Fragmented populations of leopards in West-Central Africa: facing an uncertain future

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During recent decades, most endangered species have suffered serious population declines. Little has been documented on leopards in West-Central Africa and as a result the efficiency of protection measures and wildlife managing practices can be questioned. Using 416 occurrences of leopards, we investigated the relationship between different environmental factors and leopard distribution to establish a baseline distribution of this feline. Leopards are mainly present in two large populations: one in a forest habitat, the other in a savanna habitat. Leopard populations were found to be associated with lions and hyaenas but they avoided human disturbances. Regarding potential breeding dispersal, the Gaussian representation showed a clear fragmentation among populations, suggesting that long-term survival of the species could be threatened. We found no area to be exempt from threats. The leopard has, however, declined less than other carnivore species and still shows viable populations. Furthermore, occurrences were found to be significantly more numerous than expected in protected areas, suggesting the relative efficiency of conservation.

Key words: conservation, dispersal distance, distribution, feline status, *Panthera pardus*, population fragmentation, threat, West-Central Africa.

INTRODUCTION

Most endangered species, and especially large felids, have suffered serious declines in their populations during recent decades. Hence the efficiency of the protection measures implemented can be questioned.

Knowledge of wildlife status is variable in West-Central Africa. Some species, such as lions (*Panthera leo*), elephants (*Loxodonta africana*), and *Cercopithecus* monkey species (e.g. *Cercopithecus sclateri*), have been widely studied (e.g. Tchamba 1996; Bauer 2003; Kümpel *et al.* 2008) whereas scientific literature is extremely poor concerning other species such as leopards (*Panthera pardus*), giraffes (*Giraffa camelopardalis*) or striped hyaenas (*Hyaena hyaena*) (Nowell & Jackson 1996, Henschel 2008; IUCN/PAPACO 2009). Despite various protection measures and a number of protected areas, some studies have shown that many species, including lions, wild dogs (*Lycaon pictus*), Derby elands (*Taurotragus derbianus*), and cheetahs (*Acinonyx jubatus*), are still declining (Woodroffe & Ginsberg 1999; Bauer *et al.* 2003; Angwafo 2006; Hayward *et al.* 2007). Other species, such as the black rhinoceros (*Diceros bicornis*), have even been declared extinct (Prouteau 2007). More data on species are needed to set appropriate management guidelines and to improve the existing ones.

Leopards may be the felids with the largest range in the world, occupying almost all of sub-Saharan Africa, and a great part of Asia (Nowell & Jackson 1996). Thus the species occupies various habitats, from tropical forests to woodland savannas, and shows great adaptability to the environment (Nowell & Jackson 1996). Although some researchers consider leopards as generalist feeders (Hart *et al.* 1996; Ott *et al.* 2007), others show that they exhibit prey-size preferences (e.g. Hayward *et al.* 2006; Schwartz & Fischer 2006; Martins *et al.* 2011). Their hunting behaviour also varies according to the habitat: leopards are largely nocturnal in an open environment (e.g. Stander *et al.* 1997; Bailey 2005), whereas they show diurnal and crepuscular habits in forest ecosystems (Hart *et al.* 1996; Jenny & Zuberbuhler 2005). Home-range size depends on the preferred prey availability in the habitat (Bothma *et al.* 1997; Steyn & Funston 2009). Although the specific conservation status is difficult to establish in this very elusive species (Norton 1990; Henschel 2008) it is commonly agreed that leopard populations remain widely distributed.

In West-Central Africa, the distribution of the species is supposed to be semi-continuous from the south of Senegal to Burkina Faso and Benin, although the leopard could have a more discontinuous range in Niger, Nigeria and Cameroon

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(IUCN 2010). However, the most recent analysis of its status (Martin & Meulanaer 1988) remains very controversial (Norton 1990; Henschel 2008). Despite the apparent consensus on the conservation status, the efficiency of protection measures has rarely been estimated (Rodrigues *et al.* 2004; Al-Johany 2007; Visser *et al.* 2009).

Carnivores are usually found in quite low densities, even in optimal conditions. They are sensitive to every modification of their environment, particularly those due to human activities that lead to habitat deterioration and prey depletion. For instance, aquatic carnivores have to cope with the human alteration of freshwater ecosystems (Lodé 2002; Bifolchi & Lodé 2005), while forest carnivores have to face the influence of deforestation due to forest exploitation and land reclamation (Hacker *et al.* 1998; Niedzialkowska *et al.* 2006). Habitat deterioration, which includes both habitat fragmentation and habitat loss, is fundamentally related to species fragmentation, a critical threat for endangered species (Fahrig 1997). Habitat patches are generally interspersed in damaged environments, thus leading to a heterogeneous fragmentation within wildlife populations. If the distance between continuous habitat patches is too large, their connectivity becomes too low to allow a sufficient dispersal of individuals (Fahrig & Merriam 1994), altering both breeding exchanges and genetic diversity (Frankham 1995). As it may be more difficult for individuals to mate (Comiskey *et al.* 2002; Rodriguez & Delibes 2003), fragmentation might ultimately cause a decline in populations, and could lead to local extinctions, reinforcing the threatened status of those endangered species (Fahrig & Merriam 1994; Bender *et al.* 1998).

As a top predator, the leopard might be strongly affected by habitat degradation. In West-Central Africa, fragmentation of leopard populations has been rarely documented (Henschel 2008), and little information is available concerning leopard densities (Croes *et al.* 2011). However, the conservation of this emblematic species has important economic consequences (Verbelen 1999; Nemangaya 2002) because wildlife represents a great source of income through tourism and trophy hunting (Kwabong 2008; Hemson *et al.* 2009; Lindsey *et al.* 2012).

Recently, some attention has also been given to interactions among predators (Creel *et al.* 2001; Odden *et al.* 2010). Leopards are sympatric with numerous other predators in open habitats, and such direct or exploitative competition could reduce the access to distinct resources. Nevertheless, it is commonly admitted that where large carnivores occur sympatrically, their chances of persistence are higher. The reason for this might be the greater efficiency of multispecies conservation actions (Ray *et al.* 2005; Hess *et al.* 2006; Lindenmeyer *et al.* 2006).

From a detailed investigation, the objective of this study was to analyze the ecological factors and managing practices related to leopard conservation status in Cameroon. We analyzed the leopard distribution and explored to what extent it was affected by environmental factors, interactions with other species, and other threats such as poaching, agriculture and forest logging. This study also provide an initial basis of leopard status in Cameroon. Our study uses an original approach, combining a mathematical model of dispersal with an evaluation of environmental deterioration. This research should help highlight conservation priorities and provide advice for management of carnivores in West-Central Africa.

METHODS

Study area

Cameroon has an area of 475 442 km². Human population (18 894 406 inhabitants with a density of 41 inhabitants/km²) is mainly concentrated in the cities (57% of the total population), while the rest of the country is inhabited by local village populations.

Climate varies from dry-tropical in the north, to tropical-humid/equatorial in the south, with local variations. Cameroon's vegetation is of five main types: humid forest with either monomodal or bimodal rainfall, highland vegetation, Guinean savanna (deciduous woodland), and Sudano-Sahelian savanna (deciduous shrubland) (IRAD 2009).

Leopard distribution

We documented the presence of leopard throughout the Cameroon by field work, questionnaires, and bibliographical research. We recorded various traces that indicated the occurrence of leopards (faeces, pugmarks, carcasses and sightings) in the National Park of Boubandjida (North province) from March to May 2010. We walked in dry riverbeds six days a week, the two first weeks of each month, looking for signs, from 6:00 to 10:00 and from 16:00 to 18:00. While in the field, P.T. met the hunting guides of 23 hunting zones in the Bénoué National Park Complex (North province). During informal meetings they said they had seen leopards within their areas in the past year. In order to scientifically record these testimonies, we emailed questionnaires to them in May 2010. The questionnaires consisted of descriptive questions about the hunting zone (e.g. geographical information, wildlife species present, encountered threats), as well as the presence of leopard through detailed observation records. Only nine hunting guides answered. Data were also collected through 32 published or unpublished papers or fieldwork reports (Table 1). We selected bibliographical data according to four criteria: 1) data from theses, unpublished data from extensive field research, or reports supervised by an international and independent organization (e.g. WWF, WCS), 2) the fieldwork was conducted in Cameroon after 1995, 3) the results clearly show that leopard presence has or has not been evidenced in the area for at least a decade and 4) data are original. The reliability of data was assessed by personally discussing with the authors their methods and results, and when possible, asking people we know in the area if they had observed leopards recently. From these and our field data collection we recorded the evidence indicating presence or absence of leopard in the studied areas.

To ensure the coherence of data we defined an index calculated from the number of tracks of leopards found in 10 areas of similar conditions reported to a given surface. These data were extracted from studies mentioning density estimates in their results section. We obtained a regression index of 105.03 (Fig. 1), and then defined our index as equal to one unit of presence or absence per 100 km². The value of our index in one area was thus equal to its size (in km²) divided by 100. This seemed pertinent as the median home range of leopard, calculated in previous studies (Jenny 1996; Stander *et al.* 1997; Grassman 1999; Marker & Dickman 2005; Balme *et al.* 2007; Henschel 2008; Simsharoen *et al.* 2008; Swanepoel 2008), is equal to 102 km². The use of this index implies that leopards are uniformly distributed within the delimitated area where evidence of their presence has been recorded. We applied this index to the areas previously mentioned (Table 1) and obtained numbers of data points (or occurrence) of presence or absence of leopard ($n = 661$).

In order to model potential breeding dispersal, leopard distribution was treated through a Gaussian representation (see Lodé 2002). The mapping was smoothed out through a Gaussian blur of the conventional form

$$f(j,k) = \left(\frac{1}{\sqrt{2\pi\sigma}}\right)^{\left(\frac{-(j^2+k^2)}{2\sigma^2}\right)},$$

where (*j*,*k*) represents the intensity at position (j,k) (Press *et al.*1992). Because home range size and breeding dispersal occurred over about 100 km, the Gaussian blur illustrates the potential dispersal within a radius of 100 km around every occupied site. This representation does not illustrate the population density, but it does illustrate the patchy distribution and connectivity. When numerous population exchanges are possible, the range is represented with a darker shade.

Factors potentially related to leopard presence

We defined five types of habitats, according to the five main types of vegetation: humid forest with monomodal rainfall in the western provinces, highland vegetation in the northwestern provinces, humid forest with bimodal rainfall from the south to the south of Adamawa province, Guinean savanna (with deciduous woodland) in the Adamawa province, and Sudano-Sahelian savanna (with deciduous shrubland) in the northern provinces (Fig. 2).

We used three categories for human densities: less than 10 inhabitants per km² (meaning rural areas), between 10 and 100 (rural areas with high level of exploitation), more than 100 (highly populated areas).

This study focused on two types of interactions: competition and predation. In open areas, four predator species were identified as potential competitors: lions, hyaenas, wild dogs, and jackals, while no competitors occur in forest areas. Competitive interactions between leopards and other large carnivores were tested only in open areas (i.e. highland vegetation, Guinean savanna and Sudano-Sahelian savanna). Potential prey species were divided into four categories (Hayward *et al.* 2006): small mammals (body mass <20 kg, e.g. oribi, duikers (Stuart & Stuart 2000)), medium-sized ungulates (20 kg< body mass <70 kg, e.g. bushbuck, reedbuck, kob, common warthog, and red river hog), large ungulates (>70 kg body mass, e.g. hartebeest, topi, waterbuck, sitatunga, giant forest hog) and monkeys and apes (baboon, chimpanzee).

We explored protection level through the presence of potential threats and protection status of the

Table 1. Reports, papers and unpublished data used to assess leopard presence across Cameroon (LCS = large carnivore survey, LMS = large mammal survey, HAS = human activities survey, MP = management plan; NP = National Park, S = Sanctuary, BR = Biosphere Reserve, FR = Faunal Reserve, UFA = Forestry Appointment Unit, ZIC = Zone of Cynegetic Interest; CT = camera trapping, SC = spoor count, LT = line transect, RT = recce transect, Itw = interview; ER = encounter rate, DE = density estimates, NO = number of observations, Pres. = presence, A = animal, T = trace, P = picture).

Source	Type of document	Objectives	Area	Temporal frame	Methods	Data provided	Leopard
Aboudou *et al.* 2008	M.Sc. thesis	LCS	Boubandjida NP &ZIC 11	300j in 2007	CT with baits +SC	ER(T 1 P)	Yes
Angwafo 2006	Ph.D. thesis	LMS	Bénoué NP & Faro NP	Aug 04–May 05	Itw + LT	ER (T)	Yes
de Jager 2007	M.Sc. thesis	LCS	Bénoué NP	Jan–Jun 07	CT with baits +SC	ER(T 1 P)	Yes
Astaras (unpub. data)	Ph.D. research	LMS	Korup NP	Feb–Jun 06	Itw + RT	Pres.	No
MinEF 2007	NGO report	MP	Kom NP & Mengame S	No information	LS	Pres.	No
MinEF 1997	NGO report	MP	Wasa NP	No information	LS	Pres.	No
Nzooh-Dongmo 2003	NGO report	LM & HAS	Lobéké NP	Jan 99–May 03	RT + Ponctual obs	DE/ER	Yes
Ngaudjui *et al*. 2002	Report	MP	Campo-Ma'an NP	Jun 00–May 01	RT	DE/ER	No
Ngaudjui *et al.* 2003	Report	MP	UFAs 21, 24, 25	Jun 00–May 02	RT	DE/ER	No
Nchanji 2002	Unpubl. data	LM & HAS	Banyang-Mbo S	No information	RT	DE/ER	No
Halford et al. 2002	NGO report	LM & HAS	Dja BR	Aug–Sept. 02	Itw + LT	DE/ER (A & T)	No
Sunderland-Groves & Maisels 2003	Scientific paper	LMS	Takamanda Forest Reserve	No information	LT	ER (A & T)	No
Lucy *et al.* 2003	NGO report	LMS	Bomboko Forest Reserve	Aug 02–Mar 03	RT	NO (A & T)	No
Eno-Nku 2003	NGO report	LMS	Ejagham Forest	No infomation	RT	ER (A & T)	No
Ekobo 2002	NGO report	LMS	Mont Cameroun Forest	Oct–Nov 03	RT	ER (A & T)	No
Ekinde & Wittinger 2005	NGO report	LMS	Bantakpa & Mbulu Forest	2002–2005	RT	ER (T)	No
Fomete Nembot & Tchanou 1999	NGO report	MP	Ayos, Bakossi, Douala-Edéa	No information	LS	Pres.	No
Fomete Nembot & Tchanou 1999	NGO report	MP	Koupe, Lokoundje Nyong	No information	LS	Pres.	No
Fomete Nembot & Tchanou 1999	NGO report	MP	Manengouba Mwane	No information	LS	Pres.	No
Fomete Nembot & Tchanou 1999	NGO report	MP	Mbam & Djerem, Nlonako	No information	LS	Pres.	No
Fomete Nembot & Tchanou 1999	NGO report	MP	Nta-Ali, oku, Rio dei Rey	No information	LS	Pres.	No
Fomete Nembot & Tchanou 1999	NGO report	MP	Rumpi, Tchabal Bado, Yaoundé	No information	LS	Pres.	No
Ekobo 1998	NGO report	LMS	Ngoila, Nki Ndongo-Adjala	No information	RT	ER (A & T)	Yes
Ekobo 1998	NGO report	LMS	Boumba-Bek & Nki NP	No information	RT	ER (A & T)	Yes
Ekobo 1998	NGO report	LMS	Moloundou-Mimbomimbo	No information	RT	ER (A & T)	Yes
Forboseh *et al.* 2007	Scientific paper	LMS	Etinde, Nkwende Hills, Mone	2002–2004	RT + LS	ER (T)	No
Ndeh 2004	NGO report	LMS	UFA 09-013	No information	RT	ER (A & T)	Yes
Eno-Nku 2004	NGO report	LMS	UFA 09-021	Jun 00–May 01	RT	ER (A & T)	Yes
Eno-Nku 2004	NGO report	LMS	UFA 09-024	Jun 00–May 01	RT	ER (A & T)	No
Nzooh-Dongmo *et al.* 2004	NGO report	LM & HAS	UFA 10-013	Oct–Dec 03	RT	DE/ER	No

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Table 1 (continued)

Type of document	Objectives	Area	Temporal frame	Methods	Data provided	Leopard	
Nzooh-Dongmo *et al.* 2003	NGO report	LM & HAS	UFA 10-018	Nov–Dec 02 & May 03	RT	DE/ER	Yes
JMN Consultants 2006	Report	Impact study	UFA 10-030, 039, 041, 042, 044	No information	RT	ER (T)	No
Eno-Nku 2004	NGO report	LMS	UFA 11-002	No information	RT	ER (A & T)	No
Mendomo-Biang & Nzooh-Dongmo 2007	NGO report	LM & HAS	ZIC 1 & 8	May–Aug 07	RT	ER (A & T)	No
Ghogue 2007	NGO report	LM & HAS	ZIC 2	Apr–Jun 07	RT	ER (A & T)	No
LF Veko 2007	Report	LMS	ZIC 13	Feb–Mar 07	LT	DE/ER	Yes
Boulet *et al.* 2008	NGO report	LMS	ZIC 18, 18B, 15, 03, 24	2005–2008	Testimonies	NO (A & T)	Yes
Mahop 2007	NGO report	LMS	ZIC 19	Apr–July 07	RT	ER (A & T)	Yes
LF Veko 2007	Report	LMS	ZIC 31	Jun 07	LT	DE/ER	Yes
LF Veko 2007	Report	LMS	ZIC 38	Jun 07	LT	DE/ER	Yes
Nzooh-Dongmo *et al.* 2002	NGO report	LMS	ZIC GC 2, 3, 8	Mar 01–Apr 02	RT	ER (A & T)	No
Nzooh-Dongmo *et al.* 2002	NGO report	LMS	ZIC GC 1, 9	Mar 01–Apr 02	RT	ER (A & T)	Yes

different areas. We determined eight types of threats: poaching/disturbance due to game hunting, agriculture, pasture, gathering/use of forest products (fruits, roots, fire wood, etc.), forest logging (exclusively in forest habitats), human–wildlife conflicts, areas crossed by road infrastructures, and other threats. There are 24 protected areas (excluding Hunting Zones, Forest Reserves) in the country representing 3 755 602 ha (7.9% of the country's area), 15 National Parks and nine Faunal Reserves and Sanctuaries (Table 2) (RAPAC 2010; MinFOF & MinEP 2010).

We determined five types of protection statuses: National Parks, Reserves (including Faunal Reserves, Sanctuaries, and Forest Reserves), Zones of Cynegetic Interest (ZIC), Exploited Forests (EF) gathering Units of Forestry Appointments (UFA) and Communal Forests (CF) and Other (mangroves, mountains, etc.). Leopards are integrally protected in the whole country, and in National Parks, Reserves and ZIC, this protection is applied (hunting restriction or interdiction, anti-poaching patrols), whereas Sanctuaries concentrate on protecting one species (gorilla in Mengame, chimpanzee in Banyang Mbo). In Exploited Forests and other areas, no special measures are applied.

We assessed the relationship between factors and leopard presence using chi-square (with Yates' correction) tests.

RESULTS

Environmental factors

Out of 661 data points, we evidenced 416 leopard occurrences. Leopard distribution, as a function of habitat type, was significant (χ^2 (Yates' correction), $n_{\text{presence}} = 416$, $n_{\text{absence}} = 245$, d.f. = 4, $P < 0.001$) (Fig. 3). Leopards were found to be more numerous than expected in the Sudano-Sahelian savanna habitat (31.7%) and the humid forest with bimodal rainfall habitat (55.2%). However, no leopard occurrences have been reported in western highland vegetation (0%) and few in humid forest with monomodal rainfall (8.8%) habitats.

Populations were subdivided into several demes (Fig. 2). There are two large populations in the north and in the south while three small populations in the central part of the country were very isolated. Regarding potential breeding dispersal, the Gaussian representation showed a clear fragmentation among populations and leopard distribution greatly differed among areas. The southern population exhibited some zones of fragility.

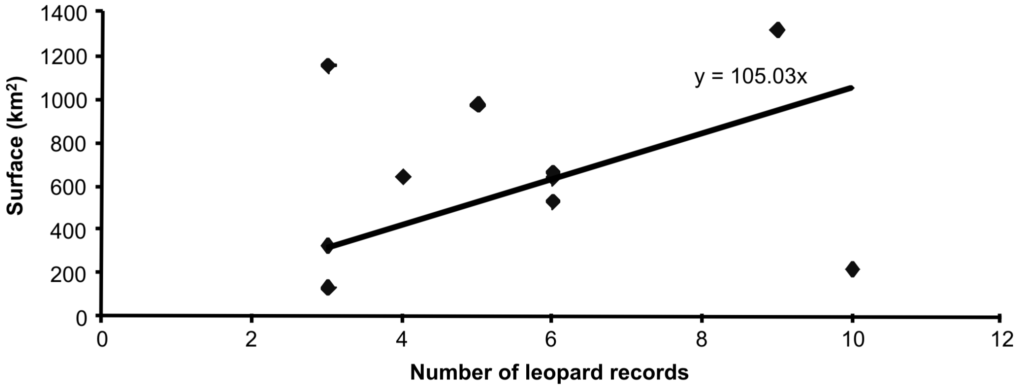

Fig. 1. Regression between size (km^2) of study area and number of leopard records (data obtained from 10 areas).

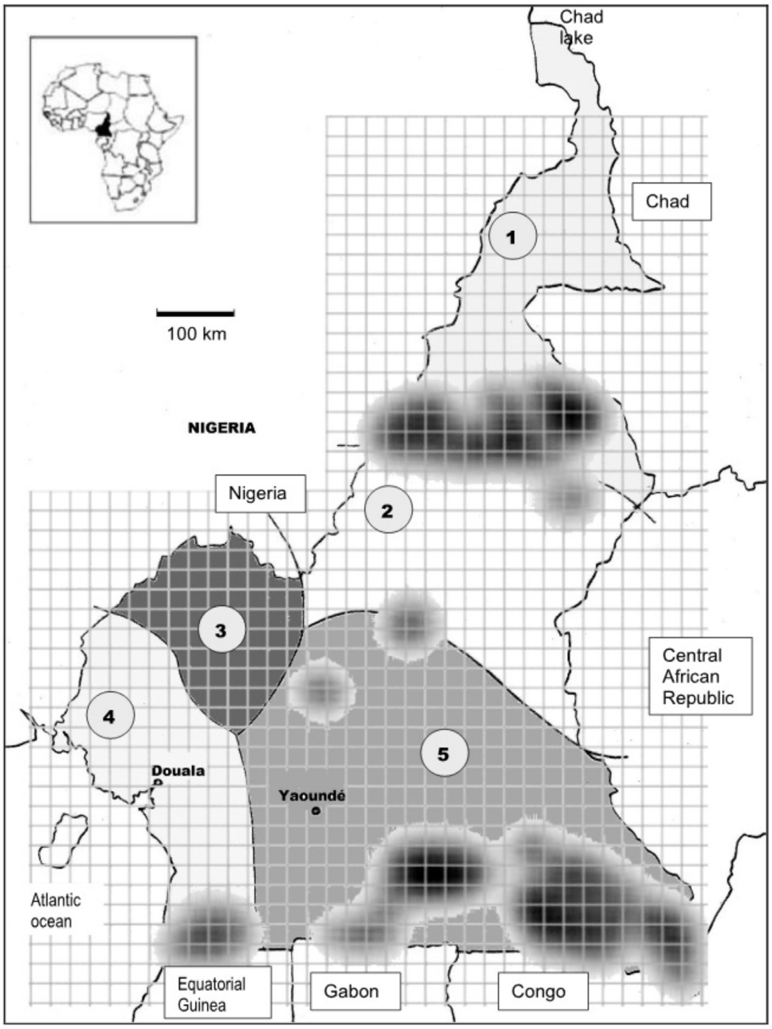

Fig. 2. Distribution and fragmentation (Gaussian representation) of leopard populations in Cameroon. Numbers refer to different habitats: 1, Sudano-Sahelian savanna; 2, Guinean savanna; 3, western highland vegetation; 4, humid forest with monomodal rainfall; 5, humid forest with bimodal rainfall

Table 2. Protected Areas in Cameroon (NP = National Park, BR = Reserve of Biosphere, FR = Faunal Reserve, S = Sanctuary).

Name	Status	Surface (ha)	'Province'
Kalamaloué	NP	4 500	extreme North
Mozoko-Gokoro	NP	1 400	extreme North
Waza	NP	170 000	extreme North
Boubandjida	NP	220 000	North
Bénoué	NP	180 000	North
Faro	NP	330 000	North
Mbéré	NP	77 760	Adamawa
Korup	NP	125 900	Southwest
Mbam et Djerem	NP	125 000	Centre
Mpem et Jim	NP	100 000	Centre
Campo-Ma'an	NP	264 064	South
Lobéké	NP	217 854	East
Boumba-Bek	NP	238 225	East
Nki	NP	309 362	East
Mefou	NP	1 044	Centre
Dja	BR	526 000	East
Mbi Crater	FR	370	Northwest
Kimbi	FR	5 625	Northwest
Douala-Edéa	FR	160 000	Littoral
Lac Ossa	FR	4 000	Littoral
Santchou	FR	7 000	West
Monts Bakossi	FR	29 300	Southwest
Banyang Mbo	S	66 000	Southwest
Mengame	S	96 010	South

In 88.2% of occurrences, evidences of leopards were found in places with very low human density. Leopard occurred significantly less frequently where human density was above 10 inhabitants/km^2 (χ^2, $n_{presence} = 416$, $n_{absence} = 245$, d.f. = 2, $P < 0.001$) (Fig. 4): 11.8% of occurrences were found in areas of medium densities and no occurrence in densely populated areas (>100 inhabitants/km^2).

Interactions with other species

Occurrences of leopards were not significantly related to prey species presence (Fig. 5, χ^2, $n_{presence} = 416$, $n_{absence} = 245$, d.f. = 4, n.s.). By contrast, there were significantly more occurrences of leopard presence than leopard absence where other predators occur (savanna habitats) (χ^2, $n_{presence} = 150$, $n_{absence} = 36$, d.f. = 4, $P < 0.001$). Lions and hyaenas were the species most frequently associated with leopard occurrence (43% of leopard occurrences were associated with lion presence and 39% to hyaena presence, Fig. 6).

Protection level

Leopard distribution was significantly related to protection statuses (χ^2, $n_{presence} = 416$, $n_{absence} = 245$, d.f. = 4, $P < 0.001$) (Fig. 7). Leopards are present more in National Parks and ZIC than in reserves, Exploited Forests, and Other areas. Actually 49% of the evidence of the occurrence of leopards was found in National Parks, 29% in ZIC, 15% in Reserves and 7% in Exploited Forests.

Numerous threats were recorded within leopard ranges, with poaching/disturbances linked to hunting (92% of considered areas) and logging (89% of considered areas) being nearly omnipresent. The number of occurrence of leopard presence was significantly related to the presence of the different types of threats (χ^2, $n_{presence} = 416$, $n_{absence} = 245$, d.f. = 7, $P < 0.001$, Fig. 8).

DISCUSSION

Leopards were evidenced in West-Central Africa, but the species exhibits fragmented populations, revealing important conservation challenges.

Habitat factors

Leopards are regarded as generalists in terms of habitat (Nowell & Jackson 1996; Bailey 2005). Accordingly, we found that leopards were widely

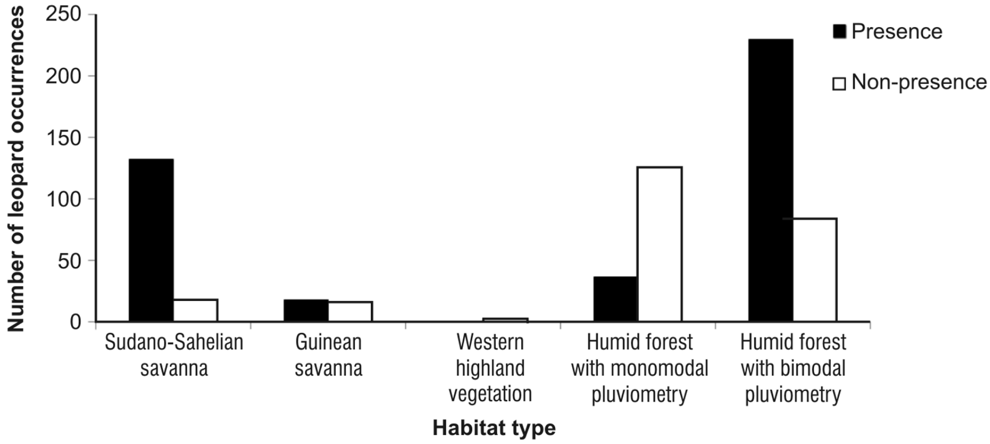

Fig. 3. Presence/absence of leopards according to habitat type.

spread in savanna areas and in rainforest habitats. However, they seem to be absent from Cameroonian rainforests; forests are widely exploited in Cameroon (Halford *et al.* 2002), causing habitat loss for leopards and for their prey populations (Verbelen 1999). Moreover, industry and trade are highly developed, in particular around Douala, which is the biggest city in the country and has a large port. Additionally, forest habitats are increasingly used for agriculture (Halford *et al.* 2002), which causes the active presence of humans. The high human density increases the pressure on the environment and often leads to high levels of bushmeat trade (Fa *et al.* 2006). Here we found few occurrences of leopards in areas with a density higher than 10 inhabitants per km^2, a density much lower than the density of 900 inhabitants/km^2 predicted as critical by Woodroffe (2000), or the density of 80 inhabitants/km^2 characterizing areas where leopards have become extinct (Fa *et al.* 2006). However, Henschel (2008) found no leopards in one of his study sites where human density was only 1–2 inhabitants/km^2. Avoidance of even barely populated areas might be due to threats presented by humans (hunting/poaching of leopards and/or prey species) more than to human density itself (Linnell *et al.* 2001; Halford *et al.* 2002).

Spacing patterns are mainly governed by the breeding system and by the general pattern of dispersal. Nevertheless, patterns of dispersal in breeding felids are expected to proceed according to a continuous or quasi-continuous distribution in which sub-population exchanges are favoured in contiguous zones (Rodriguez & Delibes 2003). As a result, the quality of contiguous habitats

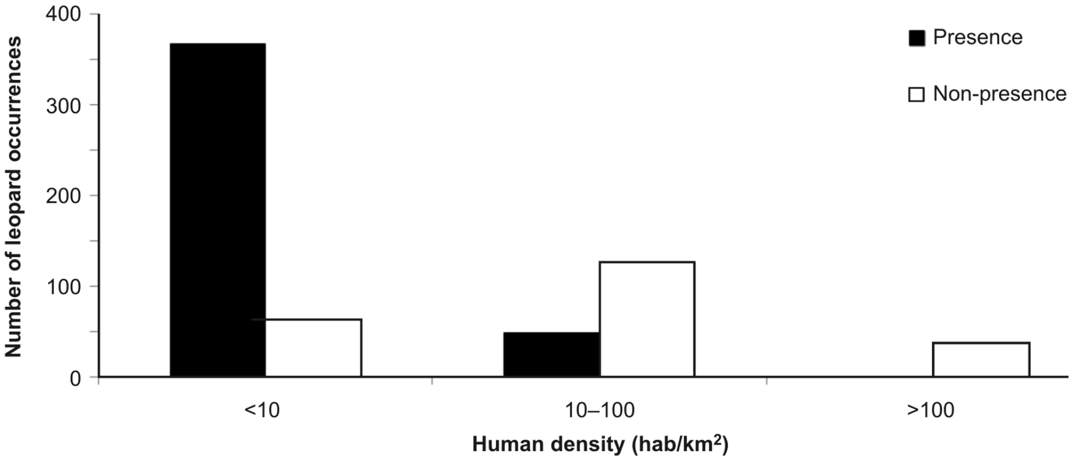

Fig. 4. Presence/absence of leopards according to human density.

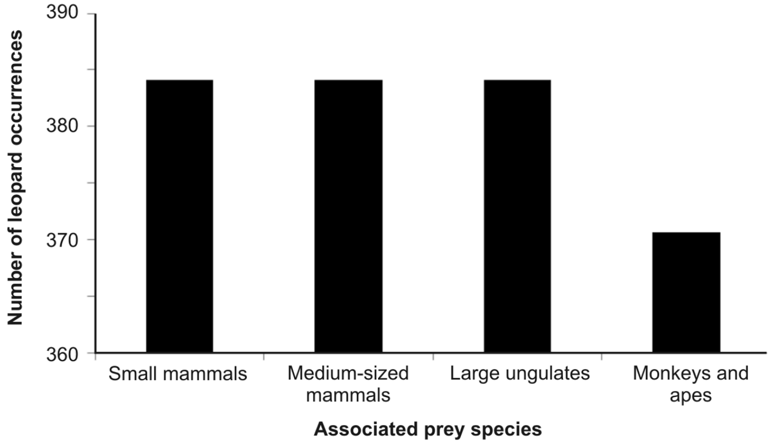

Fig. 5. Occurrence of leopards according to prey species (small mammals (body mass <20 kg, e.g. oribi, duikers (Stuart & Stuart 2000), medium-sized ungulates (20 kg < body mass < 70 kg, e.g. bushbuck, reedbuck, kob, common warthog, red river hog), large ungulates (>70 kg body mass, e.g. hartebeest, topi, waterbuck, sitatunga, giant forest hog) and monkeys and apes (baboon, chimpanzee)).

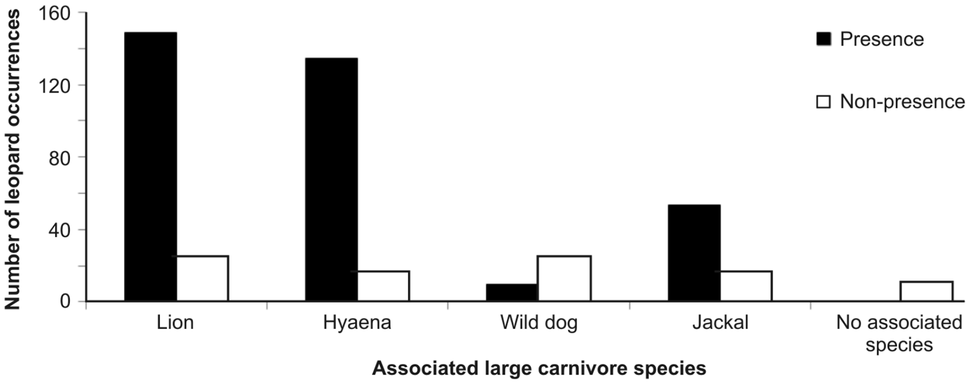

Fig. 6. Presence/absence of leopards according to associated carnivore species.

has proved to be decisive for populations and subdivision may directly affect the breeding and viability of small isolated populations because of the low number of breeding adults (Rodriguez & Delibes 2003). The 'Allee effect' hypothesis (Allee *et al.* 1950) predicts that poor or deteriorated habitats should result in home-ranges that are so extensively scattered that low densities prevent most females from finding mates. In the current study leopard populations showed a very patchy distribution, avoiding numerous areas so that breeding dispersal already seems to be highly affected. Thus, in West-Central Africa, leopards exhibited widely spaced territories, disturbing the social system. Many leopard adults may fail to breed, which supports the Allee effect hypothesis.

Associated species

The leopard has been assumed to be an opportunistic predator, showing a generalist diet (Hart *et al.* 1996), although small to medium-sized prey represent the best compromise between energy costs and benefits (Sunquist & Sunquist 2002; Al Johany 2007), and have been identified as preferred prey in several studies (Henschel *et al.* 2005; Hayward *et al.* 2006; Schwartz & Fischer 2006). Leopards tend to be found less where there are monkeys and apes. This may suggest that the presence of those species is not a shaping factor of leopard distribution (Hayward *et al.* 2006).

In areas where sympatric predators occur, leopards are present more where other large carnivore species are found. Similarly, across Africa, populations of leopards are chiefly recorded where they

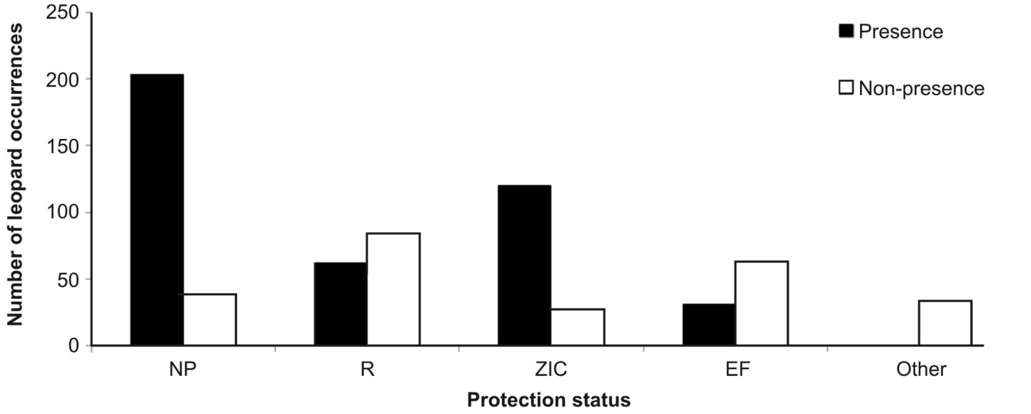

Fig. 7. Presence/absence of leopards according the conservation status of an area. (NP = National Park, R = Reserves (Faunal Reserve/Sanctuary/Forest Reserve), EF = Exploited Forest (UFA = Forestry Appointment Unit/CF = Communal Forest), ZIC = Cynegetic Interest Zone, Other = mangroves, mountains, etc.).

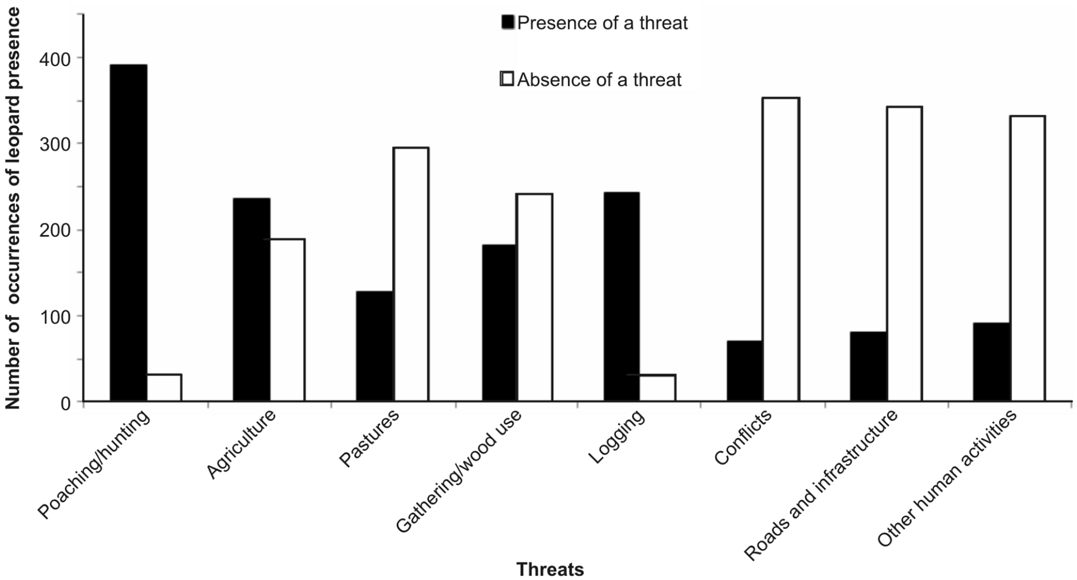

Fig. 8. Occurrence of leopards according to different types of threats or the absence of threats.

occur sympatrically with other large carnivores, especially lions and hyaenas (Nowell & Jackson 1996). It may be that competition is reduced because the leopard forages individually. As a result, dietary overlap between leopards and other large carnivores is not that important (Mills & Biggs 1993; Hayward & Kerley 2008). Conservation efforts are therefore usually more effective when addressed to an ecosystem than to a single species (Ray *et al.* 2005; Hess *et al.* 2006; Lindenmeyer *et al.* 2006). Thus, management strategies have to be improved by considering species assemblage and not only the requirements of one species.

Protection level

One of the major points of our study is that we did not find any areas where leopards are not threatened. The decline of large felids is commonly attributed to habitat degradation, and hunting and poaching of both predators and their prey (Bauer *et al.* 2003; Marker & Dickman 2005; Al Johany 2007). Forestry logging had a negative impact on leopard distribution, although we were not able to quantify the pressure this threat represented within each place. The influence of deforestation is not only due to its extent but also to its pattern (Rodriguez & Delibes 2003; Bender *et al.*

1998), thus affecting population fragmentation.

Domestic species may become a substitute for wild prey (Ogada *et al.* 2003; Kolowski & Holekamp 2006; Holmern *et al.* 2007; Kissui 2008; Gusset *et al.* 2009). Livestock owners may then remove leopards as retaliation (Dickman 2005; Holmern *et al.* 2007; Kissui 2008; Chapman & Balme 2010). Such retaliatory killing, added to widespread agriculture, may directly threaten leopard populations (Camp 2002; Ott *et al.* 2007). However, we found the leopards present more often than expected in areas where there were human–wildlife conflicts. This could be because these habitats still had numerous shelters for leopards or because we labelled conflicts as every kind of human–wildlife interaction, without specifying those involving leopards.

Nonetheless, hunting and poaching were common in the great majority of the areas covered by this study. Unexpectedly we found more evidence of leopard presence in areas where people hunt and/or poach. It could be hypothesized that both hunters and leopards choose areas where herbivores are abundant (Marker & Dickman 2005; Al Johany 2007; Hayward *et al.* 2009; Martins *et al.* 2011). Moreover, these areas are not highly populated, and Fa *et al.* (2006) and Henschel (2008) showed that human density and proximity resulted in higher pressure on wildlife and lower ungulate densities. Thus, leopards would prefer habitats with low human densities, regardless of both the threat and competition posed by hunters (Jorgenson & Redford 1993; Henschel 2008). Nevertheless, hunting and poaching were present in more than 90% of the sampled areas. This means there are few places where leopards can occur but poaching and hunting do not. Fortunately, as killing leopards is forbidden, this species is probably little threatened by direct hunting, and as a discrete animal, leopards require too much effort to be poached. Finally, leopards are sacred animals in most Cameroonian ethnic groups (Wilcox & Nambu 2007; Astaras, pers. comm.). Therefore, leopards are more likely to be threatened by habitat degradation and prey depletion, than directly by poaching (Karanth & Stith 1999). As a result, leopard distribution is determined as much by anthropological factors (human density) as by ecological ones (prey densities, habitat type) (Marker & Dickman 2005; Al Johany 2007; Hayward *et al.* 2009).

Unsurprisingly, we found that leopard distribution is highly related to the protection status of the studied area. The species is widely spread in National Parks, where the protection level is the highest (Bauer 2003; MinFOF 2005): human presence is strictly limited, habitations are forbidden inside the area, as are any kind of anthropogenic modifications (cutting trees, pasturing etc.,) and collections (of dead wood, carcasses etc.). Therefore, it seems that measures of protection are relatively efficient, when willingly applied. Leopard presence is also important in ZIC. These ZICs are mostly close to National Parks, additionally, hunting is scrupulously regulated since quotas are defined and hunters must have a license (MinFOF 2005), thus reducing human presence. By contrast, there is little evidence of leopard presence in faunal reserves, despite the fact that they are under strict protection rules (MinFOF 2005). Generally, the explored reserves were smaller than national parks. We could hypothesize that there is less wildlife in such areas, where conservation measures are less strict than in National Parks (Nowell & Jackson 1996). As home range size is correlated to prey abundance in the leopard, they should require larger home ranges in such areas, resulting in lower numbers (Rodrigues *et al.* 2004; Marker & Dickman 2005; Ray *et al.* 2005). On the whole, evidence of leopards is rare outside protected areas, and this would lead to population fragmentation.

It seems that leopards persist in small isolated populations, but are threatened by extinction. Moreover, within the southern population we found several zones of fragility, which suggests that breeding exchanges have been affected.

Our study established a baseline overview of available data on the leopard in establishing the conservation status of the feline. The decline of leopards in Cameroon is less alarming than other species, especially other big carnivores. Its wide presence in protected areas suggests that efforts made in these zones are efficient but should be improved because of the fragmentation of leopard populations.

We also highlighted the paucity of data on the species in Cameroon. There is an urgent need for further studies to propose management guidelines to improve conservation efforts based on accurate data. For instance, detailed faunal inventories should be carried out regularly in order to promote better management of animals inside and outside protected areas. Additionally, hunting policies should be modified in order to ensure better management of faunal resources, while taking into account local realities, and efforts to strengthen the anti-poaching cause should continue and be strengthened. The importance of this iconic animal in local beliefs, combined with its economic potential through its value for tourism, could be a starting point for future conservation efforts.

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