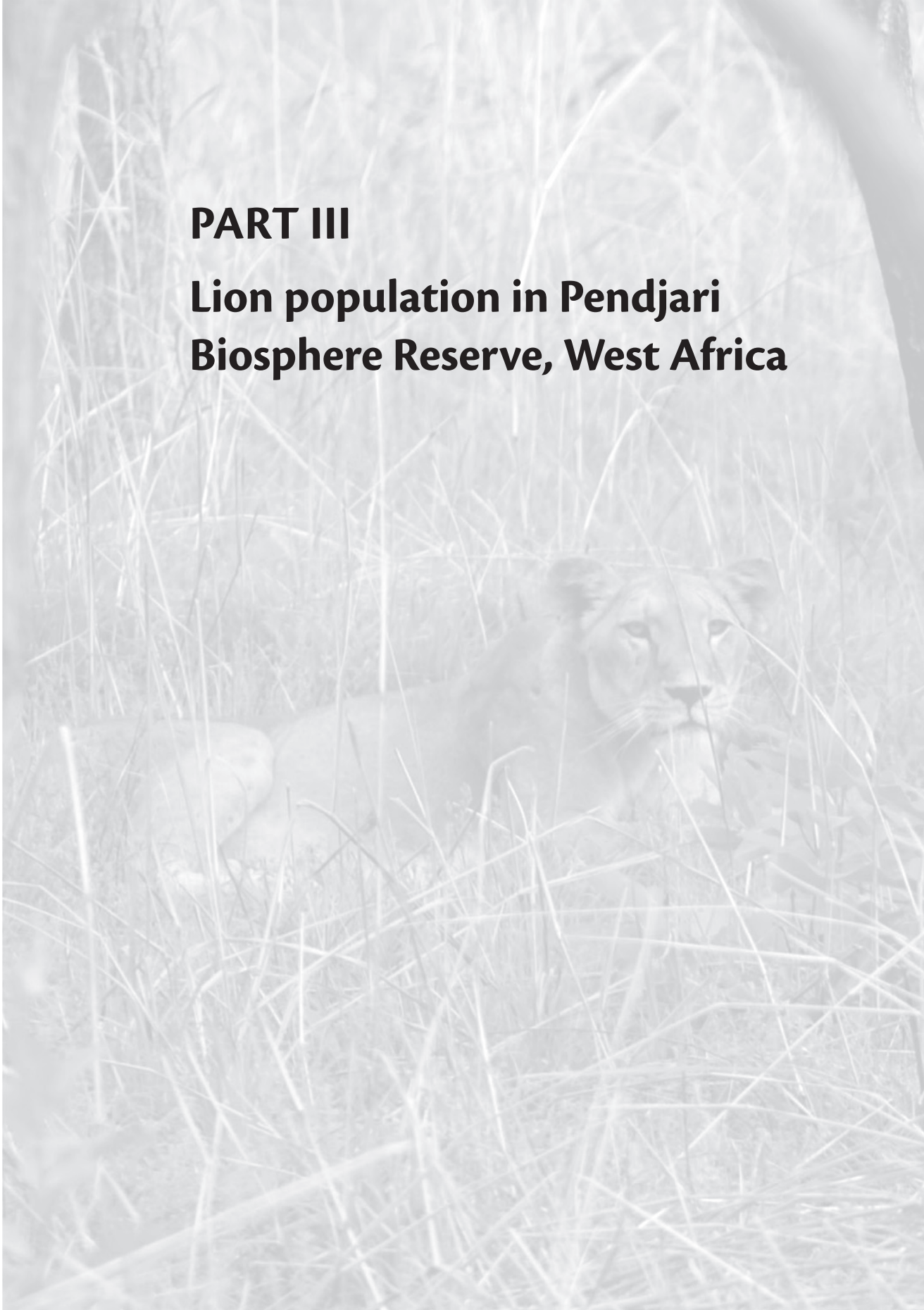
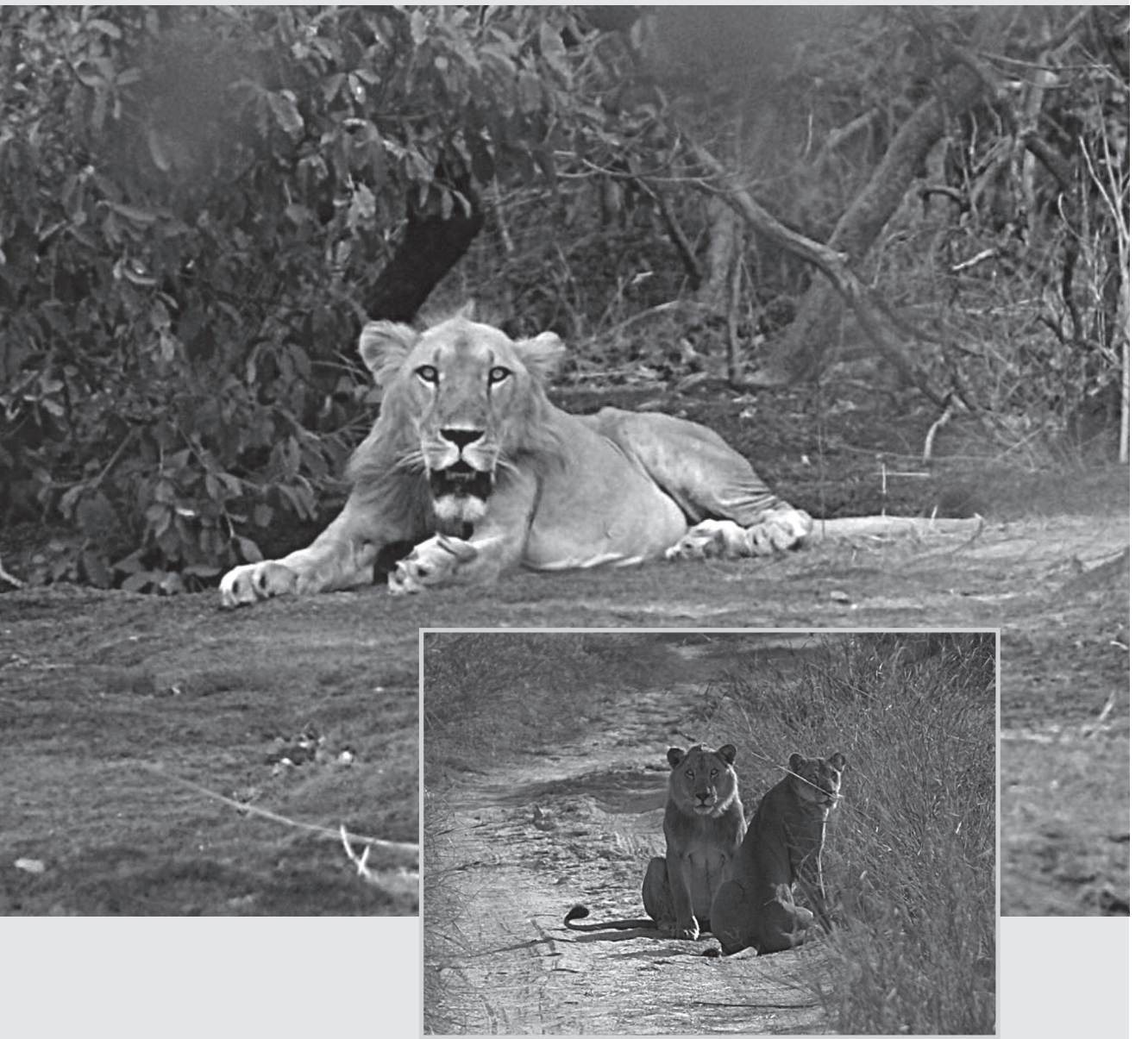
Lions of West Africa : ecology of lion (Panthera leo Linnaeus 1975) populations and human-lion conflicts in Pendjari Biosphere Reserve, North Benin

Sogbohossou, E.A.

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

Sogbohossou E.A., Loveridge A., Funston P.J., de Iongh H.H., de Snoo G.R., Sinsin B.

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.

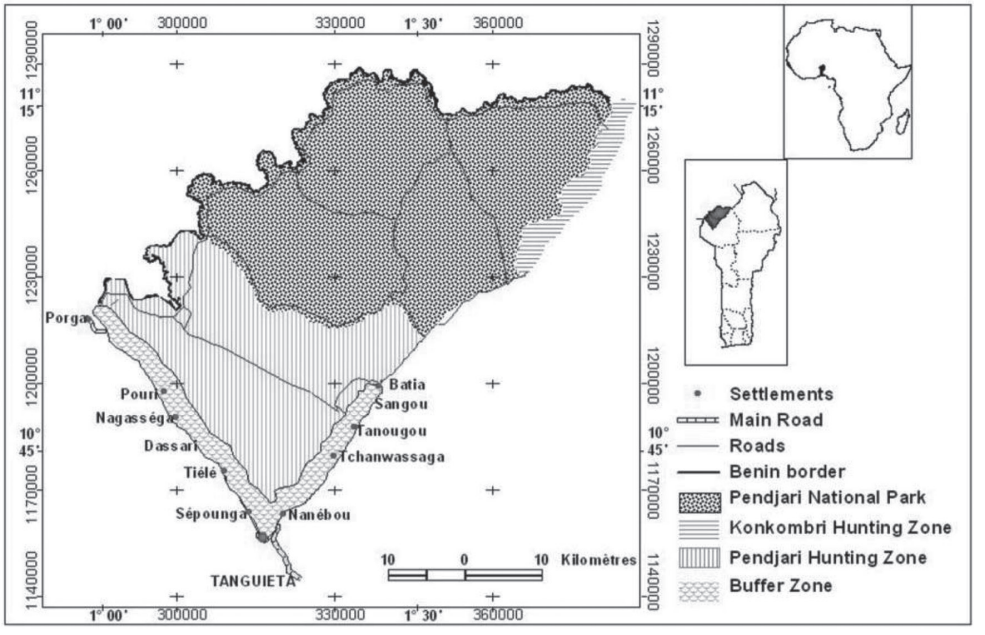


Figure 1 Location of Pendjari Biosphere Reserve in Benin.

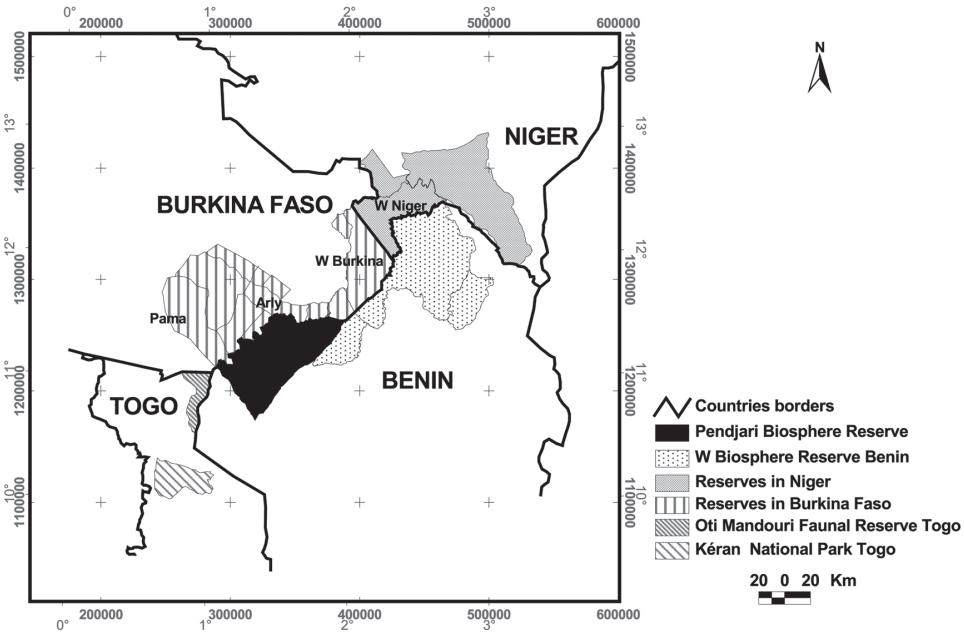


Figure 2 W - Arly - Pendjari - Oti Mandouri and Keran, the called WAPOK complex of protected areas in West Africa

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.

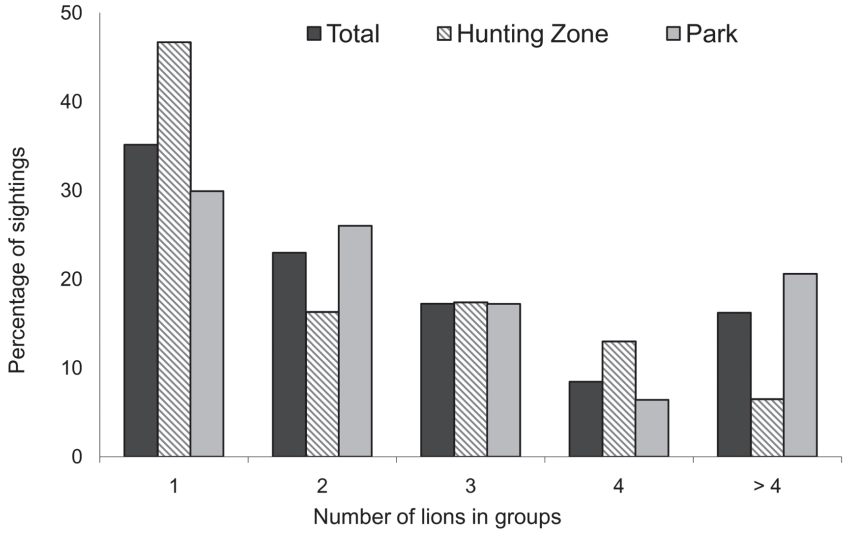


Figure 3 Frequency of different lion group sizes sightings in Pendjari Biosphere Reserve (n=296 observations from 2008 to 2010).

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.

Acknowledgements

We acknowledge the assistance of Pendjari Reserve staff especially Lange U., Tiomoko D., Tehou A. and the rangers. We thank Bauer H. for assistance, Chardonnet P. and Bernon J.P. for supplying data from hunting zones.

References

Bauer, H. (2007) Status of large carnivores in Bouba Ndjida National Park, Cameroon. *African Journal of Ecology*, **45**, 448–450.

Bauer, H., de Iongh, H.H. & Di Silvestre, I. (2003) Lion (Panthera leo) social behavior in the West and Central African savannah belt. *Mammalian Biology*, **68**, 239-243.

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

Bertram, B.C.R. (1975) Social factors influencing reproduction in wild lions. *Journal of Zoology* (London), **177**, 483-482.

Burton, C., Buedi, E.B., Balangtaa, C., Kpelle D.G., Sam, M.K. & Brashares, J.S. (2011) The decline of lions in Ghana's Mole National. *African Journal of Ecology*, **49**, 122–126.

Bygott, J.D., Bertram, B.C.R. & Hanby, J.P. (1979) Male lions in large coalitions gain reproductive advantages. *Nature*, **282**, 839–841.

Castley, J.G., Knight, M.H., Mills, M.G.L. & Thouless, C.R. (2002) Estimation of the lion (Panthera leo) population in the southwestern Kgalagadi Transfrontier Park using a capture recapture survey. *African Zoology*, **37**, 27–34.

Celesia, G.G., Peterson, A.T., Peterhans, J.C.K. & Gnoske, T.P. (2010) Climate and landscape correlates of African lion (Panthera leo) demography. *African Journal of Ecology*, **48**, 58–71.

Clerici, N., Bodini, A., Eva, H., Grégoire, J-M., Dulieu, D. & Paolini, C. (2007) Increased isolation of two Biosphere Reserves and surrounding protected areas (WAP ecological complex, West Africa). *Journal for Nature Conservation*, **15**, 26-40.

Creel, S. & Creel, N.M. (1997) Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. *African Journal of Ecology*, **35**, 83-93.

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

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

Funston, P.J., Mills, M.G.L. & Biggs, H.C. (2001) Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology* (London), **253**, 419-431.

Funston, P.J. Population characteristics of lions (*Panthera leo*) in the Kgalagadi Transfrontier Park at the millennium. *South African Journal of Wildlife Research*, in press.

Hanby, J., Bygott, J.D. & Packer, C. (1995) Ecology, demography and behavior of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. In: Serengeti II: Research, Management and Conservation of an Ecosystem (eds A.R.E. Sinclair & P. Arcese), pp. 315–331. University of Chicago Press, Chicago, US.

Henschel P., Azani, D., Burton, C., Malanda, G., Saidu, Y., Sam, M. & Hunter, L. (2010) Lion status updates from five range countries in West and Central Africa. *Cat News*, **52**, 34-37.

Loveridge, A.J., Searle, A.W., Murindagomo, F. & Macdonald. D.W. (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, **134**, 548-558.

Loveridge, A.J., Hemson, G., Davidson, Z. & Macdonald, D.W. (2010) African lion on the edge: reserve boundaries as 'attractive sinks'. In: *The Biology and Conservation of Wild Felids* (eds Macdonald D.W. & A. Loveridge), pp. 283-304. Oxford University Press, UK.

Mills, M.G.L. (1995) Notes on wild dog *Lycaon pictus* and lion *Panthera leo* population trends during a drought in the Kruger National Park. *Koedoe*, **38**, 95-99.

Mills, M.G.L., Wolff, P. & Le Riche, E.A.N. (1978) Some population characteristics of the lion (Panthera leo) in the Kalahari Gemsbok National Park. *Koedoe*, **21**, 163-171.

Mosser, A. & Packer, C. (2009) Group territoriality and the benefits of sociality in the African lion, Panthera leo. *Animal Behaviour*, **78** (2), 359-370.

Ogutu, J. O. & Dublin, H. T. (1998) The response of lions and spotted hyaenas to sound playbacks as a technique for estimating population size. *African Journal of Ecology*, **36**, 83-95.

Packer, C. & Pusey, A.E. (1982). Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature*, **296**, 740-742.

Packer, C. (1986) The ecology of sociality in felids. In: *Ecological aspects of social evolution* (eds D. I. Rubenstein & R. W. Wrangham), pp. 429-451. Princeton University Press, New Jersey.

Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. J. & Mulder, M. B. (1988) Reproductive success of lions. In: *Reproductive Success: Studies of Individual Variation*

in Contrasting Breeding Systems (ed T. H. Clutton-Brock), pp 363-383. University of Chicago Press, Chicago, US.

Packer, C., Scheel, D. & Pusey, A.E. (1990) Why lions form groups: Food is not enough. *American Naturalist*, **136**, 1-19.

Schaller, G. B. (1972) *The Serengeti lion*. Chicago: University of Chicago Press.

Schoe, M. (2007) *Ecology of lions (Panthera leo) in North Cameroon; social structure, home ranges, habitat use, movements and morphometrics of a lion population in Bénoué National Park*. Student Report no. 212, CML/Universiuty of Leiden.

Sinsin, B., Tehou, A.C., Daouda, I. & Saïdou, A. (2002) Abundance and species richness of larger mammals in Pendjari National Park in Bénin. *Mammalia*, **66**, 369-380.

Smuts, G.L. (1976) Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe*, **19**, 153-164

Smuts, G.L., Hanks, J. & Whyte, I.J. (1978) Reproduction and social organization of lions from the Kruger National Park. *Carnivore*, **1**, 17-28.

Sogbohossou, E.A., de Iongh, H.H., Sinsin, B., Snoo, G.R. & Funston, P.J. Livestock – predator conflict around Pendjari Biosphere Reserve, Northern Benin. *Oryx*, in press.

Spong, G. (2002) Space use in lions, Panthera leo, in the Selous Game Reserve: social and ecological factors. *Behavioral Ecology and Sociobiology*, **52**, 303-307.

Stander, P. (1991) Demography of lions in the Etosha National Park, Namibia. *Madoqua*, **19**, 1-9.

Stander, P.E. & Albon, S.D. (1993) Hunting success of lions in a semi-arid environment. *Symposia of the Zoological Society of London*, **65**, 127-143.

Tumenta, P.N., Kok, J.S., Van Rijssel, J.C., Buij, R., Croes, B.M., Funston, P.J., De Iongh, H.H. and Udo de Haes, H.A. (2009) Threat of rapid extermination of the lion (Panthera leo leo) in Waza National Park, Northern Cameroon. *African Journal of Ecology*, **48**, 888-894.

UICN/PACO (2009) *La grande chasse en Afrique de l'Ouest. Quelle contribution à la conservation ?* Etudes du PAPACO N°2.

Van Orsdol, K.G. (1984) Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda, *African Journal of Ecology*, **22**, 79–99.

Whitehead, H. & Dufault, S. (1999) Techniques for Analyzing Vertebrate Social Structure Using Identified Individuals: Review and Recommendations. *Advances in the study of Behavior*, **28**, 33-74.

Woodroffe, R. & Frank, L.G. (2005) Lethal control of African lions (Panthera leo): local and regional population impacts. *Animal Conservation*, **8**, 91-98.

Yamazaki, K. (1996) Social Variation of Lions in a Male-Depopulated Area in Zambia. *Journal of Wildlife Management*, **60**, 490-497.