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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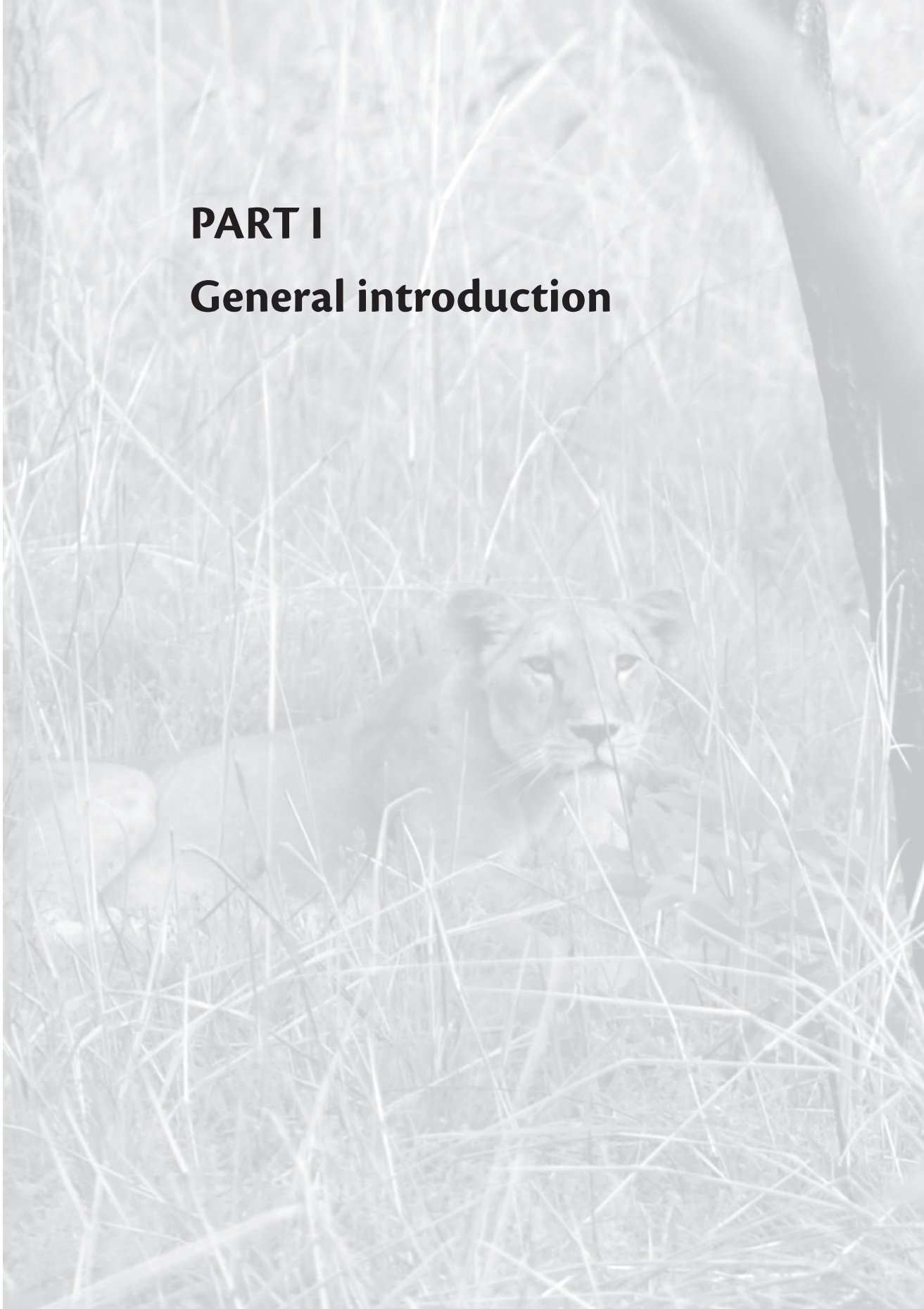

PART I
General introduction


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 en
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 re
Vous ne vous exposez pas seulement aux a
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.

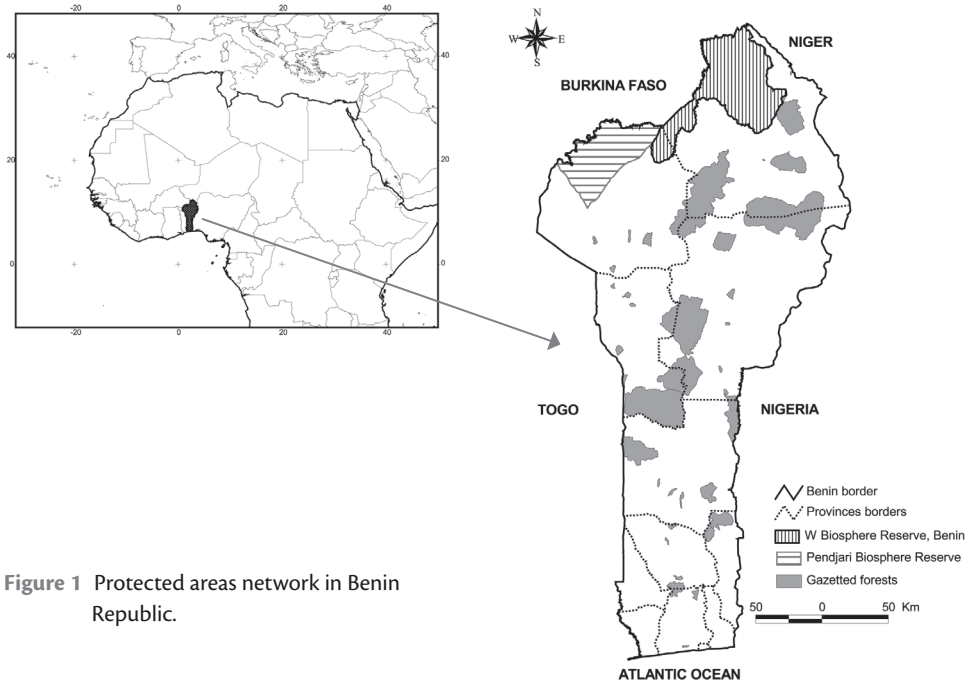

Figure 1 Protected areas network in Benin Republic.

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.

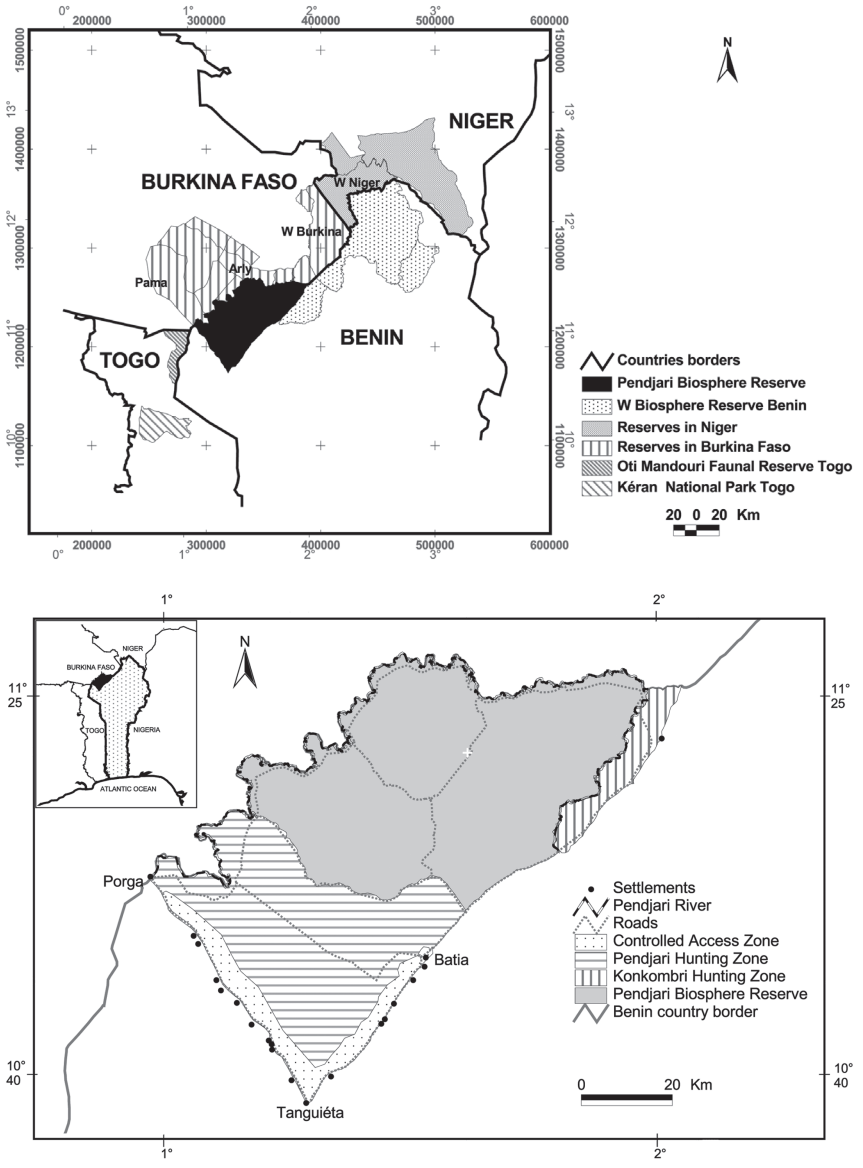

Figure 2 W – Arly – Pendjari – Oti Mandouri – Kéran complex of protected areas in Benin, Burkina Faso, Niger and Togo and Pendjari Biosphere Reserve.

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.

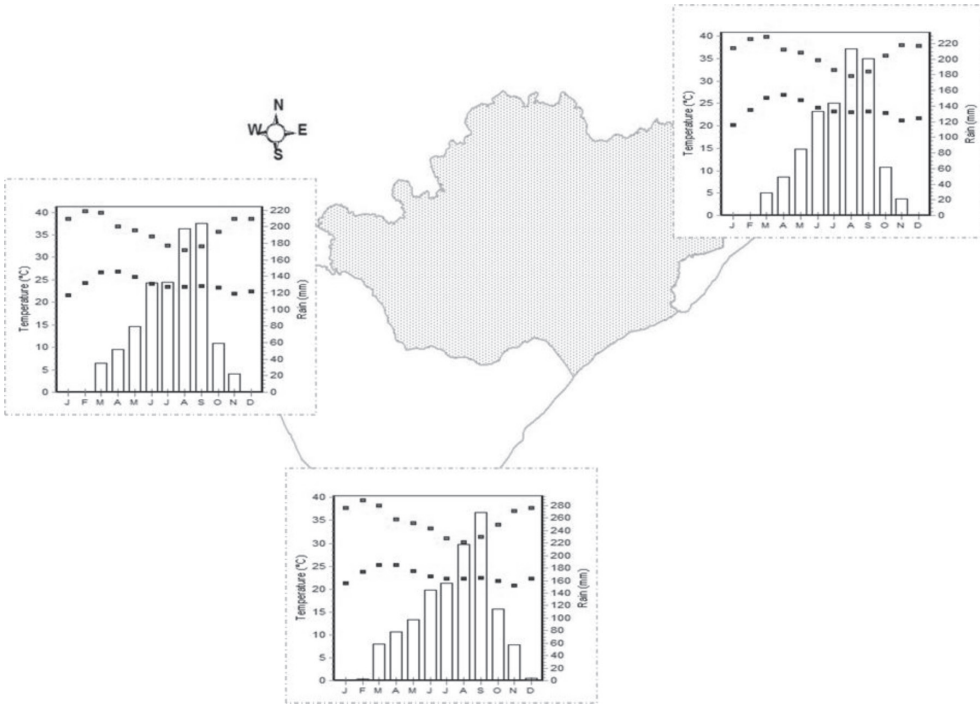

Figure 3 Climate in Pendjari Biosphere Reserve based on temperature and rainfall during 50 years (Source: Diva GIS©).

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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