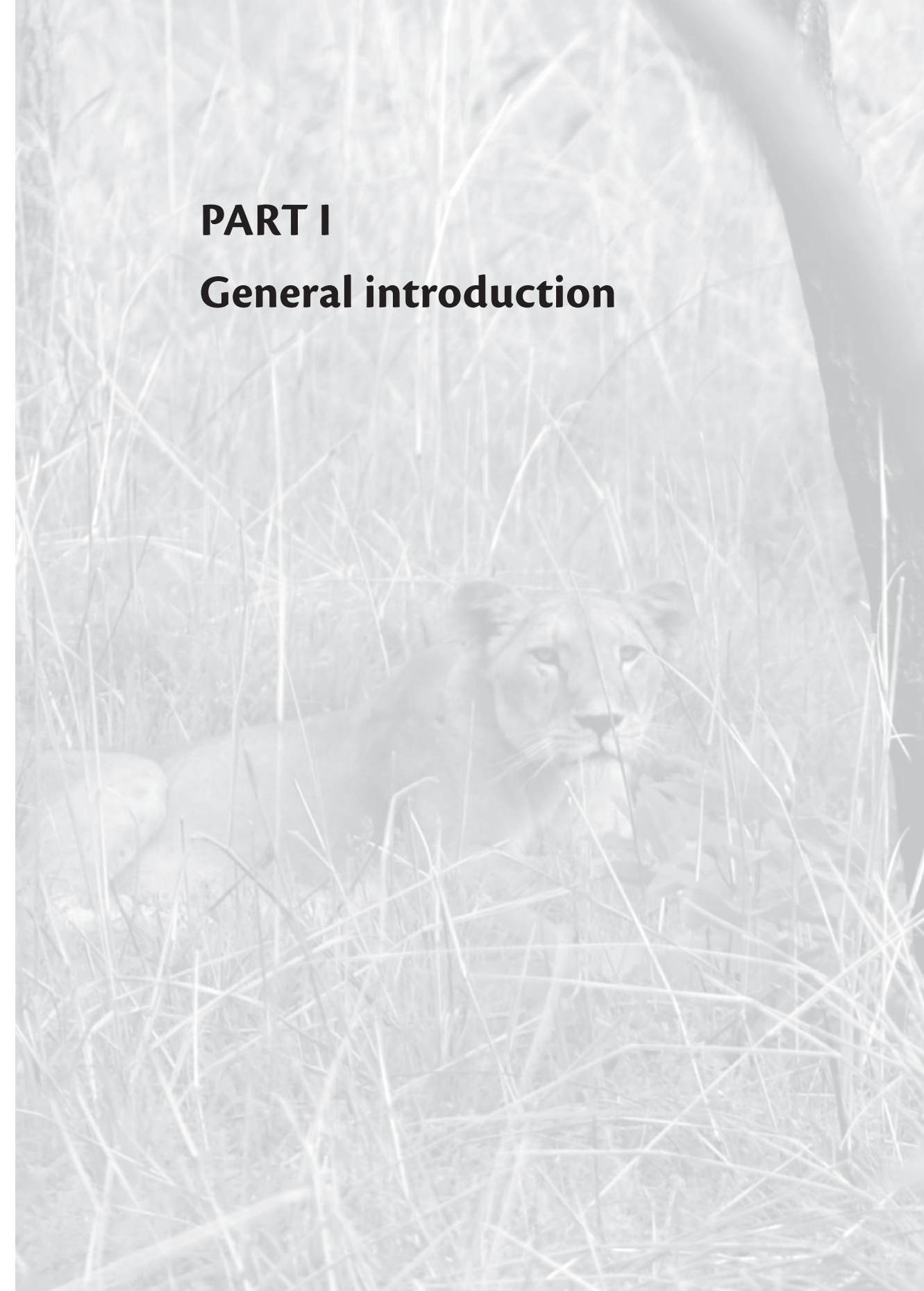
Lion population in Pendjari Biosphere Reserve

List of Acronyms

AVIGREF	Association Villageoises pour la Gestion des Réserves de Faune (Villagers Association for Wildlife Reserve Mangement)
CENAGREF	Centre National de Gestion des Réserves de Faune (National Center for Wildlife Reserve Mangement)
DED	German Development Service
ECOPAS	Ecosystèmes Protégés en Afrique Sahélienne (Protected Ecosystems in Sahelian Africa)
ESRI	Environmental Systems Research Institute
INSAE	Institut National de la Statistique et de l'Analyse Economique (National Institute of Statistics and Economic Analysis)
GIS	Geographic Information System
GTZ	Gesellschaft für Technische Zusammenarbeit (German Technical Cooperation)
IUCN	International Union for Conservation of Nature
KFW	Kreditanstalt für Wiederaufbau (Reconstruction Credit Institute)
LCU	Lion Conservation Unit
MAB	Man And Biosphere
MCP	Minimum Convex Polygon
PGRN	Projet de Gestion des Ressources Naturelles (Project for the Management of Natural Resources)
ROCAL	Réseau Ouest et Centre Africain pour la Conservation du Lion (Network for Lion Conservation in West and Central Africa)
SSC	Species Survival Commission
UNESCO	United Nations Educational Scientific and Cultural Organization
WAP	W (Benin, Burkina Faso, Niger) - Arly (Burkina Faso) – Pendjari (Benin) reserves
WAPO	W - Arly – Pendjari - Oti Mandouri reserves
WAPOK	W – Arly – Pendjari – Oti Mandouri – Kéran reserves



PART I
General introduction


PARC NATIONAL DE LA PENDJARI
VOUS SOUHAITE LA BIENVENUE
PENDJARI
GENAGIBE
Chers visiteurs
Vous entrez dans une zone de protection où
nera une expérience inédite . L'administration de l
pendjari vous demande de bien vouloir respecte
visent le bien être des animaux et votre sat
Vitesse maximale autorisée est
Ceci évite des accidents avec des animaux et autr
gradation des pistes .
Ne circulez pas hors pistes et ne tentez
Ceci va éviter l'augmentation de la distance de
Ne mettez pas feu à la végétation .
L'administration de la réserve s'est déjà chargée
la dégradation de la nature .
éviter de polluer la nature .
Déposez les ordures que vous ne pouvez pas re
réservées à cet effet .
Evitez de faire du bruit inutile
les animaux et les autres visiteurs vous e
N'introduisez pas des animaux domestiq
ils constituent des vecteurs de maladies grav
Ne donnez pas à manger aux animaux
notamment aux babouins . Ceci pourrait les
visiteurs .
Ne campez pas sauvagement dans la r
Vous ne vous exposez pas seulement aux
aussi la quiétude des animaux sauvages .
de la réserve est plus indiqué .
En cas de panne restez à côté de vot
En conséquence ravitaillez vous suffisamm
Ne provoquez pas les animaux .
(jet des pierres ou autres agressions) Ceci
rendre craintifs ou agressifs vis-à-vis

1 General Introduction

1.1 Introduction

1.1.1 Carnivore conservation worldwide

With the rapid expansion of human populations in the past decades, encroachment on land has increased. In sub-Saharan Africa in particular, there is an increasing demand for land for agriculture and husbandry, which are extensive and important space consumers (Mearns, 1997). The resulting land degradation and habitat fragmentation has had detrimental effects on wildlife (Michalsky & Peres, 2005). Protected Areas have been created for biodiversity conservation but their size does not guarantee the survival of species (Brashares *et al*., 2001). The abundance of many species has decreased and several carnivore species have become endangered (Fuller, 1995; Nowell & Jackson, 1996; Woodroffe, 2000; Bauer *et al*., 2008a). Among these species is the lion *Panthera leo*, which was one of the most widely distributed terrestrial mammals. Formerly, lions ranged over most of Africa except the driest deserts and in rainforests, as well as in Europe, the Middle East and Asia (Schaller, 1972; Nowell & Jackson, 1996; Kingdon, 2003). Proofs of the lion's presence in Europe, the Middle East and northern Africa have been found in caves and tombs (Callou *et al*., 2004; Yamaguchi *et al*., 2004). The species disappeared from Europe about 20,000 years ago and from North Africa, the Middle East and Asia between 1850 and 1900 (Nowell & Jackson, 1996; Barnett *et al*., 2006). A large part of its range in Africa collapsed during the 20th century (O'Brien *et al.* 1987, Loveridge *et al*., 2002; Kingdon, 2003; UICN/SSC Cat Specialist Group, 2006). Two sub-species of lions remain today, *Panthera leo leo* in sub-saharan Africa and *Panthera leo persica* in the Gir Forest in India (Nowell & Jackson, 1996).

As with many other predators, the lion plays the role of an indicator species as its presence reflects the health of ecosystems. As an umbrella species, it is also connected to several other species, starting with its prey. The lion can also be classified as a flagship species due to its unquestionable symbolic and ritual role in traditional and modern cultures (Simberloff, 1998). Large predators in general contribute to the maintenance of healthy ecosystems by regulating numbers of prey but also by controlling other predators' populations (Krebs *et al*., 1995; Terborgh *et al*., 1999). The disappearance of predators frequently results in changes in the herbivore community structure (Berger 1999; Terborgh et al., 2002). Large carnivores are sensitive to landscape changes because of some of their biological

traits (low population density, low fecundity and limited dispersal ability across dense or open habitat; Cardillo, 2003). Lions also have economic importance because of tourism, sport hunting and their uses for traditional medicine (Nowell & Jackson, 1996). The social and cultural importance of lions have been described in several traditional communities, for example in Kenya and Benin (Maddox, 2003; Sogbohossou, 2006).

The multiple values of the lion in African savannahs are threatened by anthropogenic and environmental developments such as habitat degradation and prey depletion. These trends justify the plethora of studies on the lion throughout Africa.

1.1.2 Status of lions in Africa and survey methods limitations

Like elsewhere in the world, lion populations have undergone a drastic decline in Africa. Nowell & Jackson (1996) made a guesstimate of 100,000 lions. The most recent estimate ranges between 23,000-39,373 lions for the whole of Africa (Chardonnet, 2002; Bauer & van der Merwe, 2004). Based on the recent estimates, this reduced population is irregularly distributed across the continent and about 1,800-3,978 lions (7.8-10.1%) live in West and Central Africa (Chardonnet, 2002; Bauer & van der Merwe, 2004; IUCN/SSC Cat Specialist Group, 2006), with West Africa sheltering only 2.9-3.7% of the total African lion population. This region has shown the most serious reduction of lion habitat in Africa, with only 9% of the historical range remaining (IUCN/SSC Cat Specialist Group, 2006). As mentioned, the main threats to lion conservation were habitat fragmentation and a decline in the natural prey base, which often result in human-lion conflicts (Nowell & Jackson, 1996; IUCN/SSC Cat Specialist Group, 2006). Other reasons for the decline are legal and illegal hunting of lions for trophy, meat and medicines as well as the impact of diseases such as bovine tuberculosis. The high level of fragmentation of lion populations and the increasing threats to lion populations in the region have resulted in a classification of the lion as Regionally Endangered in West Africa on the IUCN Red List (Bauer & Nowell, 2004). The species is listed in CITES Appendix II.

The workshop jointly organized by the IUCN Cat Specialist Group and the Wildlife Conservation Society in June 2001 in Cameroon on the Status and Needs for lion conservation in West and Central Africa (Bauer *et al*., 2003a) marked the beginning of an increased awareness of the threatened status of lion populations in West and Central Africa. This workshop highlighted the lack of knowledge of lion populations in this part of Africa. Most of the studies on lions in the region, especially in West Africa, were initiated after this workshop (Di Silvestre, 2002; Bauer *et al*., 2003b; 2008b; Di Silvestre *et al*., 2003; Sogbohossou, 2004; Sogbohossou, 2006; Garba & Di Silvestre, 2008). Approximately 14 Lion Conservation Units (LCU) have been identified in West Africa. Two LCU were considered to host a sustainable and viable lion population: the Niokolo complex between Guinea and Senegal and

the W-Arly-Pendjari-Oti complex between Benin, Niger, Burkina Faso and Togo (IUCN/SSC Cat Specialist Group, 2006). Of these areas, Pendjari Biosphere Reserve in Benin seems to be the best protected area. Recent surveys showed that the reduction of lion populations continues in the region with lions having disappeared from at least two of the LCUs in Ghana and Congo (Henschel *et al.*, 2010). Therefore, there is an urgent need to address the decline of the lion populations in West Africa in order to at least stop the decreasing trend.

Several factors favour the decline and limit the potential for recovery of lion populations. First, the real status of these populations is poorly known. Lion population densities in the region were mostly estimated through guesstimates, public interviews and surveys by calling-station methodology. Differences in the results from various authors (Chardonnet, 2002; Bauer & van der Merwe, 2004) and the results of the surveys by Henschel *et al.* (2010) revealed the need for a harmonized methodology adapted to the region. Several census and monitoring methods (Mills *et al.*, 1978; Gros, 1998; Ogutu & Dublin, 1998; Loveridge *et al.*, 2001; Castley *et al.*, 2002) are available. Each method has its advantages and disadvantages and each method requires specific conditions for successful applicability (Loveridge *et al.*, 2001).

One of the first reasons that justify a particular interest towards lions in West Africa is that their extirpation will considerably reduce the range of African lion. If we do not succeed in protecting the West African lion against extirpation, this will be considered as a great failure for conservation in the region. The possible elimination of lion populations in West Africa will not only mean a failure for lion conservation but also a failure for the conservation of many other species that share their habitat. The second reason is based on specific morphological and genetic traits of the lion in West Africa. Some morphological differences have been observed between lions of West Africa and lions from other regions of Africa, especially in relation to mane development (Patterson, 2004; 2007; Yamaguchi *et al.*, 2004) and the size of individuals (Sogbohossou, 2006). Until now, investigations on phylogenetics have not demonstrated the existence of a different sub-species of lions in West Africa (Ellerman *et al.*, 1953; O'Brien *et al.*, 1987; Dubach *et al.*, 2005; Barnett *et al.*, 2006). However, Bertola *et al.* (2011) found that lions from West and Central Africa show little genetic diversity and are more closely related to the Asiatic lion than to southern and East African lions. Better understanding the taxonomy and phylogeny of West and Central Africa lions is an additional argument for the conservation of lions in this region.

In Benin, lions are mainly present in the two Biosphere Reserves (Pendjari and W) in the northern part of the country. Some individual lions reportedly make incursions into some of the gazetted forests from the central to the northern part of the country (Pellerin *et al.*, 2010). After two decades during which there was no specific interest in the lion (Sayer & Green, 1984), the first censuses, mainly based

on calling-station surveys and public interviews, were made in 2002 (Di Silvestre, 2002). These surveys resulted in a reduction by half of the lion-hunting quota in Benin. This also resulted in a controversy, as there were critics who suggested that the methodology used underestimated the lion population and that the actual lion population could support higher a hunting quota. Long-term, integrated research on lion population census methods combined with research on lion ecology will enable us to determine the status of lions in Benin with more accuracy. Such a long-term study may serve as a reliable basis for all lion conservation activity and further research. It could also serve as example for other LCUs in the region.

1.1.3 Social structure and home range of lions

The social system of a population influences its demography and dynamics, especially in small populations (Caro & Durant, 1995; Komdeur & Deerenberg, 1997). Similarly, behaviour is assumed to influence the effective size of populations and consequently their livelihood (Gilpin & Soule, 1986). Therefore a study on social structure and behaviour is important to generate background data for conserving populations, especially threatened ones.

The lion, the most sociable of all cats, lives in families referred to as prides (Schaller, 1972). A pride consists of 2 to 18 related females, their dependent offspring and 1 to 9 males, the so-called "pride males" (Schaller, 1972; Bygott *et al.*, 1979; Packer *et al.*, 1991). A pride is defined as a fission-fusion social unit (Schaller, 1972). While membership in a pride is stable, its members are often dispersed throughout the pride's range in small subgroups (Schaller, 1972; Bauer, 2003). Several factors influence groups and pride composition. As van Orsdol *et al.* (1985) pointed out, the pride structure is correlated to food availability especially during the period of the lowest prey biomass ('the lean season') in the course of the year. The composition of a pride is usually more or less stable for several years and is primarily affected by births, deaths, emigration of sub-adults and take-over by non resident coalitions of males (Pusey & Packer, 1983; Pusey & Packer, 1987). Lions evicted from a pride may become nomadic. Average pride size varied greatly across Africa, from four (Bauer, pers. com.) to more than 20 lions (Ogutu & Dublin, 2002). Aside from environmental factors, anthropogenic activities inside and outside protected areas such as hunting (Loveridge *et al.* 2007; 2010) affect the social structure of lions throughout Africa. Prides defend exclusive territories against other prides/lions and often occupy the same range over several generations (Schaller, 1972; Packer & Pusey, 1993). Territorial defense is one of the most important activities shared by the females of a pride (van Orsdol *et al.*, 1985). Home range size of lions and their determinants have been studied in several areas in Africa. Telemetry is the most common method used (Mizutani & Jewell, 1998). However, new genetic techniques also increasingly allow the assessment of the home range and factors that influence it (Spong, 2002). Several factors such as prey availability, which is correlated with soil

nutrient status and rainfall (van Orsdol *et al.*, 1985; Bauer & de Iongh, 2005) and lion group size affect the home range of lions. Home ranges vary from 20 to 700 km^2 (Stander, 1991). Large home ranges overlap extensively with those of adjacent prides while small ranges tend to have little overlap (Schaller, 1972; van Orsdol *et al*., 1985).

In the West and Central Africa region, lion home range has been studied mainly in Cameroon and Chad. It varied from 195 km^2 in Bénoué National Park (Schoe, 2007) to 630 km^2 in Waza National Park (Bauer & de Iongh, 2005). It is hypothesised that home ranges in West and Central Africa are usually large compared to what is observed in East and Southern Africa, probably because of the lower prey densities in this region. To date, no studies have been done on lion territory size and lion movements in the different ecosystems of West Africa. This is important to know especially when lions are confined within reserves surrounded by populations whose main activities are farming and husbandry. Also most habitats where studies have been done in the region were perturbed and under heavy human pressure mainly through cattle grazing and hunting. Investigations on well-protected areas such as the Pendjari Biosphere Reserve in Benin will provide insight into determinants of home range and habitats uses by lion. It will also contribute to assessing whether lion home range remains large under such conditions and how much it depends on the lower prey base observed in West and Central African region compared to other regions. Research on lion home range and movements may allow evaluation of the potential for human-lion co-habitation and such research would also contribute to the mitigation of lion-livestock conflicts.

Information on the feeding ecology of large carnivores contributes substantially to the understanding of their behavioural ecology (Mills, 1992). The African lion consumes a broad range of prey species with the most preferred range of prey being within the body mass range of 190 to 550 kg (Hayward & Kerley, 2005). However they prefer more profitable prey (in terms of energy gained compared to energy spent to kill the prey) and they have an opportunistic hunting behaviour (Krebs, 1978; Schaller, 1972; Hayward & Kerley, 2005). Lion prey preference is affected by prey abundance, body size, distribution and antipredatory behaviour (Sunquist & Sunquist, 1997). Environmental factors such as vegetation, terrain, and time of the day may also influence hunting success and prey preference (Mills *et al.*, 1995; Funston *et al.*, 2001; Hopcraft *et al.*, 2005).

The feeding ecology of large savannah carnivores has been well studied in East and Southern Africa (Kruuk & Turner, 1967; Pienaar, 1969; Mills & Biggs, 1993; Hayward & Kerley, 2005). However it has been much less studied in West and Central Africa, especially in the savannah zone (Wanzie, 1986; Ruggiero, 1991; Gross, 1997; Di Silvestre *et al.*, 2000; Korb, 2000, Breuer, 2005; Henschel *et al*., 2005). Fewer studies concerned lions (Bodendorfer *et al*., 2006; Wiggers, 2007; Bauer *et al*., 2008). There

is a great gap in the knowledge of lion prey preferences in West and Central Africa, as shown by Hayward & Kerley's (2005) review of lion diets in Africa. The few data available in West and Central Africa showed a slight difference in prey preference between this region and East and southern Africa, with lion in West and Central Africa preferring smaller prey (Bauer *et al*., 2008b). The data presented by Bauer *et al*. (2008b) were quite general and more detailed studies would allow a better assessment of West African lion prey preferences in the region. As Pendjari seems to have enough large prey species, will the lions prefer to eat medium-sized prey or will they show preference for large prey? Under such conditions, do lions prey upon livestock when prey are lacking or because livestock are easy prey? A study of the diet will help to assess the impact of changes in prey population on lion survival and to achieve better management and improved conservation of lion population. It could also contribute to assessing the interactions between the various carnivore species and the level of competition between them.

1.1.4 Lion-human interrelations

Human-carnivores conflicts are one of, if not the main threat to the survival of large carnivore species (Woodroffe & Ginsberg, 1998). Human-lion conflicts are a common problem on the African continent (Stander, 1990; Butler, 2000; Bauer *et al*., 2003; 2008b; Loveridge *et al*., 2002; Patterson, 2004; Patterson *et al*., 2004; van Bommel *et al*., 2007). This problem is one of the major threats to lion populations, and this is especially the case in West and Central Africa (Nowell & Jackson, 1996; Bauer et *al*., 2003a; IUCN/SSC Cat specialist Group, 2006). With the rapid growth of human populations, the protected areas to which most lion populations are confined are surrounded by human settlements. The relative small sizes of protected areas (Brashares *et al*., 2001) are not enough to contain the large home range of lions. The degradation of habitat, the diminution of natural prey, and the proximity of a relatively easy prey (livestock) favour a shift in lion diet towards livestock. Habitat characteristics, the abundance and distribution of natural prey, husbandry practices and some climatic and environmental factors may influence livestock predation patterns (Ogada *et al*., 2003; Patterson *et al*., 2004; Woodroffe & Frank, 2005; Inskip & Zimmermann, 2009). Livestock depredation by lion and other carnivores occur at different intensities, according to the location and conditions in West and Central Africa (Sogbohossou, 2004; Bauer & de Iongh, 2005; van Bommel *et al*., 2007; Garba & Di Silvestre, 2008). The cost of livestock depredation varied according to places and number of livestock owned (Butler, 2000; Patterson *et al*., 2004; Garba & di Silvestre, 2008). Human-lion conflicts are not limited to livestock predation, but also imply attacks on humans and retaliatory killing of lions. Attacks on humans, common in some areas such as East Africa (Yamazaki & Bwalya, 1999; Packer *et al*., 2005) seem to happen rarely in West Africa. But in response to damages caused by lions, human populations in West and Central Africa engage in the retaliatory killing of lions, which negatively af-

fects lion populations (Kissui, 2008). In spite of the fact that the lion is generally less responsible for livestock kills than other species such as hyena (Butler, 2000; Maclennan *et al.*, 2009), the lion is probably the species most affected by retaliatory killing. Human-lion conflicts favour negative perceptions towards carnivores and conservation (Garba & Di Silvestre, 2008; Lagendijk & Gusset, 2008; Hemson *et al.*, 2009). Several solutions for mitigating these conflicts have been developed and evaluated in order to promote the cohabitation between humans and lions and other carnivores (Woodroffe & Frank, 2005; Lamarque *et al.*, 2008). Education and awareness were suggested, as well as some other techniques/deterrent methods such as guard dogs and improved livestock fences (Ogada *et al.*, 2003; Shivik, 2006; Lamarque *et al.*, 2008; Ogra & Badola, 2008; Bauer *et al.*, 2010). The human dimension of conflicts has been relatively neglected (Inskip & Zimmermann, 2009; Dickman, 2010) and needs to be better addressed in conflict resolution.

1.1.5 Gaps in lion research in West and Central Africa and research questions

Despite several studies having been done on diverse aspects of lion conservation in Africa, a huge gap remains in our knowledge of the West African lion. Almost all aspects related to conservation of the lion in this region need investigation, ranging from ecology and behaviour to genetics and morphometrics. The need to fill this gap is crucial especially as this species is classified as Regionally Endangered in West Africa (Bauer & van der Merwe, 2004). This lack of information is not only due to the limited interest on the part of scientists. Major constraints to progress are the limited interest from regional governments and policy makers in conservation and human-wildlife conflicts mitigation, combined with the difficulty to secure funding for wildlife studies in West African savannahs compared to other parts of Africa. Studies must be initiated on West African lions and these should integrate diverse aspects such as population census, ecology and behaviour and predator-prey relations. Diverse aspects of the conflicts with humans need to be investigated. As highlighted by Caro (2008), monitoring and other applied studies are essential when trying to stop the decline of populations. These studies are needed to assess the status of lions, the pressures on lion populations and their consequences for the conservation of the species.

The main questions this study will attempt to answer are:

- What are the characteristics of human-lion conflicts in the West African region? How important are these conflicts?
- Do local communities have a more positive perception of predators in general and lions in particular in areas where livestock depredation is relatively low?
- What is the status of lion populations in a well-protected wildlife reserve such as Pendjari? How does the protection status affect the social structure of the lion population?

- As large prey is less abundant in West Africa than in East and Southern Africa, which prey size dominates in lion diet in West Africa? In a well-protected area characteristic of West Africa, surrounded by human populations, with the relatively low prey base density characteristic of West and Central Africa region, do lion prey upon livestock because prey is scarce or because livestock represent easy prey?
- How do lions use the habitat of the Sudanian savannah? Could conservation efforts in a protected area counterbalance the pressures and threats from the borders? In other words, are management efforts in a protected area enough to protect the resident lion populations in West Africa?

1.2 Research aims

Overall, this research project aims to investigate the ecology of lion populations and predator-prey relationships of West African lions in the Pendjari Biosphere Reserve in Benin as a basis for their improved conservation.

The specific research objectives are:

1. To assess the characteristics and importance of human-predator conflicts around Pendjari Biosphere Reserve;
2. To examine the perceptions and attitudes of local people towards carnivores and conflicts and the factors that influence these attitudes;
3. To estimate the abundance and the social structure of the lion population in Pendjari Biosphere Reserve and assess the threats on the population;
4. To assess lion-prey relations through the lions' diet;
5. To determine the home range, movements and habitat use by lions.

1.3 Study area

To achieve the defined objectives, the field station has been established in Pendjari Biosphere Reserve in Benin Republic.

1.3.1 Benin: an overview

Named Dahomey until 1975, Benin is a country of 114,763 km² located in West Africa. Benin is divided into 12 provinces with Porto Novo as political capital and Cotonou the main city and economic capital. The population was 6,300,000 habitants in 2002 (more than 8,700,000 currently) corresponding to a mean density of 59 habitants/km² (INSAE/MPPD, 2002). The population is irregularly distributed; the density can reach 500 habitants/km² in some areas in the south while in some

regions of Atacora province in the north, the density is approximately 6 habitants/km^2. The annual population growth rate is 3.25% (INSAE/MPPD, 2002).

The official language is French, however there are about 50 ethnic groups throughout the country which have their own dialects. About a third of the human population follows traditional religious beliefs. Approximately 42.8% of the population is Christian and 24.4% Muslim.

The mixed and underdeveloped economy is largely based on subsistence agriculture, cotton production and regional trade. Several crops are planted from the south to the north, in accordance with the variability of the climate. Major crops are cotton, corn, cassava, yams, etc. The main crops exported are cotton, cashews and pineapple. Small and large livestock are raised across the country with the north being the main area of cattle husbandry.

The tropical climate is hot and humid in the south and semi-arid in the north. Mean rainfall ranges from 1200 mm in the south with two rainy seasons to 800 mm in the north with one rainy season. The topography is mainly flat to undulating plains with a few hills and low mountains.

The vegetation is diverse with 10 phytodistricts (floristic homogenous regions) in Benin (Adomou *et al*., 2006). Benin is located in what is called the "Dahomey-Gap", which explains the absence of the equatorial dense forest as compared to the south of neighboring coastal countries such as Nigeria and Ivory Coast. However there is an important biodiversity with about 2807 plant species (Akoegninou *et al*., 2009) and 4378 animal species (MEPN, 2009) counted in the country. Among these, a few endemic species are found, such as the plant species *Thunbergia atacoriensis* in the north-western region and the red-bellied monkey *Cercopithecus erythrogaster erythrogaster* in the south. The country is a refuge for several threatened species. The main threats to biodiversity conservation are natural forests degradation for farming, grazing and uncontrolled logging, poaching, uncontrolled bushfires, desertification in the north, and lands scarcity (MEPN, 2009). Fortunately, Benin has signed several International Treaties, Agreements and Conventions related to Biodiversity conservation. For example, Benin is party to the three UN Conventions on Biodiversity, Climate Change and Desertification. There are increasing efforts from the Government, the Private Sector and NGOs to conserve and sustainably manage the biodiversity. Until recently, the real status of most components of biodiversity was poorly known. There are an increasing number of studies to evaluate and monitor natural resources. This contributes to improvement of the quality of interventions of biodiversity projects. Conservation in Benin is supported by several international donors.

Benin has two National Parks in the north which are also classified as Biosphere Reserves by UNESCO (Fig. 1). Aside from those National Parks, there are about 30 gazetted forests throughout the country (Fig. 1). However, due to the lack of funds, many of these forests only exist in name and have been completely degraded by local populations.

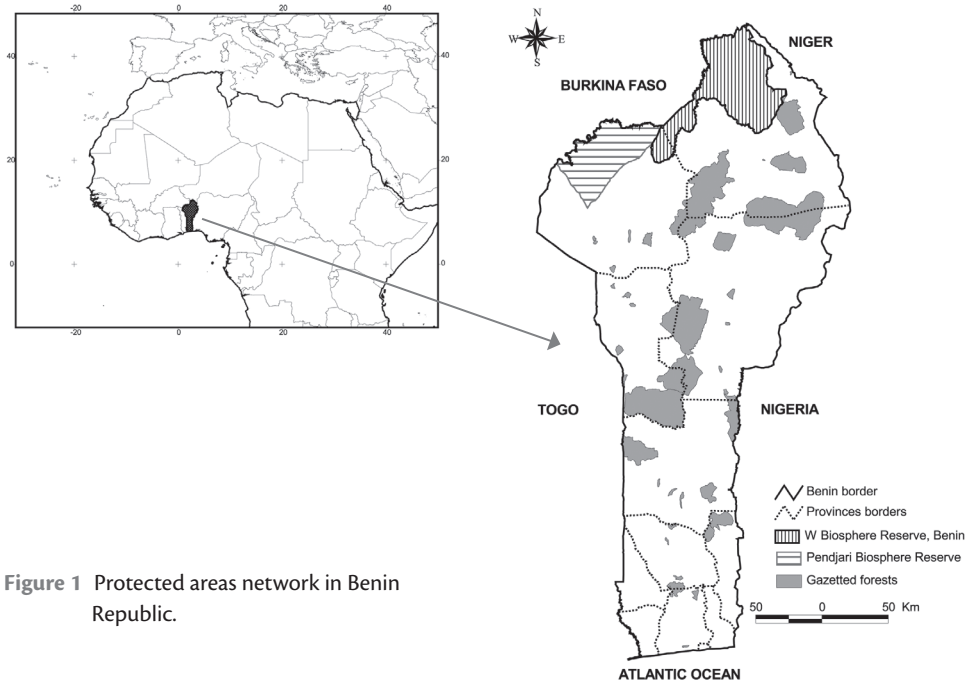


Figure 1 Protected areas network in Benin Republic.

1.3.2 The Pendjari Biosphere Reserve

First established in September 1954 as a Wildlife Reserve, Pendjari has been upgraded to a National Park in May 1961. The hunting zones were created in 1959. With these zones, the Pendjari National Park was promoted to MAB UNESCO Biosphere Reserve in June 1986. In 2007, the National Park was recognized as being of International Importance as a RAMSAR site because of its wetlands. Currently, the Pendjari Biosphere Reserve is composed of the Pendjari National Park (2,750 km²), the Pendjari (1,600 km²) and the Konkombri (251 km²) hunting zones as well as a Buffer Zone (about 300 km²). The National Park is strictly protected and only activities of tourism, research and management are allowed within its boundaries. In the two hunting zones, as their denomination indicates, sport hunting of wildlife based on a quota fixed by the Benin Wildlife Office is one of the main activities. The first years, the hunting quotas were based on the number of hunters willing to come. From 1977 to 1991, sport hunting was suspended due to the decrease noticed in wildlife abundance. Most of safari hunters come from outside Benin.

Sport hunting is managed by professional hunting guides and is controlled by the Park staff.

Like other protected areas, the management of the Pendjari Biosphere Reserve is effective only when it is supported by a project or a program with external funding. Since its creation, this reserve has been financed discontinuously by several projects. Between these projects (1982-1985; 1991-1993 and 1998 to 2000) the reserve is usually almost abandoned to poachers and populations. Since 2000, the Pendjari Project has been managing the reserve more intensively and illegal practices have been considerably reduced.

Pendjari Biosphere Reserve is part of the larger protected-areas complex in West and Central Africa (Fig. 2). This complex comprises about 36,000 km² and is composed of W Transboundary Biosphere Reserve and its annex zones (Benin, Burkina Faso and Niger), Pendjari Reserve, Arly (Burkina Faso) and Oti-Mandouri and Keran (Togo).

Before the Environmental Summit in Rio de Janeiro, the main activities of the Pendjari National Park staff were anti-poaching and anti-grazing patrols, tourism and the organization of sport hunting. In 1993, after the Rio Summit, a new project on Natural Resources Management, PGRN (*Projet de Gestion des Ressources Naturelles*) started with the goal of bringing together local populations and the park staff. One of the achievements of this project was the creation of Villagers Hunting Association (AVC: *Associations villageoises de Chasse* in French). In 1996, to reinforce the achievements of this project, the National Center for the Management of wildlife Reserves, designated by CENAGREF, has been created with the support of the German cooperation (GTZ, KFW and DED). The main aims were a modern and participatory management of protected areas in Benin. That same year, the AVCs were changed into Village Associations for the Management of Wildlife Reserves known as AVIGREF (*Associations Villageoises de Gestion des Réserves de Faune)*, having increased participation of local populations.

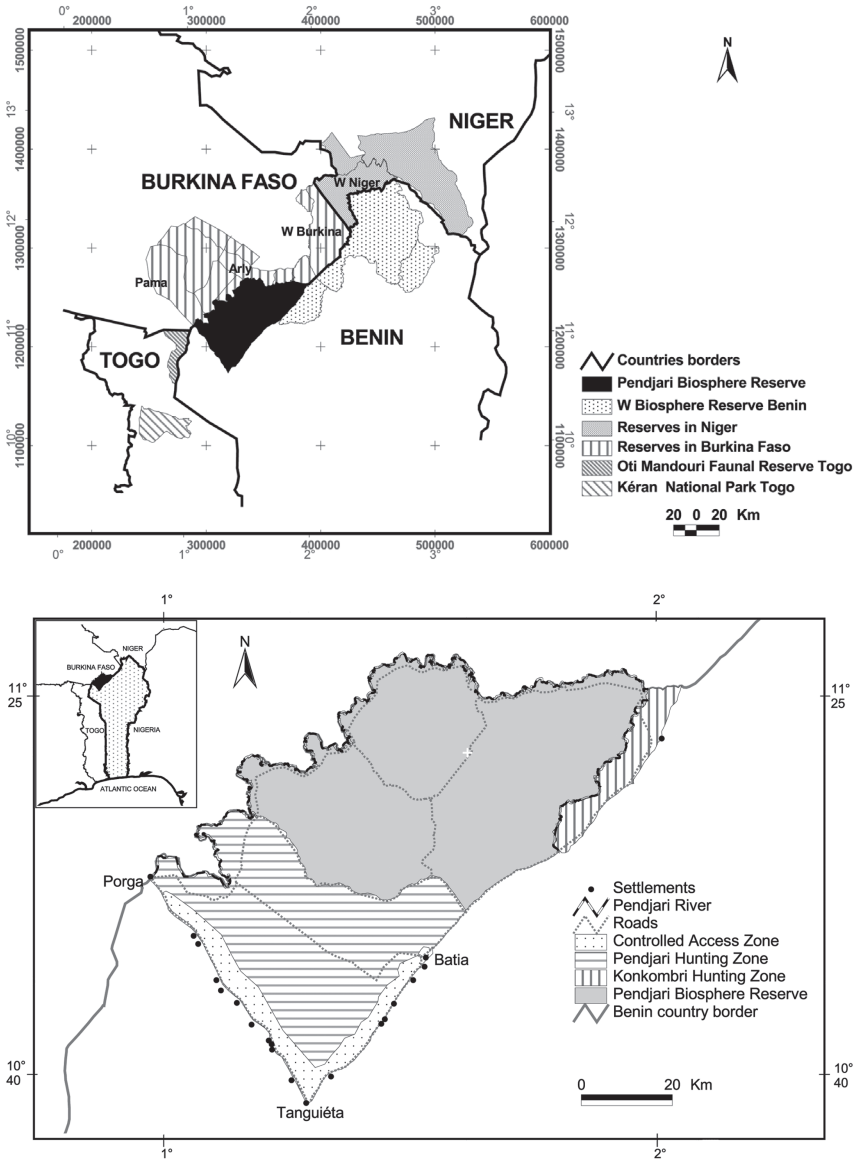


Figure 2 W – Arly – Pendjari – Oti Mandouri – Kéran complex of protected areas in Benin, Burkina Faso, Niger and Togo and Pendjari Biosphere Reserve.

1.3.3 Geomorphology & Climate of the study area

The climate in Pendjari Biosphere Reserve is a tropical one in the Sudanian savannah zone with a unimodal rainfall pattern (Fig. 3). The rainy season occurs from May to October. It is followed by a dry season with a cold period in December-January (with average monthly temperature of 19 °C) and a hot period from March to May with maximum daily temperature reaching 43 °C. The relative humidity varies from 17 to 99%. The annual rainfall varies from 800 to 1100 mm. During the cold dry period, there is the "*Harmattan*", a dry wind from the north-east that causes the vegetation and most waterpoints to dry up.

The Pendjari river has its source in the Atacora mountain, then passes over the border of the Pendjari Biosphere Reserve and continues to Togo and Ghana. This river runs through the park for 200 km of its total length of 300 km. During the rainy season, the Pendjari river overflows and floods most parts of the reserve. After the rains stop, streams dry up and only a few parts remain humid, leading to the concentration of wildlife species around river banks. Except for the river, there are few remaining water points for wildlife species from February to May.

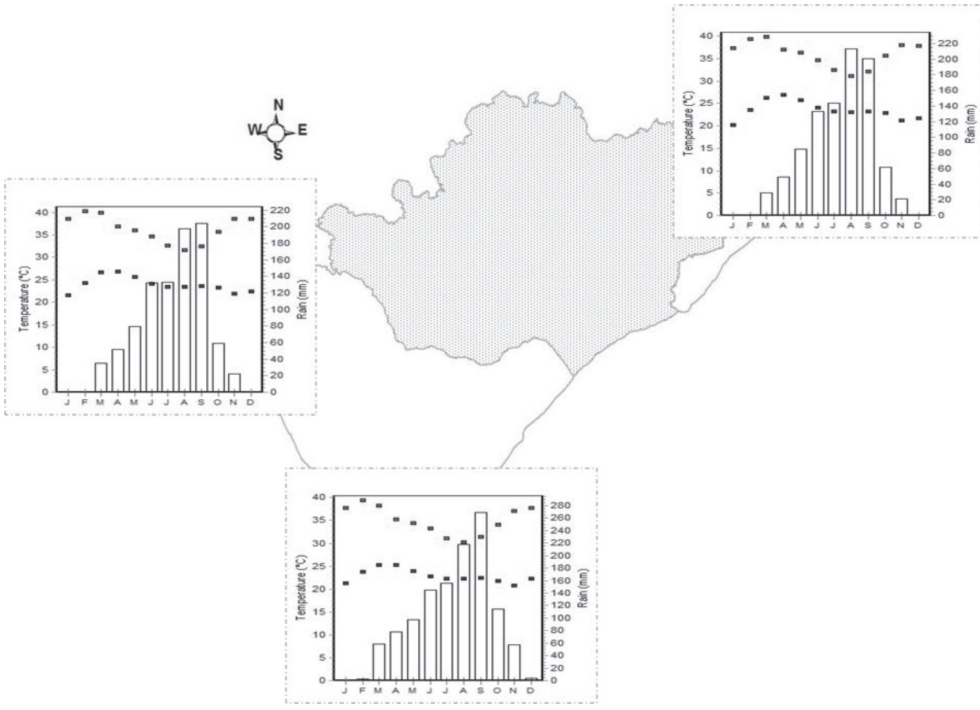


Figure 3 Climate in Pendjari Biosphere Reserve based on temperature and rainfall during 50 years (Source: Diva GIS©).

1.3.4 Wildlife and its habitat

The vegetation in the Pendjari Biosphere Reserve is a mixture of savannahs with some patches of dry forests characteristic of Sudanian area. The main vegetation types found (Sokpon *et al*., 2001) are:

- Swamp savannahs dominated by *Terminalia macroptera* in flooded plains or dominated by *Mitragyna inermis* and *Acacia sieberiana*,
- Tree savannahs with *Combretum spp*.,
- Shrub savannahs with *Acacia gourmaensis* and *Crossopteryx febrifuga*,
- Woodland savannahs dominated by *Daniellia oliveri* and *Pterocarpus erinaceus*,
- Inselbergs dominated by *Detarium microcarpum* and *Burkea africana*,
- Gallery or riparian forests with *Khaya senegalensis*, *Cola laurifolia*, *Parinari congensis* and *Pterocarpus santalinoides* along semi-permanent waterponds, and Pendjari river,
- Woodlands with *Anogeissus leiocarpa* or *Daniellia oliveri*

Furthermore there are some areas dominated by vegetation of *Borassus aethiopicum*.

Like any savannah ecosystem, the vegetation in Pendjari is burned every year. Early fires in December-January are encouraged to avoid the major damages caused by late fires which are difficult to control. These fires favor the regeneration of several species such as *Combretum*.

A variety of wildlife species inhabit Pendjari savannahs (Delvingt *et al*., 1989; Sinsin *et al*., 2002). Almost all wildlife species specific to Sudanian savannahs are found, some of them being rare and declining such as topi *Damaliscus korrigum* (Sayer, 1982) and waterbuck *Kobus ellipsiprymnus defassa* (Kassa, 2009). Three of the "big five" are commonly encountered: lion *Panthera leo leo*, buffalo *Syncerus caffer brachyceros* and elephant *Loxodonta africana*. All large carnivores are present. Lion and spotted hyena *Crocuta crocuta* are the most common, with an abundance of about 100 adult and subadult individual each (Sogbohossou & Tehou, 2007; Sogbohossou, 2009). Most small to large mammals are listed on the sport hunting quota, but among the carnivores, only lion is hunted.

A total of 28 species of bats (Djossa, 2007) and 104 species of fishes (Ahouansou Montcho, 2009) were identified in Pendjari Reserve. About 460 bird species (Grell *et al*., 2002 in DPNP/CENAGREF, 2010) with at least 37 raptors species (Bousquet, 1992) were also reported.

1.3.5 Human environment

The Pendjari Biosphere Reserve is bordered by two roads along its southern edge: Tanguiéta-Porga and Tanguiéta-Batia (Fig. 2). Most villages are established along these roads. Three main ethnic groups live in the area: the Byalbes (commonly called Berbas, 65%) living along Tanguiéta-Porga, the Gourmantchebas or Gourmantché (23%) and the Waaba or Waama (7%) living along Tanguiéta-Batia (Tiomoko, 2007). There is a fourth ethnic group, the Fulani who are not native to the area, and a fifth, the Bourba who live along Tanguiéta-Porga.

Berba and Gourmantché people used to live within the borders of the reserve and the last populations were expelled from the park in the 1980s. About 30,000 people, corresponding to 5,000 families live in the area (PNUD in Tiomoko, 2007). The density of 14 habitants/km² is quite low compared to other places in Benin. The reserve is located in one of the poorest parts of the country. Except for the Fulani, the main activity is subsistence agriculture, with cotton being the main cash crop. Husbandry is a second main activity of the local populations, with livestock representing family savings; people only sell their livestock when they need money. Fulani are primarily pastoralists and are specialized in cattle husbandry. Local people are accustomed to giving them their cattle to tend, while they raise small livestock themselves. Berba and Gourmantche were renowned hunters.

Because agriculture is extensive, there is a scarcity of agricultural land (Tiomoko, 2007), a problem exacerbated by the relative poverty of the soil. The massive use of pesticides and fertilizers presents a problem for wildlife, as river water is polluted (Soclo & Djibril, 2003).

Fishing is a common activity and local people are allowed to fish in the buffer zone. Only professional fishermen, mainly from Burkina Faso, are allowed to fish in the Pendjari river inside the park with special permits. Until recently, fishing in the park was not allowed. But as fishermen used to practice their activity on the Burkina Faso side of the river all year long, the park staff finally decided to allow this activity and to regulate it. Exceptionally, during a certain period of the year, local people are allowed to harvest oysters in the Pendjari River on the Porga side. They are also allowed to fish and to pay a tribute to their gods at the Bori waterpoint in the middle of the hunting zone. The buffer zone is an area where local people have controlled access. Farming and grazing are allowed with certain restrictions. Organic farming is encouraged. Local people may also harvest some natural resources such as hay, fruits and wood.

Tourism has created jobs around the area, for example tourist drivers or guides and rangers. The park rangers have been recruited from within the local popu-

lations. The local guides who assist rangers are former poachers, who been reformed.

Local populations, through their Association AVIGREF, receive 30% of hunting revenues every year. These revenues are used for activities such as improvement of hospital or schools, digging of wells, etc. The populations also receive most of the meat from animals killed by sport hunters.

1.4 Structure of the thesis

The first part of this thesis is a general introduction and review, stressing the importance of the study. After this review, the research questions to be addressed and the objectives of the study are presented. Then the country and the area where the study took place are described.

The second part describes conflicts between human and predators, among which the lion. In chapter 2, the characteristics and determinants of livestock-carnivore conflicts around Pendjari Biosphere Reserve are described. Chapter 3 reports local peoples' knowledge and perceptions towards carnivores and conflicts, and examines the social factors that affect the intensity of human-carnivores conflicts.

The third part focuses on lion population ecology. In chapter 4 we investigated the diet of lions in the Pendjari Biosphere Reserve based on direct observations of lion kills and scat analysis. The contribution of different prey body mass was assessed and the diet analyzed compared to lion diet in other regions. In chapter 5, the characteristics of the social structure of lion populations was explored and some 'strongholds' of the threatened lion population in Pendjari were identified. Chapter 6 presented the home range and the habitat use of lions in the Pendjari Reserve, based on telemetry.

The fourth part of this thesis (chapter 7) discusses the implications of the study, evaluates which strategies could be effective to help mitigate human-carnivores conflicts in the region and mentions some aspects that remain to be better studied in the region of West and Central Africa.

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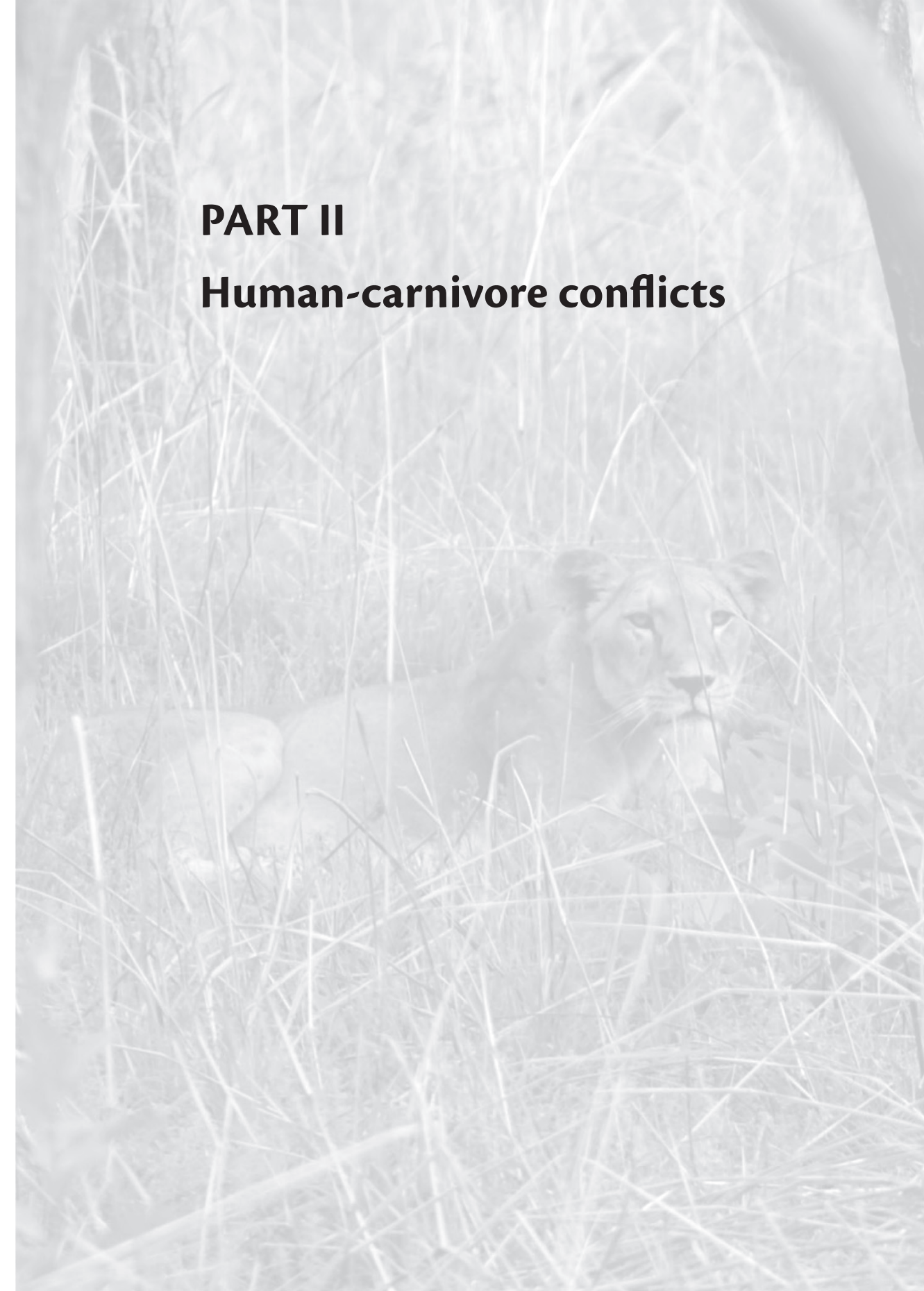

PART II
Human-carnivore conflicts

2 Human-predator conflicts around Pendjari Biosphere Reserve, Northern Benin

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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 Iongh, 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 km^2), Pendjari and Konkombri Hunting Zones (c. 1,600 and 251 km^2, respectively) and a buffer zone with controlled land-use access for local people (c. 340 km^2).

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 km^2 (Sogbohossou, 2009) and the spotted hyaena occurs at a minimum density of 1.5 per 100 km^2 (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–Batia, 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

herdsmen 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.

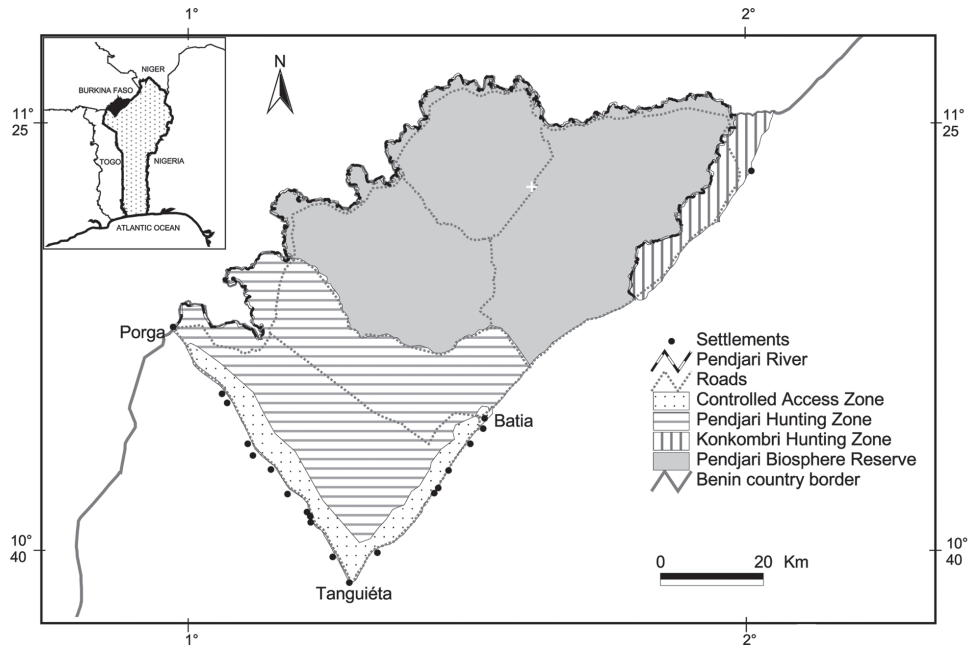

Figure 1 Location of Pendjari Biosphere Reserve in Benin Republic.

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 duringthe 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 (χ^2 = 66.28; P < 0.0001) and between livestock species (χ^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.

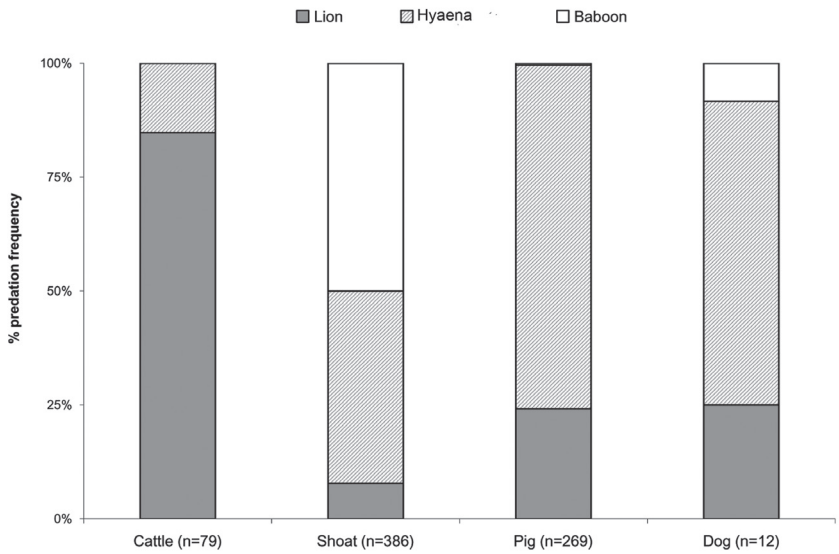

Figure 2 Percentage frequencies of attacks of baboons, hyaenas and lions on cattle, shoats, pigs and dogs from 2000 to 2007 around Pendjari Biosphere Reserve, based on our questionnaire survey.

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.

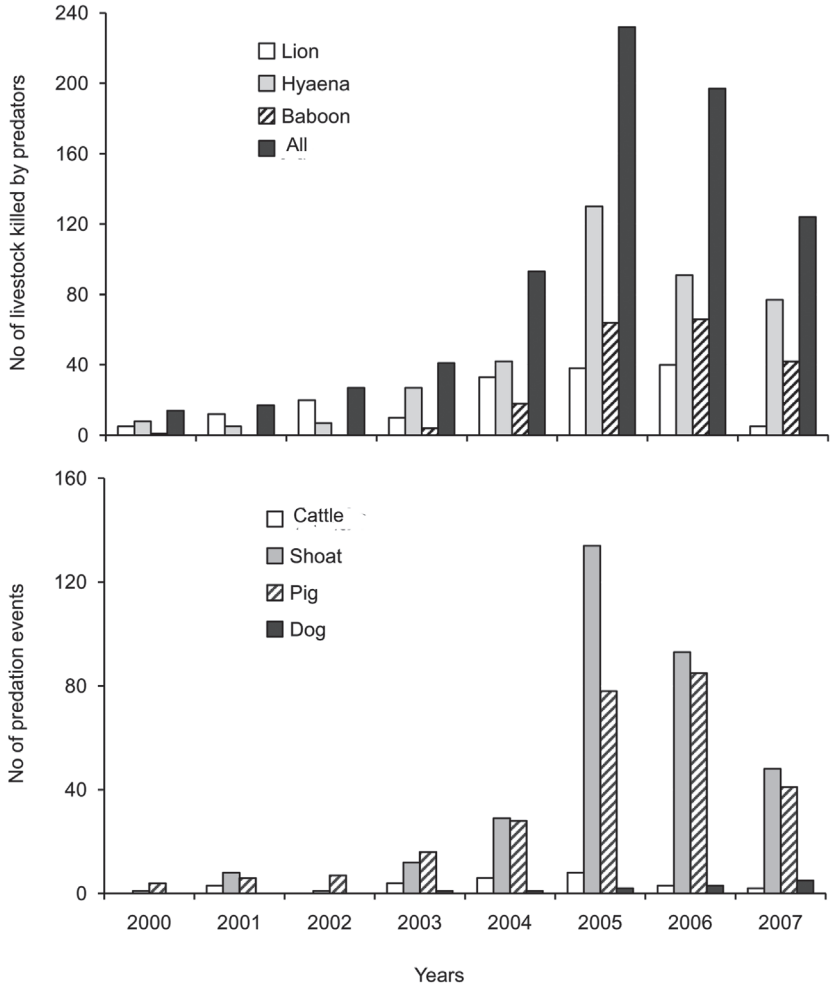

Figure 3 Number of livestock attacks predation frequencies around the Pendjari Biosphere Reserve according to livestock and predator species from 2000 to 2007 based on our questionnaire survey. Shoat represents sheep and goat.

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).

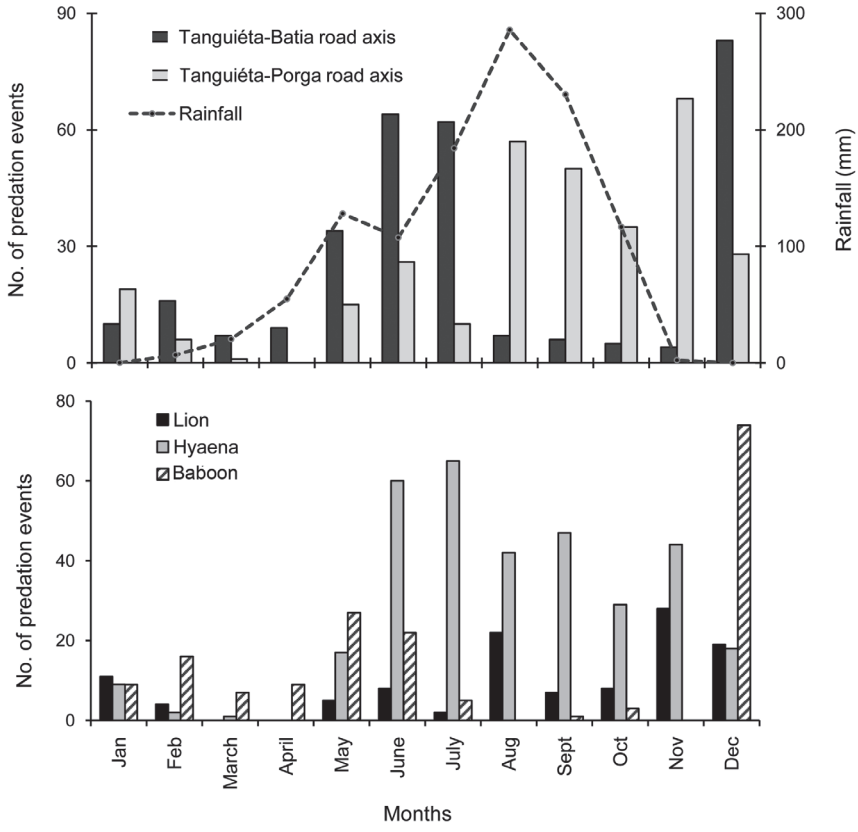

Figure 4 Monthly distribution of depredation events in relation to rainfall based on our questionnaire survey. The data used are from 2000 to 2007.

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 Tanguieta–Porga road axis and 14.2% of interviewees along the Tanguieta–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).

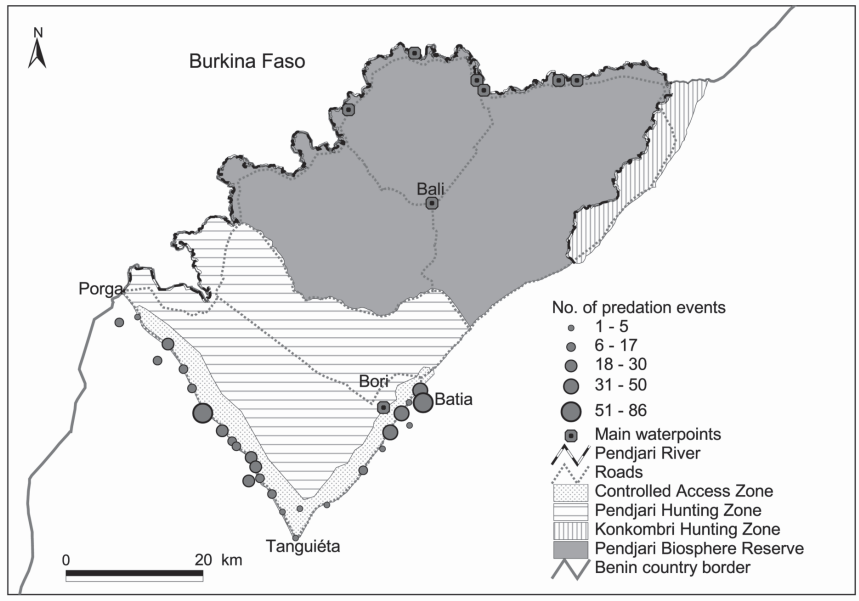

Figure 5 Predation rate in the different localities around the Pendjari Biosphere Reserve (data from 2000 to 2007).

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 predating 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 & Shivik, 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 Iongh, 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.

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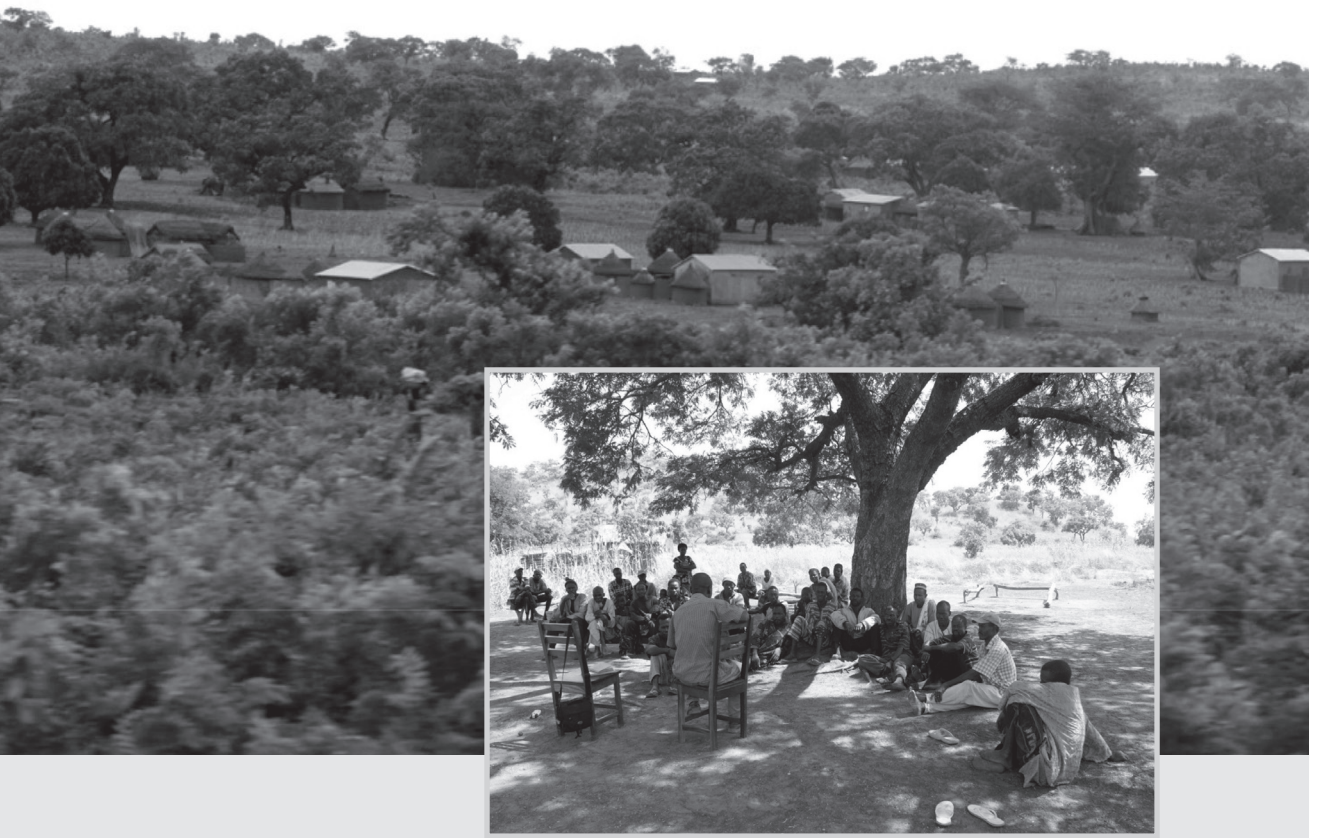

3 Conservation of carnivore species in West Africa:

Knowledge and Perceptions of local people towards human-carnivore conflicts in Pendjari Biosphere Reserve, Benin

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Submitted

Abstract

Human-carnivore conflicts are common around fragmented reserves of West Africa. A better understanding of the perceptions of local populations towards carnivores is necessary for an improved management of populations of threatened carnivore species in the region. In this paper we used door-to-door interview surveys to investigate local peoples' knowledge and perceptions of carnivore conservation and conflicts and their predicting factors in the vicinity of Pendjari Biosphere Reserve, Benin. We found that people had a moderate knowledge of carnivores. Despite the fact that general peoples'perceptions of carnivores were negative, people had a generally positive view of conservation and tolerated livestock depredation. Fortunately, few supported retaliatory killing of carnivores and many were willing to see carnivores increasing in numbers despite perceived risks. We found some differences in the perceptions of the various ethnic groups. Berba appeared to be the most negative group while Waama were likely to be more tolerant. Knowledge and perceptions were mainly predicted by the culture and ethnic group of the respondents, their previous experience with carnivores, the nature of their activity, and their age. An approach integrating education, awareness and development of economic incentives is necessary to improve conservation prospects of large carnivores in Benin and West Africa. All actions should be adapted to the different ethnic groups' needs.

Key words

communities, culture, ethnic groups, human-carnivores conflicts, management, perceptions, West Africa

3.1 Introduction

Human-wildlife conflicts are one of the most important threats to carnivore conservation worldwide (Nowell & Jackson, 1996; Woodroffe & Ginsberg, 1998). These conflicts have increased in recent decades due to human population growth and resulting habitat loss and fragmentation. They have been identified as one of the major causes of the decline of several carnivore populations in Africa (Woodroffe, 2001; Ogada *et al*., 2003; Patterson *et al*., 2004; Packer *et al*., 2005). Livestock predation and attacks on humans occurred at different intensities in Africa and involved species such as lions (Ogada *et al*., 2003; Packer *et al*., 2005; Kolowski & Holekamp, 2006; Van Bommel *et al*., 2007). Conflict-related mortality of carnivores along the border of protected areas could be very important (Woodroffe, 2001; Polisar *et al*., 2003; Kolowski & Holekamp, 2006; Kissui, 2008). High numbers of carnivores, mainly lions, are reported killed by herders in Kenya (Patterson *et al*., 2004; Kolowski & Holekamp, 2006; Hazzah *et al*., 2009), Tanzania (Kissui, 2008) and Cameroon (De Iongh *et al*., 2009; Tumenta *et al*., 2010).

Attacks and perceived dangers from carnivores generate negative perceptions and attitudes towards carnivores (Mishra, 1997; Marker *et al*., 2003; Holmern *et al*., 2007; Hazzah *et al*., 2009). A number of studies investigated the characteristics and determinants of human-carnivore conflict in Africa (Ogada *et al*., 2003; Patterson *et al*., 2004; Van Bommel *et al*., 2007; Kissui, 2008) but fewer focused on the social dimensions of this problem (Hazzah *et al*., 2009; Inskip & Zimmermann, 2009; Dickman, 2010). It is generally acknowledged that protected areas and endangered species conservation cannot be successful if local communities are not actively involved and local perceptions, behaviour and needs considered (Fiallo & Jacobson, 1995; Ite, 1996; Mehta & Kellert, 1998; Weladji *et al*., 2003).

Perceptions and attitudes about carnivores vary greatly according to several factors. Understanding and knowledge of individual species have been found to affect perceptions and attitudes towards carnivores and conflicts (Conforti & de Azevedo, 2003; Shivik *et al*., 2003; Lindsey *et al*., 2005). Taboos have existed for millennia (Gadgil *et al*., 1993) and may have an effect on the relationship between societies and their environment (Colding & Folke, 1997; Berg, 2001). The socio-economic situation of respondents also influences perception and attitudes (Oli *et al*., 1994; de Boer & Baquete, 1998; Ericsson & Heberlein, 2003; Lindsey *et al*., 2005; Morzillo *et al*., 2007). Other factors such as distance from protected areas, experience with carnivores, and benefits from conservation can affect how locals perceive carnivores (Zimmermann *et al*., 2001; Williams *et al*., 2002; Ericsson & Heberlein, 2003; Karlsson & Sjöström, 2007; Lindsey *et al*., 2005; Schumann *et al*., 2008) or not (Casey *et al*., 2005). It is difficult to predict perceptions and attitudes based on these factors (Zimmermann *et al*., 2005).

In West Africa, human-carnivore conflicts have been identified as one of the major causes of the drastic decline in populations of carnivores including the lion, which is considered as Regionally Endangered (Bauer *et al*., 2003; Nowell & Bauer, 2004). Few studies have attempted to identify the characteristics and determinants of these conflicts (Garba & di Silvestre, 2008; Sogbohossou *et al*., in press). Little research has investigated the attitudes of local people about biodiversity and conservation (Vodouhê *et al*., 2010) and to date none has tackled the human dimensions of conflicts. This knowledge is necessary in order to organize appropriate actions for conflict mitigation and carnivore conservation in this region.

The purpose of this study was to determine local people in the vicinity of the Pendjari Biosphere Reserve, Benin, perceive carnivores in order to make suggestions for mitigation of impacts and carnivore conservation in West Africa. This includes: (1) the assessment of the knowledge and perceptions of local people towards carnivores and livestock depredation, and (2) the investigation of factors that determine their various perceptions.

3.2 Methodology

3.2.1 Study area

This study was conducted in the Pendjari Biosphere Reserve (10°30' to 11°30 North; 0°50' to 2°00' East) in north-western Benin (Fig. 1). The reserve is composed of Pendjari National Park (2,660 km^2), Pendjari and Konkombri Hunting Zones (respectively 1,600 km^2 and 251 km^2), and a buffer zone with controlled land-use access for local populations. The climate, typical of the Sudanian area, is characterized by one dry season and one rainy season. Annual rainfall varies from 800 to 1,000 mm. The vegetation is a mixture of dry and gallery forests and savannahs, which are burned every year by the park staff. A variety of wildlife species characteristic of Sudanian savannahs inhabit the reserve including lion, spotted hyaena *Crocuta crocuta*, cheetah *Acinonyx jubatus*, leopard *Panthera pardus* and wild dog *Lycaon pictus* (Delvingt *et al*., 1989).

Pendjari Biosphere Reserve is bordered by two main roads (Tanguieta-Porga and Tanguieta-Batia) along which about 24 villages were established and one main city, Tanguieta. Four main ethnic groups live in the area: Berba and Bourba along Tanguieta-Porga and Waama and Gourmantché along Tanguieta-Batia road axis. There is a fifth group which did not originate in the area: the Fulani or Fufulde. Local people are mostly farmers and secondarily practise livestock husbandry. The Fulani are specialized in cattle husbandry. Mainly nomadic and transhumant in the past, Fulani are nowadays settled in villages and some continue with transhumance during the rainy or the dry season.

The park was first created in 1954, upgraded to a national park in 1961 and to a biosphere reserve with its annexes in 1986. Populations, namely of Berba and Gourmantché, used to live inside the area and the last populations were expelled from the park in the 1980s (DPNP, 2010). Until about two decades ago, local populations were excluded from the park and its management. Currently they are organized in a Local Association for the Management of Wildlife Reserves (AVIGREF in French) which is a partner of the Wildlife Office. About 30% of benefits from sport hunting are paid to this Association every year and are primarily used to build and repair infrastructure in the villages. In return, populations participate in anti-poaching patrols with the park rangers and are associated with several management activities. Populations also receive other benefits from the park through some activities and projects that have been realized in the area because of the presence of the park. On the other hand, however, the proximity of the reserve leads to conflicts with wildlife and to the insufficiency of lands for farming and grazing. Two types of conflicts were observed: crop raiding by elephants and other herbivores and livestock depredation. Some cultures such as yam were no longer planted in some regions due to heavy losses caused by elephants on these crops.

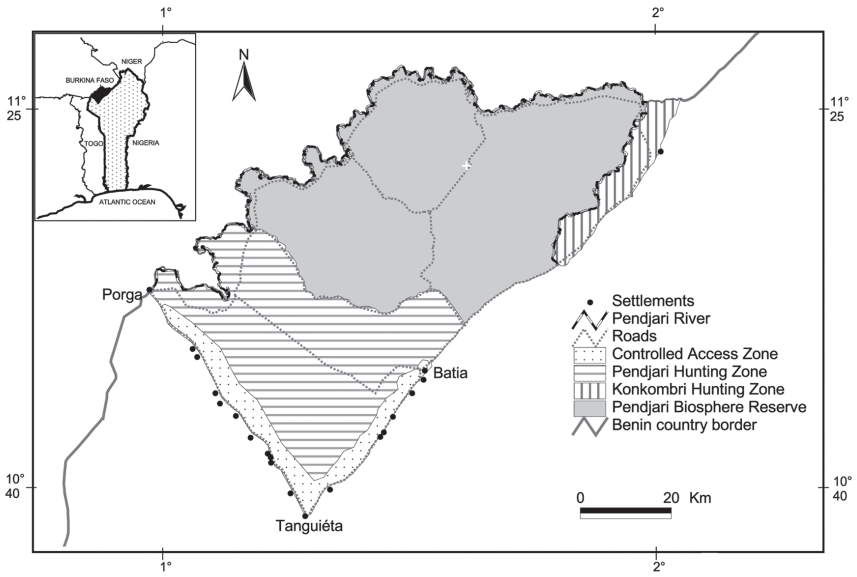

Figure 1 Map of Pendjari Biosphere Reserve in Benin

3.2.2 Interviews survey

In order to evaluate the knowledge and perceptions of local people around Pendjari Biosphere Reserve, we organized a questionnaire survey. Because distance from the reserve and social structure of the villages could have an impact on perceptions, we selected 10 villages around the reserve, based on their geographical

position and the dominant social groups within them. Each village had 80 to 100 households according to the last population census and we randomly chose 30 households per village. Fulani camps were not considered in this survey. We questioned the head of the family (usually a man) in each household. In the rare cases that he was absent, we interviewed his wife or elder son. Interviews were based on a semi-structured questionnaire divided into four sections: (1) socio-demographic characteristics; (2) knowledge of carnivores; (3) livestock husbandry; and (4) perceptions of conflicts and conservation. Data collection took place between October 2007 and October 2008. We focused our study on the six largest species of carnivores existing in the area: lion, leopard, cheetah, spotted hyaena, wild dog and jackal *Canis mesomelas*. A total of 322 respondents participated in the survey. Incomplete surveys were removed, leaving ultimately 293 in the study.

3.2.3 Variables

According to the Theory of Reasoned Action by Ajzen & Fishbein (1980), a person's behaviour is determined by his/her behavioural intentions which are a function of his/her attitude towards the behaviour and subjective norms. Attitudes are in turn determined by beliefs and reflect personal experiences and perceptions (Ajzen & Fishbein, 1980; Ajzen, 1991; Infield & Namara, 2001). Here we focused on perceptions and knowledge in order to understand the potential actions of local people living around Pendjari Biosphere Reserve. Understanding these actions can contribute to improved decision-making for mitigation of conflicts. We considered perceptions to be the opinions held by respondents based on Lucherini & Merino (2008). We distinguished perceptions related to carnivore species, to conservation in general and to depredation. As culture plays an important role in West Africa, we considered the role of totems attributed to carnivores and social knowledge related to carnivores. For the purpose of our study, a totem is a species affected by species-specific taboos as defined by Colding & Folke (2001). Knowledge here mainly refers to the recognition of species and socio-cultural knowledge. The dependent variables knowledge and perceptions were considered to be the sum of certain factors presented in Table 1. Independent variables (Table 2) were selected based on the analysis of diverse studies and the conditions in the study area. They related to socio-economic and demographic characteristics of the respondents.

Table 1 Independent variables used as descriptors for stepwise regressions

Variable	Variable description	Value
Distance	Mean distance from the village to the park	Continuous values
Age	Age of the respondent	Continuous values
Sex	Sex of the respondent	Score (1 , 2)
Ethnic group	Ethnic group to which the respondent belongs	Score (1, 2, 3, 4)
Main activity	Main activity of the respondent (agriculture, other)	Score (1, 2)
Activity related to park	Relatedness of main or secondary activity to conservation	Score (1, 2)
Household size	Number of members in the household	Continuous values
Husbandry	Livestock husbandry or not	Score (1, 2)
Total Livestock	Number of livestock owned (poultry, sheep, goat, pig, dog, donkey, cattle)	Continuous values
Total Cattle	Number of cattle owned	Continuous values
Cotton production	Cotton production or not	Score (1, 2)
Harvest months	Number of months harvest is consumed	Continuous values
Totem	Association of a carnivore as totem	Score (1, 2)
Socio-cultural knowledge	Knowledge on the uses of animal parts	Score (0, 1)
Depredation	Has the interviewee ever had livestock attacked by carnivores	Score (1, 2)
Crop raiding	Has the interviewee ever experienced farm damage by wildlife	Score (1, 2)
Human attack	Has the interviewee ever heard of carnivore attacks on humans or not	Score (1, 2)
Trend	Trend of livestock depredation (increase, decrease, stable)	Score (1, 2, 3)

3.2.4 Data analyses

Analyses were conducted with SAS® 9.1. software (SAS Institute). Descriptive Statistics were used to estimate frequencies and means of categorical and continuous variables. Percentages for each response were calculated based only on those respondents who answered the respective question. Values are expressed as means with standard deviations (SD). To assess the perceived threat to people and their livestock, we asked participants to give a score from 1 to 3 of the three most dangerous carnivores among the six carnivore species studied. For each species, the sum of scores gives the total score for the species.

Table 2 Dependent variables used for analysis

Dependent variable	Sub-variables used	Values	Total value
Knowledge	Number of carnivore species seen at least once	0 to 6	0 (none) to 15 (higher value)
	Number of carnivore species recognized from pictures	0 to 6	
	Number of carnivores that live in the region among the six	0 to 6	
	Lion spoor recognition	0 or 1	
	Hyaena spoor recognition	0 or 1	
Perception of depredation	If it possible to avoid depredation or not	0, 1, 2	0 (positive) to 6 (negative)
	If compensation is a possible solution to livestock depredation	0, 1, 2	
	Relative importance of livestock depredation and crop raiding	0, 1, 2	
Perception of carnivore	Advantages of the presence of carnivores		0 (positive) – 1 (negative)
Perception of conservation	To whom do the parks belong (people, government, other)	1, 2, 3	5 (positive) to 12 (negative)
	Is the park useful?	0,1	
	Does the interviewee think the park is useful for individuals	1, 2	
	Does the interviewee think the park is useful to communities	1, 2	
	Opinion about the wildlife office (CENAGREF)	1, 2	
	Opinion about the local organization (AVIGREF)	1, 2	
Methods used	Methods used to avoid livestock depredation	0 (none) to 2 (max)	
Will	Would the respondent like carnivore populations to increase	0 (yes) to 2 (no)	
Lethal control	Respondents think a solution to depredation is to kill carnivore or not	0 (no) to 2 (yes)	

With each dependent variable and all independent variables, we ran a descending stepwise regression with Akaike Information Criterion (AIC). The goal was to find the independent variable or the combination of independent variables which better predict the knowledge and perceptions of local people. For the selected predictors, the software yielded chi-square statistics. The model fits statistics and the summary of the stepwise selection are presented as given by the software. We used chi-square to test the relationship between the different dependent variables, sub-variables and the variable Ethnic group as the different ethnic groups could not be rank ordered. Relationships were considered to be significant at $p<0.05$. The sign * indicates that the correlation is significant at the 0.05 level while ** indicates the significance at the 0.01 level and *** at the 0.001 level.

3.3 Results

3.3.1 Respondents profile

In accordance with their importance in the area, Berba comprised 52.2% of the respondents while Bourba, Waama and Gourmantché represented 7.1, 28 and 12.7% of respondents, respectively. The respondents lived in villages along Tanguieta-Porga road axis (50.3%), along Tanguieta-Batia road (40.7%) and between these axes (9%). The average distance from the park to villages was 29.6 ± 9.1 km.

Women represented only 6.2% of the respondents, as few women are heads of households. The average age of respondents was 42.7 ± 15.6 years. The mean size of a household in addition to the head was 9.4 ± 4.6 individuals.

Some 98.1% of respondents had farming as their primary activity while 93.8% of local people practiced animal husbandry as a secondary activity. The mean number of livestock owned, all species added together, was 41 ± 42 animals per household. The mean size of the cattle herd per household was 1.7 ± 5.9 cattle. Only 3.8% of respondents had activities related to the park, such as tourists' drivers and guides. Cotton, the main cash crop in the area, was produced by 40.7% of the respondents.

When people harvest their crops, the yield is not usually enough to sustain the whole family until the next harvest. Only 2.8% of respondents harvested enough food crops to sustain their family until the next harvest. The mean period in which the harvest is consumed was 6.8 ± 0.8 months. After this period, people had to rely on selling their livestock to buy food.

Local people had a long tradition of interacting with wildlife, which is an integral part of their culture and traditions. Most of the respondents (68.6 %) had at least one carnivore species as totem. This means that they were not allowed to kill and/or to eat this species. Many (40.8%) were aware of some uses of carnivore products for medicinal and magical purposes.

Regarding conflicts with wildlife, 77.2% of local people had experienced livestock depredation at least once, and 91.2% had their crops destroyed by wildlife at least once. Only 3.1% had ever heard about attacks on humans by a carnivore. In general, 85.5% of respondents felt livestock attacks by carnivores are decreasing while 3.8% thought they are stable.

3.3.2 Knowledge about carnivores

The mean number of carnivores that have been seen at least once by a person around Pendjari Biosphere Reserve is 2.7 ± 1.6 species of the six species considered. On average, people recognized 2.6 ± 1.6 carnivore species from a picture (Fig. 2). In case of livestock depredation, when the attacking animal was not seen or heard, people used spoors to identify the carnivore responsible. Lion and spotted hyaena spoors were successfully identified by 40.3 and 36.9% of the respondents, respectively, from the six different spoors of carnivores presented to them.

The mean knowledge score was 7.1 ± 3.8 on a scale of 0 – 15, indicating that the general knowledge about carnivores in the region is moderate. There is no significant difference in knowldegd between ethnic groups. Berba and Gourmantche had a higher knowledge however there is no significant difference between ethnic groups. Among all variables tested to explain the knowledge of carnivores, only the association to a totem has been found to be a significant predictor of respondents' knowledge (Table 3).

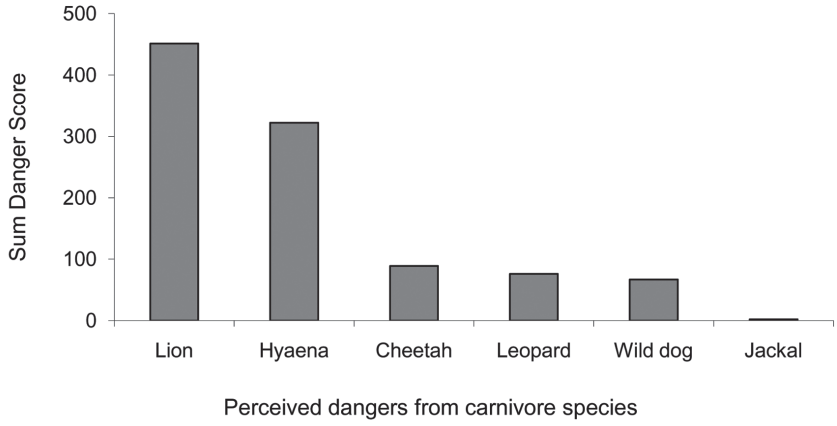

Figure 2 Proportion of people that have seen at least once and recognized pictures of the different species of carnivores living in the Pendjari Biosphere Reserve (n=322)

3.3.3 Perception of carnivores

According to local populations, the lion presents the most danger to them and their livestock, followed by spotted hyaena (Fig. 3).

All respondents agreed that the main problem with carnivores is livestock depredation. Some 26.5% of respondents found that carnivores were also advantageous. The advantages listed included tourism (mentioned by 94.8% of the respondents

who found carnivores beneficial), sport hunting (3.9%) and traditional uses of by-products for medicinal and magical purposes (3.9%).

Perception of carnivores is defined by the possibility of identifying advantages to the presence of carnivores. In general, people perceived carnivores relatively negatively, with the mean value for carnivore perception of 0.7± 0.4 with values varying from 0 (positive) to 1 (negative). Gourmantché were less negative, whereas Bourba had the most negative perception of carnivores but the difference between ethnic groups was not significant.

According to the stepwise regression (Table 3), knowledge of a carnivore attack on humans is the one significant predictor of the perception of carnivores.

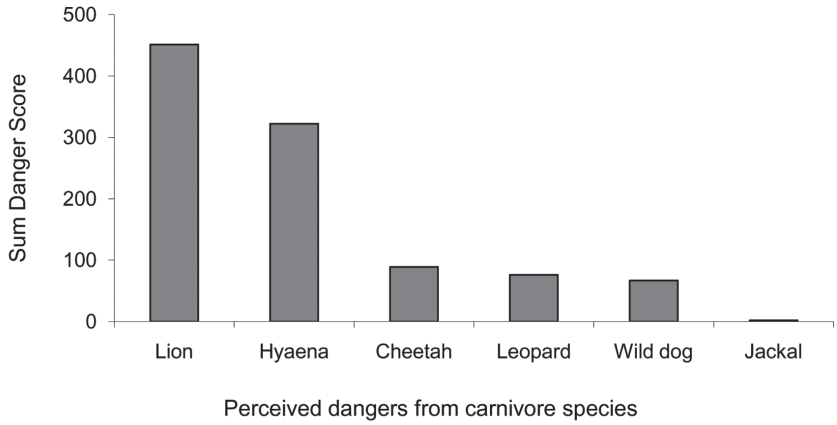

Figure 3 Ranking of the six carnivore species included in the present study according to the perceived danger they represent to local populations.

3.3.4 Perception of conservation

According to local populations, the Biosphere Reserve belongs to all Beninese (56.7% of respondents) or to the government (42.3% of respondents). Very few believed the reserve belongs to tourists (1% of respondents) or to local populations (1% of respondents). Respondents supported the work done by the actual park administration (99.7%) and their local association (100%). As shown by the Fig. 4, while almost all respondents agreed that the park is useful, they felt it was more useful to them as a community than as individuals.

The perception of conservation around Pendjari Biosphere Reserve was positive (mean score 7.6 ± 0.8 with scores varying from 5 as most positive to 12 as most negative). There was a significant difference in different ethnic groups perceived conservation (df = 12; χ^2 = 24.060; p = 0.020). Waama supported conservation

more and Bourba were the most negative towards conservation. Receiving an income from the park through an activity was the best predictor of positive conservation perception (Table 3).

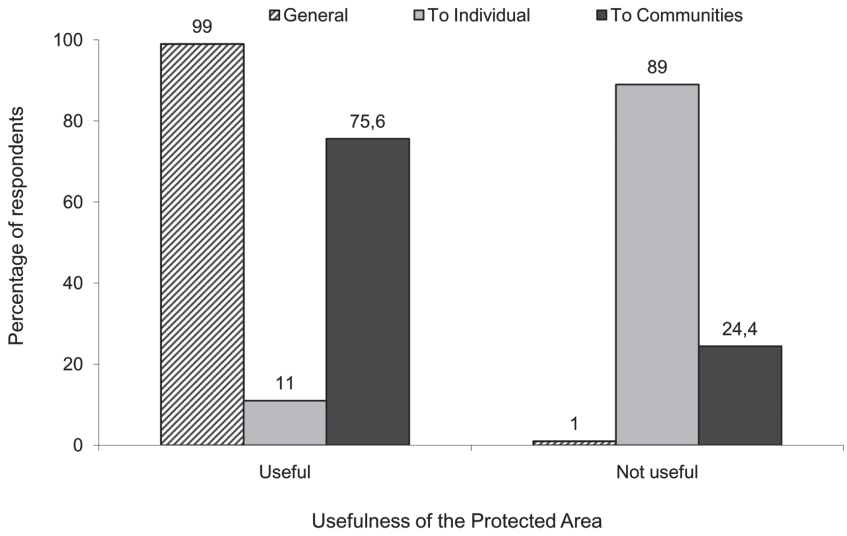

Figure 4 Perception of the use of the Pendjari Reserve by local communities

3.3.5 Perception of depredation

Fig. 5 illustrates the respondents' opinions about the effectiveness of mitigating depredation. Many respondents thought it would not be possible to avoid depredation as long as carnivores lived in close proximity. This opinion varied between ethnic groups ($df = 6$; $\chi^2 = 17.140$; $p = 0.009$). Most respondents (75.6%) thought that damage compensation could be a good method to mitigate the effects of livestock depredation as opposed to 5.4% who thought it would not be possible to compensate for losses. Ethnic groups such as the Gourmantché were more willing to be compensated for livestock losses ($df = 6$; $\chi^2 = 39.710$; $p < 0.0001$) than others. Few people (13.1%) felt that carnivore attacks on their livestock caused more damage to them than crop raiding, in contrast to 8.8% who thought the two caused similar damage.

In general, the perception of depredation in the vicinity of Pendjari was positive, which means that it was tolerated (mean score 1.87 ± 1.13, most positive 0 – most negative 6). There is no significant difference between ethnic groups although Gourmantché seemed to be more tolerant than Bourba and Berba. No factor was found to significantly predict how depredation was perceived.

Table 3 Results of stepwise selection for knowledge and perceptions

Dependent variables	Model Fit Statistics		Residual χ^2 test	Analysis of Effects Eligible for Removal	Summary of stepwise regression				
	Intercept only	Intercept & Covariates			Step	Effect entered	*df*	Score χ^2	Pr>χ^2
Knowledge	AIC =853.625 -2 Log L= 845.625	AIC =850.995 -2 Log L= 840.995	χ^2=10.331; df=17; P=0.889	Totem, DF=1; Wald χ^2 = 4.714; p=0.029	1	Totem	1	4.478	0.0340
Perception of carnivores	AIC =318.828 -2 Log L= 316.828	AIC =315.997 -2 Log L= 311.997	χ^2=18.266; df=17; P=0.372	Human attack, df=1; Wald χ^2 = 4.682; p=0.030	1	Human attack	1	5.665	0.0173
Perception of conservation	AIC =662.800 -2 Log L= 656.800	AIC =641.080 -2 Log L= 633.080	χ^2=12.726; df=17; P=0.754	Park activity, df=1; Wald χ^2= 25.326; p<0.0001	1	Park activity	1	13.879	0.0002
Perception of depredation			χ^2=21.964; df=18; P=0.234	–	–	–	–	–	–
Methods used	AIC =581.564 -2 Log L= 577.564	AIC =575.216 -2 Log L= 577.564	χ^2=9.415; df=17; P=0.926	Harvest Months, df=1; Wald χ^2= 8.187; p=0.0042		Harvest Months	1	8.174	0.0042
Lethal control	AIC =412.395 -2 Log L= 408.395	AIC =389.527 -2 Log L= 379.527	χ^2=15.347; df=14; P=0.355	Ethnic group, df=1; Wald χ^2= 13.604; p=0.0002 Age df=1; Wald χ^2= 9.829; p=0.0017 Distance df=1; Wald χ^2= 6.357; p=0.0117		Ethnic group Age Distance	1 1 1	13.775 8.242 6.317	0.0002 0.0041 0.0120
Will	AIC =258.312 -2 Log L= 254.312	AIC =239.759 -2 Log L= 231.759	χ^2=10.905 ; df=15; P=0.759	Age df=1; Wald χ^2= 12.791; p=0.0003 Totem df=1; Wald χ^2= 6.680; p=0.0097		Age Totem	1 1	15.682 7.373	<0.0001 0.007

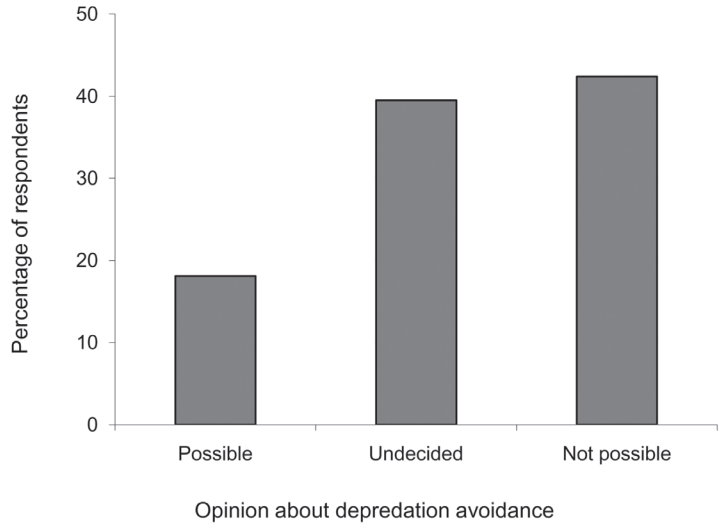

Figure 5 Respondents' opinion about the possibility of avoiding livestock depredation

3.3.6 Lethal control and tolerance towards carnivores and depredation

Most respondents (84.9 %) were willing to see populations of carnivores increase in the park. The main reason was that carnivores (especially lions) are among the species wealthy tourists want to see when they visit the reserve. If there are more carnivores, then there will be more tourists and therefore more benefits to the local populations. The second reason was related to future generations. Children nowadays do not know much about carnivore species. If wildlife was better conserved, then their children would have more opportunity to learn about them in the future. Bourba did not mind seeing numbers of carnivores increasing while Gourmantché and Berba were more reserved about an increase in populations of carnivores in the area. The willingness to see carnivore populations increase could be predicted by the age of the respondent and his or her recognition of a totem (Table 3).

To reduce livestock depredation, some people guard their livestock or put them into enclosures during the night. Most people had dogs. However, dogs were mostly used against theft and were said to be inefficient against carnivores. The number of protective methods used varied according to the ethnic group, but not significantly. It could be predicted by the food security level in the household corresponding to the number of months during which the harvest of the previous year is consumed before it becomes necessary to buy food.

Fortunately only 13.1% of respondents supported retaliatory killing of carnivores against 73.2% who thought it was not a good mitigation measure. Opinions differed significantly among ethnic groups, with Waama being the most against lion retaliatory killing and Berba supporting it ($df = 6$; $\chi^2 = 14.933$; $p = 0.021$). Attitudes related to lethal control could be predicted by the ethnic group, the age and the distance of respondents to the park (Table 3).

3.3.7 Interrelationships between knowledge and perceptions

The more people knew about the carnivore species, the more positively they perceived them ($r_s = -0.137$; $p = 0.019$). Peoples' perceptions of conservation and carnivore species were positively correlated ($r_s = 0.148$, $p = 0.011$). Perception of carnivore species is also positively correlated to the perception of depredation ($r_s = 0.130$; $p = 0.026$). People willing to find advantages to the presence of carnivores are more willing to see their number increase ($r_s = 0.187$; $p = 0.001$), less likely to kill them ($r_s = 0.191$; $p = 0.001$) and more likely to use methods to protect their cattle ($r_s = -0.158$; $p = 0.007$). Those who tolerate depredation are less likely to use retaliatory killing ($r_s = 0.199$; $p = 0.0006$) and to use diverse methods to protect their livestock ($r_s = -0.304$; $p < 0.0001$).

3.4 Discussion

Wild carnivores are often known to engender negative attitudes among people coexisting with them (Mech, 1995; Oli *et al*., 1994). These negative attitudes usually reflect a history of depredation and awareness of the species and their interactions with humans (Oli *et al*., 1994; Kellert *et al*., 1996). Around Pendjari Biosphere Reserve, where populations have a long tradition of coexisting with wildlife, their perceptions of conflicts are mixed.

3.4.1 Knowledge and traditional values about carnivores

Local populations around the Pendjari Biosphere Reserve had an average knowledge about carnivores in general, with a better knowledge of lions and hyaenas. The difference in knowledge about various species is probably because some species are more numerous and charismatic (e.g., puma and jaguar around Iguaçu National Park area in Brazil; Conforti & de Azevedo, 2003). In Pendjari Biosphere Reserve, as in Kruger National Park (Lagendijk & Gusset, 2008), the better knowledge of species such as lion and hyaena is due to the fact that these species are the ones which were more commonly observed around villages and were more responsible for attacks on livestock than other carnivore species. People who had more interaction with the protected area due to their activities and to the proximity of their village to the park had more knowledge. This supports Ericsson &

Heberlein (2003) who found in Sweden that hunters, who have much experience with wildlife, had a better knowledge than other people in their study area.

Association with a totem is an important component of certain cultures and is still a reality in West African societies as elsewhere in the world (Tobayiwa & Jackson, 1985). Lagendijk & Gusset (2008) confirmed the impact of culture on attitudes towards carnivores and conservation, as we noticed in the Pendjari. The fact that negative behaviour such as retaliation killing of carnivores was uncommon even though people have negative perceptions could be partly attributed to the existence of carnivore totems and the importance of culture in the area. Similarly, Colding & Folke (2001) found that species-specific taboos could contribute to the protection of threatened species. However, traditional beliefs could also have a negative impact, for example if the local culture encourages the killing of predators, as has been observed with Rais people in Nepal (Mehta & Kellert, 1998). The positive impact we observed in Pendjari will probably not be permanent, however, as cultural beliefs seem to regulate life in the area less and less, due to urbanization and modernization.

3.4.2 Perceptions of conflicts

The main factors found to affect perceptions and tolerance of people residing in the vicinity of Pendjari Biosphere Reserve are the nature of their activities, the awareness of human attacks and the age of the respondents. The distance to the park, the ethnic group and the ownership of a totem also influenced perceptions and tolerance.

Usually, the more benefits people receive from wildlife and conservation activities, the more positive they are towards carnivores and conservation (Fiallo & Jacobson, 1995; Lindsey *et al*., 2005; Morzillo *et al*., 2007; Romanach *et al*., 2007; Schumann *et al*., 2008). However no impact can be expected if people are not made aware of the benefits they are obtaining from conservation (Allendorf *et al*., 2007). Around Pendjari Biosphere Reserve, similarly to Vodouhê *et al.*'s (2010) findings, those who benefitted from the park through their activities displayed the most positive perception of conservation. In some cases, people can be positive even if they do not receive any benefits from conservation (Arjunan *et al*., 2006). On the other hand, benefits alone do not necessarily lead to positive perceptions and attitudes (Gillingham & Lee, 1999). Species which cause great damage are not seen positively even if they also produce benefits for the human community (for example, lion and hyaena in Namibia: Schumann *et al*., 2008). In Pendjari, despite conflicts and the lack of mitigation and compensation incentives from the government, people are more tolerant toward conservation and predators compared to some other parts of the world where perceptions and attitudes did not

improve with compensation schemes and awareness (Gusset *et al*., 2009; Majić & Bath, 2010).

Predation events have been found to affect perceptions (Ericsson & Heberlein, 2003; Naughton-Treves *et al*., 2003; Zimmermann *et al*., 2005; Baral & Henien, 2007; Dar *et al*., 2009) or not at all (Conforti & de Azevedo, 2003). People who experienced attacks on livestock were found to be less positive towards carnivores (Røskaft *et al*., 2007), were more willing to kill them in retaliation and were against the increase of carnivore populations (Palmeira & Barrella, 2007; Kissui, 2008; Hazzah *et al*., 2009). Luckily, around Pendjari, depredation experiences did not have any significant impact on perceptions. Most people who did not tolerate depredation did not think carnivores should be killed. Instead, it is the knowledge of attacks on humans which influences people's perception of carnivores. However, except for one case, respondents did not themselves experience attacks on humans around Pendjari. The assertion of Gillingham & Lee (1999) that direct experience with wildlife largely determines attitudes does not extend to Pendjari. Indirect experience of attacks on humans seemed to be more important in influencing perceptions than direct experience of livestock depredation. This raises the question of real and perceived threat or risk that was considered by Marker *et al*. (2003) and Dickman (2010). Rare events can have more impact on risk perception and this risk perception is commonly spread through popular culture (Dickman, 2010) as is the case in Pendjari. A single case of a non-lethal attack on a human within one decade and the rumour of attacks in other regions was sufficient for everyone to think carnivores and particularly lions are very dangerous to humans.

Experience with carnivores could be direct (through attacks on human or livestock) or indirect (through knowledge about the species). Around Pendjari, the positive impact of knowledge on attitude towards carnivores agrees with several previous studies (Fiallo & Jacobson, 1995; Kellert, 1996; Zimmermann *et al*., 2001; Conforti & de Azevedo, 2003; Shivik *et al*., 2003; Lindsey *et al*., 2005; Schumann *et al*., 2008).

The highest intolerance level noticed in Berba people can be partially attributed to their relationships with natural resources in the past. Like Berba, Gourmantché were expelled from the protected area a few decades ago. But the Gourmantché have been found to rely more on the park for usage ceremonies (Vodouhê *et al*., 2010) and have stronger cultural attachment to wildlife and predators. These two groups also live more closely to the park than the Waama and Bourba. They are thus more likely to suffer from insufficient land and wildlife damages. Furthermore, the different ethnic groups' perceptions are influenced by their previous experience with wildlife and conservation and the benefits they offer, as was found in other areas (Mehta & Kellert, 1998; Romanach *et al*., 2007).

In contrast to comparable studies elsewhere (Williams *et al*., 2002; Ericsson & Heberlein, 2003; Zimmermann *et al*., 2005; Arjunan *et al*., 2006; Røskaft *et al*., 2007; Majić & Bath, 2010), we found that elder respondents were more tolerant. They have experienced the benefits that local populations are receiving since 2000 with the improvement in the park management and can better assess the advantages of carnivores and wildlife in general. They were also usually more attached to their cultural practices than younger people, which may have influenced their perceptions.

3.4.3 Implications for management and conclusion

Although livestock depredation is slightly less common than crop raiding around Pendjari Biosphere Reserve, it deserves considerable attention. Conflicts that generate peoples' negative perceptions favour harmful behaviour such as poaching and retaliatory killing of carnivores. More important, these conflicts usually target endangered and flagship species such as lions.

Retaliatory killing of carnivores is yet not common in Pendjari probably due to the overall positive and fatalist attitude of populations and the importance of their culture. Still, community perceptions should be improved in order to avoid such cases in the future and to secure the conservation of all wildlife species in the area.

Compensation has been suggested by several studies as a means to improve tolerance toward conservation in general and carnivores in particular (Andersone & Ozolins, 2004; Hazzah *et al*., 2009). In Pendjari Biosphere Reserve, as in some other regions (Badola, 1998), the lack of compensation is perceived by people as an indifference on the part of the government to their losses. But in order to compensate, it is usually necessary to have evidence of depredation. This is difficult in our study area, as dogs clean up depredation evidence when it occurs in villages. If there is any meat remaining, people prefer to cook it instead of letting it decompose while waiting for the wildlife officials to arrive. Awareness campaigns did not change this behaviour. It would be necessary to have permanent staff in all villages to obtain visual evidence, and this is difficult to achieve. Contrary to the popular belief, compensation is not always effective (Cuicci & Boitani, 1998; Naughton-Treves *et al*., 2003; Gusset *et al*., 2009; Agarwala *et al*., 2010). Corruption could also be a problem (Sukumar, 1994). There is currently a compensation scheme for elephant damage around Pendjari but many find it insufficient, inefficient and complicated. A compensation scheme for carnivore damage is likely to follow the same path. Moreover, it could also be difficult to secure funding for such a scheme. Activities such as anti-poaching patrols and wildlife monitoring are not continuous, due to the lack of funding towards the end of the projects. If local populations have become accustomed to being compensated, there may

be a gap at the end of the projects, which could give rise to negative attitudes in the populations that will be ultimately be detrimental to carnivores' conservation.

Moreover, as was pointed out by Madden (2008), compensation only addresses the economic aspects of a conflict that also has social, political and ecological implications. Social factors are usually neglected (Dickman, 2010) and need to be investigated in depth if sustainable solutions are to be found.

Other methods that seem more effective are incentive-driven conservation with a better sharing of benefits from the reserve and promotion of ecotourism (Sillero-Zubiri & Laurenson, 2001; Miller, 2002; Hutton & Leader-Williams, 2003; Bagchi & Mishra, 2006; Gusset *et al*., 2008). Benefits to individuals, more than benefits to communities, will contribute to improving peoples' perceptions. Furthermore, there is a need to develop projects that address specific issues, including improvement of animal husbandry and farming techniques. Local people should not only receive benefits but should also participate to a greater extent in management actions (Gusset *et al*., 2008). Local communities should be incorporated in long-term social and ecological monitoring, development of economic alternatives, and environmental education (Fiallo & Jacobson, 1995). However, community participation is not necessarily a guarantee for the success of programs (Infield & Namara, 2001). Therefore, good preliminary research to evaluate the real needs of communities is required. Projects to be developed should not be only economically-oriented, but also be adapted to the needs of the various ethnic groups and local cultural aspects. For example, groups such as the Berba and Gourmantché had some practices related to wildlife they were obliged to abandon when they left the reserve. A few concessions have been made, however, as populations are allowed to fish and worship their gods in the Bori pond located within the hunting area. These efforts to recognize cultural practices should be extended, but not to the detriment of wildlife.

Educating people about these issues is difficult (Pierce *et al*., 2001; Shanahan *et al*., 2001; Ericsson & Heberlein, 2003). However, education and development of awareness are good strategies to improve popular perceptions (Sudarmadi *et al*., 2001; Røskaft *et al*., 2003; Zimmermann *et al*., 2005; Thornton & Quinn, 2009). Education in Pendjari would improve knowledge about carnivores and hopefully peoples' perceptions and attitudes towards conflicts. This education should focus on individuals who do not have an activity related to the park/conservation. It should also focus on ethnic groups such as Berba, who are less positive.

An integrated approach, combining education, promotion of improved husbandry methods and development of economic incentives will be more effective for conflict mitigation in the region. Cultural aspects and differences between ethnic groups should be integrated. As education and compensation programs do not

always lead to positive results (Ericsson & Heberlein, 2003; Majic & Bath, 2010), a continuous monitoring, as suggested by Inskip & Zimmermann (2009) and Dickman (2010), will allow the assessment of the impacts of these programs and introduce changes when necessary.

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Appendix 3.1
Semi-structured interview for conflicts perception surveys

1 Date:
2 Village:
3 Coordinates of the house/Location:

Socio-economic characteristics of the respondent

4 Name:
5 Gender :
6 Ethnic group
7 Age / Age class :
8 Family composition:
9 Main activity:
10 Second activity (when applicable):
11 Do you produce cotton? **a** Yes **b** No
12 Is your harvest usually enough to feed your family?
13 During how many months do you generraly consume your harvest before you start buying food?

Carnivore knowledge and perception

14 Which carnivore' species do you recognize on the pictures?

Lion Hyaena Leopard Cheetah Wild dog Jackal

15 According to you, which of these species live in this area or in the protected area?

Lion Hyaena Leopard Cheetah Wild dog Jackal

16 Which species have you ever seen?

Lion Hyaena Leopard Cheetah Wild dog Jackal

17 About the species you have seen, when and where have you sight them for the last time (for each species)?

18 According to you, for each species, what is the population evolution trend for these species? Precise for each species if the population is increasing, decreasing or stable this last decade or if you don't know?

19 Do you want these species population to increase?

a Yes b No

Why?

20 According to you, among the six species, which are the most dangerous? Give a score: 3 to the most dangerous, 2 to the second most dangerous and 1 to the third most dangerous

1 2 3

For each species, precise why it is dangerous.

21 Do you think carnivores'species have some advantages?

a Yes b No

22 If yes, which benefits could these species have?

23 What are the disadvantages of carnivore species?

24 Do carnivores species have a special meaning/importance in your culture?

25 Do you know some medicinal or magical uses of carnivore's parts?

26 Do you have totem? a Yes b No

27 Which wildlife species do you have as totem?

The protected area

28 According to you, to whom belongs the park?

a the government
b Hunting zones owners
c Local populations
d all Beninese
e Tourists
f Other (precise)

29 Is the protected area useful to you as individual?

a Yes b No

Why?

30 Is the protected area useful to your community?

a Yes b No

Why?

31 What do you think the management currently done of the protected area? Do you think the Wildlife Office is doing a good job?

a Yes b No c Don't know

32 What is your opinion of the AVIGREF? Are they doing a good job?

a Yes b No c Don't know

Livestock depredation

33 Do you breed livestock?

34 Which species? How many heads to you have for each livestock species?

35 Have you ever have livestock depredation problem?

36 If yes, please give details (year, month/period, livestock species, carnivore responsible, location, other conditions)?

37 How did you recognize the carnivore responsible?

a Spoor b Call c Other (precise)

38 Check if the respondent could identify lion and hyaena spoors on pictures

39 Do you think you can avoid depredation?

If yes, how?
If not, why?

40 Do you have a dog?

If yes, why?

41 Do you think it is possible to avoid livestock depredation?

42 How?

43 Which method do you use to limit your livestock depredation?

a Dog b Enclosures c Guard d Other

44 Do you think damage compensation could be me a good mitigation method? Why?

45 Do you think carnivotre killing could be a good method to reduce depredation?

46 According to you, what is the trend of livestock attacks these last years?

a Increasing b Decreasing c Stable d I don't know

47 Have you ever heard of human attack by carnivores?
If yes, please give details (place, date, circumstances)

48 Have you ever experienced crop raiding by wildlife? Details

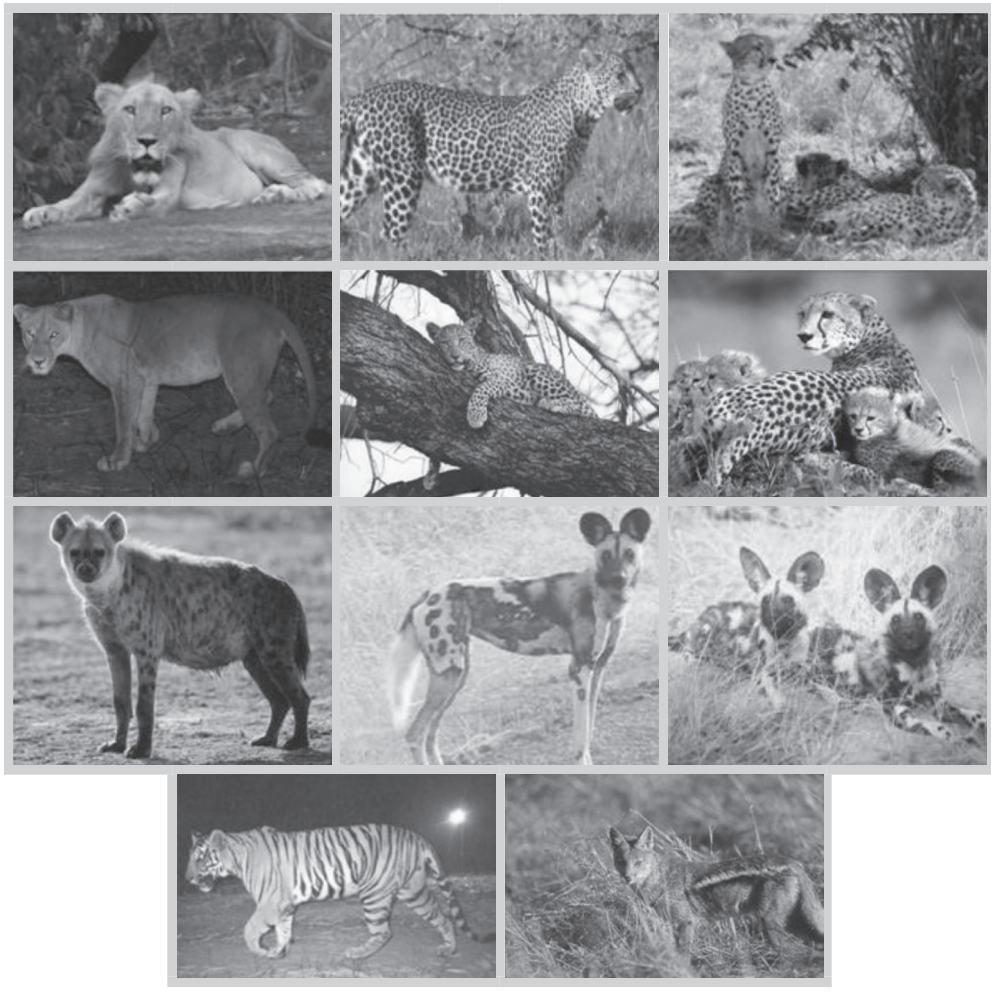
49 Between livestock depredation and crop raidng, which one is the most detrimental according to you?
Why?

50 Despite all these problems, do you think the park is important?

51 Other remarks

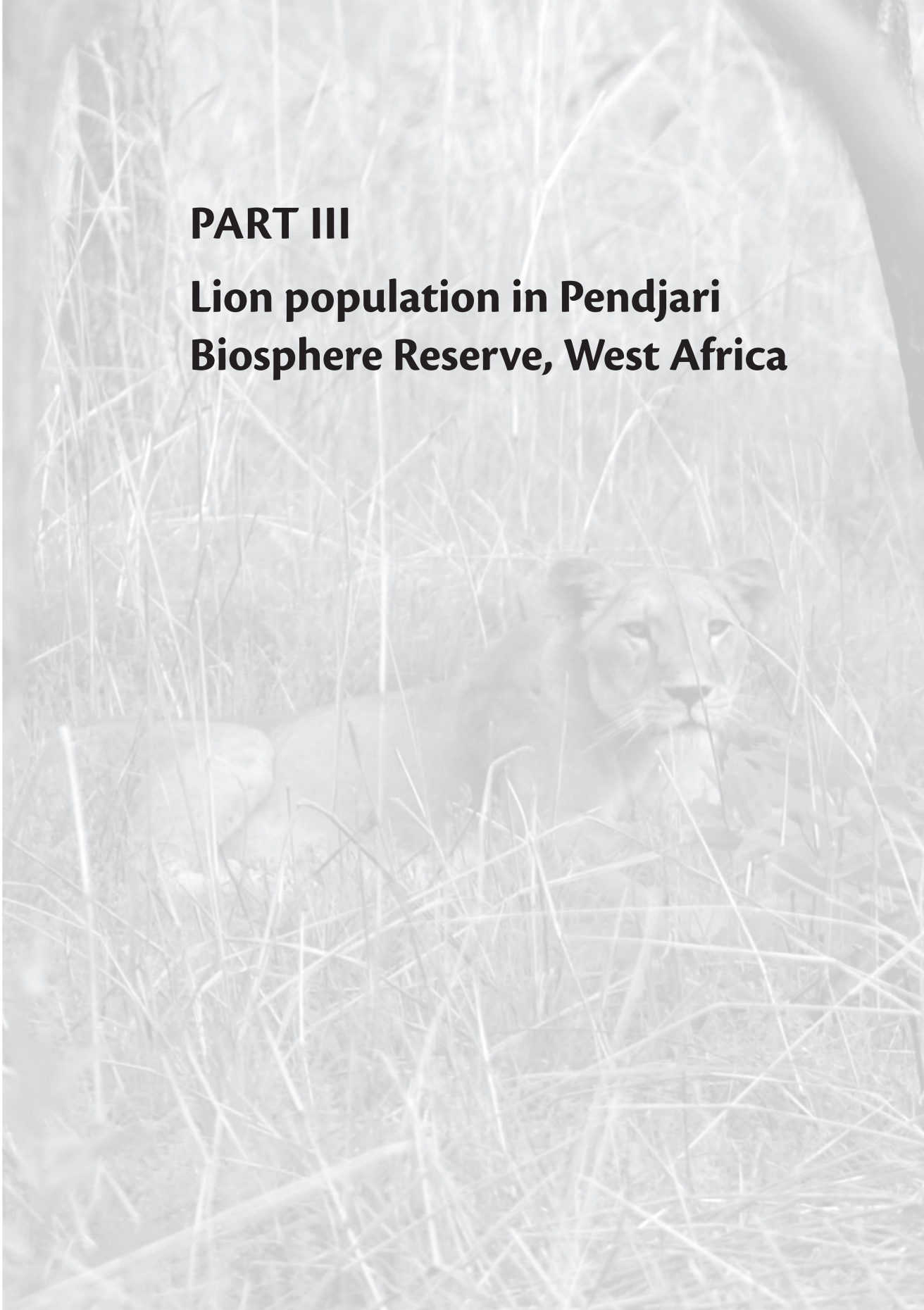
Thanks for your participation

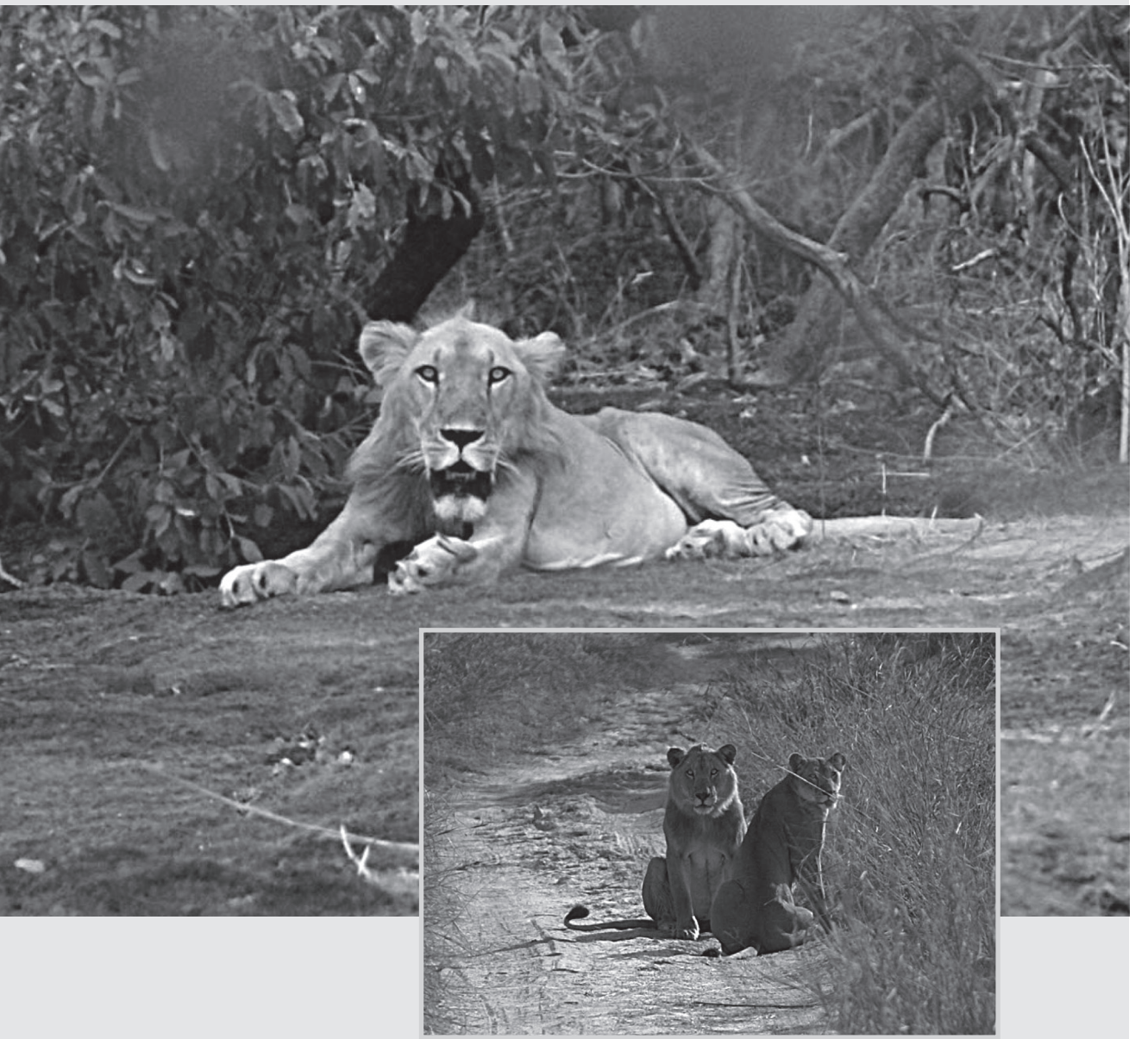
Appendix 3.2
Photographs used to identify survey species



PART III

Lion population in Pendjari Biosphere Reserve, West Africa





4 Lion population density and social structure in Pendjari Biosphere Reserve and its implication for West African lion conservation

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Submitted

Abstract

Lion populations have undergone a severe decline in Africa. In West Africa where the species is considered as Regionally Endangered while it is Vulnerable in other parts of Africa, the knowledge of the species is very limited. In order to provide baseline data for future conservation management of lions in West Africa, we assessed the density and group structure of lions in the park and hunting zones that composed Pendjari Biosphere Reserve in Benin. The density of lions determined using calling stations was 1.6 lions/100 km^2. The mean group size, highest than the average in the region, was 2.6 individuals (SD = 1.7; n = 296). A significantly highest group size was observed in the national park compared to hunting zones. Results showed an even adult sex ratio. However adult males outnumbered females in the hunting zones (1 male : 0.6 female). On average, there was 0.9 cub per adult female, indicating that the population had the potential to reproduce effectively. The lion population appears to have increased the last decade at contrary to most population in the region. However, the results showed that this population remained vulnerable to legal and illegal hunting both in Benin and neighbouring countries. For a sustainable conservation of lion in the region, conservation efforts in Pendjari should be expanded to other parts of the transboundary conservation area in neighbouring countries. There is also an urgent need to set a long-term monitoring system to assess the changes in the lion social structure and the impact of hunting and other anthropogenic activities on the lion population in the region.

Keywords

Panthera leo; density; group structure; age structure; trophy hunting; Benin; West Africa

4.1 Introduction

Lions *Panthera leo* are the most gregarious of all felids forming 'fission-fusion' social units known as prides that typically comprise four to six (range from 1 to 21) related females, their dependent offspring and a temporary, unrelated coalition of typically two (range from 1 to 9) adult males (Schaller, 1972; Bertram, 1975; Packer & Pusey, 1982; Mosser & Packer, 2009). Several factors influence lion grouping patterns among which cub defence, group territoriality, defence of kills against scavengers, synchronised female breeding patterns and communal raising of offspring are the most important (Packer, Scheel & Pusey, 1990; Mosser & Packer, 2009). Lion grouping patterns have only been weakly linked to prey availability. Despite hunting success increased with the group hunting size (Schaller, 1972; van Orsdol, 1984; Stander & Albon, 1993; Funston *et al*., 2001), grouping is not related strongly enough to improved food intake to explain sociality (Packer *et al*., 1990).

The density and possibly the social make up of lions vary greatly across the lion's range (Bauer et al., 2003). In West and Central Africa, lion populations are highly fragmented with densities of one to three lions/100 km² being typical and always less than 5 lions/100 km² (Bauer & van der Merwe, 2004; Henschel *et al*., 2010). Lions in this region thus tend to form small groups. Bauer *et al*. (2003) suggested that the main factors that drive small group size in this region are dependence on domestic livestock, low mean prey body size and low prey density. Celesia *et al*. (2010) pointed out the gap in knowledge of lion demography and population status in West and Central Africa and the fact that this region should be a priority for future field studies.

Pendjari Biosphere Reserve in Benin is part of a complex of protected areas in four countries (Benin, Burkina Faso, Niger and Togo) of West Africa named WAPOK (W -Arli - Pendjari - Oti Mandouri - Kéran). It is one of the last remaining significant lion population in West Africa (cf. Henschel *et al*., 2010) which are now regionally endangered. In order to conserve the lion in West Africa, it is important to know whether they indeed have a different social organisation from lions elsewhere or whether the patterns observed are an artefact of the prevailing conditions in terms of human and livestock densities, fragmented lion populations and generally small protected areas. Such study in a relatively well protected reserve of the region will allow assessing if the density and the population structure are characteristic of the region or mainly due to the intensity of anthropogenic pressures characteristic of the region. In the three hunting zones of Pendjari Biosphere Reserve, lion trophy hunting is allowed with a quota of two lions every two years per hunting zone. The quota is the same in the two hunting zones of the nearby W Reserve Benin. These quotas were the double from 1990 and were reduced by half in 2002 after the first specific studies on lion in Benin. It is important to note that W Benin is one of the most degraded parts of the complex with a lot of poach-

ing and illegal grazing (Clerici *et al*., 2007; Sogbohossou E.A., pers. com.). While in Niger, lion hunting is not allowed, in Burkina Faso the quota exceed 20 lions a year and about 12 lions are killed every year by sport hunters (UICN/PACO, 2009). These lions are killed in the hunting zones that are just nearby Pendjari Biosphere Reserve.

Here we present data on the density and social structure of the lion population in Pendjari Biosphere Reserve, which due to its size may approach a representative case study, but that is also exposed to the typical suite of perturbations including trophy hunting and other human activities in the reserve.

4.2 Methods

4.2.1 Study area

The study was conducted in Pendjari Biosphere Reserve (Fig. 1). This reserve, located in north-western Benin is mainly composed of Pendjari National Park (2,660 km²) and Pendjari (1,600 km²) and Konkombri (250 km²) Hunting Areas. Pendjari Hunting area is divided in Pendjari and Batia hunting blocks. Pendjari Biosphere Reserve is part of a bigger complex composed of three protected areas and their annex zones in three countries: W in Benin, Burkina Faso and Niger, Arly in Burkina Faso and Pendjari in Benin and called WAP. This complex could be extended to WAPOK including Oti-Mandouri and Keran Reserves from Togo (Fig. 2). Pendjari is probably the richest and the less degraded part of the complex. The climate is characterized by one dry season (November-May) and one rainy season (May-October). The annual rainfall varied from 800 mm in the northern part to 1,000 mm in the southern part and the mean annual temperatures range from 18°6 to 36°8 according to the season. The reserve, relatively flat, is bordered east by Atacora mountain and north by the Pendjari River. Most rivers and waterholes dried up between February/March and May with water available in only parts of the Pendjari River and a few important natural waterholes. In the rainy season, many areas of the reserve are flooded and inaccessible. The vegetation is a mosaic of shrub, woodland savannah, grasslands and forests dominated by species such as *Isoberlinia doka*, *Daniella oliveri*, *Terminalia spp*., *Combretum spp*. with *Mitragyna inermis* and *Terminalia macroptera* on the floodplains. The mammalian fauna is characteristic of the West African savannah including several species of duikers, Buffon's kob *Kobus kob*, elephant *Loxodonta africana* and roan antelope *Hippotragus equinus* (Sinsin *et al*., 2002). Five species of large carnivores are present (lion, leopard *Panthera pardus*, cheetah *Acinonys jubatus*, spotted hyaena *Crocuta crocuta*, wild dog *Lycaon pictus*) with lion and hyaena occurring at higher densities. The south-eastern and south-western parts of the reserve are bordered by

villages. W Benin park and Mekrou hunting zones are just adjacent to the eastern part of the reserve.

4.2.2 Estimating lion population size and density

In May 2009, we estimated the lion population size through call-in following a methodology adapted from Ogutu & Dublin (1998). We used mainly playbacks of buffalo calves and pig distress calls and hyena sounds played at full volume with a MP3 player connected to an amplifier and two speakers mounted on the roof of a car. We alternated 10 minutes of calls with 10 minutes of silence. When we didn't get any response, after about 1 hour 30, we played lion roar. The calling operation was done from 19h to 03.00 h and we used spotlight to check if lion respond. We chose the first point at about 10 km from one entrance of the park and from there, we called every 5 km, along all the roads of the park. 61 random calls in stations were conducted over two weeks sampling period. This represents 571.5 km² which was a 12% sample of the reserve assuming a call in radius of 2 km and a 75% response rate (following Bauer, 2007), neither of which were calibrated. The low density of roads and the inaccessibility of many parts of the reserve made it impossible to cover a higher percentage of the reserve.

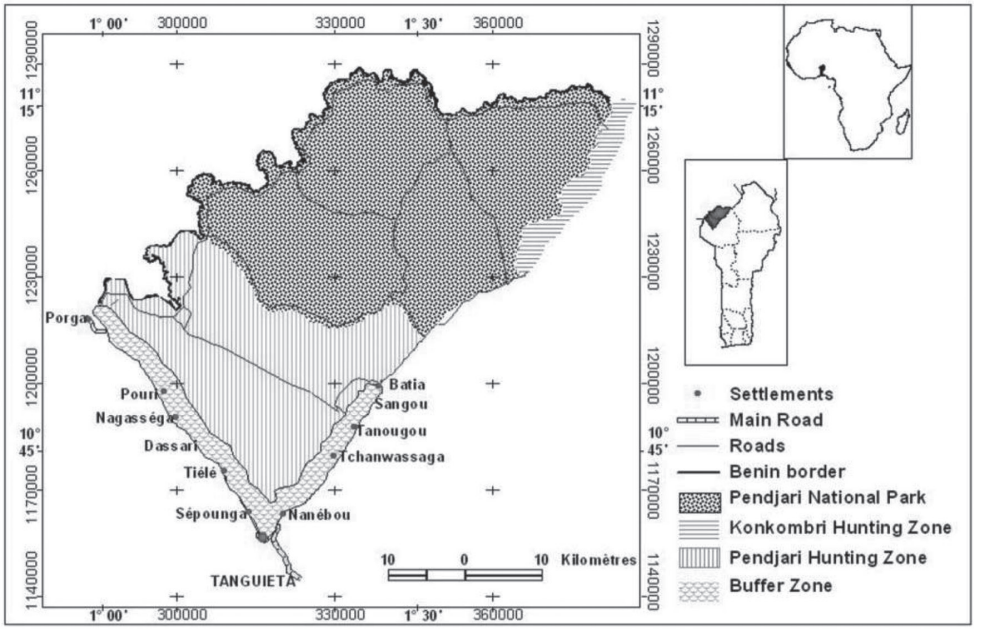

Figure 1 Location of Pendjari Biosphere Reserve in Benin.

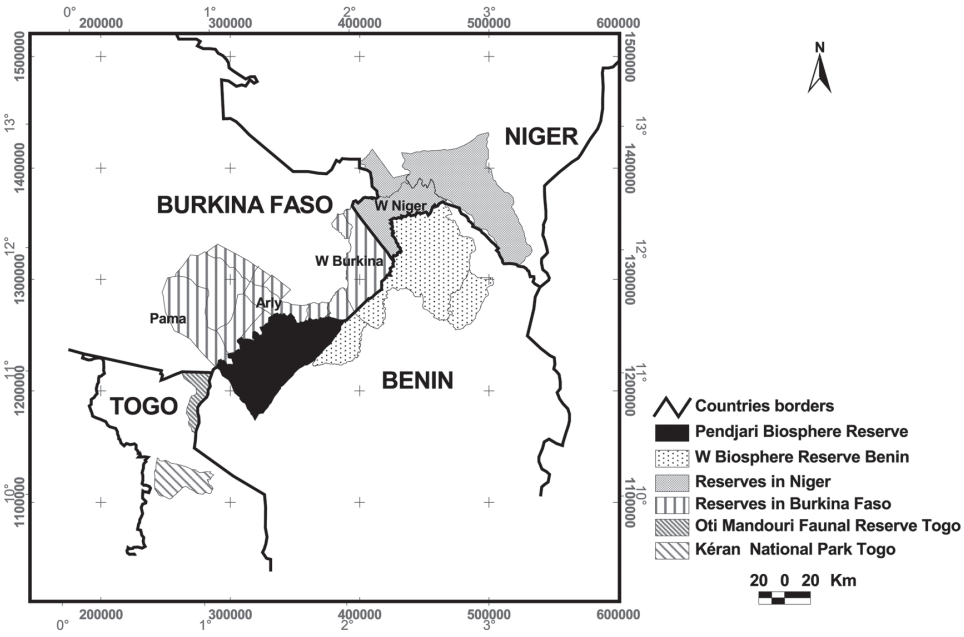

Figure 2 W - Arly - Pendjari - Oti Mandouri and Keran, the called WAPOK complex of protected areas in West Africa

4.2.3 Assessment of the social structure

To assess social structure, we systematically searched for lion by vehicle and motorbike over the park at least 15 days each month during the dry seasons of 2008-2009 and 2009-2010. We also collated all opportunistic sightings from the same period. We were able to search for lions only along the roads. This limited the percentage of the area covered due to the low density of roads and the impossibility of taking the vehicle off-road.

For hunting zones, we used mostly observations of professional hunting guides during the times when the area was accessible; research work was not possible because of hunting activities.

For each lion observation, we recorded GPS coordinates, group composition, and vegetation type. Lions were grouped in three age classes: cubs (less than two years), sub adults (two to four years) and adults (more than four years). When possible, the sex was determined. We did not use data of lion group composition from tourist guides as typically male lions lacked extensive manes and were easily confused with females. This reduced the size of the sample used for analysis but limited errors. The shyness of many lions and the fact that most observations were not close, did not allow us to base our study on the identification of individuals,

although this has been recognised to be a good method to study social structure (Whitehead & Dufault, 1999).

4.2.4 Data analysis

The mean size of the different types of observations and group compositions were calculated. We used a Kruskal Wallis (H) to test for differences between social structure in the park and the hunting zones. To evaluate the potential impact of human activities on the structure of lions in Pendjari hunting zone, the distances of each sighting in the hunting zone to the park and to villages were estimated through the function 'Calculate Distance' with Animal Movement Extension on ArcView software (ArcView GIS 3.2. Environmental Systems Research Institute Inc. 1995-1999). Then we used Spearman correlation to check the relation between distances and observations sizes and frequencies.

4.3 Results

4.3.1 Lion population size and density

The mean number of lions responding to the calls in was one response per 5.5 calls with a derived average density of 1.6 lions/100 km² (95% CI: 0.5; 2.5) suggesting that there are 77 adults and sub-adults lions in the reserve. The density of lions in the park is 2 adults and subadults lions/100 km² while in the hunting zones the density is 1.33 adults and subadults lions/100 km².

4.3.3 Structure of lion groups

Group sizes

A total of 296 lion observations were made from 2008 to 2010 in Pendjari Biosphere Reserve. Fig. 3 shows the frequencies of different group sizes observed in the park and hunting zones. There were significantly more observations of single individuals in the hunting zones population (46.7%) compared to the park (29.9%) (χ^2 = 7.89, df = 1, P = 0.005) while the proportion of groups of four and more individuals were not significantly more important in the park than in the hunting areas (20.6% of observations) than in the hunting areas (6.5%) (χ^2 = 1.87; df = 1; P = 0.17). However, significantly more groups were observed in the park (75.3% of the observations of groups of four or more lions) compared to hunting areas. In the whole reserve, 64.4% of solitary individuals were adult males while 24% were adult females, the remainder not being identified. Most (67.6 %) of observations in the park were made near waterpoints.

The average lion group size in the reserve, all ages considered, was 2.6 ± 1.7 (range 1-8). The mean group size was significantly higher (H = 6.5, df = 1; P = 0.01) in the park (2.7 ± 1.7 lions) compared to the hunting zones (2.2 ± 1.5 lions).

The mean size of adult male groups or coalitions was 1.1 ± 0.2 (range 1 - 4). The mean number of adult males found in mixed groups was 1.0 ± 0.2. There was an average of 1.2 ± 0.5 adult lionesses in groups. In the park, the mean number of female observed in a group is 1.3 ± 0.6 while it is 1.2 ± 0.6 in the hunting zones.

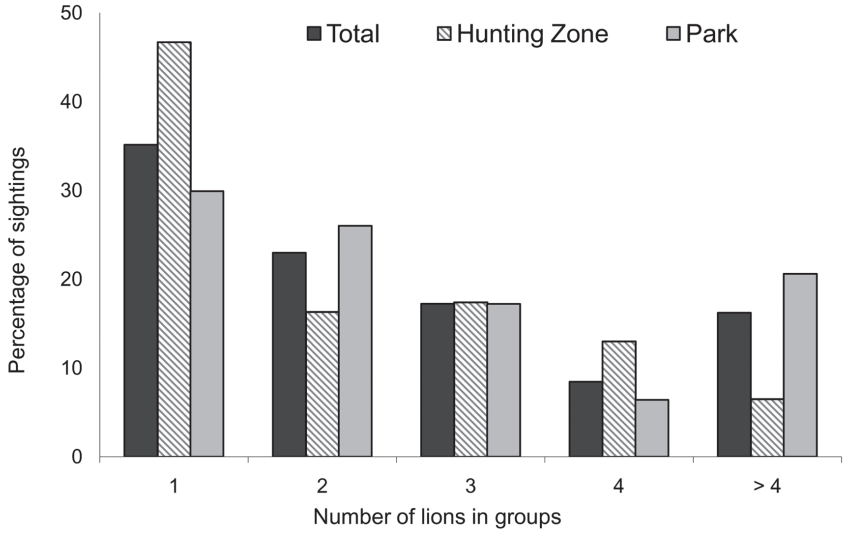

Figure 3 Frequency of different lion group sizes sightings in Pendjari Biosphere Reserve (n=296 observations from 2008 to 2010).

Age and sex composition

Adult males and females were in exactly equal proportion throughout the biosphere reserve. However male lions outnumbered lionesses in the hunting zone (1 male: 0.6 female) while we found the opposite inside the park (1 male: 1.4 females) (Table 1). Thus the proportion of adult males was significantly higher in the hunting zones than in the park (H = 11.6; df = 1; P < 0.001), the converse being the case for adult lionesses (H = 20.1; df = 1; P < 0.001).

About 20% of the lion population was composed of cubs while 72.2% were adults with no significant difference between the proportion of cubs (H = 0.58; df = 1; P = 0.45) and subadults (H = 1.79; df = 1; P = 0.18) in the park and the hunting zones. The number of cubs in groups varied from one to six with a mean size of groups with cubs was 3.8 individuals. The ratio of cub : adult lionesses in the population was 1 : 1.1.

Table 1 Age and sex composition of Pendjari

	Reserve	Hunting Zones	Park
Sex ratio adults (male: female)	1:1 (158:168)	1:0.6 (77:50)	1:1.4 (81:118)
Percentage age composition (%)			
Cubs	19.9 (n=110)	25.0 (n=50)	16.9 (n=60)
Subadult	7.9 (n=44)	8.0 (n=16)	7.9 (n=28)
Adult	72.2 (n=401)	67.0 (n=134)	75.2 (n=267)

4.3.3 Hunting zones and the impact of human activities

Most of observations in the hunting zone were made along Pendjari River, an area known for its high prey concentration, and close to the border with the park. The mean distance of observations in the hunting zones to the park was within 10 ± 9 km from the park, with 53.4% of observations made at less than 10 km from the park border. There was a significant correlation between the distance of observations to the park and the number of observations (r_s = -0.82; P = 0.011). Conversely, fewer observations were made in areas closer to the controlled access area separating the villages from the hunting zones (r_s = 0.76; P = 0.049). However there was no significant correlation between the distance to the park or villages and lion group sizes.

4.4 Discussion

The lion density in Pendjari was similar to most populations in West and Central Africa and to some other populations in arid and semi-arid, dystrophic ecosystems in southern Africa such as Etosha and Kgalagadi Transfrontier Park (Table 2). Despite this density was not the highest in the region, the lion population in Pendjari Biosphere Reserve is healthier than in most protected areas of the region. Indeed, in 2002, following the same methodology we used, Di Silvestre (2002) found a density of 0.7 lions/100 km² (95% CI: 0.07; 1.27). This increase in the lion population in Pendjari Biosphere Reserve could be attributed to the improvement in the management of the park since 2000, when active conservation actions were reinstated after a period of lax management. The estimated size of the Pendjari and indeed the WAP complex makes this one of the most important lion population in West and Central Africa where the majority of lion populations are decreasing (Henschel *et al*., 2010).

The low lion density here is consistent with the lower prey biomass found in West Africa compared to high lion density populations in East and more mesic parts of southern Africa (East, 1984). Similarly, Celesia *et al*. (2010) found that lion density mostly correlated to rainfall, temperature and landscape features and secondary

Table 2 Some characteristics of lion population structure across Africa

Region	Country	Reserve	Area (km^2)	Total population estimate (adults & subadults)	Density (lion/ $100km^2$)	Mean lion group size	References
West Africa	Benin	Pendjari	4411	39 -52	0.7	2.3	Bauer & van der Merwe, 2004; Bauer *et al.*, 2003
				77	1.6	2.6	This research
	Nigeria	Yankari	2058	15	2.41	1.9	Henschel *et al.*, 2010
		Kaindji Lake	4000	24	2.97		Henschel *et al.*, 2010
	Senegal	Niokolo Koba Ecosystem	19130	60 (20-150)	0.3		Bauer & van der Merwe, 2004
	RCI	Comoé	11500	12 - 28	0.3		Bauer & van der Merwe, 2004
	Ghana	Mole	4921	0	0.2 – 0.6		Bauer & van der Merwe, 2004
			4600				Burton *et al.*, 2011
Central Africa	Cameroon	Waza	1700	60	2.3 - 3.5	1.5	Bauer & van der Merwe, 2004
	Cameroon			14-21	0.8 – 1.2	1.6	Tumenta *et al.*, 2009
	Tchad	Bénoué	1800		2.3	1.95	Schoe, 2007
		Zakouma	3054		1.7	2.7	Vanherle, pers.com
East Africa	Kenya	Masai Mara	1530	547	30 (20-40)		Ogutu & Dublin, 2002
	Tanzania	Selous	92000	3750	16	5.3	Spong, 2002
		Ngorongoro Crater	250	97	38.8		Hanby *et al.*, 1995
Southern Africa	Namibia	Etosha	22270	191-266	1.8 - 2	5.4 (mode 2.2)	Stander, 1991
	South Africa	Kgalagadi	9591	140	1.5		Mills *et al.*, 1978;
			9593	110 - 125	1.1 – 1.3		Castley *et al.*, 2002
		Kruger	23 700		3.3 – 9.6		Mills, 1995
	Zambia	Luangwa Valley	355	49	12.7	9.7	Yamazaki, 1996

to herbivore biomass, lion density being lower in arid and higher in moister ecosystems.

The low lion density in Pendjari and most countries of West and Central Africa is accompanied by small pride/group size (Bauer *et al*., 2003). These group sizes are similar to those of arid area populations in southern Africa, such as Etosha and Kgalagadi (Stander, 1991; Funston, in press) and even more prey rich areas such as Kruger National Park (Smuts, 1976). In these southern African populations although group size was small, average pride size did not vary across the prey biomass gradient (average 11-12 lions per pride), as it is in most other lion populations in eastern and southern Africa (Schaller, 1972; Creel & Creel, 1997). However in West and Central Africa, total pride size is seemingly difficult to assess by the methods we used as members of the same pride seem to have very few interactions, largely living apart and only coalescing occasionally (Bauer *et al*., 2003). In Pendjari, larger groups up to 10-12 lions were observed on few occasions not many years ago. Thus, West African lions do at times form prides the same size as lion elsewhere. This calls in question the findings of Bauer *et al*. (2003), and implies that West and Central African lions have a similar social structure to lions elsewhere.

Bauer *et al*. (2003) suggested three hypotheses to explain the small group size of lions in West and Central Africa: low mean prey body size, low prey density and dependence of lions on livestock. Alternatively strongly group territorial lions (Mosser & Packer, 2009) may be less inclined to form larger groups in areas where relative low lion density and distribution minimises the frequency and thus risk of intergroup conflict. In other low prey density areas, such as the Kgalagadi (Funston, in press), small average lion group sizes could be driven by low prey density, but equally chances of intergroup clashes in a low lion density area with relatively few large male coalitions may account for small average group sizes.

In Pendjari, lions are not dependent on livestock (Sogbohossou *et al*., in press). Thus, either low prey density or low lion density seem to be the most likely explanations for the grouping patterns observed generally in West and Central Africa. Furthermore, intense human induced disturbance and mortality, both via persecution and trophy hunting, may be important drivers of low lion density in most protected areas in West and Central Africa (Tumenta *et al*., 2009; Henschel *et al*., 2010). In support of the group territoriality hypothesis (Mosser & Packer, 2009), lions in Kgalagadi form larger stable prides when they have young cubs and then fragment into subgroups as the cubs get older (Funston, in press). Male coalition sociality is attributed to numerical advantage in inter coalition competition as larger coalitions have greater success in pride take-overs and longer tenure times (Bygott *et al*., 1979; Packer, 1986). In Pendjari, the smaller coalitions of males could thus be interpreted as a result of small group sizes, possibly relatively smaller pride

sizes, and maybe the low levels of competition between males for pride take-over. At this stage we have no substantive explanation for the even adult sex ratio with is typically biased towards females (Mills *et al*., 1978; Smuts *et al*., 1978; Stander, 1991; Creel & Creel, 1997) or the relatively low proportion of cubs observed. The later is possibly being influenced by the relative shyness of adult lions. Indeed, on a number of occasions, we noticed that lionesses, previously believed to be alone, move and brought their cubs out of hiding. The frequency of males observation could have been biased by the fact that males more than females are nomadic and cover large distances (Schaller, 1972). We have observed it in Pendjari with a collared male which was collared in the middle of the park but was observed in the hunting zone and in the upper north of the park.

Sport hunting and other human activities may have profound impacts on the lion population in Pendjari. More than half of the lion observations in the hunting zones were made at less than 10 km from the park. This skewed distribution is probably a consequence of human encroachment through farming, illegal grazing and hunting around the reserve. Lions from the park probably fill gaps created by hunting and poaching in Benin and Burkina Faso, comparable to the 'vacuum effect' described by Loveridge *et al*. (2007; 2010). The hunting quota of 3 lions per year corresponds to about 6% of the male (adults and subadults) population of the reserve. Usually adult mortality of male lions varies from 10 to 24% (Packer *et al*., 1988) and could be higher for problem animals (Woodroffe & Frank, 2005). So sport-hunting removed fewer lions than would be expected from natural causes what is relatively positive. More fortunately, this quota is never achieved which nevertheless does suggest a very low lion density in the hunting zones. Annually one and rarely two males are hunted out of the three on the quota and it would be unwise to increase the quota to its earlier level of six lions per year without further investigations. The difficulty hunters experienced in finding suitable lion trophies (Sogbohossou, pers. obs.) suggests that the lion population despite having recovered may not yet be robust enough to sustain high levels of trophy hunting offtake. It could also suggest that hunted males are mostly young due to their high mobility and more attention should be paid to the age of removed males.

Suggestions for conservation

Compared to other populations in West and Central Africa the Pendjari lion population is characterized by higher than average group sizes for the region. In relation with the extirpation of lions in the protected areas of countries such as Côte d'Ivoire, Nigeria and Ghana (Henschel *et al*., 2010), the Pendjari lion population appears as a hope for lion conservation in West Africa. However, despite the increasing trend of this population, the proportion of females was quite low, probably due to perturbations such as hunting and other anthropogenic activities. When we consider that the park is probably the source of most of the lions

killed in the bunting zones, trophy hunting could create a problem in the future, especially if the quota is increased. Thus, the trophy hunting quota should be kept at its current level. Further investigations will assess the sustainable level of lion hunting quota in Benin and Burkina Faso in order to save the West African lion populations. Efforts should also be made to keep poaching level low in the area and improve monitoring by park staff. Reliable longitudinal data on prey density and distribution will help to estimate the real carrying capacity of the reserve for lions and better assess changes in the lion population size. The management of hunting zones should be improved and the encroachment by humans into the reserve better controlled to encourage lions to disperse more into that area. This may increase the density and the stability in the hunting zone and decrease the pressure on the park population.

This study also highlighted the need for concerted transboundary management. The conservation of lion population in one reserve should be followed by conservation actions in surrounding reserves if to be efficient.

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5 Prey selection of lions (*Panthera leo*) in Pendjari Biosphere Reserve Benin, West Africa

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Submitted

Abstract

We collected scats and feeding observations of lions in order to analyse their prey selection in Pendjari Biosphere Reserve, Benin. Twelve species of ungulates comprised the majority (89%, n = 156) of the diet. The dominant two prey species were buffalo (21.5%) and Buffon's kob (17.8%). Based on biomass, buffalo represented 50% of the diet followed by hippopotamus (17%), and roan antelope (13%). Prey selected consisted of 57.1% medium-sized prey and 38.2% large prey species. The standardized mean niche breadth of lions was 0.44 and varied according to the period and the area analyzed (park or hunting zones). The two most-preferred prey species relative to their abundance were hartebeest and waterbuck, while duikers, oribi and baboon were avoided. Buffalo, roan, and warthog were preyed upon according to their abundance. Most carcasses located were adults (73.3%, n = 156). The mean adult lion feeding group size was 1.7 ± 0.9. Despite the lower proportion of large prey species in the lions' diet in Pendjari, our results are consistent with findings in other areas, taking into account the abundance of medium-sized species in the study area. Further research will help to determine the impact of lion predation on prey populations.

Keywords

diet, prey preference, *Panthera leo*, Pendjari Biosphere Reserve

5.1 Introduction

Lion *Panthera leo* is the top predator in African savannahs ecosystems (Radloff & du Toit, 2004; Owen-Smith & Mills, 2008) but has shown a drastic range and population reduction in the last few decades (Bauer & van der Merwe, 2004; Bauer *et al*., 2008a). In West Africa, where lion populations are highly fragmented and small, they are classified as being Regionally Endangered (Bauer & Nowell, 2004). With the raising of awareness on the status of the lion in the region since 2001 (Bauer *et al*., 2003a), several studies have tackled different aspects of the species' conservation, especially population status and conflicts with humans (Bauer *et al*., 2003b, 2008b; Bauer & de Iongh, 2005; Van Bommel *et al*., 2007; Tumenta *et al*., 2009; Bauer *et al*., 2010; Henschel *et al*., 2010). Among the less-investigated fields are lion-prey relationships (Bauer *et al*., 2008b). Information on the feeding ecology of large carnivores contributes substantially to the understanding of their behavioural ecology and management (Mills, 1992). Moreover, predator-prey relationships are known to impact on the social structure and home range of carnivores (van Orsdol *et al*., 1985; Bauer & de Iongh, 2005).

The foraging behaviour of lions has been widely studied in East and Southern Africa. Several factors such as prey encounter rates (Sunquist & Sunquist, 1997), the body mass of prey (Scheel & Packer, 1995; Sunquist & Sunquist, 1997), prey herd size (Schaller, 1972; van Orsdol, 1984; Funston *et al*., 2001), habitat use of prey (van Orsdol, 1984; Sunquist & Sunquist, 1997; Harrington *et al*., 1999), and anti-predator behaviour of prey (Eloff, 1964; Makacha & Schaller, 1969; Estes, 1991) have been shown to affect lion prey preference. Hunting techniques and success rates have also been investigated (Fuller *et al*., 1992, Stander & Albon, 1993; Mills *et al*., 1995; Sunquist & Sunquist, 1997; Funston *et al*., 2001). Lions prey on a large range of species; however, they show a preference for large species within the range of 190 to 550 kg (Hayward & Kerley, 2005). Hayward & Kerley's review (2005) revealed the gap in knowledge about lion foraging ecology in West and Central Africa. Most recent efforts have focused on Central Africa (Bauer *et al*., 2008b; Breuer, 2005) with very few data available for West Africa (Bodendorfer *et al*., 2006; Bauer *et al*., 2008b). Thus, there is an urgent need to better understand the ecology, behaviour, and relationships between endangered West African lions and their prey to improve conservation efforts.

Pendjari Biosphere Reserve supports one of the largest lion population in the region (Sogbohossou, 2009; Henschel *et al*., 2010) and has a reasonably large prey base, and was thus a good place to study lion prey selection. The study aimed to determine diet composition and investigate prey preferences, thus contributing to improved knowledge of lion feeding behaviour in the region.

5.2 Study area

The study was carried out from January 2009 to June 2010 in Pendjari Biosphere Reserve, Benin (Fig. 1). Pendjari Biosphere Reserve lies in north-western Benin between 10°30' - 11°30 N and 0°50' - 2°00' E. It covers 4711.4 km² and is part of a large complex of four protected areas lying in Benin, Burkina Faso, Niger and Togo and covering about 36,500 km². Pendjari Biosphere Reserve comprises a strictly protected core area, the Pendjari National Park of 2,660 km² and two hunting zones in the West (Konkombri) and South (Pendjari) part of the park. Between the Pendjari hunting zone and villages is a buffer zone of about 340 km² with controlled land use access for local people.

The topography is mostly flat, except for the Atakora Range (400-513 m above sea level) and few isolated hills (Delvingt *et al*., 1989), in the eastern part of the reserve. The reserve is mainly irrigated by the Pendjari River, which borders the reserve in the north and west. Most of the rivers and ponds that irrigate the area dry up during the hot season.

The mean annual rainfall varies from 800 to 1,000 mm, falling mainly from May to October. Mean monthly temperatures range from 19 °C during the cold dry season (November-January) to 34 °C during the hot dry season (February-May). The monthly average relative humidity varies between 25 and 85%.

The vegetation is burned every year, which results in a mosaic of grass, bush, and woodland savannahs with some gallery forests. The predominant tree genera are *Acacia*, *Combretum* and *Terminalia*. A variety of wildlife species live in the reserve, including buffalo *Syncerus caffer*, elephant *Loxodonta africana*, roan antelope *Hippotragus equinus*, hartebeest *Alcelaphus buselaphus major*, kob *Kobus kob* and various species of duikers (Sinsin *et al*., 2002a). Cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus*, which are largely absent from other reserves of the region, are found in Pendjari, but in low densities. Leopards *Panthera pardus* are present but their status is unknown. Lions and spotted hyenas *Crocuta crocuta* are the most abundant carnivore species, with a minimal density of 1.5 adult individuals/ 100 km² for each species (Sogbohossou, 2009). Livestock depredation has been observed on small and large livestock in the area.

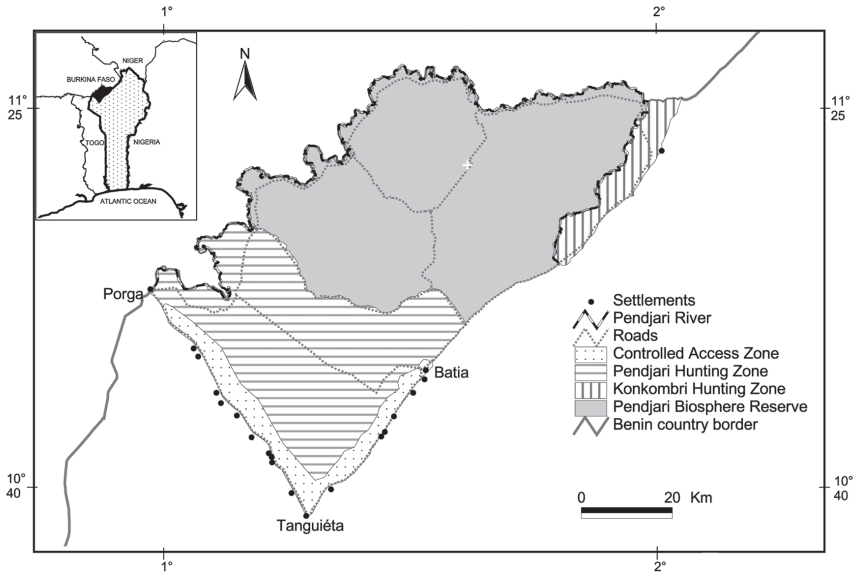

Figure 1 Location of Pendjari Biosphere Reserve

5.3 Methods

Lion diet was assessed from the combined analysis of scats and feedings observations in the study area (Schaller, 1972; Sunquist, 1981; Karanth & Sunquist, 1995, 2000; Scognamillo *et al.*, 2003; de Azevedo & Murray, 2007).

5.3.1 Scat collection and analysis

We collected lion faeces mostly in the park. Faeces identification was based on the shape, diameter, colour and odour, supplemented by the presence of associated signs of lion presence (mainly spoors and carcasses). Experienced trackers assisted us in the identification of faeces. In any case of doubt we excluded scat samples. The geographical coordinates were recorded for each scat collected.

With the hair extracted from each scat sample, we created 2 slides with 3 hairs each (n = 6 hairs). The prey species corresponding to each hair were identified based on the colour, the length, the scale with the aid of a microscope.

5.3.2 Interviews and observations

To supplement the low number of scat samples collected, we recorded all observations of lions feeding on carcasses. This method is considered to be biased

towards large preys (Mills, 1992). However, we thought direct observations of feeding would be less biased than carcass counts. This method also avoids biases about the carnivore responsible for the kill. For each observation, the location, species, and where possible the age class of the prey were recorded. We excluded a few observations of kills such as elephant carcasses because they had been killed by poachers.

5.3.3 Characterization of the lion diet

Species accumulation curves were determined following Nunez *et al.* (2000) to check if the number of scat samples and observations used could adequately depict the lion diet. We determined the frequency of occurrence of food items in scats by calculating percent composition based on relative frequency of occurrence (Neal & Sacks, 2001; Henschel *et al*., 2005; de Azevedo & Murray, 2007).

As we found no significant difference in the distribution of the frequencies of the different prey in observations and scats (Wilcoxon-Mann-Whitney test, z=-0.152; p=0.879), we put together the two data sets for the analyses.

Lion niche breadth was calculated using the niche breadth index (Levins, 1968), which corresponded to the relative frequency of occurrence of food items

$B=1/\Sigma_n\ p_i^2$

(p_i is the fraction of items in the diet that are of food category i).

The index was standardized to Bs following Colwell & Futuyma (1971), to allow comparisons. Values of Bs range between 0 (maximum specialization) and 1 (maximum niche breadth). Diet diversity (H') and evenness (E) were calculated using the Shannon-Wiener index (Pielou, 1977). The diet diversity has been calculated using the formula:

$H' = - \Sigma\ p_i \ln p_i$

in which:

p_i is the relative abundance of species i, calculated as the proportion of individuals of a given species to the total number of individuals in the community ($=n_i /N$)

n_i is the number of individuals in species i (the abundance of species i in all scats); and N is the total number of scat samples.

The formula of the eveness is: E = H'/lnS, S being the total number of species.

E varies between 0 (dominance) and 1 (equitability).

Prey preference was assessed using Jacobs' index D (Jacobs, 1974; Hayward & Kerley, 2005):

$$D=(r-p)/(r+p-2rp)$$

r is the proportion of all kills for a particular species (the fraction of a species in the diet)

p is the proportional availability of that species (the fraction of the species in the environment)

The index was calculated for each prey species using prey abundance, kills and scat analyses data. Jacobs' index ranges from +1 indicating maximum preference from -1 indicating maximum avoidance (Jacobs, 1974). Prey preference was calculated only for species for which abundance estimates were available. Data of prey abundance were derived from large mammal censuses in Pendjari Biosphere Reserve in 2000, 2001, 2002 (Sinsin *et al.*, 2001; 2002a, b). There were no more reliable or more recent censuses for all species. So we assumed that even if the density may have increased since 2002, the proportion of each species would probably have stayed approximately the same. All species of duikers, the most common being *Sylvicapra grimmia* and *Cephalophus rufilatus*, were considered as one species. We considered as large-sized prey species those that weighed more than waterbuck (180 kg), to allow direct comparison of our data with that of Bauer *et al.* (2008b). For the same reason, species weighing less than duikers are considered small prey. We used prey weight data from Kingdon (2001).

5.3.4 Data analysis

Analysis was done with SAS software. We tested the difference between the seasons and the park-hunting zones with Chi square. We checked the potential relationship between the size of the prey and the lion feeding groups with the Spearman correlation.

5.4 Results

5.4.1 Species accumulation curves in scats and observations

We identified prey species in 35 lion scats and collected 156 observations of lions feeding on carcasses. The accumulation curves (Fig. 2) show that while 50 observations seem to be enough to have a reliable estimation of the diet of lions, the 35

scats on their own would not have resulted in a reliable estimation of lion diet in our study site.

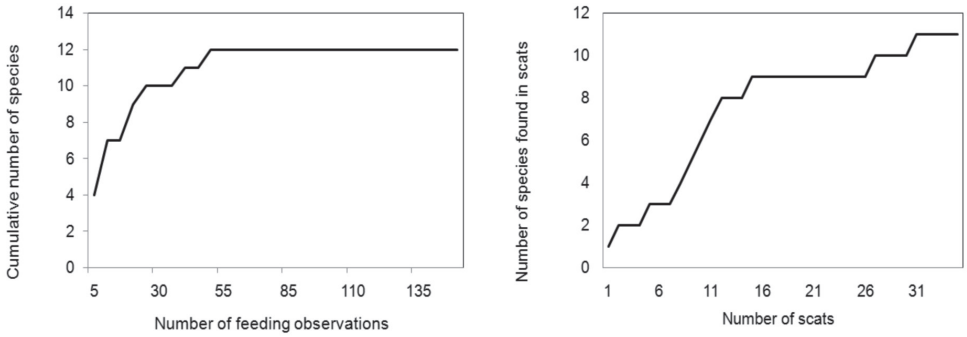

Figure 2 Species accumulations curves in scats and observations.

5.4.2 Species composition in the lion diet

Eleven species were identified in scats, while 13 species were identified by feeding observations. A total of 12 ungulate species were present in the diet of lions in Pendjari Biosphere Reserve. Table 1 presents the frequencies of the different prey items in the diet. Grass was also found in 22.8% of scats. The most frequent prey species of lions in Pendjari were buffalo (21.5% of the diet) and kob (17.3%). Hartebeest and roan antelope were also well represented in the diet, comprising 14.7 and 12.0% of the diet, respectively. With baboons (9.4%), these five species represented 74.9% of the lions' diet. Ungulates made up the largest portion of the diet (89%).

We noted the occurrence of a particular prey, hippopotamus, which represents 2.6% of the lion diet. Most (80%, n = 5) of the hippopotamuses preyed upon were young individuals, and mostly (80%) at the end of the dry season, when the majority of water ponds have dried up. When prey biomass was considered (Fig. 3), the five most represented species in the diet were buffalo (50% of the diet), hippopotamus (17%), roan antelope (13%), hartebeest (9%) and kob (5%). These five species composed 94% of the total diet biomass.

Based on direct feeding observations and scats analysis, medium-sized prey were dominant in the diet while large prey (≥180 kg) composed 38.2% of the diet and small prey composed 1.1%. Lions in the hunting zones have significantly more large prey in their diet than lions from the park (Fig. 4.) ($z = 2.45$; $p < 0.05$) however the proportion of medium-sized prey in the two areas is similar.

Table 1 Summary of kills based on feeding observations and scats in Pendjari Biosphere Reserve from 2008 to 2010.

Prey species	Number of observations	Number of scats	Total	Relative frequency (%)
Ungulates				
Buffalo *Syncerus caffer*	34	7	41	21.5
Roan *Hippotragus equines*	20	3	23	12.0
Hartebeest *Alcelaphus buselaphus major*	27	1	28	14.7
Topi *Damaliscus korringum*	2		2	1.0
Waterbuck *Kobus defassa*	3	1	4	2.1
Kob *Kobus kob*	29	4	33	17.3
Bushbuck *Tragelaphus scriptus*	4	2	6	3.1
Oribi *Ourebia ourebi*		3	3	1.6
Reedbuck *Redunca redunca*	4		4	2.1
Duikers	–	7	7	3.7
Warthog *Phacochoerus aethiopicus*	13	1	14	7.3
Hippopotamus *Hippopotamus amphibius*	5		5	2.6
Primates				
Baboon *Papio Anubis*	13	5	18	9.4
Rodents				
Cane rat *Thryonomys swinderianus*	1		1	0.5
Carnivores				
Hyaena *Crocuta crocuta*	1		1	0.5
Unidentified birds		1	1	0.5

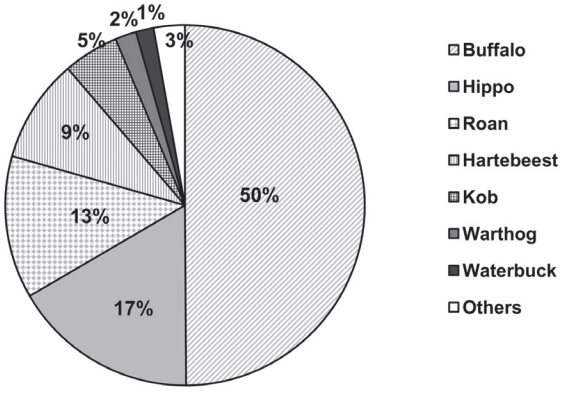

Figure 3
Proportional contribution of the different ungulate species to the total biomass of kills made by lions in Pendjari Biosphere Reserve from 2008 to 2010 (n = 191). "Others" designates species contributing least to lion kills (baboon: 0.8%; bushbuck: 0.6%; topi: 0.5%; redunca: 0.4%; duikers: 0.3%; oribi: 1%; hyena: 0.1%).

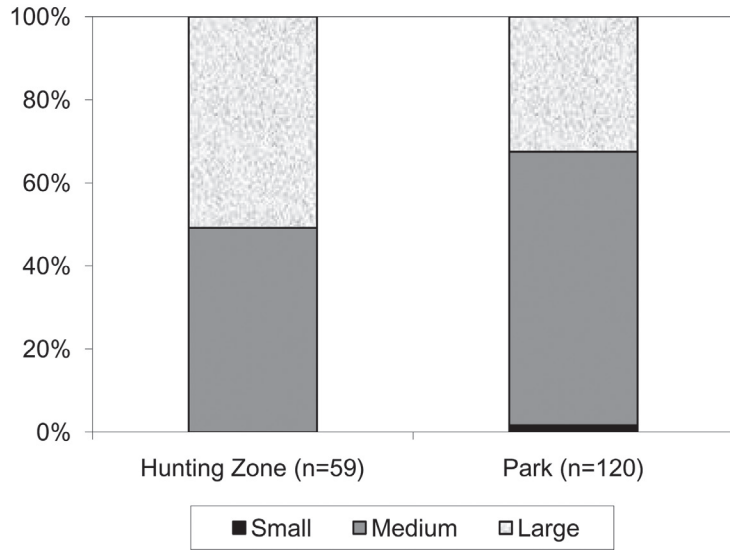

Figure 4 Proportion of different prey sizes classes in lion diet in the different parts of the reserve from 2008 to 2010 (n = 179).

5.4.3 Diet diversity and niche breadth

The calculated lion niche breadth index was B = 7.66 and the standardized index was 0.44. The diet diversity and evenness index for lions were 2.27 and 0.82, respectively. Table 2 presents the difference in the diet between the different areas of the reserve and between seasons. There were only two observations and scats collected in the rainy season so this period was left out of the analysis.

Table 2 Diet diversity and evenness and niche breadth of lion diet according to areas and to seasons in Pendjari Biosphere Reserve from 2008 to 2010.

		Diet diversity H	Diet evenness	Niche breadth	Bstan
Areas	Park (n = 124)	2.64	0.85	7.97	0.54
	Hunting Zone (n = 59)	2.20	0.89	6.05	0.63
Seasons	Dry (n = 105)	2.64	0.84	7.23	0.48
	Dry-Humid (n = 22)	2.07	0.88	5.04	0.58

5.4.4 Diet choice

The preference of lions for diverse prey species is presented in the Table 3. The most-preferred species were hartebeest and waterbuck. Warthog and buffalo were killed according to their abundance while smaller ungulates such as oribi

and duikers were generally avoided. The mean weight of non-preferred prey species, considering Jacob's index of each, was 19.4 kg. The mean weight of preferred prey species was 167.5 kg.

Table 3 Dietary preferences of lion in Pendjari Biosphere Reserve from 2008 to 2010 based on Jacob's index.

Species	Relative availability	Jacob's index
Hartebeest	0.042	0.613
Waterbuck	0.006	0.605
Kob	0.143	0.144
Bushbuck	0.028	0.084
Buffalo	0.204	0.068
Roan	0.120	0.034
Warthog	0.076	0.009
Redunca	0.025	-0.072
Baboon	0.151	-0.234
Duikers	0.119	-0.541
Oribi	0.086	-0.698

5.4.5 Diet characteristics

Lions predominantly killed adult individuals (73.3%, n = 120). The mean lion feeding group size was 2.4 ± 1.5 lions (1.7 ± 0.9 adults). We found no correlation between the prey weight and the size of the lion feeding group. However, there was a difference between the number of lions feeding on species of different weights (χ^2 = 23.37; df = 13; p = 0.04). We noted no difference among prey species between seasons. There were significantly more lions feeding on prey killed in the park than in the hunting zones (χ^2 = 5.69; df = 1; p = 0.02).

5.5 Discussion

5.5.1 Species composition and diet diversity

The number of lion prey species at a particular site usually varies from about 14 (Breuer, 2005) to more than 20 species (Pienaar, 1969; Hayward & Kerley, 2005; Funston & Mills, 2006; Lehmann *et al.*, 2008). In Pendjari, the diversity of the diet was lower, but almost all species present were recorded in their diet. Generally at most study sites about five prey species predominate, and typically make up

about 75% of the lions' diet (Stander & Albon, 1993; Funston *et al*., 1998; Druce *et al*., 2004; Radloff & du Toit, 2004; Loveridge *et al*., 2006).

Medium-sized prey dominate the lion diet in Pendjari Biosphere Reserve, which is similar to the findings of Bauer *et al.* (2008b), and Breuer (2005) in West and Central Africa. However, the proportion of medium-sized prey was slightly higher for this study (60.7% compared to 49% found by Bauer *et al*., 2008b). Conversely, there were more large prey in the diet of lions in Pendjari than in Faro National Park, Cameroon (Breuer, 2005). High proportions of medium-sized prey are also reported broadly from dry regions of eastern and southern Africa where these prey sizes predominate (Stander, 1992; Druce *et al*., 2004). Despite the high proportion of medium-sized prey in the lions' diet in Pendjari, the species most represented in the diet was buffalo, which is a large prey. This confirms at least partly the preference of lion for large prey species (Hayward & Kerley, 2005), with the mean weight of prey species being very similar to lion studies elsewhere (Radloff & du Toit, 2004; Hayward & Kerley, 2005; Owen-Smith & Mills, 2008).

A predominance of buffalo in the diet of lions has been reported in several national parks throughout Africa including Kafue (Mitchell *et al*., 1965), Hwange (Loveridge *et al*., 2006), Chobe (Viljoen, 1993), Lake Manyara (Makacha & Schaller, 1969; Schaller 1972), Mala Mala (Radloff & du Toit, 2004) and Kruger (Mills *et al*., 1995; Funston *et al*., 1998). In the few observations available for West and Central Africa, buffalo was among the most numerically abundant prey in the diet of lions only in Niokolo Koba and Zakouma (Bauer *et al*., 2008b). Due to the relative small size of lion groups in the region (Bauer *et al*., 2003b), this result was not expected and does question the generality of the findings of Bauer *et al.* (2008b). Because of the antipredatory defence behaviour of buffalo (Makacha & Schaller, 1969), it was expected that the small lion groups typically found in West and Central Africa (Bauer *et al*., 2003b; Sogbohossou *et al*., in prep.) would not easily kill buffalos. Schaller (1972) and Stander & Albon (1993) observed that lion hunting success is greater in larger groups, and notably Packer *et al*. (1990) found that large groups of lions (> five) were generally needed to capture buffalos. Although feeding groups in Pendjari varied from one to six individuals, in 46% of cases there was only one adult in the feeding group, two adults in 42% of observations and three adults in 8% of observations. If we suppose that these adults were the ones responsible for the kill, and that 71% of buffalo killed were adults, this would suggest that relatively small groups of adult lions in Pendjari are effective at killing adult buffalos. The high proportion of adult buffalo in kill records was also observed in Mala Mala Reserve (Radloff & du Toit, 2004). However, Funston *et al.* (1998) showed that lions in Kruger mainly killed buffalo calves and consumed them during the night. Thus our results must be interpreted with caution as kill remains as well as lions found feeding on carcasses does bias the results towards larger carcasses (Mills, 1992). In Beninese and West Africa savannah in general, buffaloes typically weigh about

473 ± 57 kg, n = 62 (DPNP, 2004; 2006; 2007; 2008; 2009) and occur in relatively small herds of five to fifty individuals, with exceptional herds numbering up to a hundred individuals (E.A. Sogbohossou, pers. obs.). In southern Africa, buffalos typically weigh about 750 kg and occur in herds of several hundreds. These differences could explain why lions in smaller groups in Pendjari are effective hunters of buffalo.

The predominance of large prey species consumed by the lions living in the hunting zone compared to those in the park was probably due to the relative abundance of large prey in the areas of the hunting zones where observations were made. Most observations were made along the Pendjari River, which had one of highest prey densities in the reserve. The lions' diet seemed to be less diverse at the beginning of the rains, which corresponded to the period during which lions and spotted hyaenas started predating on livestock outside the park in the village areas. With the first rains, grass starts growing and wildlife disperses (Hunter, 1952; Eltringham *et al*., 1999). At this time, some of the preferred prey species probably become more difficult to hunt, forcing lions to restrict their diet to the most available and easiest species to catch, including livestock.

The numerical importance of Buffon's kob in the diet of lions in West and Central Africa was also observed in Faro National Park in Cameroon (Breuer, 2005) and Comoé NP in Cote d'Ivoire (Bodendorfer *et al*., 2006), where kob were the primary prey species, accounting for about 35% of the diet. In other areas of West and Central Africa (Bauer *et al*., 2008b), kob was part of the diet but not as important. This species was more represented in the diet of smaller carnivores such as spotted hyaenas in the region (Di Silvestre *et al*., 2000). The position of hartebeest and roan among the top five numerically abundant species in lion diet has been confirmed by several studies in Central (Ruggiero, 1991) East and Southern Africa (Erasmus, 2008). Baboon was not a commonly eaten species.

We reported exceptional predation on hippopotamus. This is usually rare but has been observed in Kruger (Pienaar, 1969; Owen-Smith & Mills, 2008), and was reported to be quite common in Albert National Park (Bourlière, 1955). In particular the young individuals of this species are more vulnerable while grazing at night (Bourlière, 1955). This could explain the predation of the species in Pendjari, as all observations were of lions feeding on hippopotamus carcasses in the early morning hours, and all these prey were juveniles.

The absence of livestock in scat samples could be linked to the low level of livestock depredation by lions (Sogbohossou *et al*., in press). It could, however, also be due to the small number of scats collected in the hunting zones close to villages.

5.5.2 Prey selectivity

The two most-preferred species were large prey species (hartebeest and waterbuck), while the two least-preferred ones were very small species (duikers and oribi). This confirms the preference of lions for large prey species found in diverse studies (Hayward & Kerley, 2005), even sometimes despite the importance of medium-sized prey in their diet (Stander, 1992). Prey weight ranged from 1 kg (bird) to 1505 kg (hippopotamus). The preferred prey weights ranged from 69 kg to 180 kg, lower than what has been found by Hayward & Kerley (2005) and Owen-Smith & Mills (2008). As in Hayward & Kerley (2005) and Owen-Smith & Mills (2008), we noted that duikers, oribi and baboons were avoided by lions. Buffalo, the primary prey, was taken according to its abundance in the area. Like elsewhere (Hayward & Kerley, 2005), roan and warthog were killed according to their relative abundance. Hartebeest and waterbuck were also preferred prey species which was not always the case in other studies (Hayward & Kerley, 2005). The dependence of waterbuck on water (Pienaar, 1969) probably facilitated its predation by lions. Hartebeest are said to be predator-naïve compared to species such as zebra, oryx and waterbuck (Georgiadis *et al.*, 2007). This could explain why they are among the most preferred species because lions are highly opportunistic and prefer easy and accessible prey (Schaller, 1972).

The selection of adult prey was noticed elsewhere (Power, 2002; Lehmann *et al.*, 2008). The proportion of medium and small-sized prey we found in the diet is consistent with other studies in the region (Breuer, 2005; Bodendorfer *et al.*, 2006; Bauer *et al.*, 2008b), however, the main method we used is said to overestimate adults and large prey (Mills, 1992). Therefore further studies are necessary to confirm our findings.

5.5.3 Implications for conservation

The results of this study on lion diet in Pendjari revealed that lions adapt their feeding behaviour to their environment and prey availability. This supports the view that lion populations in our study area depend less on livestock than do lions in many other reserves in West and Central Africa (Bauer *et al.*, 2008b; Tumenta *et al.*, 2009). This is a positive aspect for the cohabitation of human and lion populations and also for lion conservation in the region.

The predominance of medium-sized prey that usually represents a greater part of the diet of other large carnivore species (Di Silvestre *et al.*, 2000; Breuer, 2005) suggests that these species will turn to smaller prey species or compete more with lions. Studies on feeding habits of other carnivores that inhabit Pendjari are necessary. However it is probable that this cohabitation is more harmful to other predators than to lions. As prey census data we used were not recent and some prey

abundance data was lacking, it would be interesting to have more recent and reliable data on all prey species for further analysis. Furthermore, the system for monitoring the population of ungulates should be improved in Pendjari so that we can have a more complete figure on the prey preference of lions and other predators.

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6 Preliminary results on lion home range and habitat use by lions in Pendjari Biosphere Reserve, West Africa

Sogbohossou E.A.

Abstract

Lion home range and habitat were studied using radio-tracking data collected on three lionesses in Pendjari National Park, West Africa. Mean estimates of home range using 95 and 100% minimum convex polygon were 200 ± 141 km² and 256 ± 154 km², respectively. These home ranges were in accordance with values obtained in other parts of Africa with a relatively low prey biomass. Home range sizes in Pendjari confirmed the relatively healthy status of the lion population in this reserve, compared to other parts of West and Central Africa. Habitats used by lionesses varied according to the season. During the dry season, the lionesses showed a preference for riparian forests and habitats around water, dry forests and woodlands. In the wet period, vegetation on rocks and hills, woodlands and dry forests were favoured. The preferred habitats were in accordance with the usual habitats of the main prey species. Individuals collared close to the border spent about 25% of their time in Burkina Faso reserves, which were less protected than Pendjari Biosphere Reserve. This study confirmed the vulnerability of the lion population, especially that of the prides at the edge of the park. We also suggest that particular attention should be paid to transboundary management of protected areas if lions are to be conserved in West Africa.

Keywords

lion, home range, habitat, transboundary conservation

6.1 Introduction

Large carnivores occur at low densities and need large territories (Schaller, 1996) due to their biological traits. The home range of an animal is defined as "the area traversed by the individual in its normal activities of food gathering, mating and caring for the young" (Burt, 1943). A lion's territory is the part of a lion home range avoided by other lions or defended against other lions' intrusions (Schaller, 1972). Lion home ranges vary from 20 to 600 km² (Schaller, 1972; van Orsdol *et al*., 1985). Large home ranges overlap extensively with those of adjacent prides, while small home ranges tend to have little overlap. Several factors may influence home range size. Prey availability and distribution has been shown to significantly affect the home range size of lions and other large carnivores (Macdonald, 1983; van Orsdol *et al*., 1985; Grigione *et al*., 2002; Bauer & de Iongh, 2005) while Spong (2002) found that the home range size was not correlated to pride size. The lion' sex may also influence the size their territories. Loveridge *et al*. (2009) showed that the home range size of lionesses was influenced mainly by pride size, prey abundance and dispersion, while for male lions it is also determined by prey biomass and female pride density. Intra- and interspecific competition, physical barriers, the season, food resources and water can influence home range size (Spong, 2002; Druce *et al*., 2004).

Lions are highly mobile and can disperse very far (Schaller, 1972). Their movements in different types of habitats are influenced by factors such as protection for their cubs (Donkin, 2000), cover for hunting (Van Orsdol, 1984) and prey availability (East, 1984; Creel & Macdonald, 1995; Funston *et al*., 1998). Lions have a marked preference for open woodlands and grasslands (Druce *et al*., 2004)

As pointed out by Loveridge *et al.* (2009), little is known about lion ranging behaviour in dystrophic savannahs. These types of savannahs, characterized by low herbivore density, (East, 1984; Fritz *et al*., 2002) are the most common in West and Central Africa. The first studies in the region revealed that the large home range of lions is not only due to lower prey biomass but also to livestock raiding around protected areas (Bauer & de Iongh, 2005).

This short study aimed at improving the knowledge of lion ranging behaviour in West Africa with the anthropogenic pressures known by most protected areas. Specific objectives are to evaluate the home range and the habitat preference of lions in Pendjari Biosphere Reserve, a typical West African protected area.

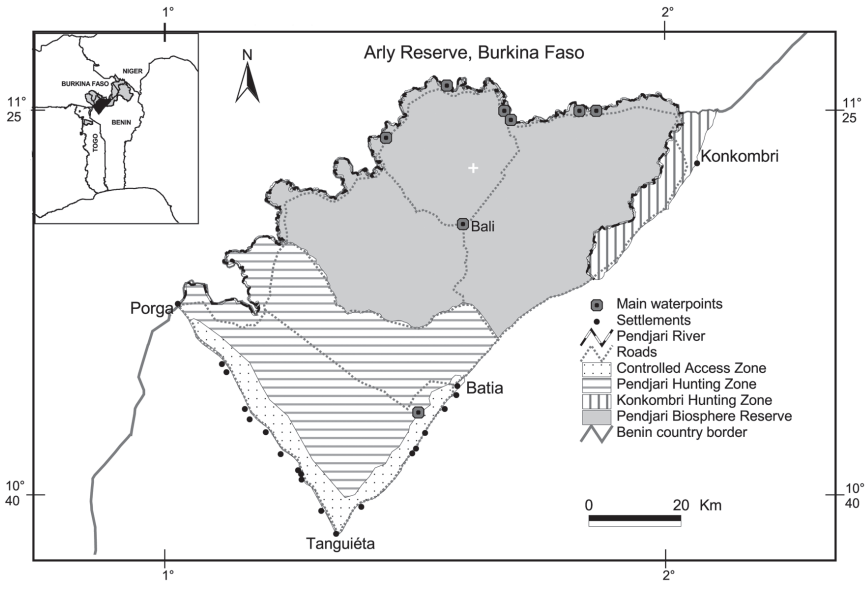

Figure 1 Pendjari Biosphere Reserve in Benin

6.2 Methodology

6.2.1 Study area

Pendjari Biosphere Reserve is a reserve located in Sudanian savannahs of West Africa. Like other areas in the region, it is characterised by low prey biomass and relatively low herbivore and carnivores densities compared to areas of eastern and southern Africa. However, as one of the best protected areas of the region, it has a relatively higher herbivore and carnivore biomass than other reserves of the region (Sogbohossou *et al*., in prep). The Pendjari Biosphere Reserve (10°30 to 11°30 N latitude and 0°50 to 2°00 E longitude) lies in northwestern Benin. The reserve is composed of a national park (2,660 km²) and Pendjari (1,600 km²) and Konkombri (250 km²) hunting zones. There is a third part, the buffer zone, also called the 'controlled access zone', where some activities such as the collection of hay and firewood as well as farming are allowed. Most human settlements are located along Pendjari hunting zone. The main activities of local populations are extensive farming and husbandry. Pendjari Biosphere Reserve is part of a complex of four protected areas laying between Benin, Burkina Faso, Niger and Togo on about 36,500 km². The climate is characterized by one rainy season from May/June to October and one dry season. The mean annual rainfall varies from 800 to 1000 mm from the northern to the southern part of the reserve. The topography is relatively flat except for the Atacora mountains range that borders the reserve on the east, and

a few hills inside the reserve. The reserve is irrigated by the Pendjari river which borders it in the north and by some waterpoints. Most waterpoints dry up during the dry season, while much of the park is flooded during the rainy season. The vegetation in the reserve is a mosaic of savannahs from grasslands to dry forests (Sokpon *et al*., 2001). Almost all species characteristic for the West African savannahs are present in the reserve (Delvingt *et al*., 1989; Sinsin *et al*., 2002). All large carnivores known to occur in West Africa are present, with cheetah and wild dog at very low densities. About seven to eight prides of lions were found to live in the reserve, with a lion density of 1.6 lions/100km² (Sogbohossou *et al*., in prep).

6.2.2 Methods

Collaring and telemetry

We used calling station surveys according to the methodology of Ogutu & Dublin (2002) to attract lions to a collaring site. Lions were anaesthetized using Zalopine and Ketaject one time and Zoletil 100 with a DAN inject immobilization gun. Lions were equipped with GPS Plus collars with a VHF transmitter purchased from VECTRONICS Aerospace. The collars were programmed to record a fix every hour. Telemetry was carried out on the ground using a vehicle or from some small hills. The vegetation, topography, and relatively few roads in the park limited the downloading of data from the collars.

Two lions and four lionesses were collared in Pendjari National Park. Data were available only for three lionesses. Table 1 presents some characteristics of the collaring operation of these lionesses.

Table 1 Description of the collaring of three lionesses in Pendjari National Park

Lionesses names	Collaring date	Sex	Age	Other lions present	Available data
Missi Sothiré	May 17, 2008 & Jan 15, 2009	Female	7-8 years	Alone in 2008 With a female and 3 cubs in 2009	May 2008 to January 2010 (4654 fixes) January 2009
Charlotte Adjima	January 16, 2010	Female	6-8 years	2 males, 1 female	January to April 2010 (1261 fixes)
Daniek Nekima	January 11, 2010	Female	5-6 years	1 male, 1 female, 2 cubs	January to May 2010 (2843 fixes)

Lion home ranges were estimated using Arcview extension Animal Movements package (ArcView GIS, version 3.2, Environmental Systems Research Institute, Redlands, CA, USA). The Minimum Convex Polygon (MCP) method (Stander,

1991; Funston *et al*., 2003; Bauer & de Iongh, 2005; Jhala *et al*., 2009) was used to allow comparison with other studies. The 95% MCP is considered to remove the effect of exploratory movements. The kernel method has also been used to estimate home range size. The Animal Movement Analyst program calculates the least squares cross validation (LSCV) for the smoothing parameter to minimize the errors (Worton, 1989; Seaman & Powell, 1996). We estimated the 50 and 95% kernel, the 50% kernel usually being considered the core home range (Druce *et al*., 2004).

Habitat selection

For the habitat use analysis, Arcview Geoprocessing Tool (Assign data by location) has been used to assign a vegetation type to each fixes. According to the most recent vegetation map available of the reserve, there were 18 types of vegetation. We combined the most similar ones in order to obtain seven types of vegetation:

- Riparian forests and water
- Swamp savannahs and grasslands
- Woodlands with *Anogeissus* and dry forests
- Woodland savannahs dominated by *Burkea africana*, *Vitellaria paradoxa*, *Crossopterix febrifuga* or *Acacia sp*.
- Shrub savannahs with *Acacia* sp. or with *Crossopteryx febrifuga*
- Inselberg vegetation or savannahs on rocks.
- Other: woodlands or shrubland dominated by *Combretum sp.* and farms

With the proportion of time spent in each type of vegetation, habitat preference was assessed through the Resource Selection Program (Ecological Methodology; Krebs, 1999) based on Manly's selection index (Manly *et al*., 1993). The selection index is measured by the formula:

$$w_i = {}^{oi}/_{pi}$$

where

w_i = Ratio for vegetation type *i*
o_i = Proportion or percentage of time spent (corresponding to number of fixes) in vegetation *i*
p_i = Proportion or percentage of vegetation *i* available in the environment

Values above 1.0 indicate preference while values less than 1.0 indicate avoidance. The standardized index B_i allows comparisons:

$$Bi = {}^{wi}/_{\sum_{i=1}^{n} \hat{w}i}$$

where B_i is the standardized selection index for vegetation *i* and $\hat{w}_i$ is the ratio for vegetation *i*. Values below 0.143 (corresponding to 1/number of vegetation types) indicated relative avoidance while values above indicate relative preference.

6.3 Results

6.3.1 Lionesses' home range

The mean home range size estimated by 100% MCP is 256 ± 154 km² (range from 96 to 403 km²). The home range size considering 95% MCP was 200 ± 141 km² (range from 50 to 330 km²). The mean home range used in the dry season was 285 ± 190 km², MCP 100% (133 ± 171 km², MCP 95%). The mean core home range (50% kernel) is 33.57 ± 18.43 km². The 95% kernel home range is 170.87 ± 95.75 km². The home ranges of the three females are presented in Fig. 2 and Table 2. The two lionesses that were collared not too far from the border with Burkina Faso regularly crossed the Pendjari River to spend some time in Arly Reserve in Burkina Faso. Approximately 31.40% of lioness Nekima's fixes were in Burkina Faso compared to 27.10% of Charlotte's. When we considered the 100% MCP home range, 35.37% of Nekima's and 27.56% of Charlotte's home ranges were in Burkina Faso. If we consider 95% MCP, 41.40 and 33.67% of the home ranges of Nekima and Charlotte extend to Burkina Faso, respectively.

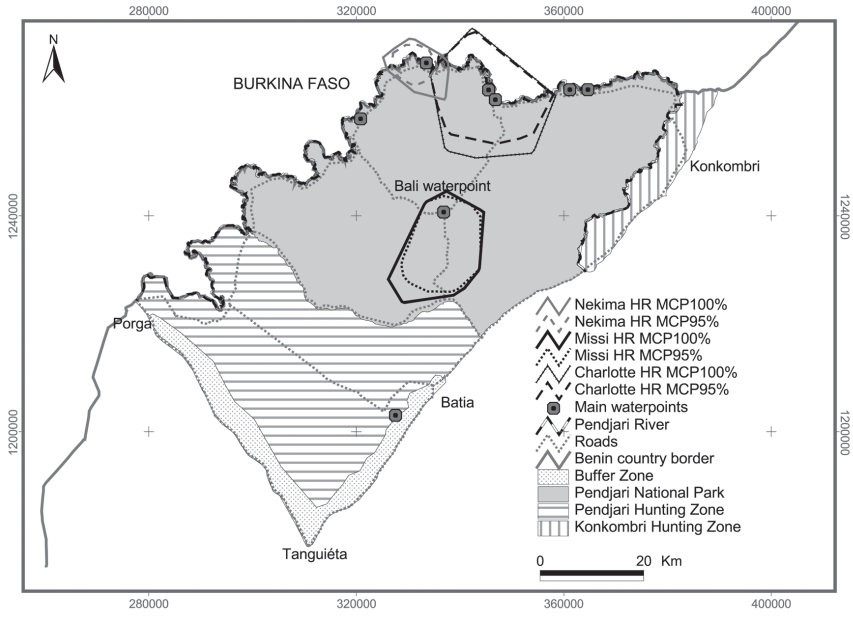

Figure 2 - Home ranges of three collared lionesses in Pendjari Biosphere Reserve.

Table 2 Home range sizes

Lionesses	Home range			
	MCP 100%	MCP 95%	Kernel 50%	Kernel 95%
Nekima Daniek	95.98	50.46	12.68	61.21
Charlotte Adjima	403.32	330.15	40.50	237.92
Missi Sothiré	267.86	219.72	47.53	213.48

6.3.2 Selection for habitats

The lionesses in Pendjari spent most of their time in swamp savannahs and grasslands and in woodlands (Table 3). When the availability of each habitat type is considered, the results are different. During the dry season, the three most preferred habitats by the lionesses were in order of preference: riparian forest and water > Woodlands with *Anogeissus* and dry forests > grasslands and swamps (Table 4). Grasslands and swamps, however, were used according to their availability. The lionesses avoided vegetation on rocks and hills. Rainy season data, available only for the lioness Missi, indicated that during this period, inselbergs and vegetation on rocks that were avoided during the dry season were preferred lion habitat, along with woodlands with *Anogeissus* and dry forests. After the start of the rains, the lionesses avoided grasslands and swamps, which were the first habitats to be flooded.

Table 3 Time spent by lionesses in each type of habitat

Habitat type	Proportion of time spent in each type of vegetation by lionesses			
	D. Nekima	C. Adjima	S. Missi	Mean
Woodlands	18.96	32.31	29.49	26.92
Shrub savannah & shrublands	7.58	21.66	10.76	13.33
Dry Forest	6.43	4.54	7.73	6.23
Gallery & water	25.71	8.96	9.79	14.82
Swamp savannahs& grasslands	40.44	30.05	28.36	32.95
Inselbergs	0.05	0.45	9.07	3.19
Others	0.83	2.03	4.8	2.55

Table 4 Habitat selection indices for lionesses in Pendjari Biosphere Reserve (Manly's alpha if non-selective habitat = 0.143) (w_i, selection index; B_i, Standardized selection index)

Habitat	All lionesses, dry season		Missi, dry season		Missi, rainy season	
	w_i	B_i	w_i	B_i	w_i	B_i
Woodland savannahs	1.033	0.060	1.003	0.055	1.4	0.099
Shrub savannahs	0.329	0.019	0.103	0.006	0.549	0.039
Woodlands with *Anogeissus* and dry forests	2.292	0.134	2.691	0.148	3.252	0.232
Riparian forests and water	11.471	0.669	12.044	0.662	1.254	0.089
Grasslands and swamps	1.829	0.107	2.124	0.117	0.506	0.036
Inselberg vegetation or savannahs on rocks	0.107	0.006	0.140	0.008	6.489	0.463
Other	0.099	0.006	0.099	0.005	0.57	0.041

6.4 Discussion

Despite the relatively low success of lion monitoring through the GPS-VHF collars used in Pendjari, the high number of fixes suggests that data collected were reliable, particularly concerning the home range and habitat use patterns for the dry season. In fact, for the dry season, data from the three lionesses for a mean period of 3 months with at least 6 fixes per day was available. The type of vegetation, the few roads and restricted accessibility in Pendjari limited the amount of data collected. For future studies, it would be interesting to test or combine other methods such as aerial search for collared lions.

Compared to the mean MCP home range value of 806 km² found for lionesses in Waza National park (Bauer & de Iongh, 2005), the mean territory size of Pendjari lionesses, 256 km², was not very large. The home ranges of the lionesses in our study fitted with the values of 20 to 400 km² found by several studies in eastern and southern Africa (Schaller, 1972; van Orsdol *et al*., 1985; Loveridge *et al*., 2009), taking into consideration the lower prey biomass expected in the area (East, 1984). The home range sizes in Pendjari were small, compared to home ranges of 600 to 1000 km² reported for arid zones of eastern and southern Africa such as Etosha (Stander, 1991). This suggests that resources to sustain lion populations are not so scarce in Pendjari. Indeed prey biomass in Pendjari ranged between 615 to 1665 kg/km² (Sinsin *et al*., 2006; 2008) while it was between 400 and 800 kg/km² in Waza National Park (Bauer & de Iongh, 2005). As with to the social structure of lion population in Pendjari Biosphere Reserve, the home range indicated that the Pendjari lion population is relatively healthy and has a good growth potential.

Results revealed a large difference between the home range sizes of different individuals, which could be attributed to several factors. The smaller home range of Nekima could be explained by the fact that she had two large cubs which may have limited her movements. Bauer & de Iongh (2005) also noticed in their sample that a female with cubs had the smallest home range.

The annual home range of lionesses in Pendjari reserve could be higher than what has been obtained. Usually the home range changes according to seasons in relation to prey availability and abundance (Schaller, 1972; Macdonald, 1983). Conversely, in some areas, home ranges do not change significantly with seasons (Druce *et al*., 2004; Loveridge *et al*., 2009). In our area, most water sources dry up during the dry season, as noticed elsewhere (Thrash *et al*., 1995; Loveridge *et al*., 2009). Herbivores and their predators are concentrated along the remaining waterpoints. During the rainy season, grass and water are available everywhere. Prey are randomly distributed throughout the reserve. Lions are then obliged to disperse, increasing their home range, as found by Bauer & de Iongh (2005). Whether the displacement of the home range led to a significant increase of the home range needs to be confirmed by further studies in Pendjari Biosphere Reserve.

The preference for a certain habitat type was in accordance with home range variations. During the dry season, as found by Spong (2002) and Loveridge *et al.* (2009), lions focused their activities along watercourses and waterpoints where prey were most abundant. They then preferred riparian forests and vegetation surrounding waterpoints. Usually these habitats and woodlands offer moist shade against the heat of the dry season. These habitats also provide a good cover to protect their cubs and to ambush prey (Donkin, 2000). According to Hopcraft *et al.* (2005), lions prefer to feed in areas with high prey catchability rather than high prey density. During the dry period, riparian forests and woodlands provide both. The preferred habitats also harbored many common prey species in Pendjari. Species such as waterbuck, Buffon's kob and buffalo are commonly found in riparian forests and woodlands. This preference for denser vegetation is not a rule as in reserves such as Makalali (Druce *et al*., 2004) and Phinda (Hunter, 1998) in South Africa, grasslands and low open woodlands were favoured.

During the rainy season, when vegetation around waterpoints, swamps and grasslands are flooded, rocks, inselbergs and woodlands are preferred. The hills and rocks probably facilitate the view and hunting by predators such as lions. These habitats also shelter the hartebeest (Sinsin *et al*., 2002) which is the most preferred prey species of lions in Pendjari (Sogbohossou *et al*., in prep). The rainy season is the period during which livestock depredation in villages by lions is the highest. Probably some lion individuals avoid flooded areas by occasionally going into human settlements to prey upon livestock, which represent easy prey. Further

studies will reveal whether certain problem animals are responsible for attacks on livestock or if depredation is due to any lion that is occasionally present in villages.

Implications for conservation

According to Woodroffe & Ginsberg (1998), the average female home range size is a good predictor of critical reserve size. If we considered that the mean home range found for the lionesses correspond to the mean home range of a pride, then the eight to ten prides thought to live in Pendjari Biosphere Reserve could fit in the reserve. Although this is a positive finding, the lion population is still vulnerable. Our observations mainly covered the dry season movements and we cannot exclude that during the wet season these lionesses would have larger home range. Even in the dry season when home ranges are smaller, a large part of the lion population lives at the edge of the park. These lions move easily and regularly to Burkina Faso, where protection is less effective than in Pendjari. The analysis of the home range of a lioness such as Missi suggested that the lions that live in the hunting areas could also easily move into villages and then be vulnerable to anthropogenic activities from human settlements. Most of the lion groups or prides are thus subject to edge effects and to human threats from hunting zones in Benin and Burkina Faso. This study confirmed that the conservation of the lion population and other resources within a protected area are not limited to the conservation inside the boundaries of this area but should be extended to all neighbouring areas. In order to cope with these edge effects, the reserve management should be intensified both in the park and in hunting zones. Also, conservation actions should be concerted between all countries which share contiguous protected areas. Transboundary management of resources is the key to lion and wildlife conservation in West Africa.

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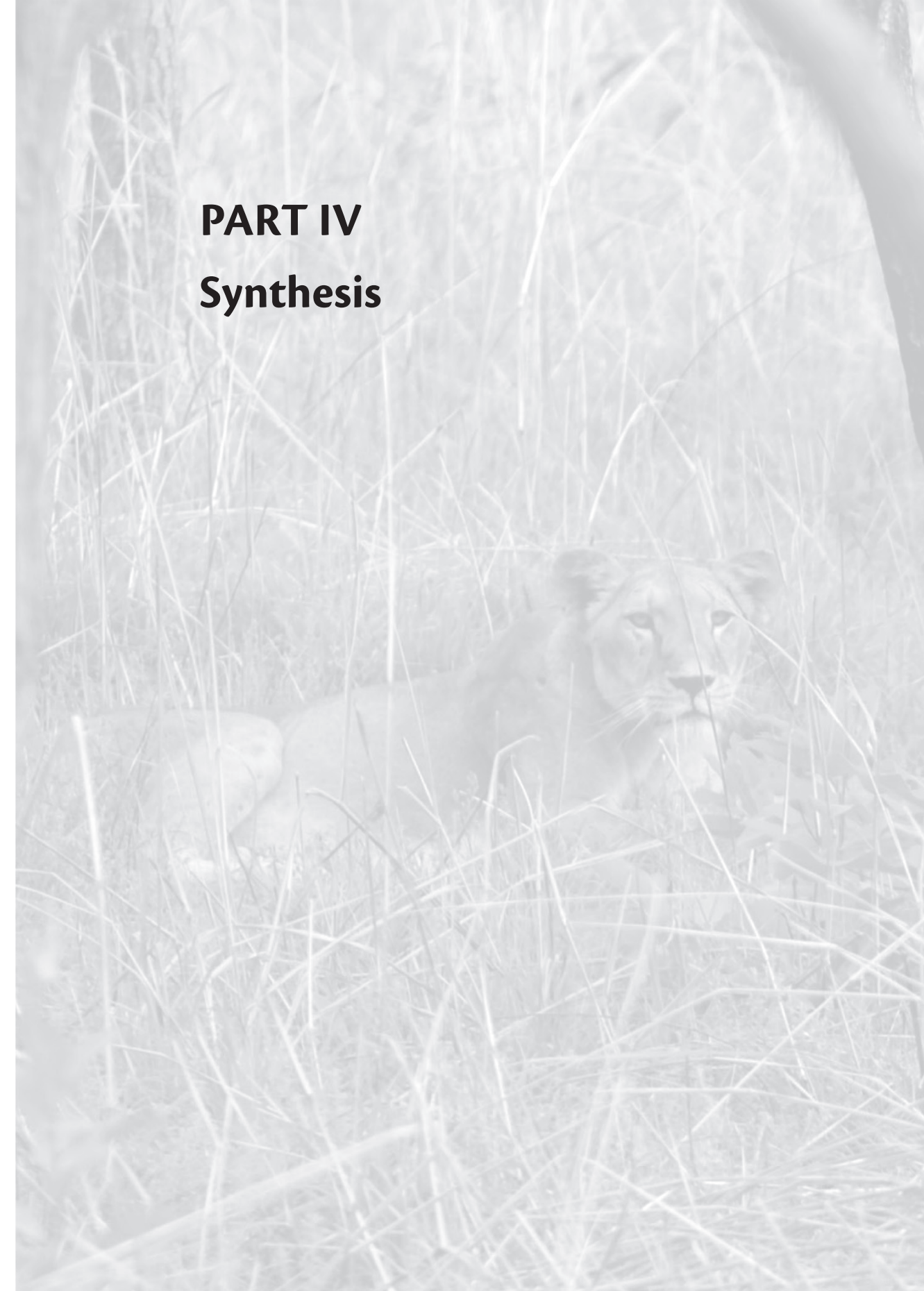

PART IV
Synthesis

7 Synthesis

7.1 Introduction

As set out in the introduction, this research aimed to address some aspects of the ecology of lions and their conflicts with humans in the Pendjari Biosphere Reserve, West Africa. The objectives of the study were to assess the characteristics of human-predator conflicts and how people perceive these conflicts, examine lion population social structure, analyse lion diet and determine habitat use by lions. We aimed at obtaining a better understanding of a typical lion population from West Africa in order to identify the threats faced by such populations, to identify challenges for their conservation and to raise awareness among policymakers so as to develop policies aimed at conserving regionally endangered lion populations.

7.2 Carnivore-livestock conflicts

Since the improvement of conservation activities in the Pendjari Biosphere Reserve in 2000, human-carnivore conflicts have been increasing. Lion, the third livestock depredator after spotted hyaena and baboon, is responsible for 18% of livestock attacks reported in this study. Like in many other areas (Patterson *et al.*, 2004), carnivore attacks peaked in the rainy season. During this period, wild prey are randomly dispersed in the area where visibility is reduced due to the height of the grass, making hunting more difficult than during the dry season when most species are concentrated around the few remaining waterpoints. Lion predated mostly on cattle but also on small livestock. As expected, predation was higher closer to the protected area. Livestock depredation in Pendjari, like in many other areas in the region and elsewhere in Africa (Ogada *et al.*, 2003) was favoured by poor husbandry techniques. The minor significance of lion-human conflicts suggests that lions in the Pendjari region do not depend on livestock, in contrast to many other parts of Africa (Patterson *et al.*, 2004; van Bommel *et al.*, 2007) where the frequency and intensity of conflicts is greater.

People living around the Pendjari Biosphere Reserve were tolerant of conflicts. Most people supported conservation activities but they have a generally negative perception of carnivores. The local population has a moderate knowledge of

carnivore species, probably due to the proximity of the reserve and their tolerance to conflicts could be partly attributed to their cultural background, which favors the conservation of carnivore species. It is important to note that the tolerance varied according to ethnic groups: the Berba were the least tolerant, while the Waama were the most tolerant group. Other factors such as age and cultural background also affect how people perceive conflicts. With modernization and the associated loss of traditional values, more efforts should be done to encourage local communities to participate in conservation efforts. An integrated approach, combining education, the promotion of improved husbandry techniques and the development of economic incentives together with the effective participation of local populations could help to mitigate conflicts and save the threatened carnivore species of West and Central Africa. The economic incentives to be developed should be chosen after effective consultation with local people. Projects such as those of the Network for Lion Conservation in West and Central Africa (ROCAL) conflict-mitigation projects around Pendjari Biosphere Reserve (Tehou, 2009) should be developed on a larger scale. Projects should take into account the needs of each ethnic group or each socio-professional class, with special consideration for women. As it has been pointed out in chapter 3 on perceptions, people should be aware that all these projects exist because of the protected areas and that they are a form of compensation for losses and damages. Wildlife and environmental education could be added to school programs in order to develop awareness among the youth. Children are the future, and properly educating them will help to guarantee conservation of the lion and of wildlife in general.

Fortunately despite the occurrence of predator-livestock conflicts, disturbing behaviour such as the retaliatory killing of lions and other carnivores was not common in Pendjari Biosphere Reserve. Improved participation of the local population in conservation programmes helps prevent negative behaviour. The park staff is already making appreciable efforts in this direction (Tiomoko, 2007), however local peoples' perceptions revealed that these actions were not yet sufficient.

If possible, future projects should integrate traditional knowledge. A preliminary study has been done on how cultural aspects and traditional hunters could be used in conservation activities around Pendjari Biosphere Reserve (Ratié, 2010). However this initiative, that would empower local people, also carries a certain risk so it will be important to conduct it gradually and take enough safeguards to prevent any failure.

7.3 Elements of lion ecology in Pendjari Biosphere Reserve

The three top factors that threaten lions with extermination in West and Central Africa have been identified by the Lion Conservation Strategy (IUCN/SSC Cat Specialist Group, 2006) as the loss, degradation and fragmentation of the habitat, the loss of a wild prey base and human-lion conflicts. The assessment of human-carnivore conflicts in Pendjari Biosphere Reserve suggested that these conflicts were not as important as in most other parts of West and Central Africa (Bauer *et al.*, 2003; Bauer *et al.*, 2010). Other factors such as human encroachment on lion habitat and hunting have probably more impact on the survival of lion populations in this reserve.

Lion occurred in Pendjari Biosphere Reserve at a density of 1.6 lions/100 km^2. In contrast to most populations in West and Central Africa (IUCN/SSC Cat Specialist Group, 2006; Tumenta *et al.*, 2009; Henschel *et al.*, 2010), the lion population in the Pendjari Biosphere Reserve is increasing. This reserve thus offered a more effective protection to lion populations than most protected areas in the region. The mean group size of 2.6 individuals was significantly higher in the National Park than in the hunting zones. Although pride size has not been estimated, we know that lions do form prides in West Africa. Human disturbance, mainly through poaching and sport hunting led to high mortality and considerable edge effects, thereby contributing to the small group size of lions in West Africa. Surprisingly, the sex ratio was not in favour of females as it is normally observed in lion populations. This may be partly due to the monitoring method used that could lead to overestimate males' proportion in the population. However the low proportion of females and cubs suggested a high mortality and pressure on lions in the reserve. This sex ratio suggested particularly a high female mortality that could not be explained in Pendjari. This implies that either the threat comes from adjoining reserves in Burkina Faso or there is poaching of lionesses in Pendjari that is unknown to us. Considering that the hunting quotas are relatively low and that the known poaching level is also low, it is likely that the pressure may come from neighbouring areas. Indeed Pendjari is part of an ensemble of five protected areas with their annex zones in four countries: W in Benin, Burkina Faso and Niger, Arly in Burkina Faso, Oti-Mandouri and Kéran in Togo. Currently Pendjari and probably the Niger part of the W transboundary reserves are the best-protected parts of the complex. Pendjari is just adjacent to the hunting zones of Burkina Faso, where the protection status is lower than in Benin (UICN/PACO, 2009). One of the indicators of this lower protection level in Burkina Faso is the large number of poachers and herders that come into Pendjari from the Burkina Faso side. In addition, in the neighbouring areas in Burkina Faso, the lion hunting quota is the highest in the region: more than 20 lions annually (IUCN/PACO, 2009). Similarly, in the neighboring W Benin reserve, there are more conflicts with humans than in Pendjari due to the fact that cattle herders often frequent the park. In contrast to Pendjari, evidence of retali-

atory killing of lions has been found in the past in W Biosphere Reserve in Benin and herders from W admitted to poisoning lions that kill their cattle. The Pendjari lion population probably serves as a source population and the lion population in Burkina Faso and W Benin as a sink. All of this has raised the question of transboundary management of adjoining protected areas. This form of management is very important, as any effort in one country could be destroyed by a lack of action in a neighbouring country. In spite of the relatively good state and increasing trend of the lion population in Pendjari Biosphere Reserve, this population is vulnerable to threats from neighbouring protected areas.

The home range of lionesses in Pendjari reserve is relatively large, but lower than in several other parts of the region (Bauer & de Iongh, 2005). This suggests that prey populations are in a relatively good state. It also probably confirms the lower pressure on lions in the Pendjari Biosphere Reserve. However, considering the size of the territories and the location of most known lions groups or prides in the area, lion populations are vulnerable, due to the edge effects described by Loveridge *et al.* (2007; 2010). Most prides are relatively close to borders, making them vulnerable to sport hunting in Benin, and poaching and sport hunting in Burkina Faso and in the neighbouring W Benin. The size of the home range confirmed that lions from the Park could easily move to hunting zones or to neighbouring protected areas. The role of source population played by Pendjari lion population proves the importance of concerted transboundary management of protected areas between Benin and Burkina Faso.

Assessment of lion diets revealed that diet was predominantly composed of medium-sized prey (60.7% of lion diet) in Pendjari while large-sized prey comprised 38.2% of the diet. However, despite the small group size of lions in the Pendjari, the dominant prey species is large: buffalo, which comprised 21.5% of the prey species in the diet and 50% of the prey biomass. Thus, large groups of lions do not appear to be necessary to capture large prey in Pendjari in contrast to what has been observed elsewhere (Lamprecht, 1978; Packer *et al*., 1990). The most preferred prey were all rather large, i.e., hartebeest and waterbuck, whereas smaller prey such as duikers, oribi and baboon were avoided as was also found by Hayward & Kerley (2005). Therefore, the predominance of small prey in the lion diet in West Africa as found by Bauer *et al*. (2008) is not a consequence of lion preference for small prey but of the greater availability of small prey. The absence of livestock in the diet confirms the relatively low importance of livestock in lion diet inside the Pendjari Biosphere Reserve, contrary to many other areas of the region (Bauer *et al*., 2008; Tumenta *et al*., 2009). Therefore, in a stable habitat with sufficient prey base in West and Central Africa, lions do not frequently prey on livestock even if they are present and represent easy prey. The increasing poaching and illegal grazing level observed recently in the reserve are worrying, as they could affect the predator-prey equilibrium and could be detrimental to large predators such as lions.

7.4 What future for lions in West Africa?

The lion population in the Pendjari Biosphere Reserve has been recovering over the past decade. If the threats to lions can be maintained at a relatively low level, this could help to recolonize the whole WAPOK complex. However even though the lion population is in good condition in Pendjari Biosphere Reserve, it is vulnerable to anthropogenic activities mainly from neighbouring protected areas. In West Africa, two LCUs offer the best hope for lion conservation. These are the W-Arly-Pendjari (WAP) (Benin-Burkina Faso-Niger) and the Niokolo complex (Senegal-Guinea). In each of these conservation units, research efforts and management actions should be implemented in close cooperation. If this is not done, efforts in one country could be easily offset by the lack of action in the neighbouring country. Decision-makers and politicians should be aware of the importance of concerted actions, not only for the conservation of lion and other large carnivores but also for biodiversity in general. A start has already been made, with projects such as the European Union supported WAP project or the European Union project ECOPAS which have been implemented in at least the three countries Benin, Burkina Faso and Niger covered by the WAPO complex. But more efforts are needed. Activities such as periodic and concerted anti-poaching patrols could be organized along the borders by a team with members from several countries. Research should also be conducted in close collaboration with staff of all involved countries. For example, in 2008, hundreds of cattle coming from Burkina Faso were killed in the Pendjari National Park by rangers and military personnel. The effects of cattle on wildlife are known (Fritz *et al*., 1996; Treydte *et al*., 2005) and if efforts had been made in Burkina Faso to protect their area, these cattle would not have intruded into the Pendjari National Park.

Livestock depredation occurred at different densities in the various parts of the complex of protected areas. It seemed to be worse in parts where human encroachment was higher (Sogbohossou, pers.obs) however this needs to be confirmed by further studies. Increased attention to conflicts with particular consideration of human needs would contribute to saving lions and large carnivores in West Africa.

One limit to carnivore conservation is the poor monitoring system of prey species and carnivore populations in many protected areas. The methods used (call-ups or questionnaires) are not always suitable, and the way they are used do not always yield reliable results. It is necessary to organize a reliable and continuous monitoring of wildlife (predators and prey) and habitats in the protected areas of Benin and other countries of West and Central Africa. Limited financial resources are the reason often cited by managers of protected areas for the absence of reliable monitoring programmes. However it would be better to try to secure sufficient funding than to collect incomplete data that cannot be reliably used.

Another limiting factor for large mammal conservation in Benin and in West Africa is the low number of funding organizations working in the area. Scientists and managers should approach international conservation organizations to secure more funding.

In summary, the survival of lions in West Africa depends on concerted management actions and research efforts. Safeguarding protected areas and developing research to improve knowledge of the lion and other species that share its habitat are crucial for the improved conservation of the species.

7.5 Research needs

This first long-term study on lions in West Africa has provided initial information about lions' home range and their habitat use and has contributed to a better knowledge of the species ecology. However, in order to save lions and other carnivores in West Africa, several aspects still need to be investigated.

- Home ranges, movements and habitat use of lions should be extended to the WAPOK complex to assess the impact of anthropogenic pressures on the structure of populations and the dispersal of individuals. This would also help to measure the difference in impacts within one complex.
- Monitoring of sport hunting and its impact on carnivores and prey populations would enable the assessment of its sustainability.
- The investigation of the determinants of livestock-carnivore conflicts should continue in order to find appropriate and sustainable solutions for West Africa.
- Further phylogenetics and morphology studies should contribute to measuring how much the environment of the region influences the genes and the morphology of lions in West and Central Africa.
- A continuous monitoring of prey populations would elucidate their population dynamics and how they interact with lions and other carnivore populations.
- Other carnivores that inhabit the ecosystem should be studied to find out how predators limit each other.

It is important to note that studies should be conducted in the whole complex, as all protected areas are connected.

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Summary

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

Keywords

lion *Panthera leo*; human-wildlife conflicts; social structure; feeding ecology; habitat use; West Africa;

Earth's biodiversity is disappearing at an alarming rate in the last decades. Many species, including carnivores, are becoming endangered. The lion was one of the most widely distributed terrestrial mammals and is today restricted to Gir ecosystem in India and to more or less fragmented populations in sub-saharan Africa. The species is considered as Vulnerable on IUCN Red List. In West Africa, due to its small and fragmented populations, the species is listed as Regionally Endangered. While the species is widely studied in other parts of Africa, it is poorly known in West Africa. The threats to lions, their ecology and their behaviour have not been assessed in the context of this region. In order to fill this gap, this research aims at investigating the ecology of the lion population and conflicts with humans in a West African protected area: Pendjari Biosphere Reserve, Benin. Pendjari Biosphere Reserve is one of the best-managed protected areas in West Africa and is part of the two most promising Lion Conservation Units in the region. It covers about 5,000 km² and is composed of the Pendjari National Park, and the Pendjari and Konkombri hunting zones.

Local populations surrounding the Pendjari Biosphere Reserve suffer from livestock depredation mainly by hyena (53.6% of attacks), baboon (24.8% of attacks) and lion (18% of attacks). Most attacks occur during the rainy season when wild prey are scattered and more difficult to hunt. The depredation level is relatively low compared to many other regions in Africa. However the losses are significant, as local populations live below the poverty line. Fortunately, despite these losses and the fear of carnivores, people tolerated conflicts. No retaliatory killing of predators was reported. This could be partly attributed to the social and cultural importance of carnivores. The low level of conflicts in Pendjari is confirmed by the absence of livestock in the diet of lions. In the relatively well protected Sudanian savannah area that Pendjari represents, buffalo is the most consumed species (50% of the prey biomass consumed). However, like in other areas of West and Central Africa, the lion diet is dominated by medium prey (61.7%) while large prey composed 38.2% of the diet. Similarly to what is observed across Africa, smaller prey

such as oribi and duiker were avoided and relatively large prey such as waterbuck and hartebeest were preferred. The predominance of small prey in the diet is then due to the relative abundance of these prey and not to the small size of lion groups in the region. There are about 1.6 lions/100 km² in the Pendjari Biosphere Reserve. The mean lion group size is of 2.6 lions with a significantly higher group size in the park compared to that in hunting zones. The adult sex ratio of 1 male : 1.04 female is skewed towards males. The small group size could be linked to the low prey and lion densities in the area. The lion population is particularly vulnerable to trophy hunting both in hunting zones of Pendjari and hunting zones of Burkina Faso, as the park's lion population plays the role of source population while the hunting zone lions represent the sink populations. The mean home range of lionesses (95% MCP: 200 ± 141 km²) is consistent with findings across Africa. Riparian forests, woodlands and dry forests were the preferred lion habitats during the dry season while grasslands and swamps were used according to their availability. The few available results showed that during the rainy season, when most of the reserve is flooded, lions preferred woodlands on hills and avoid grasslands and swamps. The study of the home range and the social structure of lions in Pendjari highlighted the need for a concerted management of Benin and Burkina Faso lion populations for better efficiency. In summary, when protected areas are safe enough, lion population ecology and behaviour are similar across Africa. The Pendjari lion population was increasing and did not represent a great threat to livestock and humans surrounding the reserve. The lion population remained vulnerable, however, mainly because of legal and illegal hunting and human encroachment from neighbouring reserves. The impact of hunting and human activities on the social structure need to be better investigated. To save the lion in the region of West Africa, efforts should be made to safeguard only protected areas but also their surrounding areas. Studies on other issues such as the impact of lion trophy hunting and the relationship between the different large predators will contribute to improve the status of lions and other predators in West Africa.

Samenvatting

Leeuwen van West-Afrika
Ecologie van leeuwenpopulaties (*Panthera leo* Linnaeus 1975) en mens-leeuwconflicten in Pendjari Biosphere Reserve, Noord-Benin

Trefwoorden

leeuw *Panthera leo*; mens-natuurconflicten, sociale structuur; voedselecologie; habitatgebruik; West-Afrika

Het uitsterven van soorten neemt de laatste decennia wereldwijd alarmerend toe. Steeds meer soorten, waaronder carnivoren, zijn bedreigd met uitsterven. De leeuw was één van de meest verspreide terrestrische zoogdieren en wordt nu nog slechts gevonden in gefragmenteerde populaties in Afrika en in het Gir-reservaat in India. De leeuw is geclassificeerd als *Vulnerable* (kwetsbaar) op de IUCN Rode Lijst. In West-Afrika, vanwege de aanwezigheid van kleine en gefragmenteerde populaties, wordt de leeuw beschouwd als *Regionally Endangered* (regionaal bedreigd). Hoewel er veel onderzoek is gedaan naar de leeuw in Oost- en Zuidelijk-Afrika, is er weinig bekend over de leeuw in West-Afrika. De bedreigingen, de ecologie en het gedrag waren tot voor kort onbekend en deze kennis is nodig voor een betere bescherming van de leeuw in West-Afrika. Om deze leemte in kennis te vullen, heeft dit onderzoek als doel om de ecologie van de leeuw en conflicten met lokale gemeenschappen te onderzoeken in een West-Afrikaans beschermd gebied, het Pendjari Biosphere Reserve in Noord-Benin. Dit is een van de best beheerde gebieden van West-Afrika. De oppervlakte is ongeveer 5000 km² en bestaat uit het Pendjari Biosphere Reserve en de Konkombri jachtzones.

Lokale gemeenschappen die wonen rond het Pendjari Biosphere Reserve ondervinden vooral schade als gevolg van predatie door hyena's (53,6% van de aanvallen), bavianen (24,8% van de aanvallen) en leeuwen (18% van de aanvallen). De meeste aanvallen vinden plaats gedurende het regenseizoen, wanneer de wilde prooidieren zich verspreiden en moeilijk te vangen zijn door predatoren. Het niveau van schade is relatief laag vergeleken met andere gebieden in Afrika. Echter, voor de lokale gemeenschappen zijn de verliezen toch belangrijk, omdat de lokale bevolking onder de armoedegrens leeft. Wel is het zo dat, ondanks deze verliezen en ondanks hun angst voor carnivoren, lokale gemeenschappen toch redelijk tolerant zijn ten aanzien van deze conflicten. Gedurende het onderzoek werden geen gevallen van door de bevolking gedode carnivoren gemeld als wraakactie. Dit ontbreken van wraakacties kan gedeeltelijk verklaard worden uit het bestaande sociale en culturele belang van carnivoren. Het relatief lage niveau van predatie

van vee door leeuwen wordt bevestigd door het ontbreken van vee als prooi in het dieet van leeuwen. In het goed beschermde Pendjari Biosphere Reserve is de Afrikaanse buffel het belangrijkste prooidier voor leeuwen (50% van de geconsumeerde prooi biomassa). In andere gebieden van West- en Centraal-Afrika bestaat het dieet van leeuwen vooral uit middelgrote prooidieren (61,7%) en grote prooidieren (38,2%). In dit onderzoek tonen leeuwen een voorkeur voor grote prooidieren en vermijden ze kleinere prooidieren, hetgeen overeenkomt met bevindingen in de rest van Afrika. De aanwezigheid van kleinere prooidieren in het dieet van leeuwen is vooral een gevolg van de beschikbaarheid van deze kleine prooidieren en heeft geen verband met de relatief kleine groepsgrootte van leeuwen in de regio van West-Afrika. Er wordt in het Pendjari Biosphere Reserve een dichtheid gevonden van 1,6 leeuwen per 100 km². De gemiddelde omvang van leeuwengroepen is 2,6 en in het nationaal park zijn de groepen significant groter dan in de jachtzones. De sex ratio man : vrouw is 1 : 1,04. De relatief kleine groepsomvang is mogelijk te verklaren door de relatief lage prooidierdichtheden, met als gevolg ook lage dichtheden aan leeuwen. De leeuwenpopulatie is in het bijzonder gevoelig voor safari-jacht in de jachtzones rond Pendjari Biosphere Reserve en in het aangrenzende Burkina Faso. De leeuwenpopulaties in het nationaal park lijken de rol van 'source'-populatie te spelen, de populaties in de jachtzones zijn de 'sink'-populatie. De gemiddelde 'home range' van leeuwinnen (95% Minimum Convex Polygon: 200 ± 141 km²) is vergelijkbaar met 'home ranges' die in andere delen van Afrika gevonden worden. Rivierbos, boomsavanne, graslanden en moerassen bleken de habitat van leeuwen te zijn gedurende het droge seizoen. In het natte seizoen bleken leeuwen een voorkeur te hebben voor boomsavannes en heuvels en ze leken graslanden en moerassen te mijden. De resultaten van het onderzoek naar 'home ranges' en de sociale structuur toonden de noodzaak aan voor een gecoördineerd beheer van het Pendjari Biosphere Reserve en de jachtzones in Benin en Burkina Faso met het doel het verbeteren van het management. Samenvattend maakt dit onderzoek duidelijk dat, indien een beschermd gebied in West-Afrika goed beheerd wordt, het gedrag en de ecologie van leeuwen vergelijkbaar is met grote gebieden van Afrika. De leeuwenpopulatie in Pendjari neemt toe en vormt geen grote bedreiging voor het vee en de lokale bevolking die rond het reservaat leeft. De leeuwenpopulatie wordt wel beïnvloed door legale en illegale jacht en andere illegale activiteiten. Om de leeuw in West-Afrika te behouden is het niet alleen nodig om nationale parken te beschermen maar ook om de omliggende gebieden goed te beheren.

Résumé

Les lions de l'Afrique de l'Ouest
Ecologie des populations de lion (*Panthera leo* Linnaeus 1975) et conflits hommes-lion dans la Réserve de Biosphère de la Pendjari au nord-Bénin.

Mots clé

lion *Panthera leo*; conflits hommes-faune; structure sociale; regime alimentaire; utilisation de l'habitat; Afrique de l'Ouest

La biodiversité disparait à un rythme alarmant des dernières décennies. Plusieurs espèces, parmi lesquelles les carnivores, deviennent de plus en plus menacées. Le lion, l'un des mammifères terrestres les plus largement distribués dans le monde autrefois, est aujourd'hui réduit à l'écosystème du Gir en Inde et à des populations plus ou moins fragmentées en Afrique sub-saharienne. L'espèce est considérée comme Vulnérable d'après la Liste Rouge de l'UICN. Les populations étant de petite taille et très fragmentées en Afrique de l'Ouest, l'espèce y est classée comme 'Régionalement En Danger d'extinction'. Le lion africain a fait l'objet de diverses études. Mais les menaces, l'écologie et le comportement du lion dans le contexte ouest-africain, dont la connaissance est nécessaire pour la conservation de l'espèce dans la sous-région ont fait l'objet de peu d'études. Dans le but de combler ces lacunes relatives à la conservation du lion en Afrique de l'Ouest, la présente recherche vise à étudier l'écologie des populations de lions et les conflits hommes-lion dans une aire protégée ouest-africaine : la Réserve de Biosphère de la Pendjari au Bénin. Les objectifs spécifiques sont de: (i) déterminer les caractéristiques des conflits hommes-prédateurs dans la Réserve de Biosphère de la Pendjari au Bénin , (ii) examiner la perception qu'ont les populations locales de ces conflits, (iii) étudier l'abondance et la structure sociale des populations de lions dans la Pendjari ; (iv) étudier les relations lions-proies et enfin (v) déterminer la taille des territoires et les habitats utilisés par les lions dans la réserve.

La Réserve de Biosphère de la Pendjari est l'une des aires protégées les mieux conservées dans la région. Elle fait partie de l'un des deux ensembles d'aitres protégées les plus prometteurs pour l'avenir du lion en Afrique Occidentale d'après la Stratégie de Conservation du lion en Afrique Occidentale et Centrale. Elle couvre un peu moins de 5000 km² et se compose du parc national de la Pendjari ainsi que des zones cynégétiques de la Pendjari et de Konkombri.

Les populations humaines vivant autour de la Réserve connaissent des problèmes avec les prédateurs sauvages, principalement à travers l'élevage qui est la deuxième activité dans la région après l'agriculture. L'hyène est la première espèce de prédateur concernée, étant responsable de 53,6% des attaques de bétail dans la zone. Viennent ensuite le babouin (responsable de 24,8 % des attaques) puis le lion (responsable de 18% des attaques). La majorité des attaques se produisent durant la saison des pluies, quand les proies sauvages sont distribuées aléatoirement et régulièrement dans l'aire protégée et ainsi un peu plus difficiles à chasser. Le niveau de déprédation est néanmoins faible comparé à ce qui est observé dans beaucoup d'autres régions du continent africain. Malgré cela, les pertes sont d'une importance significative pour les populations qui vivent pour la plupart en dessous du seuil de pauvreté. Heureusement, en dépit des pertes et de la crainte pour les espèces de carnivores, les populations semblent tolérer les conflits. De façon générale, la perception qu'ont les populations des carnivores et des conflits est déterminée par l'ethnie d'appartenance, les expériences antérieures avec les carnivores, les bénéfices individuels tirés du parc, l'âge de l'enquêté. Les Berbas, de l'ethnie dominante dans la région, apparaissent comme le groupe ayant les perceptions les plus négatives tandis que les Waama ont tendance à être plus tolérants. L'abattage de revanche des lions, qui aurait été très nuisible à la population des lions et autres prédateurs, n'a pas été observé dans la zone. Ceci est probablement en partie dû à cause de l'importance socioculturelle des grands carnivores. L'ampleur relativement faible des conflits hommes-lion autour de la Réserve de Biosphère de la Pendjari est confirmée par l'absence de bétail dans le régime alimentaire du lion à travers l'analyse des crottes et les observations.

Dans la Réserve de Biosphère de la Pendjari, le buffle est l'espèce la plus consommée par les lions. Il représente 50% de la biomasse consommée. Toutefois, comme dans les autres régions d'Afrique Centrale et Occidentale et contrairement à l'Afrique Australe et Orientale, le régime alimentaire du lion dans la Pendjari est, en terme d'effectifs consommés, dominé par les proies de taille moyenne. Elles composent 61,7% du régime contre 38,2 % pour les proies de grande taille. Néanmoins, les lions marquent une préférence pour les proies plus grandes telles que le waterbuck et le bubale tandis que les petites proies telles que l'ourébi et les céphalophes sont évitées. Le buffle est prélevé conformément à son abondance dans la réserve. La prédominance des petites proies dans le régime alimentaire n'est pas donc pas due à une préférence de ces espèces ou à la petite taille des groupes de lions dans la région mais plutôt à la relative abondance de ces petites proies dans le milieu.

La densité moyenne des lions dans la Réserve de la Pendjari est de 1,6 lions/100 km² avec une densité beaucoup plus élevée dans le parc (2 lions/100km²) comparativement aux zones cynégétiques (1,3 lions/100 km²). Contrairement à la majorité des populations de lions en Afrique Centrale et Occidentale, les lions connaissent

une augmentation de leur population dans la Réserve de Biosphère de la Pendjari ces dernières années. La taille moyenne des groupes de lions est de 2,6 lions. Elle est significativement plus élevée dans le parc que dans les zones cynégétiques. La faible taille des groupes est en accord avec la relative faible densité de proies et de lions dans la zone. La proportion des males dans la population est beaucoup plus élevée que ce qui est communément observé avec un sexe ratio chez les adultes de 1 male pour 1,04 femelle. Bien que ce biais soit en partie imputable à la méthode d'étude utilisée, il révèle un dysfonctionnement au niveau de la population. La population de lions de la Pendjari est particulièrement vulnérable à la chasse sportive faite aussi bien dans les zones cynégétiques du Bénin que dans celles du Burkina Faso. La population du parc, population source, sert à combler le vide créé par la chasse dans les zones. La taille des territoires des lions de la Pendjari, s'inscrivent dans le même ordre de grandeur que dans d'autres aires d'Afrique. Elle est en moyenne de 200 ± 141 km² (Méthode du Minimum Convex Polygon). Les galeries forestières, les savanes arborées et forêts claires constituent des habitats privilégiés des lions en saison sèche. Les résultats préliminaires indiquent qu'en saison des pluies, les habitats entourant les points d'eau, les savanes herbeuses et marécages sont évitées au profit des végétations saxicoles et des forêts claires et denses sèches. L'étude de la structure sociale et de l'utilisation de l'habitat par les lions révèle l'importance de la gestion concertée des aires protégées de la sous-région et principalement du Bénin et du Burkina Faso pour la conservation du lion et de la faune en général.

En résumé, il ressort de cette étude que malgré les particularités environnementales, quand la protection est effective, les lions se comportent de la même façon en Afrique de l'Ouest que dans les autres parties du continent. Les lions de la Réserve de Biosphère de la Pendjari, malgré l'augmentation constante de la population, restent menacés par les prélèvements légaux et illégaux ainsi que les pressions sur l'habitat provenant essentiellement des aires contigües du Bénin et du Burkina Faso. Pour sauver l'espèce, il faudra faire des efforts pour protéger non seulement les aires protégées concernées mais aussi leurs alentours. Aussi l'aménagement concerté des aires transnationales est-elle une nécessité. Des facteurs tels que les impacts de la chasse sportive et les relations entre les différentes espèces de prédateurs restent à explorer pour améliorer le statut de conservation des lions et autres prédateurs en Afrique de l'Ouest.

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Etotépé A. Soghohossou
July 2011

Curriculum Vitae

Etotépé A. Sogbohossou was born on 4 June 1978 in Parakou, Benin. From 1995 to 2000, she studied at the Faculty of Agricultural Sciences, University of Abomey-Calavi, then at the National University of Benin, where she obtained an "Ingénieur Agronome" degree in December 2000. Just after her graduation, she became Research Assistant at the Laboratory of Applied Ecology at the University of Abomey-Calavi. She mainly participated in research on wildlife census and monitoring, rangeland management, and biodiversity conservation. She lectures to BSc and MSc students on fields related to wildlife census & monitoring methods, management of protected areas and large carnivore monitoring. She is also a member of CERGET NGO now CRGB (Research Centre for the Management of Biodiversity), a Beninese NGO working for the conservation of biodiversity. From 2001 to 2003, she has been in charge of the botanical part of the project African Medicinal Plants on the Net (PLAMENET) in Benin. She participated in several studies in Cameroon, Kenya and South Africa to nourish her passion for wildlife and large carnivores. With some other colleagues from the region, she participated to the creation of the Network on Lion Conservation in West and Central Africa (ROCAL in French) in 2002. She is in charge of Communication and Training of this network. She designed and led projects on carnivore conservation and human-predator conflict mitigation in Benin. From 2005 to 2008, with CERGET NGO, she led a project on the conservation of threatened medicinal plants with the creation of botanical gardens managed by local communities in northern Benin. In 2006 she came back as a student to the University of Abomey-Calavi to complete an MSc in Natural Resources Management. This MSc was an opportunity to explore phylogenetics of lion in West Africa with the Brookfield Zoo laboratory of Genetics, Chicago, US. After this MSc, she started a PhD on lion ecology in Pendjari Biosphere Reserve, Benin between the University of Leiden and the University of Abomey-Calavi. In addition to a NUFFIC scholarship, she received a Kaplan Graduate Award from Panthera Foundation (2009-2010) and a Charlotte Fellowship from the African Wildlife Foundation (2010) to fund her PhD research.

Etotépé A. Sogbohossou is member of several networks among which the Cat Specialist Group and the World Commission for Protected Areas of the IUCN, the African Lion Working Group and the Society for Conservation Biology. As one of the first experts in carnivore conservation in West and Central Africa, she expects to significantly contribute to the sustainable conservation of endangered carnivores and other wildlife species in West Africa and to work for their sustainable cohabitation with human populations.