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Leopards (*Panthera pardus pardus*) in Gashaka Gumti National Park, Nigeria: historical records and recent sightings

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Abstract: West-African populations of the African subspecies of leopards (*Panthera pardus pardus)* are very fragmented, particularly so in Nigeria, Africa's most populous nation. We compile historical and recent information about the occurrence of these big cats in what is likely their last remaining stronghold: Gashaka Gumti National Park (GGNP) in Adamawa and Taraba States along the border with Cameroon. Leopards in GGNP's northern Gumti sector are close to extinction, given that its open plains of savannah are heavily encroached upon by illegal cattle grazing. However, in GGNP's southern Gashaka sector, leopards are better protected, given its often mountainous and densely forested landscape. We present specific data for a 30 km^2 forest-savannah area around a research station at Kwano, which harbours sizeable populations of 35 species of prey species leopards target elsewhere. Here, direct evidence for leopard presence (e.g., footprints, scratchmarks, predation incidences, vocalizations, sightings, camera-trap images) amounts to 1 per year. Albeit this encounter rate is very low, it is relatively steady throughout the last 30 years and into the present. We assume that GGNP's Gashaka sector represents one of the best chances for leopards to survive in Nigeria.

Key words: *Panthera pardus*; leopard prey; forest habitat; population fragmentation; West Africa.

Introduction

Gashaka Gumti National Park (GGNP) might very well be one of the few protected areas where leopards (*Panthera pardus* (Linnaeus, 1758)) have a chance to survive in Nigeria, particularly in the more forested Gashaka sector which encompasses most of the park's biodiversity (Jesus 2020).

In the vast landscapes of West Africa, especially in regions with rainforests, the dense vegetation offers leopards an abundance of hiding spots. This, combined with their solitary and primarily nocturnal nature (Bothma and Bothma 2006), means that they are seldom seen during the day. Their tendency to avoid human-populated areas and their activity dur-

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ing hours when most humans are inactive further contributes to their elusive reputation (Henschel et al. 2011). Moreover, the leopard's spotted coat, which is perfectly evolved for camouflage, allows it to blend seamlessly with its environment, particularly in the low light of the forest understorey (Hunter 2011).

Regrettably, the chances of encountering leopards in West Africa have diminished in recent times. Factors such as habitat loss, escalating human-wildlife conflicts, and poaching have led to a marked decline in their populations (Toni and Lodé 2013). Their innate wariness of humans means they tend to retreat if they sense human presence, which, coupled with the aforementioned challenges, makes them a rare sight (Jacobson et al. 2016).

Human-wildlife conflict goes hand in hand with population growth, land use and consequent deforestation and natural habitats destruction (Woodroffe 2000). Typically, such conflicts are the result of food competition between humans who need to produce food and increase production yields and animals that take advantage of easy food accessibility (Bennett and Ross 2011). When it comes to terrestrial carnivores, the competition for animal protein can lead to disastrous outcomes which go from the loss of livestock, to the loss of human life or, often the local extinction of such megafauna (Graham et al. 2005).

Nigeria is Africa's most populated country and among the top ten countries reporting the greatest annual net loss of forest area (5.0 % in 2010–2015, FAO 2016). As deforestation and land-use changes continue to occur in many parts of Nigeria, leopards are increasingly coming into contact with people, which can result in conflicts.

This study focuses on the occurrence of leopards at GGNP which lies in the north-eastern part of Nigeria at the northern edge of the Gulf of Guinea Biodiversity Hotspot and though being the country's largest National Park its wilderness is still largely unexplored (Dunn 1999; Oates et al. 2004; Sommer and Ross 2011).

The Gashaka region has been a stronghold for Fulani populations since the mid 19th century, and their presence within the park is mostly due to its tstse fly free, montane pastures which allow for the raising of healthy herds (Dunn 1999). Livestock is an integral part of Fulani culture and the ones residing within the GGNP highland enclaves practice a combination of agriculture and cattle herding (Bennett and Ross 2011). Most large carnivores are now extinct from the park. Lions, hyenas and wild dogs were regularly seen until the late 1990's but have since been exterminated by poisoning, shooting or trapping (Barnwell 2011). Such situation is echoed across many large mammalian carnivores' habitats, where larger and more predatory species seem to be suffering the most population declines, often due to misconceptions about the threat they pose both to livestock and humans (Karanth and Chellam 2009). While leopards display remarkable ecological adaptability, anthropogenic forces such as habitat destruction, prey depletion, trophy hunting and retaliatory killings have extirpated these big cats from two-thirds to three-quarters of their historic ranges in Asia and Africa (Jacobson et al. 2016). The African subspecies (*P. p. pardus*) still occurs in relatively large numbers in Sub-Saharan habitats of east, central and southern Africa, but populations in West Africa are largely fragmented (ibid.).

This is particularly true for 21st century Nigeria where only a few locales still harbour small numbers of leopards (Toni and Lodé 2013; Eniang et al. 2016). Our report compiles evidence about the occurrence of these big cats in Gashaka Gumti National Park in Nigeria's Adamawa and Taraba States along the border with Cameroon. Apart from being of historical interest, our records will hopefully inform management strategies to prevent or at least delay the extinction of these big cats from Africa's most populous nation.

Materials and Methods

Our data collection on leopard presence was opportunistic and is based on both direct field work evidence (scratchmarks, vocalizations, footprints, scats, direct sightings, predation incidences) as well as interviews with locals, including recollections of leopard poaching.

We monitored wildlife and potential leopard prey via foot surveys from March 2005 to December 2008 for a total of 14.493 hours. For these foot surveys, typically a single observer (and sometimes teams of 2-3 individuals) went on predetermined routes that systematically covered 1x1 km quadrants of the about 30 km^2 Kwano study area. The observers would adhere to a rota of walking and pausing to record sightings of pigs, antelopes and primates but also collected anecdotal information on other taxa. Our survey methods did not use direct line transects or grid systems, which means we cannot provide specific numbers on the abundance or exact locations of different species within the area. We recognize there's a possibility of recording the same animals or groups more than once over consecutive days, leading to potential duplicate records. To minimize double counts within a single day, we have considered any sightings of the same species within a 3-hour period as a single observation. Nevertheless, since the data is gathered from a broad area (approximately 30 km^2), it's improbable that repeat observations will significantly skew the overall results. Our data analysis was concentrated on the prey species that were most frequently observed, specifically those with a minimum of 50 sightings throughout the study period. We conducted all statistical analyses using RStudio (RStudio Team 2020).

Our research took place in Gashaka Gumti National Park, with 6.731 km^2 Nigeria's largest national park (06°55′ – 08°13′ N, 11°13′ N – 12°11′ E; Gumnior and Sommer 2012). The park encompasses most of the catchment of the Taraba river, largest tributary to the Benue. Pronounced wet and dry seasons correspond with fluctuations in temperature and humidity. GGNP is divided into the undulating Gumti sector in the north, with its open plains of grassland and woodland-savannah, and the hilly to mountainous Gashaka sector in the south, which apart from savannah-woodland also includes more or less closed riverine, lowland and montane forests (Dunn 1999). Here, elevations rise to 2.419 m at Mount Gangirwal (also called Chappal Wade), West Africa's highest peak. Few humans have set foot into the escarpment's north-western slopes as they are incised by heavily forested and steep valleys carved out by often copious watercourses (Sommer 2008).

The park is surrounded by villages that practice subsistence farming, with fields sometimes encroaching into the reserve. The park itself contains various enclaves, mainly inhabited by settled cattle herders – as per 2012 with an estimated human population of 5.000 along with about 10.000 cattle. The park's vegetation cover is subject to various deteriorating forces, such as livestock grazing, burning, artisanal mining and tree cutting (Adanu et al. 2011; Nyanganji et al. 2011). Since 2015, these illegal activities include removal of "rosewood" trees (*Pterocarpus erinaceus)* destined for consumption in east Asia (Gaworecki 2016).

GGNP's Gumti sector in particular has, over the last 20 years, experienced wide-scale destruction, largely brought about by illegal hunting and cattle grazing by cattle herders who also poison carnivores and other animals considered resource competitors for their cows. Consequently, iconic species have been lost or driven close to extinction, including elephant (*Loxodonta africana* (Blumenbach, 1797)) and giant eland (*Tragelaphus derbianus* (Gray, 1847)) as well as large carnivores such as wild dog (*Lycaon pictus* (Temminck, 1820)), spotted hyena (*Crocuta crocuta* (Erxleben, 1777)) and lion (*Panthera leo* (Linnaeus, 1758)) (Kamaya et al. 2002; Saidu et al. 2010).

By comparison, GGNP's Gashaka sector still represents one of West Africa's most biodiverse wildernesses, due to its remoteness and often rugged profile. However, the area is likewise not without anthropogenic disturbances, such as cattle grazing, hunting for bushmeat and tree-cutting. Still, albeit humans access the Gashaka sector on foot or, where possible, on motorcycles, mostly to ferry goods between the park's enclaves, no permanent all-weather road criss-crosses these habitats as per 2020. Thus, the Gashaka sector of GGNP constitutes an important habitat reservoir for many plants and animal taxa that are elsewhere already extiguished (Gumnior and Sommer 2012).

Most of our research was carried out in the Gashaka sector from a field station maintained by the Gashaka Primate Project (GPP) at the site of the abandoned village of Kwano (583 m asl; 07°19′ N–011°35′ E), 11 aerial km from the nearest village of Gashaka. At the Kwano site, between 2000 and 2012, mean minimum temperature was recorded as 20,8°C, mean maximum as 31,9°C, and annual mean rainfall as 2.021 mm (range 1.683-2.337 mm). As for seasonality, 5 months with very little or no rainfall are followed by heavy downpours from mid-April to mid-November that constitute 97 % of all precipitation. The proportion of forest (72%) to woodland (28%) in the Kwano range is typical for much of GGNP's Gashaka sector. Research permits were issued by Nigeria's National Park Service.

Results

General statements about the existence of leopards in the area date back to the 1970s (Barnwell 2011: 44) and 1980s (Dunn 1999: 26).

We were able to assemble about 30 specific records dating back more than 30 years (Table 1) – based on fieldwork at Kwano supplemented by interviews with locals, reports from park ranger patrols and foot-surveys of the Gangirwal escarpment and Gumti sector. These accounts confirm the existence of leopards based on footprints (n=13), direct sightings (n=10), narratives of poaching (n=5), scratchmarks (n=2), leopard predation (n=5), vocalizations (n=2) and scats (n=1). However, despite extensive camera-trapping efforts of wildlife at the Kwano site from 2012–2017, only a single image captured a leopard. Interviews with local people did not reveal a single testimony about an unprovoked leopard attack on humans.

As for localities (Figure 1), few records (2/30=7%) come from the flat and open northern Gumti sector, while the vast majority (28/30=93%) stems from the mountainous and often forested Gashaka sector. Within the Gashaka sector, half of the records (14/28=50%) came from the vicinity of the GPP station at Kwano, and the other half mostly from park enclaves (11/28=39%), supplemented by a few reports (3/28=11%) from Serti town, Gashaka village and the Mt. Gangirwal slopes. Of the 30 records examined, habitat types were successfully identified for 22 instances. Among these, the majority, 15 occurrences (68%), were in forested areas, while the remaining 7 (32%) were in grasslands.

Our records are not systematic but biased towards field work at Kwano, because here, between 1999 and 2016, local field assistants, students and researchers associated with GPP visited a forest-savannah segment of about 35 km^2 on an almost daily basis. Over these 18 years, we accumulated 14 opportunistic records of leopard presence. We never came across leopard scats – albeit there was no targeted effort to find them. During the first decade, at least one record was obtained during most of the years, with a subsequent gap from 2011 till 2016, after which leopard presence was again confirmed by a camera trap. Overall, the 30 records for 30 years from 1991–2020 amount to 1.0 incidence per year, with relatively steady distribution, except for a 5-year gap from 2011–2016.

As for potential leopard prey species, the Kwano study area and other forests of the Gashaka sector harbour 35 species that are leopard prey elsewhere (Hayward et al. 2006; Henschel et al. 2011) (Table 2). In particular, the habitat supports sizeable populations of pigs, antelopes and primates, which occur in often large groups and at high density.

A chi-square test of independence was performed to examine the relationship between habitat type (forest and grassland) and the presence of different leopard prey species. There was a significant association between habitat type and species distribution, $X^2(8)=1237.9$, $p<0.001$. This finding aligns with the patterns observed in leopard sightings, indicating a preference for certain prey species to inhabit forested areas rather than grasslands. This is further supported by the data in Figure 2, which, with the exception of olive baboons and bushbucks, shows a higher frequency of sightings for all other species in forest habitats.

Our analysis revealed no significant relationship between rainfall patterns and the frequency of sightings of potential leopard prey (Figure 3, Spearman's rank correlation: rho=0.107, p=0.490), suggesting that seasonal changes do not notably influence the visibility or presence of potential prey, and by extension, this may also apply to leopard sightings themselves.

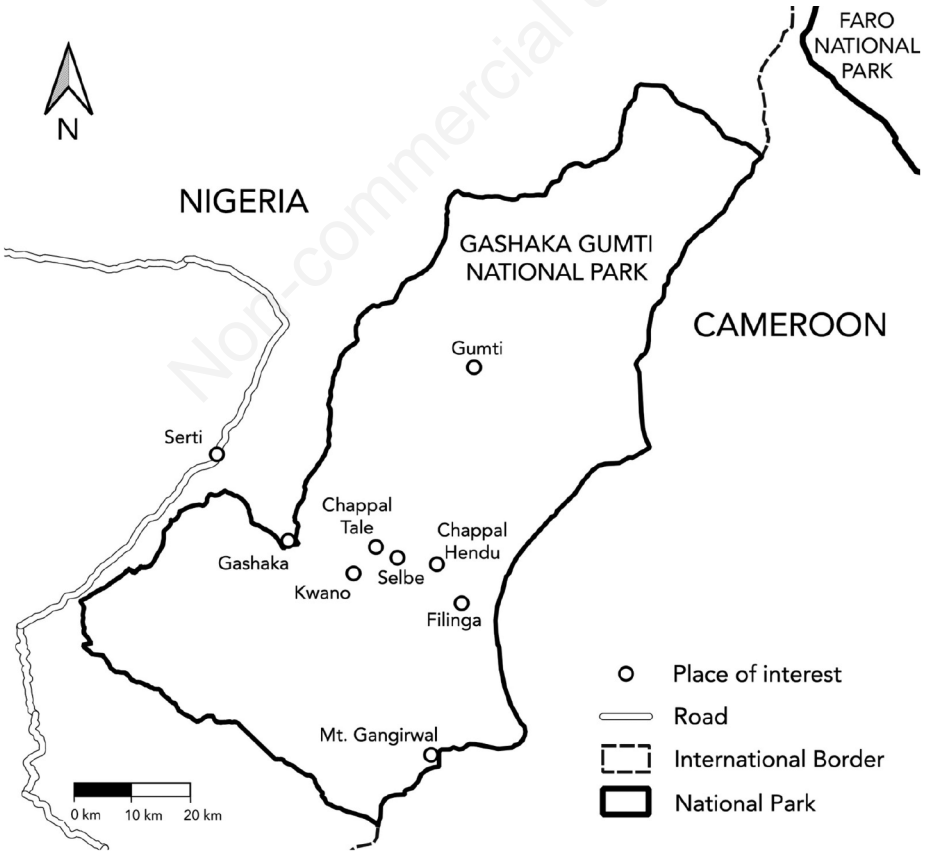

Figure 1. Localities of records of leopard occurrence in Gashaka Gumti National Park (cf. Table 1).

Table 1. Leopards in Gashaka Gumti National Park: local narratives and evidence of occurrence.

Date	Evidence	Description or interview quote	Location	Informant or source
Before 1991	Poaching	"Before area was national park, people used to come buy skins, which are liked by big men"; "one man from Serti, now dead, used to deal in leopard skins"	Gashaka sector of GGNP	FA (HG)
1989 ca	Poaching	"Sule of Kwano village caught a leopard in a snare, and sold skin to Wakili of Gashaka, who sold it on"	Near KW village (abandoned in 1990s)	FA (HG)
1993	Sighting	1 female leopard	Between GV and Serti town	FA (HI, BuBe)
1997 ca	Poaching	"Man caught leopard in snare. He tried to shoot it, but hit the wire. The leopard attacked his face, broke his eye-socket towards ear; they carried him to Cameroon for treatment"	Near Filinga EN	FA (HG)
1999-2000	Vocalisation	Growls heard	KW	FW (IF)
1999-2000	Scratchmark	Seen	KW	FW (IF)
2000 or earlier	Sighting	1 leopard	Near Hendu EN	FA (BoBu)
2003 ca	Poaching	"Park rangers arrested a man near Gashaka who carried a skin from Cameroon to Serti"	Near GV	FA (HG)
2005	Footprint	1 footprint	KW	FA (HG), RE (AF)
2006 Jan	Sighting	Encountered 1 leopard (or other large cat?) on forest trail (daytime)	KW	FW (VG)
2006 Mar	Footprint	1 large footprint, riverbed	Mt. Gangirwal north-western slope	FW (VS), PR (several)
2006 Jun	Sighting, footprint	"I saw a quick movement of the animal. When I told others they could not believe me until we went back and saw its fresh footprints."	Near Tale EN (Gidan Hitler, below Tonga)	PR (NL)
2008	Predation	"Fulani people say leopard ate a cow calf; they say leopard is sometimes coming close to their home stead"	Near Tale EN	FA (HG)
2008	Footprint	Several	KW	FA (HI)
2008	Scratchmark	On bark of *Uapaca* tree	KW	FA (HI)
2008 ca Sep	Vocalisation	"Many growls" heard 1 evening (19:00)	KW	FA (HG, HI)
2009 May	Footprint, scats	Footprints and scats of 1 leopard found; three interviewed groups of cattle herders all confirmed presence of leopards	Northern Gumti sector of GGNP	Saidu et al. 2010, p. 11f
2009 Jun	Predation	"Hidden under a fallen tree and covered with leaves, the carcass of a pregnant red-flanked duiker female was found, its left front leg and shoulder are missing; part of the leg is buried under vegetation a few metres away"	KW	FA (BoBu)
2009 Feb	Footprint	3 footprints, open hillside	KW	FA (HG)

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Table 1. Continued from previous page.

Date	Evidence	Description or interview quote	Location	Informant or source
2009 Feb	Sighting	Close-up encounter with 1 leopard on forest trail (ca. 17:30)	KW	FW (GJ)
2009 Sep	Footprint	Many	KW	FA (HG)
2009 ca Sep	Sighting	"A man told he had seen a leopard. The man ran away."	KW	FA (HI)
2011	Sighting, footprint, predation	"I herd cattle close to the edge of the enclave. Below a cliff I frequently see them or their footprints. My herdsman also sometimes found a sheep carcass suspected to have been killed by the leopard. We have them a lot here."	Near Shirgu EN	ER (AD)
(2012 Apr - 2016 Feb)	(Camera trap)	(Not caught on grid of up to ca 50 camera traps)	(KW)	GPP
2017	Camera trap	1 camera trap image	KW	GBP (Briggs 2018)
2017 May	Footprint, poaching	"Even for a hunter like me, leopards are a very clever animals to see, but the footprints can never be missed. I saw the prints a few times, mostly in forested areas."	Near Nyumti EN (Tunga Aboye)	ER (CG)
2017 Dec	Footprint	"The prints were fresh across a soft patch of soil in a dense forest."	Filinga EN (Nderem hill)	PR (DL)
2020 Mar	Sighting	"I was resting by a stream after drinking my full and the forest was quite. It appeared walking and suddenly turned back in a twinkle of an eye."	Nyumti EN (Dakka)	ER (MA)
2020 Apr	Footprint	Along a footpath	Near Gumti EN (Mayim River)	PR (PB)

Abbreviations: Location: KW = Kwano research station; forest and savannah woodland in the vicinity of Gashaka Primate Project (GPP) field station at site of the abandoned former Kwano settlement; GV = Gashaka village at the edge of the national park, 11 km from Kwano; EN = enclave settlement within the national park. Informants: FA = local field assistant to Gashaka Primate Project from Gashaka village (BoBu = Bobbo Buba, BuBe = Buba Bello, HG = Hammaunde Guruza, HI = Halidu Ilyasu; pre-2011 reports based on interviews conducted by GPP director Volker Sommer in March 2010); FW = non-Nigerian field worker affiliated with GPP (AF = Andrew Fowler, PhD researcher; GJ = Gonçalo Jesus, PhD researcher; IF = Isabelle Faucher, PhD researcher; VG = Volker Gallitz jun., engineer; VS = Volker Sommer, GPP director); PR = national park rangers resp. officers (BP = Proverb Benjamin; DL = Dahiru Lawal; NL = Nuhu Lagu; PK = Pepeh Kamaya); ER = resident of enclave inside park (AD = Ahmadu Dajji; CG = Caleb Godwin; MA = Mai'anguwa Hammanshehu Aliyu; interviews conducted by GGNP officer Pepeh Kamaya); GBP = Gashaka Biodiversity Project led by Chester Zoo.

Table 2. Potential leopard prey species encountered in the forest-savannah habitat in the surroundings of the Gashaka Primate Project research station at Kwano, Gashaka Gumti National Park.

Taxon	Common name	Latin name	Prey status (1)	Group size (2) Mean	Min	Max	SD	Counts	Survey method (3)
Antelopes	African buffalo	*Syncerus caffer* (Sparrman, 1779)	a	5.8	1	12	3.2	29	a
	Waterbuck	*Kobus ellipsiprymnus* (Ogilby, 1833)	a	3.0	1	8	1.4	397	a
	Bushbuck	*Tragelaphus scriptus* (Pallas, 1766)	a	1.3	1	2	0.5	65	a
	Yellow-backed duiker	*Cephalophus silvicultor* (Afzelius, 1815)	a	1.1	1	2	0.6	129	a
	Red-flanked duiker	*Cephalophus rufilatus* Gray, 1846	a	1.1	1	2	0.3	40	a
	Blue duiker	*Cephalophus monticola* (Thunberg, 1789)	a	1.6	1	2	0.5	5	c
	Hartebeest	*Alcelaphus buselaphus* (Pallas, 1766)	a	3.0	1	8	2.9	5	a
Pigs	Red river hog	*Potamochoerus porcus* (Linnaeus, 1758)	a	5.3	1	13	2.1	271	a
	Giant forest hog	*Hylochoerus meinertzhageni* Thomas, 1904	(p)	3.8	1	11	3.0	16	a
	Warthog	*Phacochoerus africanus* (Gmelin, 1788)	a						
Primates	Olive baboon	*Papio anubis* (Cuvier, 1824)	(a)	22.3			6.5	7	b, Higham et al. 2009
	Putty-nosed monkey	*Cercopithecus nictitans* (Linnaeus, 1766)	a	20.9	1	34	6.5	54	b
	Mona monkey	*Cercopithecus mona* (Schreber, 1775)	a	15.0	1	30	6.3	46	b
	Tantalus monkey	*Cercopithecus aethiops* (Linnaeus, 1758)	a	6.0	1	19	3.3	92	a
	Black-and-white colobus	*Colobus guereza* Rüppell, 1835	a	10.7	1	15	2.2	45	b
	Chimpanzee	*Pan troglodytes ellioti* (Matschie, 1914)	a	4.0	1	21	2.6	306	a, Sommer et al. 2004
	Grey-cheeked mangabey	*Lophocebus albigena* (Gray, 1850)	a						
Scaly ant-eaters	Tree pangolin (N)	*Phataginus tricuspis* (Rafinesque, 1821)	(p)						
	Giant Pangolin	*Smutsia gigantea* (Illiger, 1815)	(p)						
Hares	Scrub hare	*Lepus saxatilis* F.Cuvier, 1823	a						
Rodents	Gambian sun-squirrel	*Heliosciurus gambianus* (Ogilby, 1835)	(a)						
	Brush-tailed porcupine (N)	*Atherurus africanus* Gray, 1842	(a)						

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Table 2. Continued from previous page.

Taxon	Common name	Latin name	Prey status (1)	Group size (2) Mean	Min	Max	SD	Counts	Survey method (3)
	Crested porcupine (N)	*Hystrix cristata* Linnaeus, 1758	(a)						
	Gambian giant rat (N)	*Cricetomys gambianus* Waterhouse, 1840	(a)						
	Marsh cane-rat	*Thryonomys swinderianus* (Temminck, 1827)	(a)						
Aardvarks	Aardvark (N)	*Orycteropus afer* (Pallas, 1766)	a						
Hyraxes	Rock hyrax	*Procavia ruficeps* (Hemprich & Ehrenberg, 1832)	(a)						
Carnivores	Long-snouted mongoose	*Herpestes naso* de Winton, 1901	a						
	African civet	*Civettictis civetta* (Schreber, 1776)	a						
	Genet	*Genetta* sp.	a						
	Golden cat	*Felis aurata* Temminck, 1827	p						
	Honey badger	*Mellivora capensis* (Schreber, 1776)	p						
	Side-striped jackal	*Canis adustus* Sundevall, 1847	(a)						
Birds	Francolin	*Francolinus* sp.	a						
	Guineafowl	*Numida meleagris* (Linnaeus, 1758)	a						

(1) Hayward et al. (2017) list these species as: a = actual prey, p = potential prey; (brackets) = Hayward et al. (2017) list a closely related prey species. (2) Records of group sizes are restricted to antelopes and most pigs and primate taxa. (3) Survey methods (details in Jesus 2020): (a) opportunistic counts during 2005-2008 habitat survey; (b) dedicated group counts, May-Dec 2000; (c) 2012-2014 GPP camera traps.

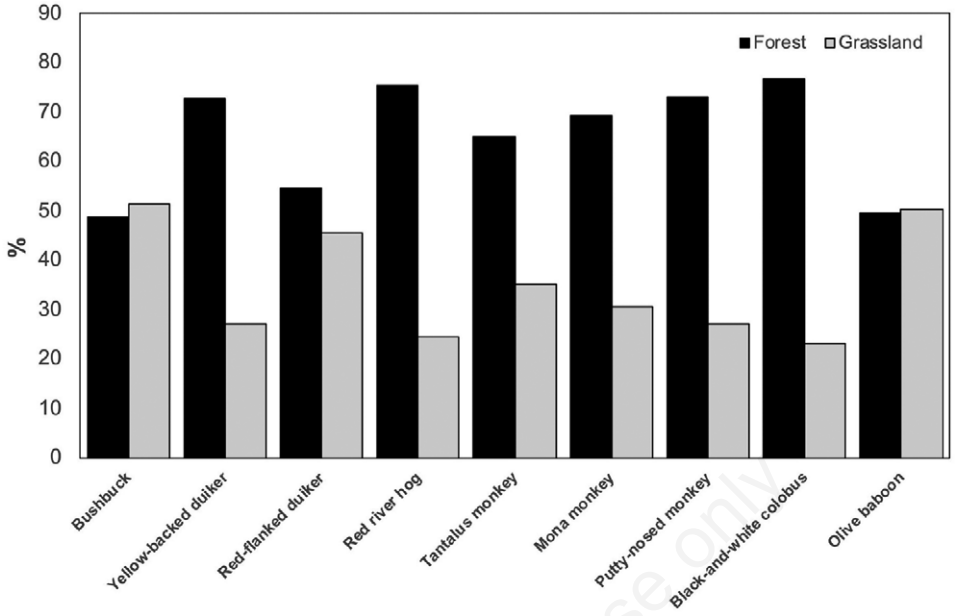

Figure 2. Sighting proportions across the two habitats (forest and grassland) for the nine most frequently observed potential prey species of leopards.

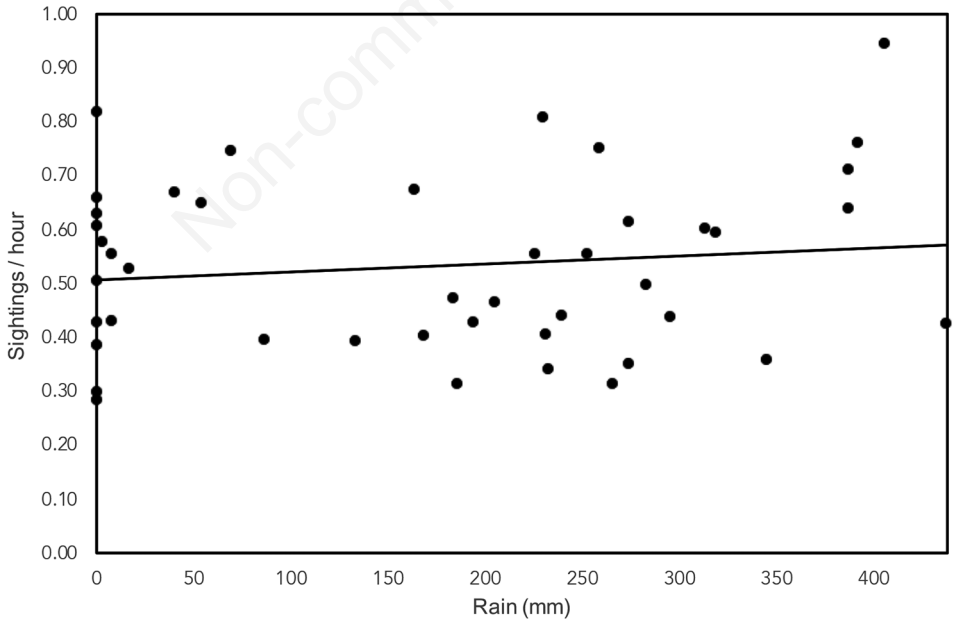

Figure 3. Scatter plot of prey sightings per hour against rainfall (mm). Each point represents the number of sightings per hour for a given amount of rainfall. The overlaid line suggests a weak positive trend, although statistical analysis indicates no significant correlation between rainfall and sightings (Spearman's rho=0.107, p=0.4902).

Discussion

Our record compilation confirms a historical presence of leopards in the Gashaka sector of Gashaka Gumti National Park (GGNP) which continues into the present. GGNP comprises close to 7.000 km^2, and while the human population of its various enclaves is steadily increasing, human density is still low, with probably less than 1 inhabitant / km^2. Theoretically, this might bode well for the existence and survival prospects of leopards in GGNP, given that 88 % of occurrences in west-central Africa (Cameroon) are found in locales with human densities below 10 inhabitants / km^2, and that leopard distribution is significantly related to the protection status of their habitat (Toni and Lodé 2013, see also Jacobson et al. 2016, Havmøller et al. 2019).

Nevertheless, despite intensive and virtually daily field work on foot in the study area around the Kwano field station in GGNP's Gashaka sector, where researchers, students and local assistants regularly cover about 35 km^2 of forest and savannah, our records of leopard presence are at the rate of one per year (cf. Table 1). While scats are more difficult to find in wet closed rainforests than dry open habitat (Angelici et al. 1998), it is still surprising that no sample was ever obtained from Kwano. Moreover, the low, albeit relatively steady, annual rate until the year 2011 is followed by a 5-year gap. It is likely that this lack reflects idiosyncratic data gathering and not an actual reduction in leopard numbers, as the four years from 2017-2020 saw another 6 records.

The installation of a grid of dozens of still- and video-camera traps in the Kwano study area between 2012 and 2017 only produced a single image (Briggs 2018). However, it is possible that leopards avoid proximity to these cameras. In addition, the cameras covered an area of only about 35 km^2. This is a fraction of the about ~2.500 km^2 sampled in Tanzania where arrays of 25-34 pairs of traps captured 185 events pointing to 62 different leopards, i.e., 1 animal/40 km^2 (Havmøller et al. 2019). The camera capture of just 1 leopard at Kwano is therefore not necessarily out of the ordinary with respect to density.

While sizes of leopard home ranges are considerable, and often in the order of 100 km^2 (Kingdon et al. 2013), their extent varies greatly. Figures for open savanna average 42 km^2 with a maximum of 487 km^2. This contrasts with range data for the Tai forest of Ivory Coast where a male roamed over 86 km^2, overlapping with ranges of 2 females that stretched over only 25 km^2 (Jenny 1996). Theoretically, the extent of the Kwano study area could therefore well represent the home range of a single leopard, albeit it is hard to say if this should indeed translate into higher rates of evidence for the presence of such a big cat, in particular because leopards are notoriously secretive (Jacobson et al. 2016).

A promising new method of establishing the presence of certain animal taxa in a given habitat is based on metabarcoding of vertebrate DNA found in invertebrates (iDNA). In fact, DNA obtained from flies (n=105) trapped in the Kwano habitat could be traced back to a dozen mammalian species (Gogarten et al. 2019). However, numerous high-density taxa including ungulates and primates were not detected via fly-DNA. It is therefore not surprising that leopard DNA was likewise not sampled – albeit this method will likely become increasingly important and effective for biomonitoring at broad spatial and temporal scales.

Leopards living in open environments are known to be largely nocturnal, whereas in forested ecosystems they are more diurnal and crepuscular as they follow activity patterns of their main prey (Jenny and Zuberbühler 2005). This is confirmed by our records for the largely forested Kwano habitat, where some direct sightings occurred during the daytime (cf. Table 1). Forest leopards tend to not stalk their prey, but ambush it at fruiting trees and along game trails (Hart et al. 1996). Forest leopards may also benefit from a lack of com-

petition by other large predators, such as lions (*Panthera leo*), spoted hyenas (*Crocuta crocuta*) and wild dogs (*Lycaon pictus*) (Jenny 1996).

Availability, abundance and catchability of prey have been highlighted as important factors for habitat selection by leopards (Balme et al. 2007; Carbone et al. 2010; but see Havmøller et al. 2019). However, it is unlikely that the Gashaka sector's low leopard density reflects a lack of predation opportunities, because its forests and savannahs were and are rich in wildlife. Compared to a compilation of prey items elsewhere in Africa and Asia (Hayward et al. 2006), the Gashaka sector's fauna includes 35 taxa considered to be leopard prey (cf. Table 2). The habitat harbours 16 species of ungulates and primates that occur in often large aggregations. These potential prey species for leopards inhabit both the dense forests and the more open grasslands within the Kwano region (cf. Figure 2). Although certain species may show a preference for one habitat type over another, this preference does not appear to limit the overall distribution of leopards across the region and leopard presence has been attested in both types of habitats. Such group-living animals may not constitute preferred prey, given that leopards seem to favour small herds or solitarily animals, presumably to reduce the risk of injury during capture for what is a solitary hunter (Hayward et al. 2006). It is also assumed that leopards only hunt primates when larger prey are scarce, and that pigs are avoided as too aggressive and dangerous (ibid.). However, such potential constraints are certainly mitigated in GGNP's Gashaka sector. Firstly, while ungulates and primates tend to live in groups of large mean size, they are often also encountered in small herds or as single individuals (cf. Table 2). Secondly, the Gashaka sector overall offers an abundance of small to medium-sized prey which leopards prefer, in particular duiker and bushbuck (Hayward et al. 2006). Thirdly, the density of the habitat significantly reduces visibility, which may lead to occasional chance encounters. Despite the distinct seasonality of the region, rainfall appears to have no effect on the temporal distribution and encounter rate of potential prey species (cf. Figure 3).

Certain behavioural and grouping features of mammals at the Kwano study site, including primate gregariousness (Miller 2002), likely reflect a risk to fall victim to predators such crowned eagles (*Stephanoaetus coronatus* (Linnaeus, 1766)), rock pythons (*Python sebae* (Gmelin, 1789)), golden cats (*Felis aurata*) , chimpanzees (*Pan troglodytes*), baboons (*Papio anubis*) (Sommer et al. 2016), and, of course, leopards. Thus, there are indications that chimpanzees may select certain sleeping sites to minimize encounters with leopards (Fowler 2006). Moreover, experiments with acoustic and visual leopard models caused putty-nosed monkeys to alarm-call and adjust group movements (Arnold and Zuberbühler 2006; Arnold et al. 2011), indicating that these primates perceive large-cat predation as an ongoing threat.

In sum, leopards were and are present in GGNP's southern Gashaka sector, albeit at low density. As for the Kwano study area in particular, hunting with shotguns had decreased since about the year 2000, snare-traps are extremely rare and logging is absent. However, since about 2015, there has been a noticeable upturn in cattle grazing and motorcycle traffic. Looking into the future, this may lead leopards to increasingly avoid this part of the park which, traditionally, is perceived as one of the best protected areas.

The situation is different in GGNP's northern Gumti sector with its vast plains. Here, illegal cattle grazing is rampant since decades. This has caused the recent extinction of lions, hyenas and wild dogs and a stark reduction in the numbers of leopards and jackals. Herdsmen aim to shoot or poison these carnivores, who, in addition, are deprived of their natural prey animals because these are likewise eradicated due to cattle grazing (Saidu et al. 2010; see also Kamaya et al. 2002). The rarity or absence of large carnivores in the

Gumti sector is reflected in the fact that most herdsmen camps lack protective fences to corral livestock at night (Saidu et al. 2010).

Our compilation also indicates that leopards have always been targeted by hunters to obtain their valuable spotted skin, for which there exists continued and widespread demand, including in Nigeria itself (Nowell 2014). Perhaps because of this traditional hunting pressure, leopards have learned to avoid humans – which might at least partially explain, why, unlike elsewhere in Africa or Asia (Löe and Röskaft 2004), GGNP leopard attacks on humans are almost inexistent.

Apart from GGNP, leopards have survived into the present in at the most four other areas in Nigeria, albeit with precarious statuses:

- Niger Delta. A 2016 publication revealed only 6 confirmed records in the last 15 years, concluding that their population is regionally functionally extinct, with just a few vagrant individuals surviving (Eniang et al. 2016).
- Yankari Game Reserve. In September 2017 (WCS 2017) and June 2019 (WCS 2019), leopards were captured with camera traps.
- Kainji National Park. "Remnant leopard populations" still persisted here in 2015 according to Eniang et al. (2016: 174).
- Cross River National Park. In 2015, rangers reported footprints of a leopard with two cubs (Eniang et al. 2016: 174).

In comparison, the steady pace of leopard records for GGNP's Gashaka sector throughout decades indicates that this remote wilderness of GGNP may constitute the best prospects for these big cats to survive in Nigeria.

Authors' contributions

All the authors made a substantive intellectual contribution. All the authors have read and approved the final version of the manuscript and agreed to be held accountable for all aspects of the work.

Conflict of interest

The authors declare no potential conflict of interest.

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Availability of data and materials

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