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

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Submitted

Abstract

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

Keywords

diet, prey preference, *Panthera leo*, Pendjari Biosphere Reserve
Part III  Lion population in Pendjari Biosphere Reserve

5.1  Introduction

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

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

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

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

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

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

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

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

5.3.1 Scat collection and analysis

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

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

5.3.2 Interviews and observations

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

5.3.3 Characterization of the lion diet

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

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

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

$$B=1/\sum \pi_i^2$$

($\pi_i$ is the fraction of items in the diet that are of food category $i$).

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

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

in which:

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

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

The formula of the evenness is: $E = H'/\ln S$, $S$ being the total number of species.
E varies between 0 (dominance) and 1 (equitability).

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

\[ D = \frac{r-p}{(r+p-2rp)} \]

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

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

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

5.3.4 Data analysis

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

5.4 Results

5.4.1 Species accumulation curves in scats and observations

We identified prey species in 35 lion scats and collected 156 observations of lions feeding on carcasses. The accumulation curves (Fig. 2) show that while 50 observations seem to be enough to have a reliable estimation of the diet of lions, the 35
scats on their own would not have resulted in a reliable estimation of lion diet in our study site.

[Figure 2] Species accumulations curves in scats and observations.

### 5.4.2 Species composition in the lion diet

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

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

Based on direct feeding observations and scats analysis, medium-sized prey were dominant in the diet while large prey (≥180 kg) composed 38.2% of the diet and small prey composed 1.1%. Lions in the hunting zones have significantly more large prey in their diet than lions from the park (Fig. 4.) (z = 2.45; p < 0.05) however the proportion of medium-sized prey in the two areas is similar.
## Table 1 Summary of kills based on feeding observations and scats in Pendjari Biosphere Reserve from 2008 to 2010.

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

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

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

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

### 5.4.4 Diet choice

The preference of lions for diverse prey species is presented in the Table 3. The most-preferred species were hartebeest and waterbuck. Warthog and buffalo were killed according to their abundance while smaller ungulates such as oribi...
and duikers were generally avoided. The mean weight of non-preferred prey species, considering Jacob’s index of each, was 19.4 kg. The mean weight of preferred prey species was 167.5 kg.

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Relative availability</th>
<th>Jacob’s index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hartebeest</td>
<td>0.042</td>
<td>0.613</td>
</tr>
<tr>
<td>Waterbuck</td>
<td>0.006</td>
<td>0.605</td>
</tr>
<tr>
<td>Kob</td>
<td>0.143</td>
<td>0.144</td>
</tr>
<tr>
<td>Bushbuck</td>
<td>0.028</td>
<td>0.084</td>
</tr>
<tr>
<td>Buffalo</td>
<td>0.204</td>
<td>0.068</td>
</tr>
<tr>
<td>Roan</td>
<td>0.120</td>
<td>0.034</td>
</tr>
<tr>
<td>Warthog</td>
<td>0.076</td>
<td>0.009</td>
</tr>
<tr>
<td>Redunca</td>
<td>0.025</td>
<td>-0.072</td>
</tr>
<tr>
<td>Baboon</td>
<td>0.151</td>
<td>-0.234</td>
</tr>
<tr>
<td>Duikers</td>
<td>0.119</td>
<td>-0.541</td>
</tr>
<tr>
<td>Oribi</td>
<td>0.086</td>
<td>-0.698</td>
</tr>
</tbody>
</table>

5.4.5 Diet characteristics

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

5.5 Discussion

5.5.1 Species composition and diet diversity

The number of lion prey species at a particular site usually varies from about 14 (Breuer, 2005) to more than 20 species (Pienaar, 1969; Hayward & Kerley, 2005; Funston & Mills, 2006; Lehmann et al., 2008). In Pendjari, the diversity of the diet was lower, but almost all species present were recorded in their diet. Generally at most study sites about five prey species predominate, and typically make up
about 75% of the lions’ diet (Stander & Albon, 1993; Funston et al., 1998; Druce et al., 2004; Radloff & du Toit, 2004; Loveridge et al., 2006).

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

A predominance of buffalo in the diet of lions has been reported in several national parks throughout Africa including Kafue (Mitchell et al., 1965), Hwange (Loveridge et al., 2006), Chobe (Viljoen, 1993), Lake Manyara (Makacha & Schaller, 1969; Schaller 1972), Mala Mala (Radloff & du Toit, 2004) and Kruger (Mills et al., 1995; Funston et al., 1998). In the few observations available for West and Central Africa, buffalo was among the most numerically abundant prey in the diet of lions only in Niokolo Koba and Zakouma (Bauer et al., 2008b). Due to the relative small size of lion groups in the region (Bauer et al., 2003b), this result was not expected and does question the generality of the findings of Bauer et al. (2008b). Because of the antipredatory defence behaviour of buffalo (Makacha & Schaller, 1969), it was expected that the small lion groups typically found in West and Central Africa (Bauer et al., 2003b; Sogbohossou et al., in prep.) would not easily kill buffalos. Schaller (1972) and Stander & Albon (1993) observed that lion hunting success is greater in larger groups, and notably Packer et al. (1990) found that large groups of lions (> five) were generally needed to capture buffalos. Although feeding groups in Pendjari varied from one to six individuals, in 46% of cases there was only one adult in the feeding group, two adults in 42% of observations and three adults in 8% of observations. If we suppose that these adults were the ones responsible for the kill, and that 71% of buffalo killed were adults, this would suggest that relatively small groups of adult lions in Pendjari are effective at killing adult buffalos. The high proportion of adult buffalo in kill records was also observed in Mala Mala Reserve (Radloff & du Toit, 2004). However, Funston et al. (1998) showed that lions in Kruger mainly killed buffalo calves and consumed them during the night. Thus our results must be interpreted with caution as kill remains as well as lions found feeding on carcasses does bias the results towards larger carcasses (Mills, 1992). In Beninese and West Africa savannah in general, buffaloes typically weigh about
473 ± 57 kg, n = 62 (DPNP, 2004; 2006; 2007; 2008; 2009) and occur in relatively small herds of five to fifty individuals, with exceptional herds numbering up to a hundred individuals (E.A. Sogbohossou, pers. obs.). In southern Africa, buffalos typically weigh about 750 kg and occur in herds of several hundreds. These differences could explain why lions in smaller groups in Pendjari are effective hunters of buffalo.

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

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

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

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

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

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

5.5.3 Implications for conservation

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

The predominance of medium-sized prey that usually represents a greater part of the diet of other large carnivore species (Di Silvestre et al., 2000; Breuer, 2005) suggests that these species will turn to smaller prey species or compete more with lions. Studies on feeding habits of other carnivores that inhabit Pendjari are necessary. However it is probable that this cohabitation is more harmful to other predators than to lions. As prey census data we used were not recent and some prey
abundance data was lacking, it would be interesting to have more recent and reliable data on all prey species for further analysis. Furthermore, the system for monitoring the population of ungulates should be improved in Pendjari so that we can have a more complete figure on the prey preference of lions and other predators.

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References


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