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Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters

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Abstract

Analyses of leopard *Panthera pardus* prey choice reveal a strong preference for species weighing 10–40 kg. In the Congo Basin rainforests, species within this weight range are also targeted by bushmeat hunters, potentially leading to exploitative competition between leopards and hunters. We investigated leopard prey choice along a gradient of human disturbance, hypothesizing that leopards will exploit smaller prey where competition is strong, possibly resulting in reduced leopard densities at highly hunted sites. We determined leopard diet by means of scat analysis at four rainforest sites in central Gabon, which varied according to their distance from human settlements. Camera trap data collected at each of the four study sites revealed that human hunting intensity increased with proximity to settlements, while the abundance of potential leopard prey species decreased. We found no evidence of leopards at the site nearest to settlements. At the remaining sites, the number of scats collected, mean leopard prey weight and the proportion of large prey (>20 kg) in leopard diet increased with distance from settlements. Camera trap data demonstrated that leopard population density increased with distance from settlements, from 2.7 ± 0.94 leopards/100 km^2 to 12.1 ± 5.11 leopards/100 km^2. Our results document an increasing use of smaller prey species and a decrease in leopard density in proximity to settlements, supporting our hypothesis. Comparison of leopard diet with hunter return data revealed a high dietary niche overlap between leopards and hunters at sites situated at similar distances from settlements. Our results suggest that bushmeat hunting may precipitate the decline in leopard numbers through exploitative competition and that intensively hunted areas are unlikely to support resident leopard populations. Conserving the leopard in the Congo Basin will rely on effective protected areas and alternative land management strategies that promote regulated human hunting of leopard prey.

Introduction

The leopard *Panthera pardus* has the greatest geographic distribution of the wild cats (Nowell & Jackson, 1996) and is the most abundant large felid in Africa (Hunter, Henschel & Ray, in press). This success appears to be rooted in its wide habitat tolerance, occupying hyper-arid areas and rainforests alike (Hunter *et al.*, in press), and its versatility as a generalist predator (Nowell & Jackson, 1996). Despite a celebrated ability to exploit prey ranging from arthropods to elands (Kingdon, 1977), leopard diet is generally dominated by medium-sized ungulates with a weight range of 10–40 kg (Hayward *et al.*, 2006), and leopard population density is strongly and positively correlated to the biomass of prey species within this weight range (Hayward, O'Brien, & Kerley, 2007). In areas where their preferred ungulate prey is scarce, leopards have been reported to switch to smaller bodied prey (Nowell & Jackson, 1996). However, felid species exceeding 21.5 kg generally tend to specialize on large vertebrate prey (Carbone *et al.*, 1999), and predation on prey species well below a large carnivore's preferred weight range has been suggested as an early indicator for a population at a risk of extinction (Hayward, 2009).

In the Congo Basin rainforest, the leopard is the largest mammalian predator. Previous studies on the species' feeding ecology at three different forest sites revealed a relatively broad diet, with leopards using between 17 and 32 different prey species (Hart, Katembo & Punga, 1996; Ray & Sunquist, 2001; Henschel, Abernethy & White, 2005). Diet was uniformly dominated by ungulate prey, occurring in 44.9–53.5% of analyzed scats, followed by primates, large rodents, pangolins and small carnivores (Hart *et al.*, 1996;

Ray & Sunquist, 2001; Henschel *et al.*, 2005). The mean prey weight varied from a low of 7.3 kg (Ray & Sunquist, 2001) to 29.2 kg (Henschel *et al.*, 2005).

Anecdotal evidence suggests that large forest felids are negatively affected by the depletion of their prey base through exploitative competition with humans hunting for bushmeat (Jorgenson & Redford, 1993; Ray, 2001). The potential for exploitative competition between leopards and hunters is very high in the Congo Basin rainforest; human populations in this region rely primarily on bushmeat for their protein requirements (Robinson & Bennett, 2000), and between one (Wilkie & Carpenter, 1999) and five (Fa, Peres & Meeuwig, 2002) million metric tons of wild meat are estimated to be traded annually. Hunters appear to target larger-bodied species (Fa, Ryan & Bell, 2005), and extraction rates for species >5 kg are considered to be unsustainable in the majority of studies on bushmeat exploitation (e.g. Noss, 1998; Muchaal & Ngandjui, 1999; van Vliet & Nasi, 2008). The result is generally a sharp decline in the number of medium-sized and large ungulates and larger primates in the vicinity of settlements, where hunting is most intense (Laurance *et al.*, 2006; van Vliet & Nasi, 2008).

In the present study we sought to investigate, for the first time, how leopard populations in the African rainforest are affected by humans hunting for bushmeat. We determined leopard diet at four rainforest sites inside and adjacent to Ivindo National Park (NP), Gabon. All study sites were similar, regarding topography and forest type, but were situated at varying distances from settlements. Using available camera-trap data (Henschel, 2008), we compared leopard population density and the relative abundance of prey and of human hunters across all four study sites. We further compared leopard diet with bushmeat hunter returns from one of our sites (Coad, 2007), and from four other matched Congo Basin rainforest sites (Fa *et al.*, 1995; Muchaal & Ngandjui, 1999), to assess the potential for exploitative competition between leopards and hunters. Using these data, we investigate the hypothesis that leopards will exploit smaller, less preferred prey at sites where competition with hunters is intense, possibly resulting in reduced leopard densities at sites where larger prey has been depleted by human hunting. Finally, we evaluate whether unregulated bushmeat exploitation can contribute to the decline of leopard populations across the Congo Basin, and therefore, their likelihood of persisting in forested Africa.

Materials and methods

Study sites

All four study sites were situated within the same contiguous forest landscape in central Gabon, which contains the Ivindo (3000 km^2) and Lopé (4950 km^2) NPs (Fig. 1). The human population density in this central part of Gabon is particularly low, with 1.5–2.0 inhabitants km^{-2} (WNN, 2006), and >95% of the region is covered by mature lowland semi-evergreen rainforest, with elevations ranging between 100 and 1000 m (White & Abernethy, 1997; Vande weghe, 2006). The mammalian fauna of Gabon has been well studied in the northern part of Lopé NP (e.g. White,

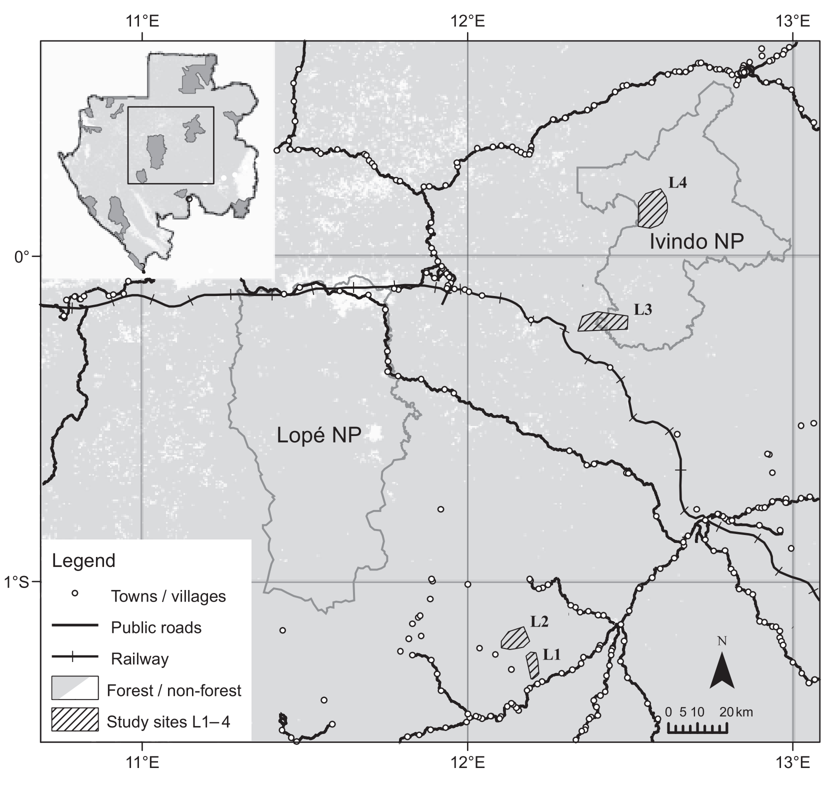

Figure 1 Location of the four study sites in central Gabon relative to villages, public roads, railway tracks and protected areas.

Table 1 Characteristics of each study area (L1–L4), describing the study period, predominant form of land use, legal status of hunting in the area and distance from the nearest settlement and point of market access

Study site	Study period	Land-use type/legal status of hunting	Distance from settlement (km)	Distance from road/railway (km)
L1	9-10/2004	Village hunting territory/permitted	2–12	2–12
L2	4-5/2005	Logging concession/tolerated	3–14	14–21
L3	8-10/2003	National park/prohibited	13–20	13–20
L4	5-6/2004	National park/prohibited	19–29	49–63

1994; Abernethy, White & Wickings, 2002), and 45 species of medium-sized and large mammal species have been identified in this area, including 14, 12 and 11 species of primates, ungulates and carnivores, respectively (Tutin, White & Mackanga-Missandzou, 1997). The fauna of Ivindo NP is less well studied, but species composition for medium-sized and large mammals is very similar to Lopé (Vande weghe, 2006). Mandrills *Mandrillus sphinx*, however, are only present in study sites L1 and L2 and absent in sites L3 and L4 (Abernethy *et al.*, 2002).

Forests surrounding these two protected areas are largely managed by timber companies (WRI, 2009), and small-scale slash-and-burn agriculture is practiced in the direct vicinity (<3 km radius) of settlements. Hunting intensity is generally the highest in the direct vicinity of settlements (Laurance *et al.*, 2006; Coad, 2007), and access to roads and other routes of transport has been identified as a driver of unsustainable levels of hunting, because it facilitates the commercialization of local bushmeat hunting (Wilkie & Carpenter, 1999; Laporte *et al.*, 2007). The study sites were therefore chosen based on their distance from the nearest settlement and point of market access. Two sites were at least partly inside Ivindo NP and the remaining two sites were located about 100 km to the south between Lopé and Ivindo, close to a public road linking two provincial capitals (Fig. 1). Details on all four study sites are provided in Table 1.

Determination of leopard diet at the study sites

We assessed leopard diet through the analysis of scats (Putman, 1984) collected at each study site over periods of 2–3 months (Table 1). We collected leopard scats along prominent game trails and abandoned logging roads, predominantly during patrol trips to inspect remote camera traps set up to determine leopard population density and prey abundance (Henschel, 2008). We distinguished leopard scats from those of the substantially smaller African golden cat *Caracal aurata* based on their diameter, using 21 mm minimum width as a cut-off point (Hart *et al.*, 1996; Ray & Sunquist, 2001). Storage and analysis of scat content followed the protocol established by Henschel *et al.* (2005). We compared prey remains with a reference collection of African rainforest taxa, by examining prey hair retrieved from scats macroscopically, or microscopically, if the macroscopic examination did not permit species identification (Henschel *et al.*, 2005).

For scats containing remains of multiple prey species, we calculated a corrected frequency of occurrence (Karanth & Sunquist, 1995). In studies relying on scat analysis, the importance of smaller prey for a predator can be considerably overestimated, if only the frequency of occurrence of the prey species in the scat samples is considered (Ackerman, Lindzey & Hemker, 1984). We therefore used a correction factor developed by Ackerman *et al.* (1984) based on the linear relationship found between ingested biomass per predator scat and the live weight of the prey species, to convert the frequency of occurrence to the relative biomass consumed by leopards. We used live weights for prey species from White (1994).

Analysis of dietary composition and cross-site comparison

To determine whether leopard prey use differed significantly across study sites, we compared the corrected frequencies of occurrence using Fisher's exact test. Leopard prey selectivity could not be tested, because camera traps rarely detected prey species <10 kg (Henschel, 2008), and abundance data for smaller prey species were consequently unavailable. For larger-bodied species and hunters, we present camera-trap data from Henschel (2008) in the form of a relative abundance index (RAI), given as the number of photographs/100 trap-days. RAI has previously been demonstrated to be a reliable indicator of ungulate abundance in studies on tigers and their prey in Asia (O'Brien, Kinnaird & Wibisono, 2003), and leopards and prey in Africa (Balme, Slotow & Hunter, 2010).

To assess the potential for exploitative competition between leopards and hunters, we compared leopard diet to hunter return data collected concurrent with our study at study site L1 (Coad, 2007). This dataset represents a sample of 1242 hunter kills, 1119 of which were mammals (Coad, 2007). As no hunter return data were available for our study sites L2–L4, we compared our leopard diet data with hunter return data from four Congo Basin rainforest sites matched for habitat, hunting intensity and distance from human settlements (Fa *et al.*, 1995; Muchaal & Ngandjui, 1999). Fa *et al.* (1995) collected data in Rio Muni, Equatorial Guinea (hereafter referred to as site H1), which had easy road and market access, and was hence comparable to our site L1 (Table 1). Muchaal & Ngandjui (1999) collected hunter follow data in three zones within the Dja Reserve, Cameroon (sites H2–H4), which were situated at 0–10, 10–30 and 30–40 km from a relatively remote village, and thus similar to our sites L2–L4 regarding their respective distances from the nearest settlement (Table 1).

For each study site, we calculated the dietary niche breadth, which reflects the degree of specialization on certain prey items exhibited by a given species or population. We used Levins' (1968) niche breadth index, which ranges from 1 to the number of prey species used. We likewise calculated a standardized dietary niche breadth, B_{sta} (Colwell & Futuyma, 1971), to permit comparisons between sites that differed regarding the number of prey species used. The B_{sta} ranges between 0 and 1, where a value of 1 means that all prey species used by a predator are taken at equal proportions, while a value approximating 0 signifies that a few species were taken at disproportionately higher frequencies than the remainder (Colwell & Futuyma, 1971). We furthermore calculated dietary niche overlap between leopard and hunter datasets from all study sites, using Pianka's (1973) index, which varies from 0 (exclusive food niches) to 1 (complete dietary overlap).

Results

Leopard diet

We found no leopard scats at site L1, and 32–83 scats at the remaining three study sites, with the number of scats collected per site increasing with distance from settlements (Table 2). Across sites, 99.1% of prey items in scats could be identified to the genus level; only the medium-sized duikers could not be identified to the species level and were therefore grouped as 'red' duikers (*Cephalophus* spp.). Eight to 17 prey taxa were identified at sites L2–L4, and leopards used exclusively mammalian prey (Table 2). At all sites, 'red' duikers were the most frequently used prey taxon, followed by brush-tailed porcupine *Atherurus africanus* at site L2 and red river hog *Potamochoerus porcus* at sites L3 and L4 (Table 2). In terms of the relative biomass consumed, 'red' duikers were the single most important prey taxon at sites L2 and L3, whereas red river hogs were more important at site L4, accounting for almost 50% of the biomass consumed (Table 3).

Table 2 Composition of leopard diet in three of the four study sites in central Gabon; no leopard scats were found in site L1

		Corrected frequency of occurrence[a]		
Scientific name	Common name	Site L2 (n=32)[b]	Site L3 (n=65)[c]	Site L4 (n=83)[d]
Ungulates				
Neotragus batesi	Bates' pygmy antelope	–	–	1.2
Philantomba monticola	Blue duiker	3.1	3.8	–
Hyemoschus aquaticus	Water chevrotain	–	0.8	–
Cephalophus spp.	'Red' duikers	34.4	36.9	49.4
Cephalophus silvicultor	Yellow-backed duiker	–	4.6	–
Tragelaphus spekii	Sitatunga	–	1.5	–
Potamochoerus porcus	Red river hog	20.3	16.2	36.7
Syncerus c. nanus	Forest buffalo	–	0.8	–
Primates				
Cercopithecus nictitans	Putty-nosed guenon	–	10.0	1.8
Cercopithecus cephus	Moustached guenon	–	2.3	2.4
Lophocebus albigena	Grey-cheeked mangabey	–	1.5	0.6
Colobus satanus	Black colobus	4.7	–	–
Mandrillus sphinx[e]	Mandrill	6.3	–	–
Pan t. troglodytes	Central African chimpanzee	–	3.1	2.4
Gorilla g. gorilla	Western lowland gorilla	–	5.4	–
Rodents				
Atherurus africanus	Brush-tailed porcupine	23.4	6.9	1.8
Unknown small rodent	Unknown small rodent	1.6	0.5	–
Carnivores				
Genetta servalina	Servaline genet	–	1.3	1.2
Atilax paludinosus	Marsh mongoose	6.3	–	0.6
Pangolins				
Uromanis tetradactyla	Long-tailed pangolin	–	0.8	0.6
Phataginus tricuspis	African tree pangolin	–	3.6	1.2

[a]Corrected for the occurrence of multiple prey items (see text).
[b]Thirty-two scats, containing 39 prey items (1.22 items per scat).
[c]Sixty-five scats, containing 81 prey items (1.25 items per scat).
[d]Eighty-three scats, containing 93 prey items (1.12 items per scat).
[e]Mandrills do not occur at sites L3 and L4 (see text).

Table 3 Estimates of the relative biomass consumed by leopards at three of four study sites in central Gabon; no leopard scats were found at site L1

Species	Body weight (kg)[a]	Correction factor (kg/scat)[b]	Relative biomass consumed (%)		
			Site L2 ($n=32$)	Site L3 ($n=65$)	Site L4 ($n=83$)
Ungulates					
Neotragus batesi	3.8	2.11	–	–	0.8
Philantomba monticola	3.9	2.12	2.5	2.8	–
Hyemoschus aquaticus	10.4	2.34	–	0.6	–
'Red' duikers	15.5	2.52	32.8	32.2	40.4
Cephalophus silvicultor	56.7	3.96	–	6.3	–
Tragelaphus spekii	62.8	4.18	–	2.2	–
Potamochoerus porcus	61.9	4.15	31.9	23.2	49.4
Syncerus caffer nanus	118.8	6.14	–	1.6	–
Total ungulates			67.2	68.9	90.6
Primates					
Cercopithecus nictitans	3.2	2.09	–	7.2	1.2
Cercopithecus cephus	2	2.05	–	1.6	1.6
Lophocebus albigena	4.1	2.12	–	1.1	0.4
Colobus satanus	8.4	2.27	4.0	–	–
Mandrillus sphinx[c]	10.2	2.34	5.5	–	–
Pan t. troglodytes	38.7	3.33	–	3.6	2.6
Gorilla g. gorilla	78.1	4.71	–	8.8	–
Total primates			9.6	22.3	5.8
Rodents					
Atherurus africanus	2.3	2.06	18.3	4.9	1.2
Unknown small rodent	0.1	0.1[d]	0.1	0.1	–
Total rodents			18.3	5.0	1.2
Carnivores					
Genetta servalina	1.6	2.05	–	0.9	0.8
Atilax paludinosus	3	2.09	4.9	–	0.4
Total carnivores			4.9	0.9	1.2
Pangolins					
Uromanis tetradactyla	2.3	2.06	–	0.6	0.4
Phataginus tricuspis	1.9	1.9[d]	–	2.4	0.7
Total pangolins			0.0	2.9	1.1

[a]Estimated mean live weight (kg) from White (1994).
[b]Correction factor calculated following Ackerman *et al.* (1984).
[c]Mandrills do not occur at sites L3 and L4 (see text).
[d]No correction factor is applied for species <2 kg (Ackerman *et al.*, 1984).

Dietary comparison across sites

The frequency of occurrence of prey items in leopard diets differed significantly between sites L2–L4 (Fisher's exact test, $P<0.0001$, Table 2). When we grouped prey taxa into small prey (≤ 5 kg), medium-sized prey (>5 kg, <20 kg) and large prey (≥ 20 kg), we found that leopard use of small prey increased at sites in proximity to settlements (Fisher's exact test, $P=0.002$), whereas the use of large prey decreased at these sites, and was the highest at the most remote site L4 (Fisher's exact test, $P=0.001$; Fig. 2a). The use of medium-sized prey did not differ significantly between sites (Fisher's exact test, $P=0.766$). Leopard diet was dominated by ungulates at the more remote study sites, whereas the use of primates and rodents increased at sites nearer to settlements (Fig. 2b). Hunter return data from site L1 showed that hunter catch consisted almost exclusively of small-bodied prey (Fig. 2a). Our camera-trap data revealed that medium-sized and large prey were virtually absent at site L1 (Fig. 3), whereas the abundance of larger-bodied prey increased with the distance from settlements (Fig. 3, Henschel, 2008). Similarly, camera traps at site L1 failed to detect leopards, while population density increased with the distance from settlements at the remaining sites (Fig. 3). Hunting intensity, calculated as the RAI of hunters filmed in camera traps (Henschel, 2008), decreased with distance from settlements, and no hunters were recorded at the most remote site L4 (Fig. 3).

The highest mean prey weight was recorded for leopards at site L4, and leopard and bushmeat hunter mean prey weight decreased with proximity to the settlements (Table 4). For both leopards and hunters, the standardized dietary niche breadth (B_{sta}) was the smallest at the most remote sites (L4 and H4) and increased at sites nearer to settlements (Table 4). The dietary niche overlap between leopards and hunters was the highest between pairs of study sites located at similar distances from settlements (Table 5).

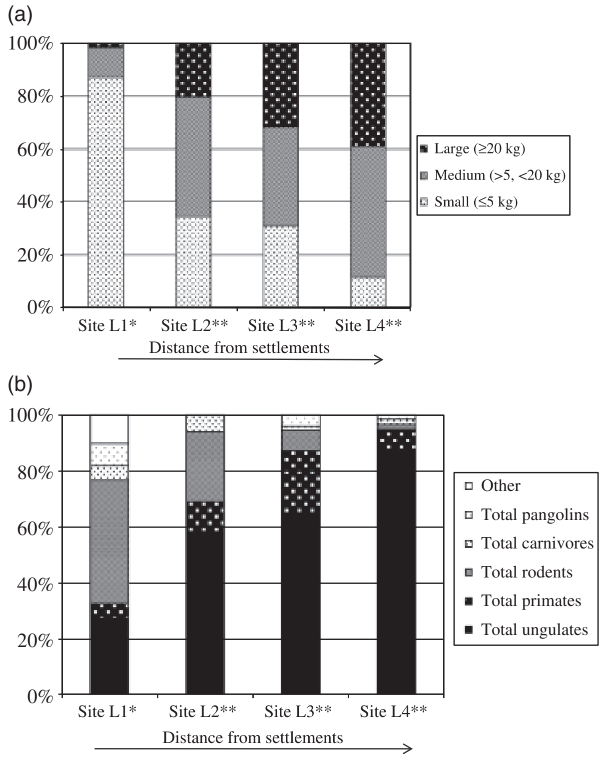

Figure 2 Representation of different prey size classes (a) and prey taxa (b) in hunter return data* (site L1) and leopard scats** (sites L2–L4) at four study sites in central Gabon. Data sources: site L1, Coad (2007); sites L2–L4, this study.

Discussion

Our study is the first to indicate the deleterious effects of human bushmeat exploitation on leopard populations. With increasing proximity to settlements and concomitant human hunting pressure, leopards exploited smaller prey and occurred at considerably reduced population densities, strongly supporting our hypothesis. In the presence of intensive bushmeat hunting surrounding human settlements, leopards appeared entirely absent. Our comparison of leopard diet with hunter return data reveals that both species exhibit the highest mean prey weight and the narrowest dietary niche at the remotest site, suggesting selective predation on larger prey species (Table 4). Closer to settlements, leopards and bushmeat hunters alike exhibit a wider diet and exploit an increasing proportion of smaller prey (Table 4), most likely in response to a reduced abundance of larger prey species (Fig. 3; Fa *et al*., 1995; Muchaal & Ngandjui, 1999). As both species appear to exhibit a very similar response to changes in prey abundance, dietary niche overlap between leopards and hunters at sites located at similar distances from settlements is high (Table 5). Large predators like leopards are limited by prey availability (Hayward *et al*., 2007), and for food-limited species, the degree of dietary niche overlap provides evidence for the occurrence of exploitative competition (Hayward & Kerley, 2008). The high dietary niche overlap observed between leopard and human hunters in our study consequently suggests strong exploitative competition between both species.

At site L1, where bushmeat hunting intensity was the highest (Fig. 3), we found no leopard scats nor was the species recorded during 2 months of intensive camera trapping (Henschel, 2008). Given the intensity of our survey effort, which was similar across all four study sites, it is unlikely that leopards were present at this site during the study (Henschel & Ray, 2003). This result is of even more concern, considering that site L1 consisted of $>30\,km^2$ of unfragmented, prime rainforest habitat, contiguous to the north with a vast forest area also containing site L2 (Fig. 1), where leopards occurred (Henschel, 2008). Immigration of

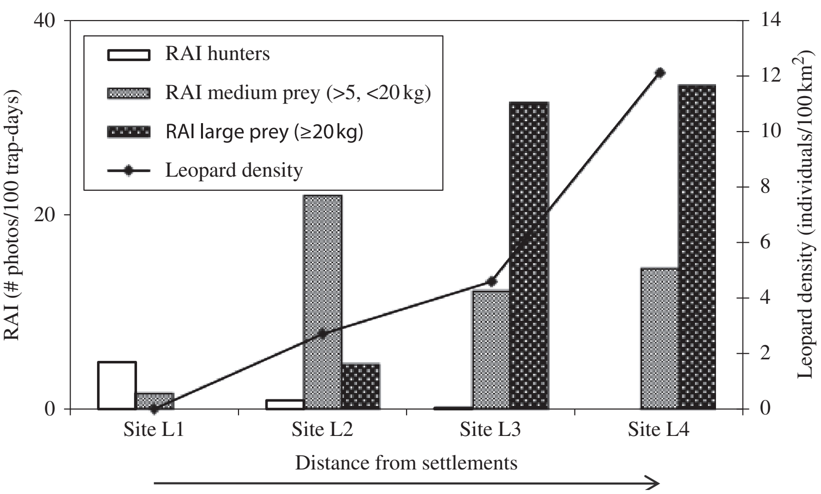

Figure 3 Camera trap estimates of the relative abundance index (RAI) of hunters and leopard prey, and leopard population density at four study sites in central Gabon. Data source Henschel (2008).

Table 4 Number of mammalian prey species, mean weight of mammalian prey, dietary niche breadth (B) and standardized dietary niche breadth (B_{sta}) for leopards (sites L2–L3) and hunters (sites L1, H1–H4) in eight Congo Basin rainforest sites

Site	# prey species	Mean prey weight (kg)	B^a	$B_{sta}{}^b$	Data type and source
L2	8	19.8	4.43	0.49	Leopard diet[c]
L3	17	26.5	5.34	0.27	Leopard diet[c]
L4	12	31.6	2.62	0.15	Leopard diet[c]
L1	22	5.0	5.88	0.29	Hunter returns[d]
H1	17	5.2	5.00	0.27	Hunter returns[e]
H2	21	6.8	5.27	0.25	Hunter returns[f]
H3	17	8.6	4.52	0.25	Hunter returns[f]
H4	8	14.1	1.80	0.13	Hunter returns[f]

[a]Dietary niche breadth (Levins, 1968).
[b]Standardized dietary niche breadth (Colwell & Futuyma, 1971).
[c]This study.
[d]Coad (2007).
[e]Fa *et al.* (1995).
[f]Muchaal & Ngandjui (1999).
Study sites: L1–L4, this study; H1–H4, matched bushmeat study sites (see text); numbers indicate proximity to settlements (1 = closest; 4 = furthest). Data sources are indicated by different alphabets.

Table 5 Food niche overlap across eight Congo Basin rainforest sites with data on leopard diet (sites L2–L4) or hunter returns (sites L1, H1–H4)

Site	L2	L3	L4	L1	H1	H2	H3	H4	Data type and source
L2	X								Leopard diet[a]
L3	**0.88**	X							Leopard diet[a]
L4	**0.86**	**0.92**	X						Leopard diet[a]
L1	0.64	0.42	0.25	X					Hunter returns[b]
H1	0.51	0.42	0.21	**0.83**	X				Hunter returns[c]
H2	0.65	0.63	0.46	0.74	**0.91**	X			Hunter returns[d]
H3	**0.81**	0.75	0.61	0.78	**0.81**	**0.94**	X		Hunter returns[d]
H4	0.75	**0.84**	**0.80**	0.35	0.35	0.68	**0.82**	X	Hunter returns[d]

[a]This study.
[b]Coad (2007).
[c]Fa *et al.* (1995).
[d]Muchaal & Ngandjui (1999).
Study sites: L1–L4, this study; H1–H4, matched bushmeat study sites (see text); numbers indicate proximity to settlements (1 = closest; 4 = furthest). Food niche overlap values >0.8 are highlighted in bold. Data sources are indicated by different alphabets.

leopards from adjacent forest areas would be expected, if conditions at site L1 were favorable for the species. Direct persecution of leopards at site L1 is the most obvious explanation for their absence. However, hunters using site L1 belonged exclusively to the Pouvi ethnic group, whose members are prohibited to kill leopards (Coad, 2007) or even consume their meat (Starkey, 2004). Furthermore, Balme *et al.* (2010) demonstrated, using a monitoring effort very similar to ours, that leopards persist under high levels of anthropogenic persecution, albeit in lowered densities, provided suitable prey is available. We believe, therefore, that the apparent absence of leopards at site L1 was due to the extremely low abundance of medium-sized and large prey at the site (Fig 3), as a direct result of intensive bushmeat exploitation at the site (Coad, 2007). Hunters at site L1 catch almost exclusively small-bodied (≤ 5 kg) prey (Fig. 2a), with almost 50% of the 1242 kills recorded at this site being represented by two species: the blue duiker *Philantomba monticola* and the brush-tailed porcupine (Coad, 2007). Although large felids (e.g. López González & Miller, 2002) and canids (e.g. Woodroffe *et al.*, 2007) are reportedly able to subsist on small prey species occurring at high densities, our results suggest that leopards are incapable of subsisting entirely on small-bodied prey at rainforest sites subject to intense bushmeat exploitation.

Our site L1 is representative of much of rural Gabon (Coad, 2007), suggesting that the factors leading to poor prospects for leopards there are widespread in the Congo Basin. Studies on the impact of commercial bushmeat hunting on multi-prey communities throughout the Congo Basin clearly demonstrate that unsustainable hunting quickly leads to the disappearance of larger-bodied species (Noss, 1998; Muchaal & Ngandjui, 1999). Smaller species, such as brush-tailed porcupines and blue duikers, may decrease at a lower rate, and/or may persist under higher levels of hunting pressure while at even higher exploitation rates only rodent species are still extant (Cowlishaw, Mendelson & Rowcliffe, 2005; Waite, 2007). Considering that the human population in the Congo Basin is likely to double in 25–30 years (UN, 2005), and that there is little evidence of implementation of strategies to reduce the drivers of bushmeat hunting [e.g. urban market regulation, environmental education, provision of alternative protein sources for rural communities (Wilkie & Carpenter, 1999; Wilkie *et al.*, 2006)], it is likely that larger-bodied prey species will be extirpated from all areas of forest close to population centers (Wilkie & Carpenter, 1999).

Under these circumstances, other land-use types that mitigate the effects of bushmeat hunting will be essential for effective conservation of leopards in the Congo Basin. Our data clearly demonstrate the value to leopards of well-managed, inviolate protected areas such as Ivindo NP. However, only 12% of the Congo Basin rainforests currently receive formal protection, while >30% of the forests are under logging concessions (Laporte *et al.*, 2007). Although logging concessions can increase commercial hunting access (Poulsen *et al.*, 2009), pilot studies in concessions in north-eastern Congo suggest that, if managed appropriately, logged forests can support larger rainforest taxa at densities comparable to protected areas (Clark *et al.*, 2009). In the absence of strong management of village bushmeat hunting, the combination of well-managed, large protected areas and similarly large and well-managed logging concessions may provide leopards with the highest chance for long-term survival in the Congo Basin.

Our results have similar implications for large felid conservation efforts in tropical America and Asia, where rural populations equally exploit large prey species at extraction rates generally considered to be unsustainable (e.g. Robinson & Bennett, 2000). Although the decline of jaguars and tigers is primarily explained by direct persecution of felids and destruction of their habitat (e.g. Naughton-Treves *et al.*, 2003; Linkie *et al.*, 2008), a recent analysis of predator–prey ratios across multiple sites and involving 11 carnivore species revealed that the largest species are disproportionately more vulnerable to decreases in the abundance of their prey (Carbone, Pettorelli, & Stephens, 2011). Overhunting of prey is undoubtedly a factor affecting the viability of tiger populations (Karanth & Stith, 1999), and it is also likely a key factor in the ability of jaguars to persist in human-modified landscapes and move between them (Rabinowitz & Zeller, 2010). As for forest leopards in Africa, conservation of these felids will rely on focused interventions that address their immediate persecution as well as the overhunting of prey.

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