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

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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 $200 \pm 141 \text{ km}^2$ and $256 \pm 154 \text{ km}^2$, 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 longh, 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 longh, 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.

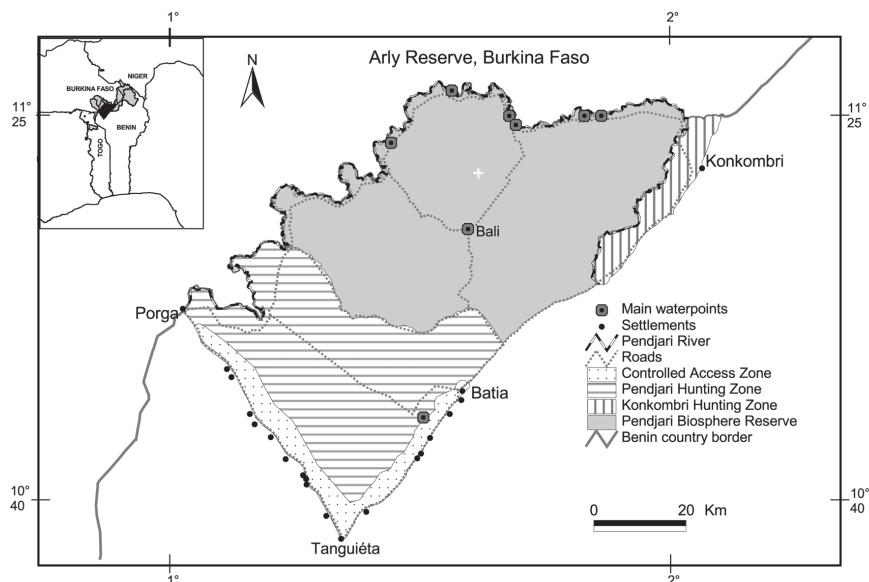


Figure 1 Pendjari Biosphere Reserve in Benin

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 longh, 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*, *Crosopteryx febrifuga* or *Acacia* sp.
- Shrub savannahs with *Acacia* sp. or with *Crosopteryx 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:

$$w_i = \frac{o_i}{p_i}$$

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:

$$B_i = \frac{w_i}{\sum_{i=1}^n w_i}$$

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 $256 \pm 154 \text{ km}^2$ (range from 96 to 403 km^2). The home range size considering 95% MCP was $200 \pm 141 \text{ km}^2$ (range from 50 to 330 km^2). The mean home range used in the dry season was $285 \pm 190 \text{ km}^2$, MCP 100% ($133 \pm 171 \text{ km}^2$, MCP 95%). The mean core home range (50% kernel) is $33.57 \pm 18.43 \text{ km}^2$. The 95% kernel home range is $170.87 \pm 95.75 \text{ km}^2$. 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.

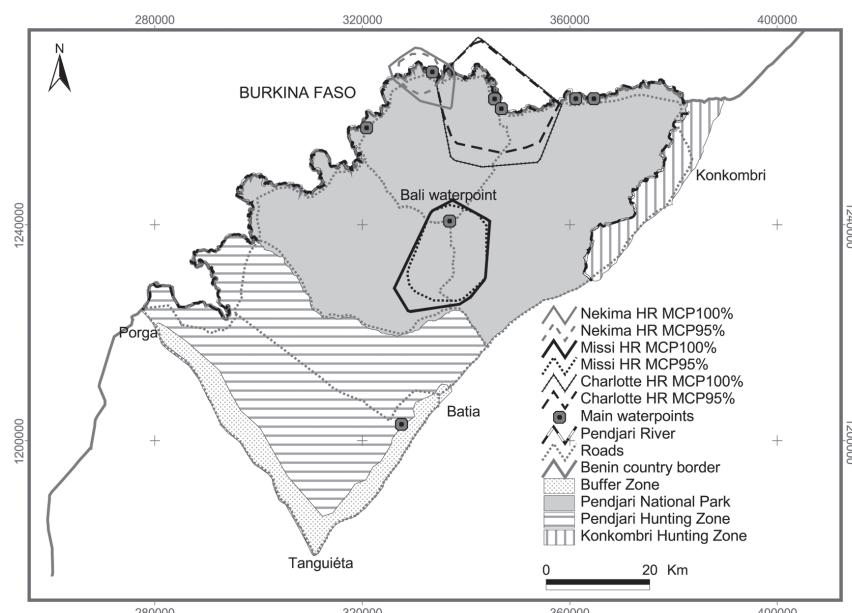


Figure 2 - Home ranges of three collared lionesses in Pendjari Biosphere Reserve.

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 <i>Anogeissus</i> 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 longh, 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 longh, 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 longh (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 longh (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.

References

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

Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346-352.

Creel, S. & Macdonald, D. (1995) Sociality, group size and reproductive suppression among carnivores. *Advances in the Study of Behavior*, **24**, 203-257.

Delvingt, W., Heymans, J.C. & Sinsin, B. (1989) *Guide du Parc National de la Pendjari*. CECA-CEE-CEA, Bruxelles, Belgique.

Donkin, D.A. (2000) *Lion spatial ecology: The effect of habitat on lion group dynamics*. MSc thesis, University of Natal, Durban.

Druce, D., Genis, H., Braak, J., Greatwood, S., Delsink A., Kettles, R., Hunter, L. & Slotow, R. (2004) Population demography and spatial ecology of a reintroduced lion population in the Greater Makalali Conservancy, South Africa. *Koedoe*, **47**, 103-118.

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

Fritz, H., Duncan, P., Gordon, I.J. & Illius, A.W. (2002) The influence of megaherbivores on the trophic guilds in African ungulate communities. *Oecologia*, **131**, 620-625.

Funston, P.J., Mills, M.G.M., Biggs, H.C. & Richardson, P.R.K. (1998) Hunting by male lions: ecological influences and socioecological implications. *Animal Behaviour*, **56**, 1333–1345.

Funston, P.J., Mills, M.G.L., Richardson, P.R.K. & van Jaarsveld, A.S. (2003) Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology* (London), **259**, 131-142.

Grigione, M.M., Beier, P., Hopkins, R.A., Neal, D., Padley, W.D., Schonewald, C.M. & Johnson, M.L. (2002) Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). *Animal Conservation*, **5**, 317–324.

Hopcraft, J.G.C., Sinclair, A.R.E. & Packer, C. (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, **74**, 559–566.

Hunter, L.T.B. (1998) *The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, Kwazulu-Natal, South Africa*. PhD thesis, University of Pretoria.

Jhala, Y.V., Mukherjee, S., Shah, N., Chauhan, K.S., Dave, C.V., Meena, V. & Banerjee, K. (2009) Home range and habitat preference of female lions (*Panthera leo persica*) in Gir forests, India. *Biodiversity and Conservation*, **18**, 3383–3394.

Krebs, C.J. (1999) *Ecological Methodology*. Addison-Wesley Educational Publishers, Inc., Menlo Park, Canada.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D.W. (2009) Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography*, **32**, 953-962.

MacDonald, D.W. (1983) The ecology of carnivore social behaviour. *Nature*, **301**, 379–383.

Manly, B., McDonald, L. & Thomas, D. (1993) *Resource selection by animals. Statistical design and analysis for field studies*. Chapman and Hall, London, UK.

Ogutu, J.O. & Dublin, H.T. (2002) Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology*, **40**, 120–129.

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

Schaller, G.B. (1996) Carnivores and conservation biology. In: *Carnivore behavior, ecology and evolution Vol 2* (ed. J.L. Gittleman), pp. 1-10. Cornell University Press, Ithaca, New York, US.

Seaman, D.E. & Powell, R.F. (1996) An evaluation of the accuracy of kernel estimators for home range analysis. *Ecology*, **77**, 2075–2085.

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

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.

Sinsin, B., Akpona, A.H. & Ahokpe, E. (2006) *Dénombrement aérien de la faune dans la Réserve de Biosphère de la Pendjari*. Unpublished Report. Projet Pendjari GTZ, Cotonou, Benin.

Sinsin, B., Sogbohossou, E.A. & Nobime, G. (2008) *Dénombrement aérien de la faune dans la Réserve de Biosphère de la Pendjari*. Unpublished Report. Projet Pendjari GTZ, Cotonou, Benin.

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.

Sokpon, N., Biaou, H., Hounhyet, O., Ouinsavi, C. & Barbier, N. (2001) *Inventaire et caractérisation des formations végétales du complexe national de la Pendjari, zone cynégétique de la Pendjari et de l'Atacora: région de Konkombri*. Unpublished Report. UNB/CENAGREF, Cotonou, Bénin.

Thrash, I., Theron, G.K., & du P. Bothma, J. (1995) Dry season herbivore densities around drinking troughs in the Kruger National Park. *Journal of Arid Environment*, **29**, 213–219.

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.

Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. (1985) Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology (London)*, **206**, 97–112.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology*, **70**, 164–168.

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