The conservation value of Dja Faunal Reserve for tropical forest mammal communities

Rajan Amin, Tom Bruce, Oliver Fankem, Tim Wacher, Gilbert Oum Ndjock, Anne Stephanie Kobla, David Olson, Andrew Fowler

Zoological Society of London

MINISTERE DES FORETS ET DE LA FAUNE
MINISTRY OF FORESTRY AND WILDLIFE

Cover page images: *Clockwise from top-left:* Central Chimpanzee (*Pan troglodytes troglodytes),* Peter's duiker (*Cephalophus callipygus)* & Fire-crested Alethe (*Alethe castanea),* Giant pangolin (*Smutsia gigantea*), and African forest elephant (*Loxodonta cyclotis*).

Citation: Amin, R., Bruce, T., Fankem, O., Wacher, T., Oum Ndjock, G., Kobla, AS., Olson., D & Fowler., A. (2023). *The conservation value of Dja Faunal Reserve for tropical forest mammal communities.* Zoological Society of London. pp 1 – 102.

Contents

The conservation value of Dja Faunal Reserve for tropical forest mammal communities

Summary

The 5,280 km² Dja Faunal Reserve (DFR) is Cameroon's largest protected area (Figure 1). Designated a World Heritage Site in 1987 (the DFR and its buffer zone constitute the Dja Biosphere Reserve), the Dja is one of Africa's most biodiverse rainforests supporting extensive wildlife communities. It is a stronghold for several flagship species, including the Critically Endangered western lowland gorilla (*Gorilla gorilla gorilla*), the Endangered central chimpanzee (*Pan troglodytes troglodytes*) and the Critically Endangered African forest elephant (*Loxodonta cyclotis*). The Reserve also supports a diverse community of forest antelopes and three threatened pangolins, namely the Vulnerable black-bellied pangolin (*Phataginus tetradactyla*), and the Endangered white-bellied pangolin (*Phataginus tricuspis*) and giant pangolin (*Smutsia gigantea*). Despite its importance, the conservation status of DFR is uncertain due to continuing impact of pervasive and uncontrolled hunting and other illegal activities (MINFOF & IUCN, 2015); consequently, it is at risk of being added to the List of World Heritage in Danger (https://whc.unesco.org/en/decisions/7889).

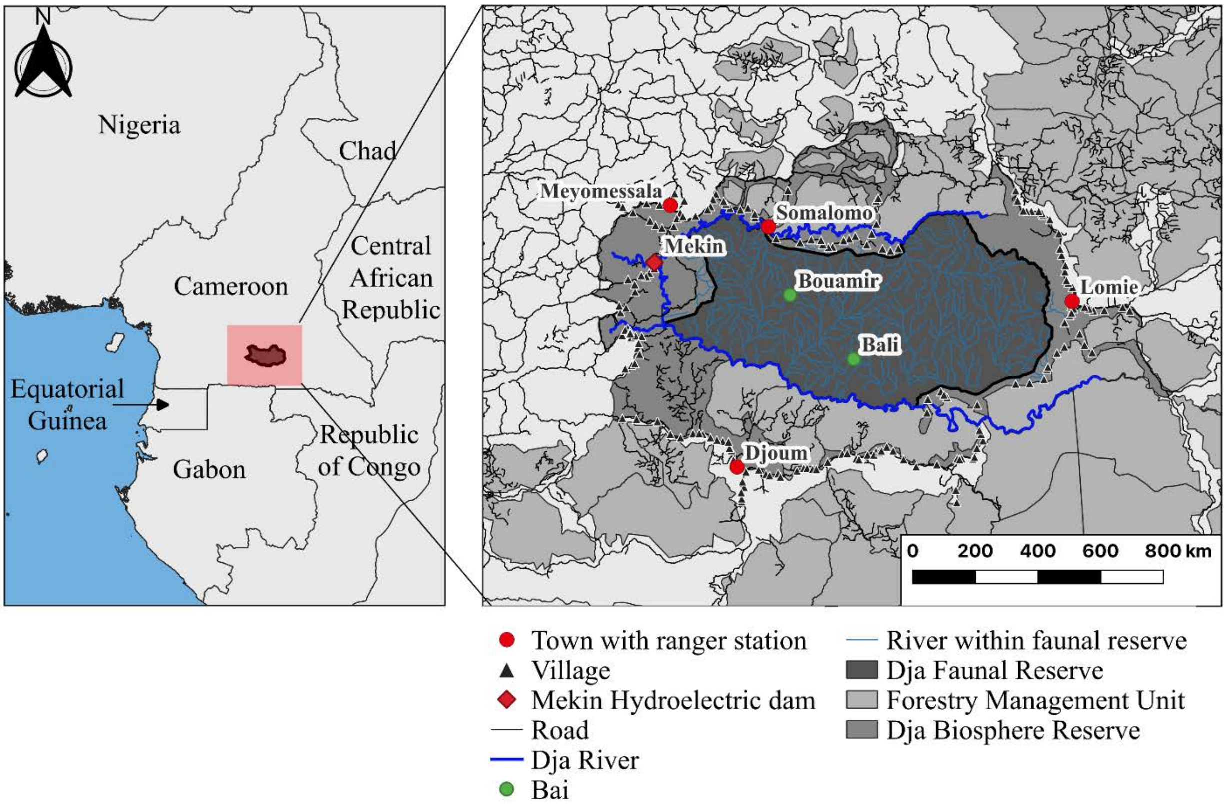


Figure 1. Location of the Dja Faunal Reserve, Cameroon.

The Cameroon Ministry of Forest and Fauna (MINFOF) in partnership with the Zoological Society of London (ZSL) carried out an extensive baseline survey of medium-to-large (>= 0.5 kg) terrestrial mammals, using a combination of two standardised approaches, within the DFR over the period 2016-2020. Eight camera-trap grids (305 camera-trap sampling points) were deployed across the Reserve with a total survey effort of 28,277 camera-trap days (Figure 2). A line transect survey comprising of 286 one-km transects systematically positioned across the whole Reserve was undertaken, from the 4 April 2018 to 3 June 2018, to assess the status of forest elephants (from dung) and great apes (from nests) (Figure 3).

This document provides a reference source, summarising measures of abundance and distribution for most medium to large terrestrial mammals in the Dja over the period 2016-2020 (with some limited information on the larger terrestrial birds found in the system). It also references the methods used to achieve these results. As such it is the most comprehensive baseline available against which to measure progress in mammal conservation at the DFR into the future.

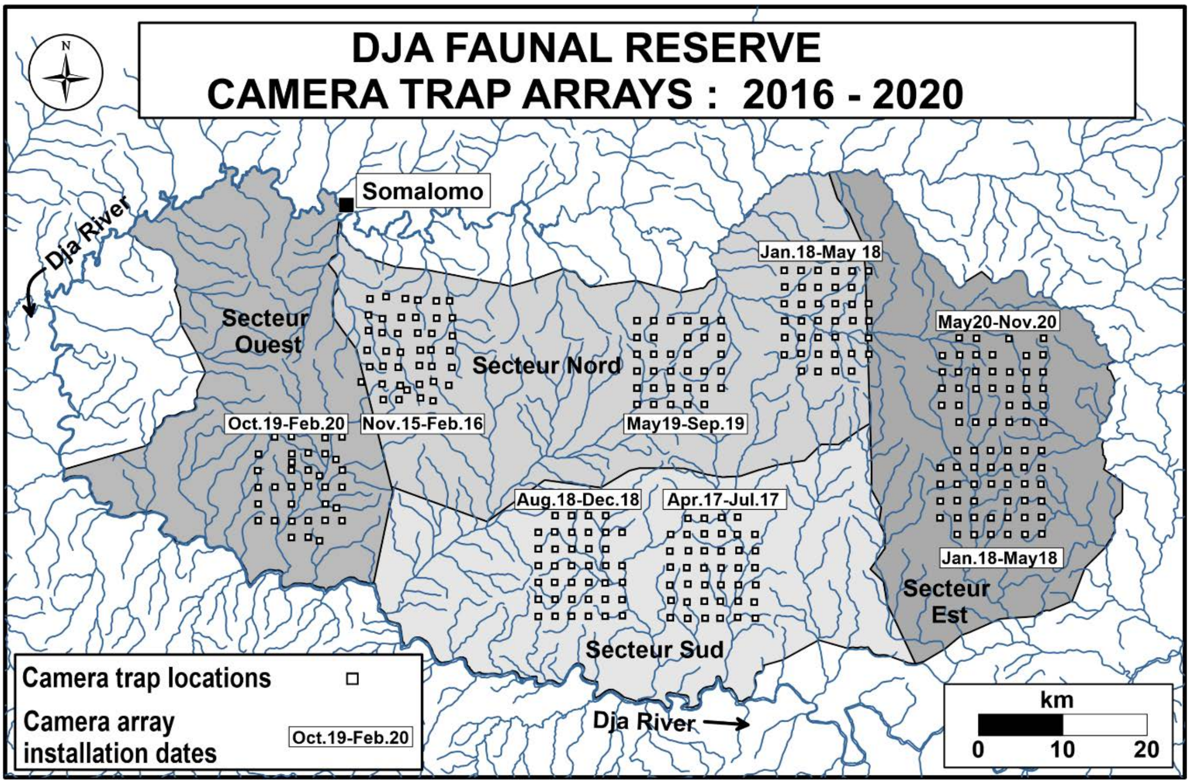


Figure 2. Location of eight camera-trap survey grids, and operational dates [label format month.year (start)–month.year (end)], Dja Faunal Reserve, Cameroon, 2016–2020.

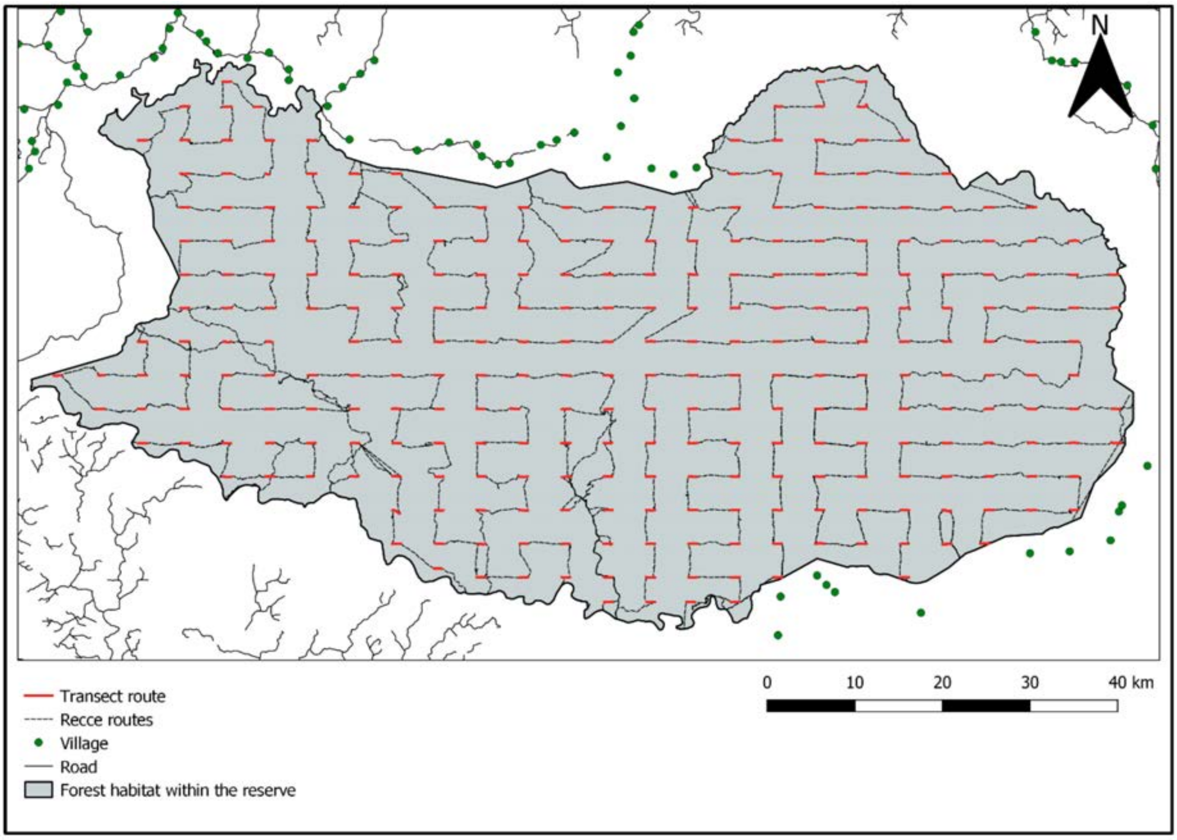


Figure 3. Locations of line transects and the associated routes between them (recces), systematically covering the entire Dja Faunal Reserve, Cameroon, 2018.

A total of 34 medium-to-large terrestrial mammal species were photographed in the camera-trap surveys (Table 1). A further seven medium-to-large arboreal mammals were documented, although they were not the target of the surveys (Table 1). Demidoff's galago (*Galagoides demidovii*) and five species of squirrels (< 0.5 kg) were also detected. No photographs of humans were taken, other than project staff at setup and recovery of camera-traps.

The species accumulation curves for medium-to-large terrestrial mammals show more species detected per unit effort in the South Sector (Figure 4, Figure 5), with the highest number of species recorded in South Sector-2017 (32 species, jackknife estimate (JE)=33), followed by North Sector-2019 (31 species, JE=33). The lowest number of species detected per unit effort occurred in North Sector-2018 (25 species, JE=26). There was a marked difference in the number of medium-to-large terrestrial mammals detected between adjacent grids: South Sector-2017 (32 species) and 2018 (28 species; missing species aardvark, forest buffalo, sitatunga, black-fronted duiker), and North Sector 2018 (25 species; missing species African golden cat, leopard, African civet, mandril, greater cane rat, western tree hyrax) and 2019 (31 species).

Further reading: Bruce *et al*. (2018).

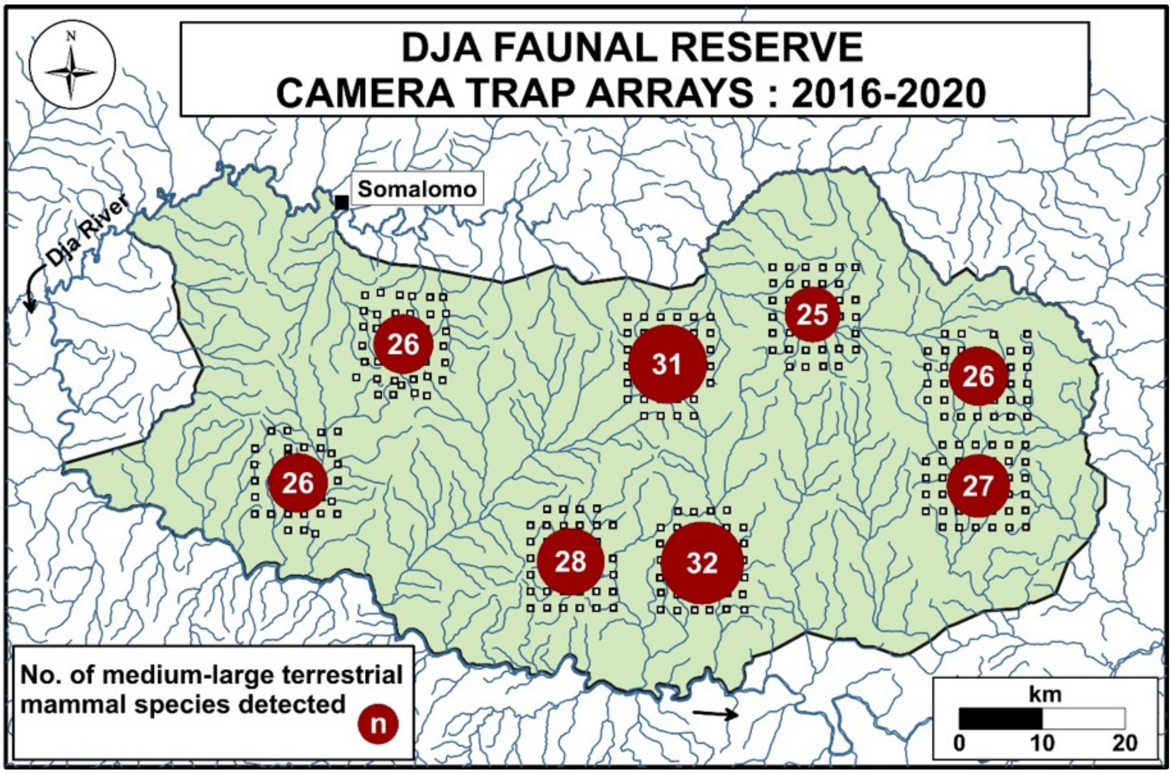


Figure 4. Total number of medium-to-large (>0.5 kg) terrestrial mammal species detected in each camera-trap survey grid, Dja Faunal Reserve, Cameroon. The camera-trap locations are also shown.

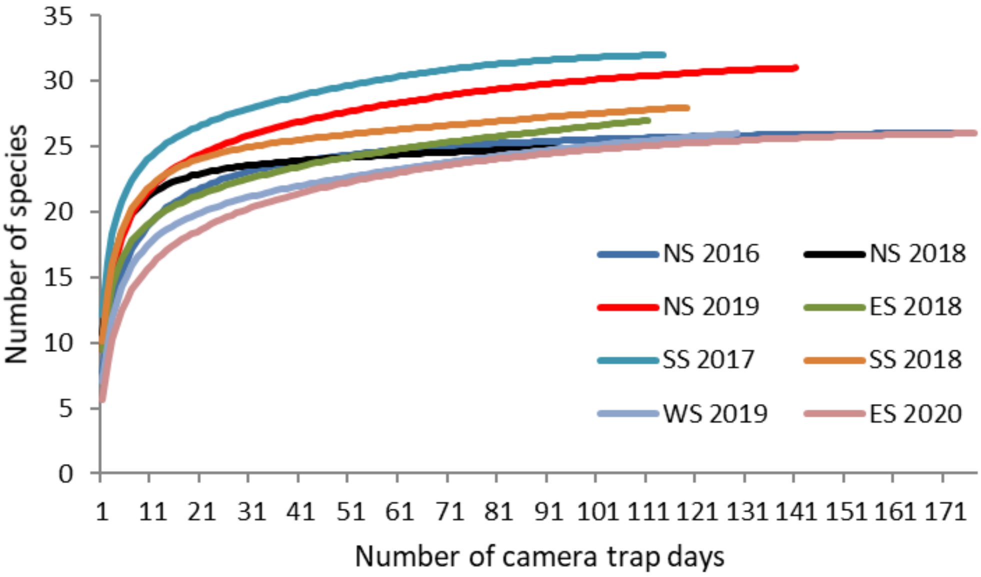


Figure 5. Medium-to-large (>0.5 kg) terrestrial mammal species accumulation curves: NS=North Sector, ES=East Sector, SS=South Sector, WS=West Sector, Dja Faunal Reserve, Cameroon.

Table 1. Camera-trap trapping rates (relative abundance index[1] "RAI" = events/100 days) of mammal species recorded in Dja Faunal Reserve, 2016-2020. NS=North Sector, ES=East Sector, SS=South Sector, WS=West Sector.

Family	**Species**	**Common name**	**Grid NS-2016**	**Grid SS-2017**	**Grid NS-2018**	**Grid ES-2018**	**Grid SS-2018**	**Grid NS-2019**	**Grid WS-2019**	**Grid ES - 2020**	**IUCN status**
Carnivora											
Felidae	*Caracal aurata*	African Golden Cat		0.62			0.65	0.15			VU
Felidae	*Panthera pardus*	Leopard		1.36			0.24	0.06	0.03		VU
Herpestidae	*Atilax paludinosus*	Marsh Mongoose	0.62	0.09	1.59	0.03	1.08	0.85	1.22	0.16	LC
Herpestidae	*Bdeogale nigripes*	Black-legged Mongoose	2.12	4.39	5.37	2.64	5.2	4.33	1.01	0.95	LC
Herpestidae	*Crossarchus platycephalus*	Cameroon Cusimanse	3.7	0.95	0.85	0.95	0.49	0.91	1.89	0.41	LC
Herpestidae	*Herpestes naso*	Long-nosed Mongoose	1.42	0.98	0.14	2.11	0.87	0.53	1.52	0.41	LC
Nandiniidae	*Nandinia binotata*	African Palm Civet	1.29	1.04	2.25	2.64	1.95	1.4	2.2	2.31	LC
Viverridae	*Civettictis civetta*	African Civet						0.03			LC
Viverridae	*Genetta maculata*	Large-spotted Genet		0.03	0.03		0.03	1.05			LC
Viverridae	*Genetta servalina*	Servaline Genet	3.79	2.34	2.96	1.56	1.95	1.46	2.4	1.6	LC
Artiodactyla											
Bovidae-Antilopinae	*Neotragus batesi*	Bates' Pygmy Antelope	0.51	0.42	0.33	0.53	0.22	0.15	0.03	0.11	LC
Bovidae-Bovinae	*Syncerus caffer nanus*	Forest Buffalo	0.16	0.06							NC
Bovidae-Cephalophinae	*Cephalophus callipygus*	Peters' Duiker	22.26	**113.14**	26.62	11.14	**75.52**	43.5	13.28	6.91	LC
Bovidae-Cephalophinae	*Cephalophus dorsalis*	Bay Duiker	8.64	10.53	7.4	0.84	8.35	14.06	3.18	2.09	NT
Bovidae-Cephalophinae	*Cephalophus leucogaster*	White-bellied Duiker		5.22	0.44	0.13	4.93	1.55	0.47	0.16	NT
Bovidae-Cephalophinae	*Cephalophus nigrifrons*	Black-fronted Duiker	1.99	0.62	0.08	0.21		0.2	0.07	0.46	LC
Bovidae-Cephalophinae	*Cephalophus silvicultor*	Yellow-backed Duiker	5.05	6.88	3.29	1.51	4.77	3.77	0.84	1.58	NT
Bovidae-Cephalophinae	*Philantomba monticola*	Blue Duiker	**100.67**	**62.36**	**71.87**	16.45	48.63	42.41	49.07	11.34	LC
Bovidae-Tragelaphinae	*Tragelaphus eurycerus*	Bongo	0.08	0.06			0.03				NT
Bovidae-Tragelaphinae	*Tragelaphus spekii*	Sitatunga	0.27	0.09	0.25	0.03		0.03	0.03	0.05	LC
Suidae	*Potamochoerus porcus*	Red River Hog	5.34	25.33	1.12	0.84	1.95	1.9	1.22	0.52	LC

[1] Species relative abundance index (RAI) = number of "independent detections" per trap day times 100; "independent detection" is defined as any sequence of images for a given species occurring after an interval of ≥60 min from the previous trigger (three-image sequence) of that species. IUCN status = Status of species from IUCN redlist. NC = Not categorised, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered, EW = Extinct in the Wild, EX = Extinct.

Tragulidae	*Hyemoschus aquaticus*	Water Chevrotain	0.46	6.47	2.25	0.05	3.06	0.96	0.64		LC
Hyracoidea											
Procaviidae	*Dendrohyrax dorsalis*	Western Tree Hyrax		0.06		0.03	0.16	0.06	0.2	0.03	LC
Pholidota											
Manidae	*Phataginus tricuspis*	White-bellied Pangolin	0.78	0.92	1.18	2.93	1.36	0.79	0.54	1.58	EN
Manidae	*Smutsia gigantea*	Giant Pangolin	0.3	0.86	0.47	0.08	0.43	0.35	0.17	0.16	EN
Primates											
Cercopithecidae	*Cercocebus agilis*	Agile Mangabey	1.1	14.15	15.57	4.12	0.73	4.03		3.02	LC
Cercopithecidae	*Cercopithecus cephus*	Moustached Guenon*	0.21		0.14			0.15	0.17	0.19	LC
Cercopithecidae	*Cercopithecus erythrotis*	Red-eared Guenon*						0.09			VU
Cercopithecidae	*Cercopithecus neglectus*	De Brazza's Guenon*						0.03	0.03		LC
Cercopithecidae	*Cercopithecus nictitans*	Greater Spot-nosed Guenon*	0.24	0.12	0.16	0.16	0.16	0.53	0.17	0.3	NT
Cercopithecidae	*Colobus guereza*	Eastern Black-and-white Colobus*					0.03				LC
Cercopithecidae	*Colobus satanas*	Black Colobus*		0.03		0.03	0.11	0.06			VU
Cercopithecidae	*Lophocebus albigena*	Grey-cheeked Mangabey*			0.11						VU
Cercopithecidae	*Mandrillus sphinx*	Mandrill	0.05	0.06		0.11		0.06		0.05	VU
Hominidae	*Gorilla gorilla*	Western Lowland Gorilla	0.21	0.71	1.43	0.4	0.7	0.85	0.27	0.08	CR
Hominidae	*Pan troglodytes troglodytes*	Central Chimpanzee	2.58	6.73	2.22	0.63	2.3	2.22	1.69	0.9	EN
Proboscidea											
Elephantidae	*Loxodonta cyclotis*	African Forest Elephant	2.6	4.51	0.96	0.48	0.68	0.2	0.07	0.08	CR
Rodentia											
Hystricidae	*Atherurus africanus*	African Brush-tailed Porcupine	24.13	9.76	26.73	13.73	13.2	12.8	9.94	5.79	LC
Muridae	*Cricetomys emini*	Emin's Pouched Rat	47.09	9.52	30.57	27.59	17.08	13.27	21.19	47.85	LC
Sciuridae	*Funisciurus Isabella*	Lady Burton's Rope Squirrel**		0.03	12.09	8.87	14.48	5	10.1	3.94	LC
Sciuridae	*Funisciurus leucogenys*	Red-cheeked Rope Squirrel**			0.03						LC
Sciuridae	*Funisciurus pyrropus*	Fire-footed Rope Squirrel**	0.05	0.03	1.65	1.69	4.45	1.55	1.76	1.88	LC
Sciuridae	*Heliosciurus rufobrachium*	Red-legged Sun Squirrel**			3.76	2.83	11.28	9.03	7.3	9.71	LC

Sciuridae	*Protoxerus stangeri*	African Giant Squirrel*	0.11	0.12	0.22		0.54	0.56	0.24	0.38	LC
Thryonomyidae	*Thryonomys swinderianus*	Greater Cane Rat				0.03	0.03	0.06	0.07	0.05	LC
Tubulidentata											
Orycteropodidae	*Orycteropus afer*	Aardvark		0.09							LC

* arboreal species; ** species < 0.5kg

		Trapping rate/100 days
		<=1
		>1 and <=50
		>50

Forest elephants

Central African forest elephants have declined by an estimated 62% between 2002 and 2011, largely due to poaching for the illegal ivory trade. They are now considerably more threatened than the African savannah elephant. The dung-based distance-sampling survey population estimates of 0.042 individuals/km^2 (CV: 19.4%; 95% CI: 0.029–0.061) and 219 individuals (95% CI: 50–319) confirmed a significant decline over recent years in the Reserve. The low density of forest elephants in the DFR reflects similar losses experienced in other parts of Central Africa such as the heavily impacted Korup National Park (0.04 individuals/km^2). Elephants mainly persisted in pockets within the northern part of the DFR during the April-May 2018 survey (Figure 6). However, camera trapping at other times indicates that they also utilise the south-central (April-July 2017 and August-December 2018) and south-eastern part (February-March 2018, most likely a single group) of the Reserve.

Further reading: Amin *et al*. (2020).

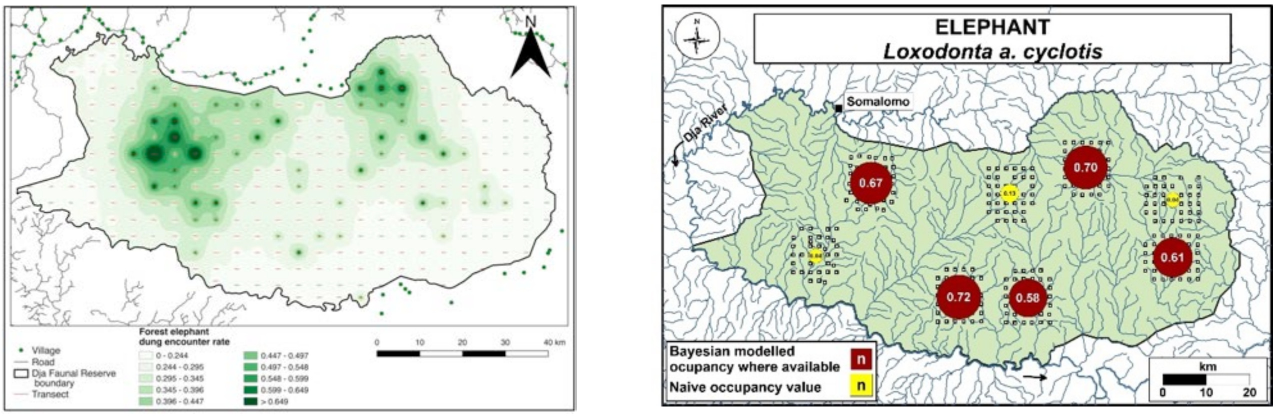


Figure 6. Forest elephant distribution (dung/km) from line transect survey (April-May 2018) (left) and occupancy by camera-trap grid (2016-2020) (right), Dja Faunal Reserve, Cameroon.

Great apes

Central chimpanzee and western lowland gorilla populations are rapidly declining due to habitat loss, poaching, and disease epidemics. Gorilla population estimates of 0.38 (95% CI: 0.28–0.53) individuals/km^2 and 2,004 (95% CI: 1,447–2,774) individuals confirmed a significant decline since the 1995 survey in the north-central part of the Reserve (a 57% decline for the area) and the Reserve-wide survey in 2015 (a 70% decline), although some of these differences could be due to methodology differences. The population was also much lower than in most other protected areas in the region.

The chimpanzee population with an estimated 0.53 (95% CI: 0.38–0.73) individuals/km^2 and 2,785 (95% CI: 2,020–3,839) individuals also revealed a marked decline of 34% and 23% compared to the 1995 and 2015 surveys, respectively. Occupancy estimates from camera-trap grid surveys showed great apes persisting mainly in the north-eastern part of the Reserve (Figure 7).

Further reading: Amin *et al*. (2022).

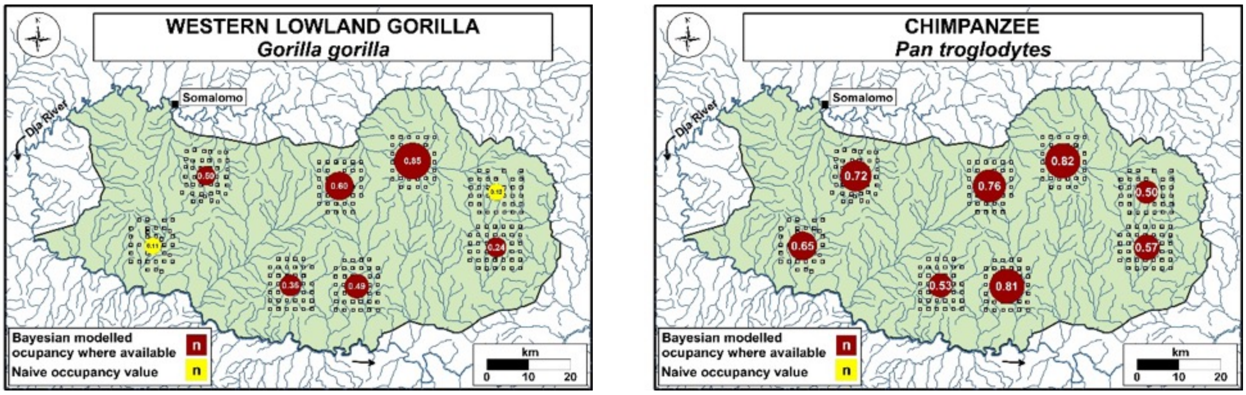


Figure 7. Western lowland gorilla (left) and central chimpanzee (right) occupancy by camera-trap grid, Dja Faunal Reserve, Cameroon.

Mandrill

The survey documented the first record of the occurrence of the mandrill (*Mandrillus sphinx*) in the DFR (Figure 8), east of the Dja River, which represents the northernmost extent of their range. A single mature male was photographed each time at widely separate locations, so the actual status of the species within the reserve is very uncertain. Although nationally protected, it is likely to be declining through hunting and habitat loss. The only other protected area in Cameroon where the species is known to occur is Campo Ma'an NP.

Further reading: Bata *et al*. (2017).

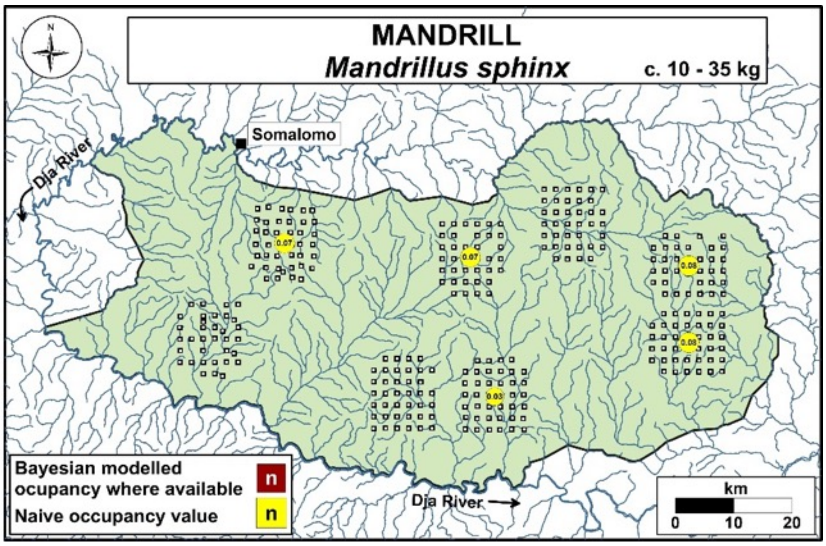


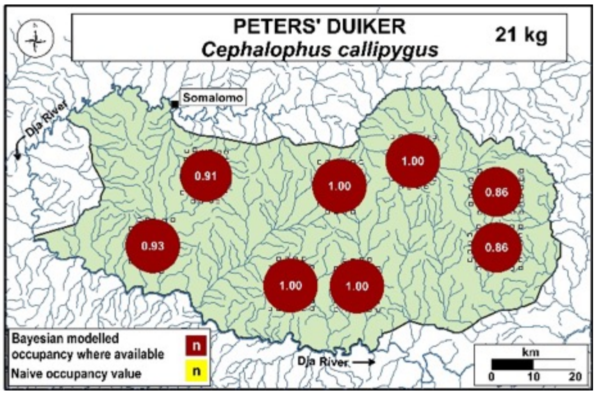
Figure 8. Mandrill occupancy by camera-trap grid, Dja Faunal Reserve, Cameroon.

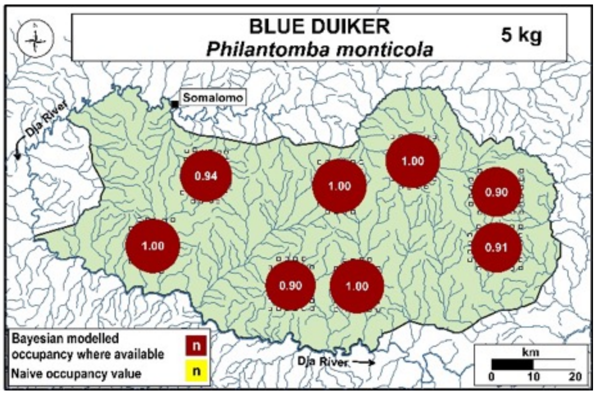
Forest ungulates

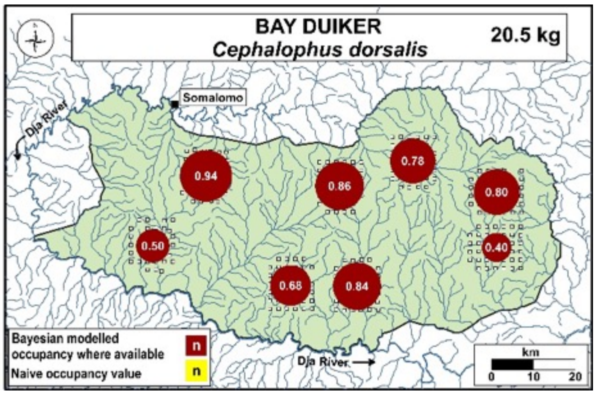
Ungulates have undergone major declines in Central and West African forests as a result of bushmeat trade and habitat loss. The camera-trap surveys recorded 30,601 independent detections of 12 species of forest ungulate. The blue duiker (*Philantomba monticola*) and Peters' duiker (*Cephalophus callipygus*) were the most abundant, together accounting for 82% of all ungulate detections, both with occupancy >85% in all survey grids. The black-fronted duiker (*Cephalophus nigrifrons*) was relatively widespread but rare. The white-bellied duiker (*Cephalophus leucogaster*) and water chevrotain (*Hyemoschus aquaticus*) were found mostly in the southern part of the Reserve (Figure 9). There were very few detections of sitatunga (*Tragelaphus spekii*), forest buffalo (*Syncerus caffer nanus*) and bongo (*Tragelaphus eurycerus*). There was also evidence of ecological partitioning among the more abundant duikers based on activity pattern and body size.

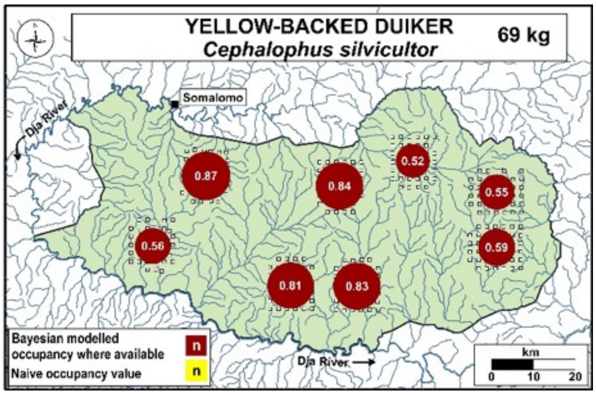
Camera-trap distance sampling was also trialled in the North and South Sector to obtain density and abundance estimates as traditional transect survey methods for forest antelopes often underestimate density for common species and do not provide sufficient data for rarer species. Density estimates for the bay duiker (*Cephalophus dorsalis*), blue duiker, Peters' duiker, and yellow-backed duiker (*Cephalophus silvicultor*) were higher in the North Sector than the East Sector. Bates pygmy antelope (*Neotragus batesi*), black-fronted duiker and white-bellied duiker had densities of <1 individual per km^2.

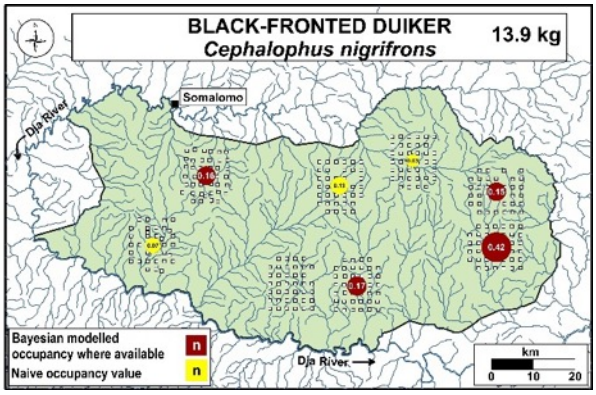
Further reading: Amin *et al*. (2019); Amin *et al*. (2021); Amin *et al*. (2022).

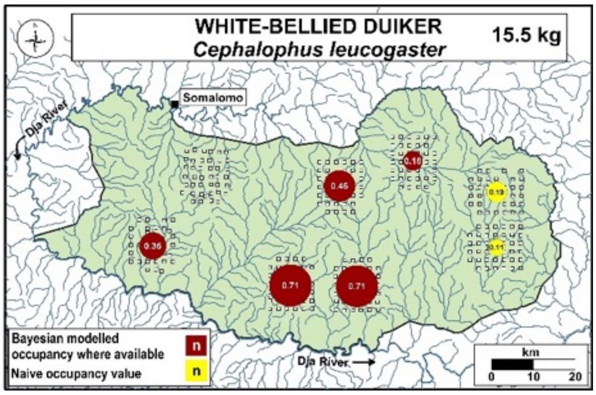


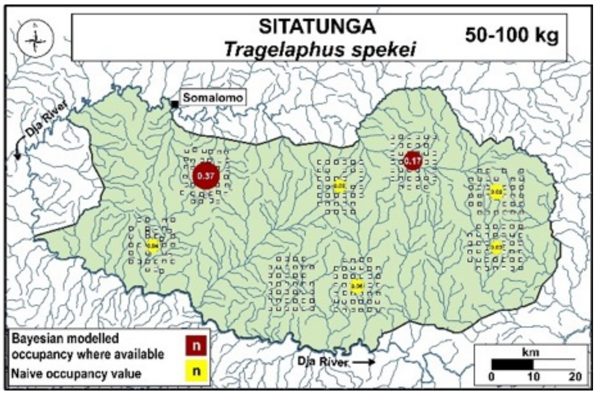


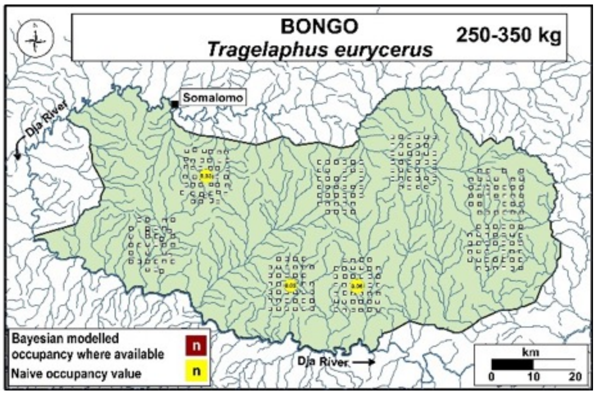

BAY DUIKER
Cephalophus dorsalis
20.5 kg
Somalomo
Dja River
0.94
0.86
0.78
0.80
0.50
0.40
0.68
0.84
Bayesian modelled occupancy where available
Naive occupancy value
n
km
0 10 20

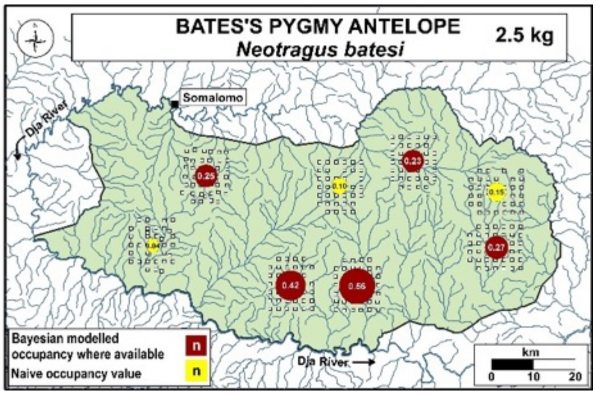

YELLOW-BACKED DUIKER
Cephalophus silvicultor
69 kg
Somalomo
Dja River
0.87
0.84
0.52
0.55
0.56
0.59
0.81
0.83
Bayesian modelled occupancy where available
Naive occupancy value
n
km
0 10 20

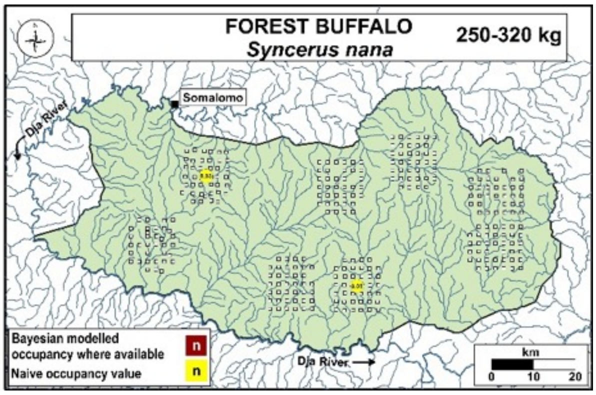

BLACK-FRONTED DUIKER
Cephalophus nigrifrons
13.9 kg
Somalomo
Dja River
0.16
0.15
0.42
0.17
Bayesian modelled occupancy where available
Naive occupancy value
n
km
0 10 20


WHITE-BELLIED DUIKER
Cephalophus leucogaster
15.5 kg
Somalomo
Dja River
0.45
0.36
0.71
0.71
Bayesian modelled occupancy where available
Naive occupancy value
n
km
0 10 20


SITATUNGA
Tragelaphus spekei
50-100 kg
Somalomo
Dja River
0.37
0.17
Bayesian modelled occupancy where available
Naive occupancy value
n
km
0 10 20


BONGO
Tragelaphus eurycerus
250-350 kg
Somalomo
Dja River
Bayesian modelled occupancy where available
Naive occupancy value
n
km
0 10 20


BATES'S PYGMY ANTELOPE
Neotragus batesi
2.5 kg
Somalomo
Dja River
0.25
0.23
0.27
0.42
0.56
Bayesian modelled occupancy where available
Naive occupancy value
n
km
0 10 20


FOREST BUFFALO
Syncerus nana
250-320 kg
Somalomo
Dja River
Bayesian modelled occupancy where available
Naive occupancy value
n
km
0 10 20

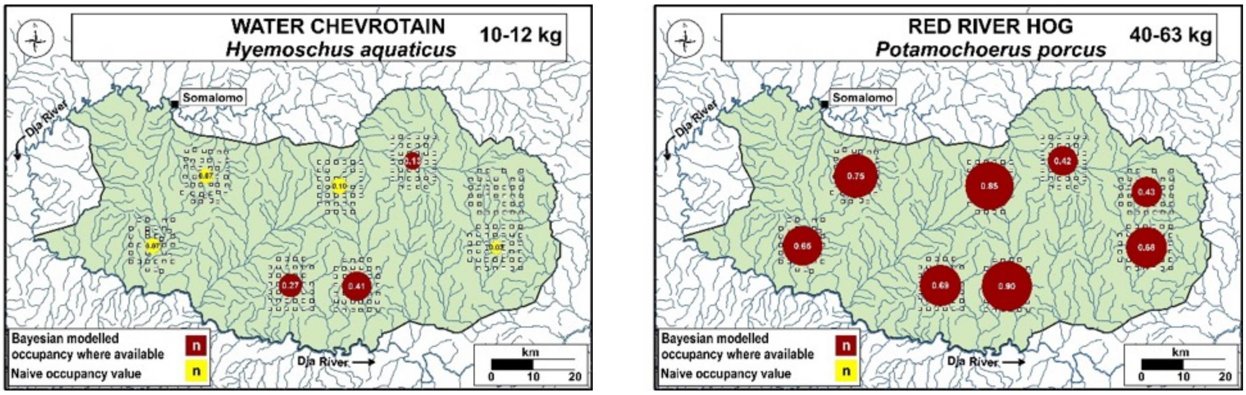
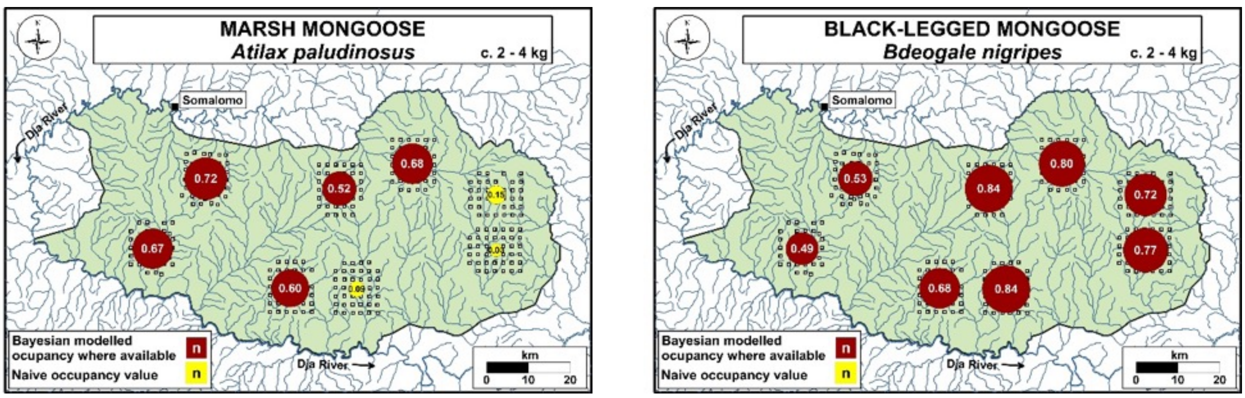


Figure 9. Occupancy by camera-trap grid for Peters' duiker and blue duiker; bay duiker and yellow-backed duiker; black-fronted duiker and white-bellied duiker; sitatunga and bongo; Bates' pygmy antelope and forest buffalo; water chevrotain and red river hog, Dja Faunal Reserve, Cameroon.

Carnivores

Ten species of medium-to-large terrestrial carnivore were recorded. The community differed in structure between the sectors. The black-legged mongoose (*Bdeogale nigripes*) was the most frequently encountered carnivore (Table 1). Marsh mongoose (*Atilax paludinosus*), long-nosed mongoose (*Herpestes naso*), Cameroon cusimanse (*Crossarchus platycephalus*), African palm civet (*Nandinia binotata*) and servaline genet (*Genetta servalina*) were also recorded throughout the Reserve (Figure 10). The large-spotted genet (*Genetta maculata*) was detected in the North and South Sector at very low frequency, although differentiating genet species was not possible in many images and other species (such as *Genetta cristata*) may occur. The African civet (*Civettictis civetta*) was only detected on one occasion in the North Sector. The two felids, leopard (*Panthera pardus*) and African golden cat (*Caracal aurata*), were mostly detected in the South Sector.

Further reading: Bruce *et al.* (2018).



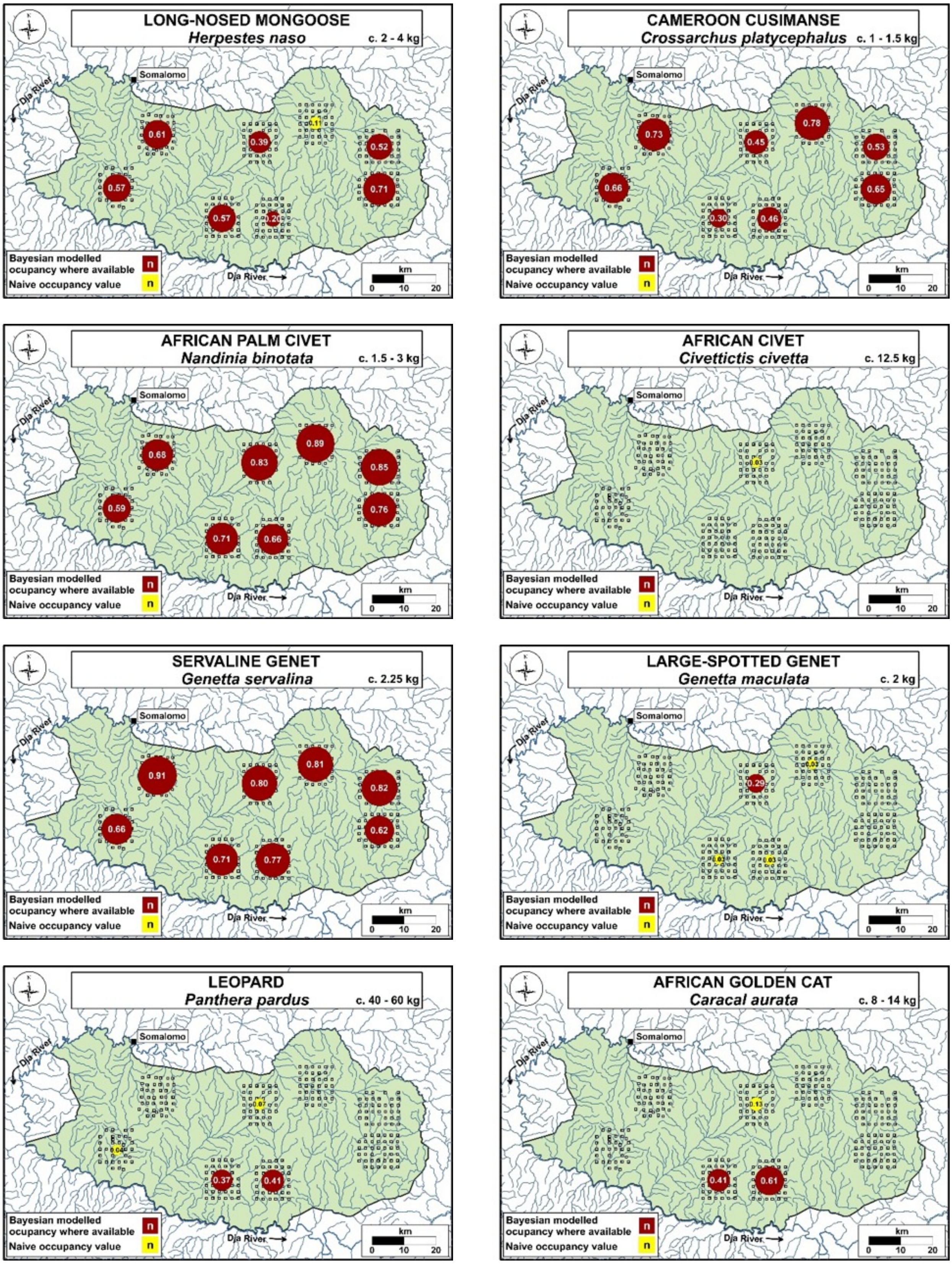


Figure 10. Occupancy by camera-trap grid for marsh mongoose and black-legged mongoose; long-nosed mongoose and Cameroon cusimanse; African palm civet and African civet; servaline genet and large-spotted genet; leopard and African golden cat, Dja Faunal Reserve, Cameroon.

Pangolins

Pangolins are one of the most threatened mammal groups, as a result of habitat loss and exploitation for their meat, scales, and other body parts. However, there is a lack of quantitative data on pangolin populations; their behaviour and ecology make them challenging to survey. The Reserve-wide camera-trap survey recorded 768 images of giant pangolin in 99 independent detections at 57 sites (Relative Abundance Index (RAI) =0.35), and 2282 images in 355 detections (RAI=1.26) of white-bellied pangolin at 137 sites. Ground-dwelling giant pangolins were largely confined to the core of the Reserve. Semi-arboreal white-bellied pangolins were predominantly distributed in the northeast, east and south of the Reserve (Figure 11). The study also suggests that at the ground-level the two species do not spatially segregate, and both were active throughout the night but with different activity peak times. There was also evidence of white-bellied pangolin possibly exhibiting fine-scale temporal avoidance of giant pangolin. The camera-trap study obtained no information on the strictly arboreal, black-bellied pangolin. Targeted arboreal camera-trap surveys and focussing on features such as fallen trees have the potential to confirm its presence and to estimate occupancy, and may also provide insight into their activity and ecology.

Further reading: Amin *et al*. (2023), Bruce *et al.* (2018).

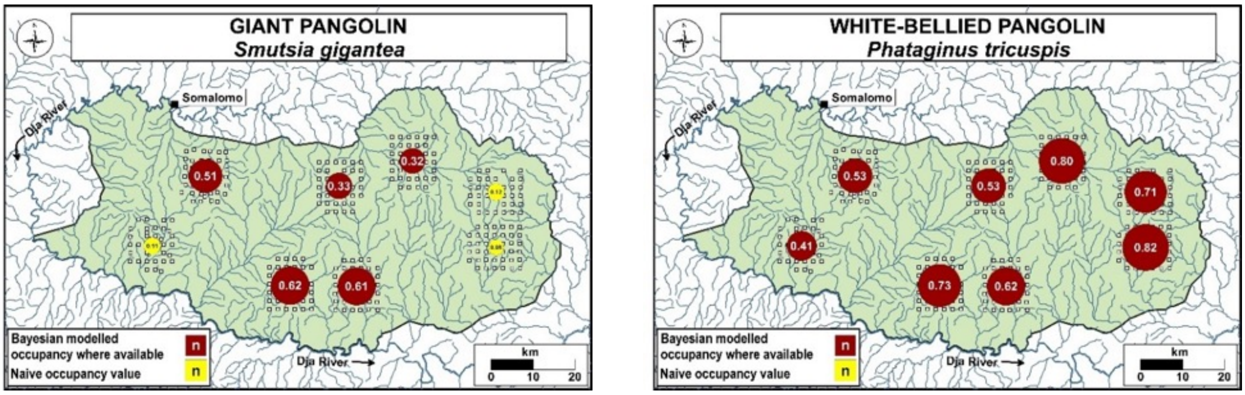


Figure 11. Giant pangolin (left) and white-bellied pangolin (right) occupancy by camera-trap grid, Dja Faunal Reserve, Cameroon.

Terrestrial birds

Six ground-dwelling birds were detected in the camera-trap surveys. The black guineafowl (*Agelastes niger*), plumed guineafowl (*Guttera plumifera*), Latham's forest francolin (*Peliperdix lathami*) and Nkulengu rail (*Himantornis haematopus*) occurred throughout the Reserve. The scaly francolin (*Pternistis squamatus*) and grey-throated rail (*Canirallus oculeus*) were detected at very low frequencies (Figure 11). The guineafowls are known to be hunted for food, possibly unsustainably.

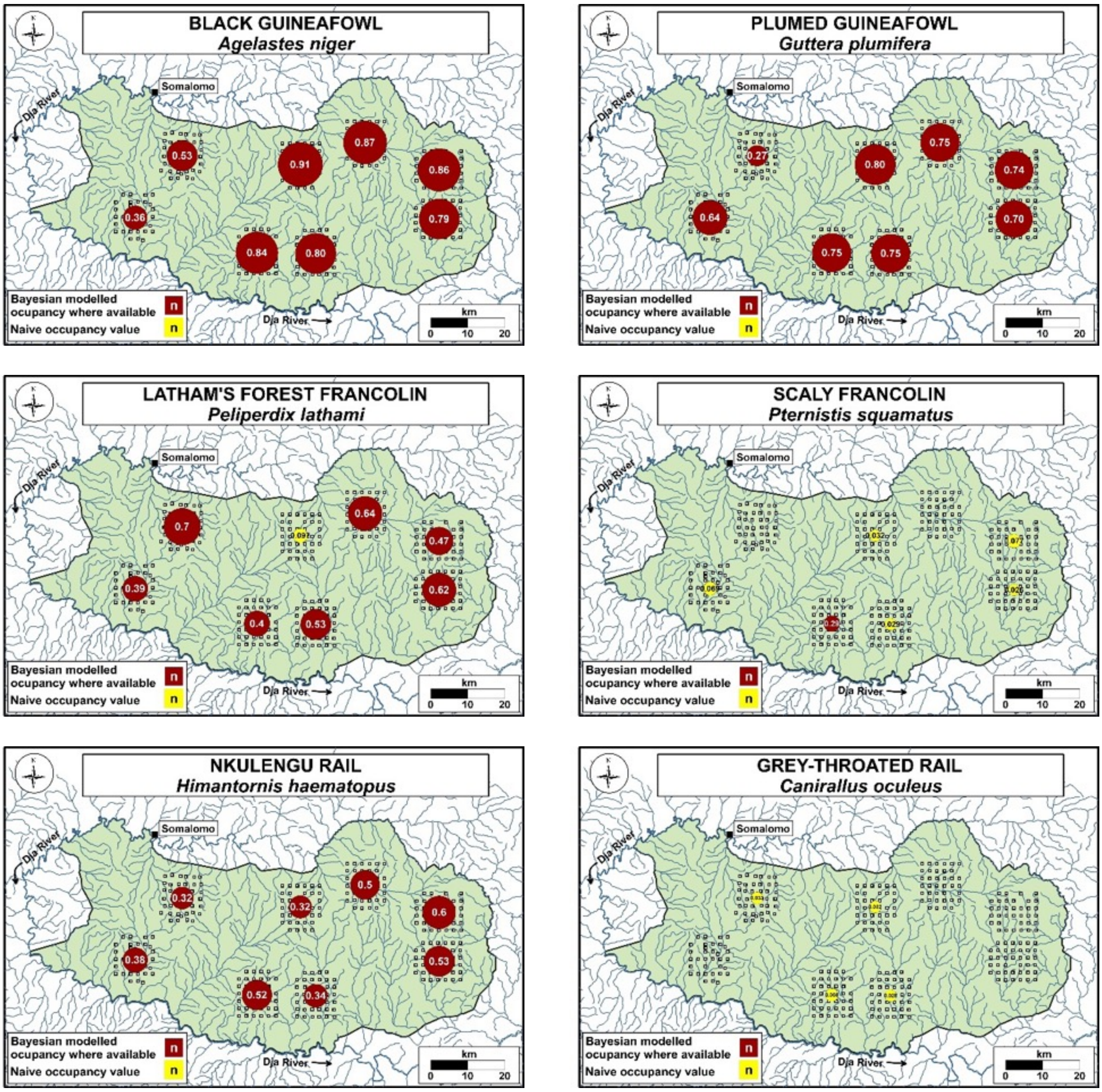


Figure 11. Occupancy by camera-trap grid for black guineafowl and plumed guineafowl; Latham's forest francolin and scaly francolin; Nkulengu rail and grey-throated rail, Dja Faunal Reserve, Cameroon.

The baseline surveys have confirmed that the DFR remains of major importance to African tropical forest mammal conservation, holding complete communities of predators and herbivores. Forty-six mammal species were recorded in DFR with 34 terrestrial medium-to-large mammal species. The terrestrial medium-to-large mammal community structure differed between management sectors. The eastern and western part of the Reserve had the lowest number of medium-to-large mammal species recorded, and trap rate and occupancy for many larger mammals were comparatively lower. Camera-trap distance sampling in the northern and eastern sector also revealed higher densities of bay duiker, blue duiker, Peters' duiker and yellow-backed duiker in the north.

In the North Sector, the presence of a long-term research station permanently manned by rangers, provides a deterrence to poaching, and a community surveillance network has also been established in the sector. Along the Reserve's southern boundary, the Dja River forms a natural barrier providing some protection from developed areas to the south, in conjunction with a permanent ecoguard river post being present on the Reserve side of the river. There is potentially greater pressure in the eastern and western part of the Reserve. Adjacent to the eastern boundary is a 276 km^2 buffer zone and two towns (Lomié and Mindourou) inhabited by over 30,000 people according to 2005 Cameroon population census (https://www.citypopulation.de/en/cameroon/admin/). Historically, indigenous people and local communities were very close to the Reserve forests and were sustainably utilizing the forests. With the gazettement of the Reserve, the communities have reluctantly respected the limit of the Reserve and over time with increased human population and the cost of bushmeat and pangolin scales, the impact of the towns and villages seems to have increased. On the western edge of the Reserve, there is significant infrastructure (Hydromekin Dam and Sud-Cameroun Hévéa rubber plantation) and associated human settlements.

The Dja Faunal Reserve is integral to the 167,000 km^2 TRIDOM conservation landscape across Cameroon, Gabon, and the Republic of Congo. The landscape is recognised as a global conservation priority and the management of forest concessions for biodiversity within the landscape is essential for maintaining connectivity especially for large mammals, such as the forest elephants and great apes. Viable populations of these keystone species are vital for the maintenance of forests due to their roles in fruit dispersal of large long-lived forest trees and lateral nutrient transport across vast distances. The protection of the Central African forests is all the more urgent given it is now recognised as a globally important factor in inter-continental weather patterns and for maintaining climate stability.

Publications

Amin R., Wacher T., Fankem O., Bruce T., Gilbert O.N., Ndimbe M.S. & Fowler A. (2023). Giant pangolin and white-bellied pangolin observations from a world heritage site. *Mammalia*. https://doi.org/10.1515/mammalia-2021-0173

Amin R., Wacher T., Fankem O., Gilbert O.N., Ndimbe M.S. & Fowler A. (2022). Status and ecology of forest ungulates in the Dja Faunal Reserve, Cameroon. *Mammalia*. https://doi.org/10.1515/mammalia-2021-0175.

Amin R., Fankem O., Gilbert O.N., Bruce T., Ndimbe M.S., Kobla A.S., Olson D. & Fowler A. (2022). Assessing the status of great apes in the Dja Faunal Reserve using distance sampling and camera-trapping. *Primate Conservation* (36).

Amin R., Klair H., Wacher T., Ndjassi C., Fowler A., Olson D. & Bruce T. (2021). Estimating Central African forest antelope population densities using distance sampling with camera traps. *Oryx* 56 (3): 345-351. doi:10.1017/S0030605320001209.

Amin R., Fankem O., Gilbert O.N., Bruce T., Ndjassi C., Olson D. & Fowler A. (2020). The status of the forest elephant in the world heritage Dja Faunal Reserve, Cameroon. (2020). Pachyderm 61: 78-89.

Amin R., Klair H., Wacher T., Bruce T., Ndjassi C., Olson D. & Fowler A. (2019). Estimating forest antelope population densities using distance sampling with camera traps: Blue Duikers in the Dja Faunal Reserve, Cameroon. *Gnusletter* 36 (1).

Bruce, T., Amin, R., Wacher, T., Fankem, O., Ndjassi, C., Ngo Bata, M., Fowler, A., Ndinga, H. and Olson, D., 2018. Using camera trap data to characterise terrestrial larger-bodied mammal communities in different management sectors of the Dja Faunal Reserve, Cameroon. *African Journal of Ecology*, *56*(4), pp.759-776. https://doi.org/10.1111/aje.12574

Bruce, T., Ndjassi, C., LeBreton, M., Wacher, T., Fowler, A., Tabue Mbobda, R.B. and Olson, D., 2018. African golden cat and leopard persist in Dja Faunal reserve Cameroon. *CAT News*, *68*(68), pp.00-01.

Bruce, T., Kamta, R., Tabue Mbobda, R.B., Talla Kanto, S., Djibrilla, D., Moses, I., Deblauwe, V., Njabo, K., LeBreton, M., Ndjassi, C. and Barichievy, C., 2018. Locating giant ground pangolins (Smutsia gigantea) using camera traps on burrows in the Dja Biosphere Reserve, Cameroon. *Tropical Conservation Science*, *11*, p.1940082917749224.

Bata M.N., Easton J., Fankem O., Wacher T., Bruce T., Eliseé T., Taguieteu P.A. & Olson D. (2017). Extending the Northeastern distribution of mandrills (*Mandrillus sphinx*) into the Dja Faunal Reserve, Cameroon. *African Primates* 12: 65-67.

Acknowledgements

We sincerely thank the Cameroon Ministry of Forestry and Wildlife (MINFOF), the Dja Conservation Service, Hilaire Ndinga (late Conservator of Dja Faunal Reserve) and the technicians, porters and guides involved in carrying out the fieldwork, without whom this collection of work would not have been possible.

We also thank Mike Hoffmann, Chris Ransom, Hannah Klair, Eleanor Harvie, Paul D'Ornelas, Malenoh Sewah Ndimbe, Constant Ndjassi, Madeleine Ngo Bata, Rebecca Sennet Day, Anthony Dancer and Romeo Tene for their support.

The authors are grateful for the generous financial support from the United States Fish and Wildlife Service (USFWS)—African Elephant Conservation, IUCN SOS—Fondation Segré Pangolin Conservation Initiative, and European Union - Programme de Conservation et Utilisation Rationnelle des Ecosystemes Forestiers en Afrique Centrale 6 (ECOFAC6). We also thank Save the Elephants, Arcus Foundation, Darwin initiative, USFWS - Illegal Wildlife Trade (IWT) – Grey Parrots, and UNESCO - Central Africa World Forest Heritage Initiative (CAWFHI) for contributing financially to the overall programme of work.

We finally thank the editors of CAT News and Mammalia for granting permission to make the articles published in their journals available in this compendium. We also acknowledge the journals Oryx, Primate Conservation, Pachyderm, Gnusletter, African Journal of Ecology, Tropical Conservation Science, and African Primates for making their content open access.

The status of the forest elephant in the world heritage Dja Faunal Reserve, Cameroon

Rajan Amin[1], Oliver Fankem[2], Oum Ndjock Gilbert[3], Thomas Bruce[2], Constant Ndjassi[2], David Olson[4], Andrew Fowler[4]*

[1]Zoological Society of London, Regents Park, London, United Kingdom
[2]Zoological Society of London – Cameroon, Yaoundé, Cameroon
[3]Ministry of Forests and Fauna, Yaoundé, Cameroon
[4]WWF Hong Kong, New Territories
*corresponding author: raj.amin@zsl.org

Abstract

Central African forest elephants (*Loxodonta africana cyclotis*) have declined by an estimated 62% between 2002 and 2011, largely as a result of poaching for the illegal ivory trade. They are now considerably more threatened than the Vulnerable African savannah elephant (*Loxodonta africana*), and effective monitoring of refugia populations is essential to inform management and conservation plans to secure a future for this megafaunal species.

Our forest elephant dung-based distance-sampling survey of the 5,260 km^2 World Heritage Dja Faunal Reserve (DFR) in Cameroon systematically covered 298.2 km of line transects with a further 1,681.4 km covered as recces. The population estimates of 0.042 individuals/km^2 (CV: 19.4%; 95% CI: 0.029–0.061) and 219 individuals (95% CI: 150–319) confirmed a significant decline over recent years. The low density of forest elephants in the DFR reflects similar losses experienced in other parts of Central Africa such as the heavily impacted Korup National Park (0.04 individuals/km^2).

Elephants now mainly persist in pockets within the northern part of the DFR, where the Cameroon Ministry of Forests and Fauna (MINFOF) has initiated a community support partnership agreement on sustainable access to forest resources, and increased law enforcement patrols and rapid response. The southern sector of the DFR is much more vulnerable to organised wildlife crime gangs operating from trafficking hubs outside traditional communities. The DFR management is implementing a community surveillance network and increasing SMART based patrolling, especially along the DFR's southern boundary, as well as in the south-eastern corner to secure the only existing forest elephant corridor. With improved security and appropriate engagement with local communities and private sector operators in the region, the remaining elephant population should start to expand across the DFR and its buffer zone, and numbers gradually increase across the wider landscape.

Résumé

Les éléphants de forêt de l'Afrique centrale (*Loxodonta africana cyclotis*) ont diminué d'environ 62% entre 2002 et 2011, ceci en grande partie à cause du braconnage pour le commerce illégal de l'ivoire. Ils sont à présent plus menacés que l' éléphant de savane (*Loxodonta africana*) et un suivi efficace de ces populations refuges est essentiel pour la mise à jour et l'implemenation des plans de gestion afin d'assurer un avenir pour cette espèce de mégafaune.

Cet inventaire par la méthode distance sampling a permis de couvrir 5,260 km^2 de la Réserve de Faune du Dja (RFD) site du patrimoine mondial avec 298.2 km de transects linéaires et 1,681.4 km de recces. Une estimation de la population d'éléphants à 0.042 individu/km^2 (CV: 19.4%; IC à 95%: 0.029 à 0.061) et 219 individus (IC à 95%: 150 à 319) a confirmé un déclin significatif de la population de cette espèce au cours des dernières années. La faible densité d'éléphants de forêt dans la RFD reflète les tendances à la baisse observées dans d'autres parties de l'Afrique centrale telle que le Parc National de Korup, fortement touché (0.04 individu/km^2).

Les éléphants persistent maintenant principalement dans les poches du la partie RFD, principalement dans les poches du secteur nord de la RFD où le Ministère Forêts et de la Faune (MINFOF) du Cameroun à initier un accord de partenariat d'appui aux communautés pour l'accès durable aux ressources forestières en plus de l'intensification des patrouilles de surveillance et de réponses rapides. Le secteur sud de la RFD semble être plus vulnérable aux gangs de la criminalité faunique opérant à partir de petites localités qui échappent à l'influence des communautés locales. L'unité de gestion de la RFD met en œuvre un réseau de surveillance communautaire et augmente les patrouilles avec l'approche SMART, en particulier le long des limites Sud et Sud-Est de la RFD pour sécuriser le seul possible couloir de migration des éléphants de cette aire protegée. Avec une protection améliorée, une implication appropriée des communautés locales et des opérateurs du secteur privé opérant autour de la RFD, la population d'éléphants restants devrait commencer à augmenter à l'interieur puis dans la zone tampon avant de progressivement se redistribuer dans l'ensemble du paysage.

Introduction

Central African populations of forest elephant (*L. a. cyclotis*) are in serious decline (Maisels et al. 2013). African forest elephants are estimated to have declined by 62% between 2002–2011 across the Central African forests (hereafter, the region), largely as a direct result of poaching for the illegal ivory trade (Maisels et al. 2013). Acting UNEP Executive Director Achim Steiner in 2013 stated that "In Central and West Africa, the elephant may soon disappear from whole areas unless urgent action is taken" (UNEP 2013). An important population of forest elephants inhabiting the south-east of Cameroon, representing a stronghold, has been recognised as a priority for conservation efforts (Brittain 2013). Monitoring population trends of this species across the region is essential to inform protected area (PA) management and conservation strategies aimed at securing a future for this megafauna species. To enable PA managers and governments to make informed decisions, reliable estimates of population size, density and distribution, and trends in these estimates, at regional and local scales are required. An understanding of the anthropogenic and ecological factors that influence the distribution of this species within its environment is also vital for adaptive management strategies (Stokes et al. 2010).

Elephant assessments are undertaken at landscape, national and regional scales (Thouless et al. 2016). Regional estimates are useful for gathering an overall status and trend of wide-ranging species, such as elephant. For such species, the concept of a conservation landscape (that is, a network of PAs separated and surrounded by alternative land use) provides a more effective framework for conservation actions (Stokes et al. 2010). Assessments at the spatial scale of individual reserves are also needed to help ensure they can continue to function as source populations and refugia in the future (Stokes et al. 2010, N'Goran et al. 2017). Regular surveys can provide early warning signs of precipitous declines as a result of intense poaching (Stokes et al. 2010). For example, within a decade (2004–2014), forest elephants within Minkébé NP declined by 78–81% (a loss of more than 25,000 elephants, Poulsen et al. 2017). This highlights that even in one of Central Africa's most remote PAs, potentially irreparable population declines can occur undetected, in less than the time taken for a single generation of elephants to advance to sexual maturity (Turkalo et al. 2017).

The primary objective of our study was to assess the status of forest elephant (and great apes, Bruce et al. 2018) in the Dja Faunal Reserve (DFR), in south-east Cameroon a World Heritage Site (UNESCO 2018; the DFR and its buffer zone constitute the Dja Biosphere Reserve). The DFR's extant megafauna is considered one of the Outstanding Universal Values (UNESCO 2018). This paper presents the study's findings on forest elephants. Distance sampling carried out through transect surveys of elephant dung was employed to estimate elephant population density and abundance (Hedges 2012). We used a standardised survey protocol to provide robust estimates for monitoring changes in the population over the long-term.

The survey also gathered information on the type, frequency, and distribution of human activities within the DFR. When combined with the information on the distribution of species, human activity data can provide insight into the importance of hunting pressure and human disturbance in diminishing wildlife populations. This also provides a robust baseline of data against which the effectiveness of management activities can be measured.

Materials and Methods

Study area and field data collection

The DFR, the largest protected area in Cameroon, is 5,260 km^2 (3°08′58.9″N, 13°00′00.1″E, fig. 1). Approximately 80% of the DFR is bordered by the Dja River, which forms a natural barrier and provides some limited protection, though crossing in canoes is common. The Biosphere Reserve outside the formal DFR is largely comprised of Forestry Management Units (FMUs), settlements, and community forests. There is also a 450 km^2 rubber plantation and a hydroelectric dam on the Dja River in the western buffer zone, both adjacent to the DFR boundary (fig. 1). There are no

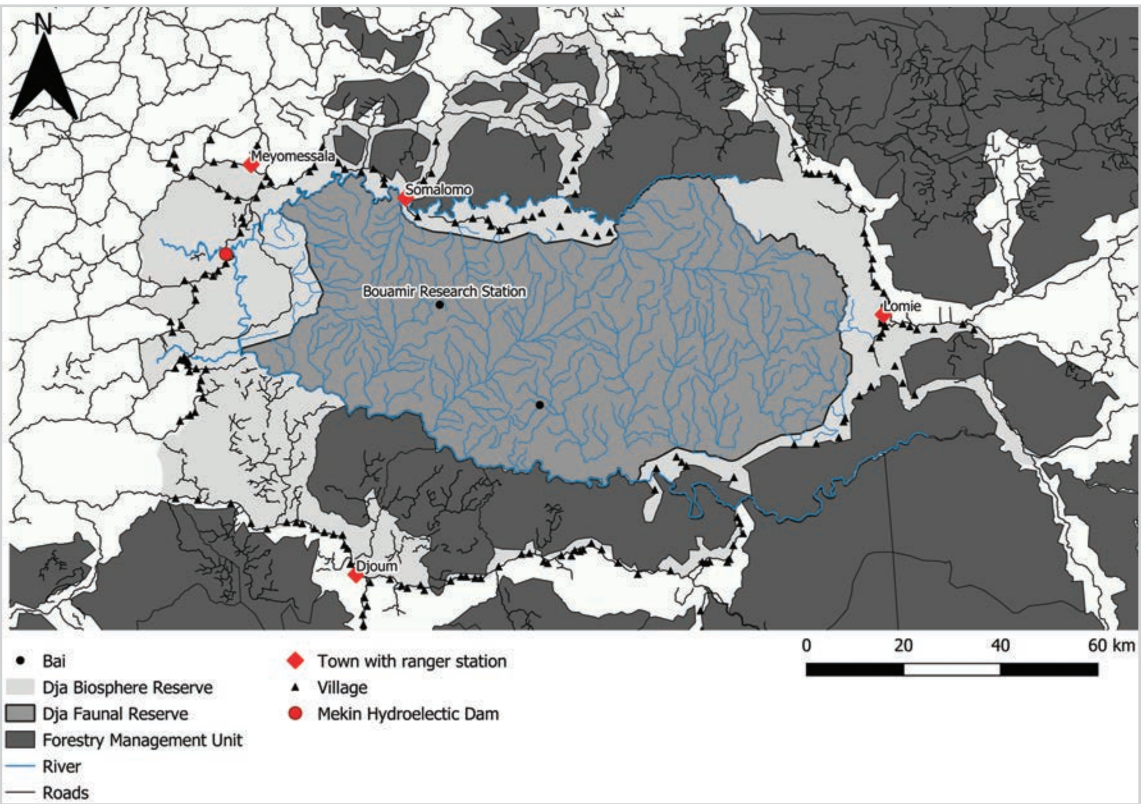


Figure 1. Location of the Dja Faunal Reserve, Cameroon.

recent reliable estimates of human population size surrounding the DFR. Estimates vary from 19,500 village inhabitants within the core zone to a further 30,000 within the wider area directly surrounding this zone (Fowler 2019, Ngatcha 2019). Expanding settlements and transport corridors to the south and east of the DFR are rapidly clearing natural forest and may soon result in isolation of the DFR, as intact forest corridors are lost, particularly in the south-eastern corner.

The DFR is a relatively flat plateau of round-topped hills and ranges in altitude from 600–800 m asl (MINFOF and IUCN 2015). The topography is mainly shallow valleys on either side of a ridgeline that cuts through the DFR east to west (MINFOF and IUCN 2015). On the floor of valleys, swamp habitat becomes more common. Tributaries throughout the DFR flow into the Dja River (UNESCO 2018, MINFOF and IUCN 2015). The three major types of forest in the DFR are *terra firma* mixed-species forest, mono-dominant forest where *Gilbertiodendron dewevrei* is the most abundant species, and periodically flooded forest (Djuikouo et al. 2010). The DFR supports a rich medium-to-large mammal fauna, including the Vulnerable African forest elephant, which is considerably more threatened than the Vulnerable *Loxodonta africana* (the African savannah elephant), with which it is merged by some specialists (Blanc 2008). The Critically Endangered Western lowland gorilla (*Gorilla gorilla gorilla*) and the Endangered central chimpanzee (*Pan troglodytes troglodytes*) also occur in the DFR. The DFR also has a diverse community of forest antelopes and three Vulnerable species of pangolins, namely the black-bellied pangolin (*Phataginus tetradactyla*), white-bellied pangolin (*Phataginus tricuspis*), and giant pangolin (*Smutsia gigantea*).

There are four main seasons: the long rains (August-November); the dry season (November-March); the short rains (March-May); and a shorter dry season (June-July) (MINFOF and IUCN 2015). During the dry season there is on average <100 mm of rainfall from a mean annual rainfall of approximately 1,570 mm (UNESCO 2018). The mean annual temperature is 23.5˚C–24.5˚C. The maximum temperature is reached in February and the minimum in July (MINFOF and IUCN 2015).

Within and around the DFR, poaching is occurring for subsistence, but largely through non-traditional means, such as guns and wire snares; and for the commercial and illegal wildlife trade (UNESCO 2018, Bruce et al. 2018). Around the DFR, other significant threats to biodiversity include mining, a proposed concrete plant on the river, logging, agricultural clearance for subsistence crops and commercial crops such as pineapple, loss of the last remaining large forested corridor if the south-eastern road is developed, rubber plantations (e.g. Sud-Cameroun Hévéa) and the associated demands for bushmeat, and the ecological impacts of existing (the Hydro Mekin) and planned hydroelectric dams (Muchaal and Ngandjui 1999, MINFOF and IUCN 2015).

Cameroon's Ministry of Forests and Fauna (MINFOF) is responsible for the management of the DFR and the Biosphere Reserve. In order to facilitate management, the DFR has been divided into four sectors with a base responsible for each sector in the nearest town: Lomié (East Sector), Djoum (South Sector), Meyomessala (West Sector), and Somalomo (North Sector).

Line transect surveys

We first estimated the total length of transect we would need to achieve a desired precision in the density estimate for the forest elephant using the methodology from Hedges (chapter 9, 2012). We used the following equation (Buckland 2001) and data from a previous transect survey (MINFOF and IUCN 2015).

$$L = (b/\{cv_t(\hat{E})\}^2).(Lo/no),$$

where

L = estimate of total transect line length to be surveyed to achieve target coefficient of variation,

b = dispersion factor (= 3; Buckland et al. 2001),

cv_t = target coefficient of variation of density estimate $\hat{E}$,

Lo = total length of all transects (from previous survey)

no = total number of observations on all transects (from previous survey).

We estimated 286 km of transects were needed to achieve a 10% coefficient of variation for forest elephants (based on the 2015 MINFOF and IUCN survey comprising of 612 km of transects, MINFOF and IUCN 2015).

The survey, therefore, consisted of 286 one km transects systematically positioned with orientation east to west as the majority of watercourses in the DFR run north–south (fig. 2). We conducted the survey at the end of the dry season between 4 April 2018 and 3 June 2018 using eight teams. Each team had two observers, one looking up for great ape nests, while the other looking at ground level for elephant dung, human signs, and great ape nests. Each team also had two data recorders and four porters who walked at a distance behind the team and were responsible for carrying supplies and camping equipment. The observers were trained in identifying and ageing elephant dung and great ape nests. Forest elephant dung piles were aged according to the S-system (Hedges 2012), namely: S1: all boli are intact; S2: one or more boli (but not all) are intact; S3: no boli are intact, but coherent fragments remain (fibres are held together by faecal material); S4: no boli are intact; only traces (e.g., plant fibres) remain; no coherent fragments are present (but fibres may be held together by mud); S5: no faecal material (including plant fibres) is present. Perpendicular distance from the centre of each individual dung pile to the line transect was measured to the nearest cm.

The survey also recorded sign of human activity, both along line transects and during the approximately 3.8 km walk (hereafter recce) between transects. Types of human sign recorded were trails, snares, signs of passage, machete cuts, shelters and camps, firearms and ammunition, timber exploitation, direct encounters with people, and gunshots heard. Camps were defined as any structure used for sleeping within the forest evident from cleared ground and the presence of a fire pit or structures. However, as a caveat, it is impossible to differentiate poacher's trails and cuts from those of ecoguards and NGO work within the DFR.

All data was recorded using the Spatial Monitoring and Reporting Tool–Ecological Records (SMART-ER

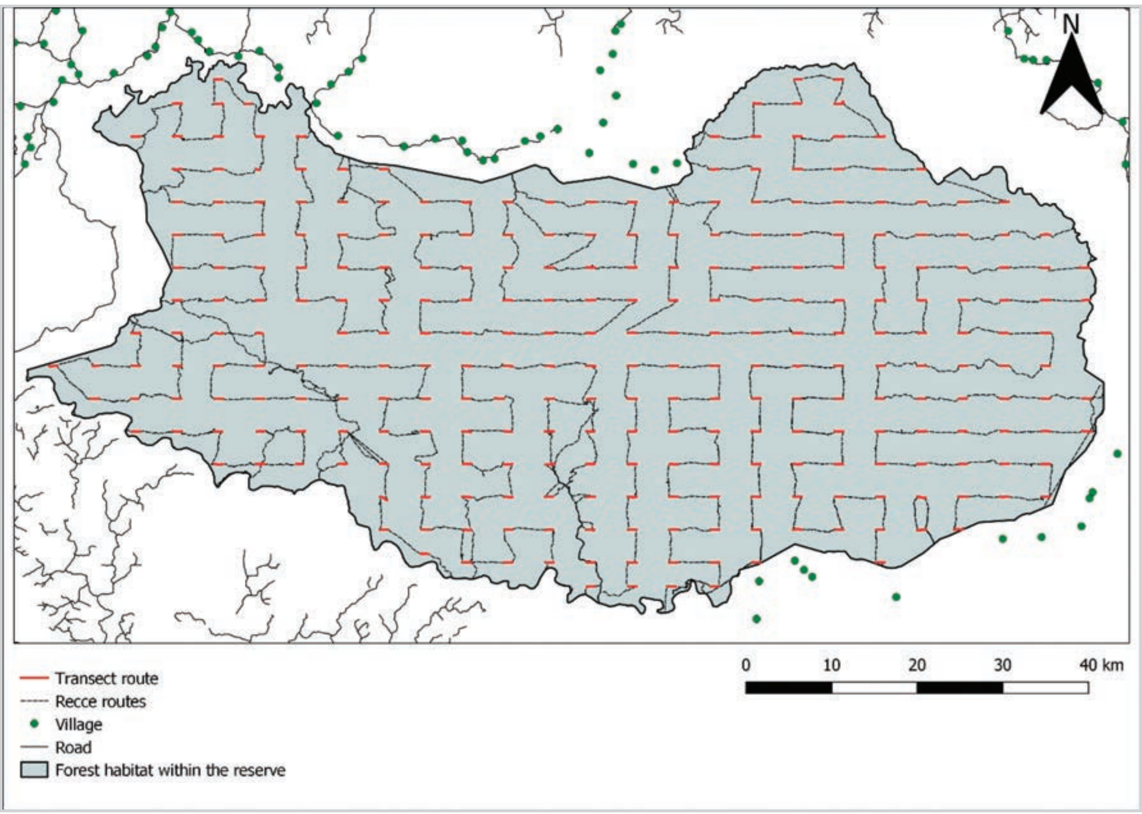


Figure 2. Location of transects and the associated routes between them (recces), systematically covering the entire Dja Faunal Reserve, Cameroon.

https://smartconservationtools.org) on Cedar Personal Digital Assistants (PDAs), and also in notebooks to back up data on the Cedar device. A Global Positioning Satellite (GPS) point with date and time was also taken for each observation and recorded in the notebook.

All data was exported from the PDAs into SMART. We checked all data entries within SMART against their paper counterparts to ensure that both were consistent with one another. We then exported the cleaned data in SMART into Excel and converted into suitable format for analysis in DISTANCE 7.2 software package (http://distancesampling.org/distance). We considered models of the detection function with the half-normal, hazard rate and uniform key functions with up to five cosine, simple polynomial and Hermite polynomial adjustment terms. Adjustment terms were constrained, where necessary, to ensure the detection function was monotonically decreasing. We selected among candidate models of the detection function by comparing AIC values. We also performed absolute model fit to the data using Chi-square test. All maps were produced using Quantum Geographic Information System (QGIS, http://qgis.osgeo.org).

Estimation of elephant dung decay rate

Over a period between April 2018 and September 2018, 85 fresh elephant dung piles were located and carefully marked across the study area. At the end of the study, the marked elephant dung piles were checked to see which had disappeared and which were still visible. The data on the state of the dung piles and time since dung deposition were analysed using logistic regression in R software package (http://www.R-project.org) to estimate the elephant dung mean decay rate and its variance. For the production rates, we used 19.77 elephant dung piles per day (Tchamba 1992).

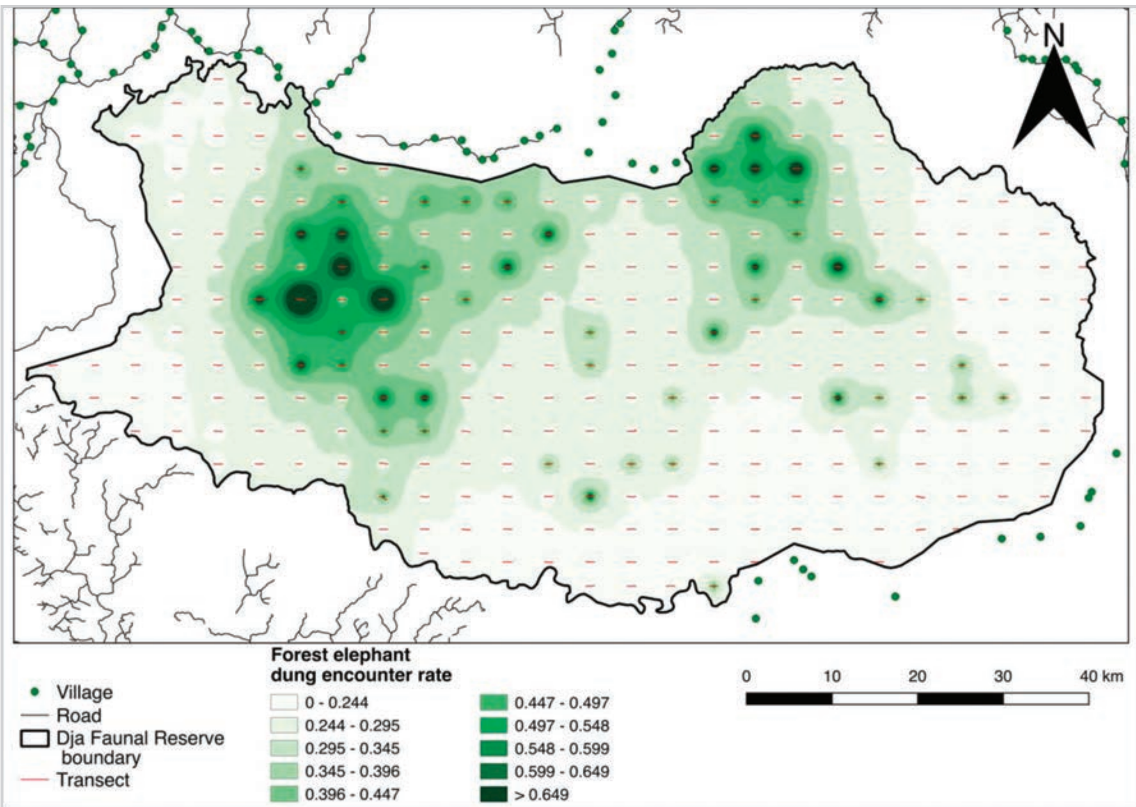


Figure 3. Distribution of forest elephant dung (dung/km) within the Dja Faunal Reserve, Cameroon. Locations of dung encounters along both transects and recces are also shown.

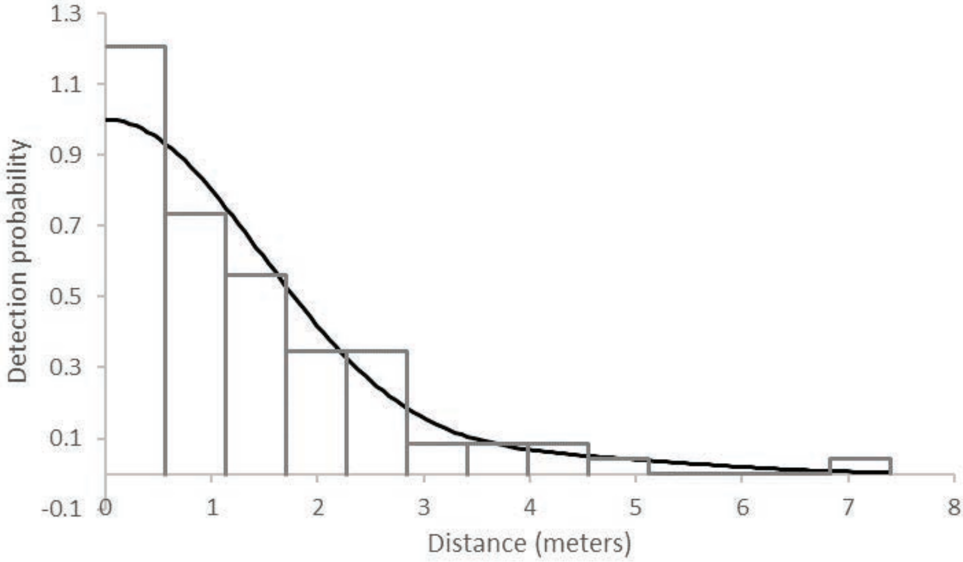


Figure 4. Detection probability as function of distance from half-normal line transect model fitted to forest elephant in the Dja Faunal Reserve, Cameroon (2018). The histograms of the observed distances are also shown.

Results

283 transects, totalling 298.2 km were completed. Two transects had to be abandoned due to flooding. One was abandoned as part of it was within a village. Recces covered a total distance of 1,681.4 km (fig. 2). In total, 167 elephant dung piles were encountered on transects during the survey. Of these, 82 were in the S1–S3 categories used for the distance analysis. The distribution of forest elephant dung observations is shown in fig. 3, as an encounter rate (dung/km) density contour map.

We estimated an elephant dung mean decay rate of 83.2 days (SE: 6.19). Exploratory analyses revealed no evidence of data collection errors. The half normal model with 2 cosine adjustments minimised AIC along with chi-square P value >>0.05 and was used to estimate density (fig. 4). Forest elephant dung density estimate was 68.43 piles/km^2 (95% CI: 48.24–97.07) and detection probability was 0.27 (SE: 0.02; 95% CI: 0.23–0.32). Effective strip width was 2.01 m (SE: 0.16; 95% CI: 1.71–2.36). Elephant density was estimated as 0.042 individuals/km^2 (CV: 19.4%; 95% CI: 0.029–0.061) with a population estimate of 219 individuals (95% CI: 150–319).

Human disturbance

A total of 359 human signs were encountered on the transects and 1,309 signs on recces resulting in an overall encounter rate of 0.84/km. The most prevalent signs encountered were established trails (0.27/km), machete cuts (0.17/km) and signs of passage such as marked trees and bent sticks (0.15/km). Of the signs directly attributable only to poaching the most prevalent was firearm accoutrements and ammunition (0.11/km), followed by snares (0.06/km). The distribution of human signs encountered on recces and transects is shown in fig. 5 as an encounter rate (signs/km) density contour map.

Discussion

This reserve–wide survey confirms that the forest elephant population within the DFR has diminished markedly over recent years in comparison to two earlier surveys by Williamson and Usongo (1995) and MINFOF and IUCN (2015) (Table 1). However, the MINFOF and IUCN (2015) survey used a dung decay rate of 90 days from Tchamba (1992), which also wasn't based on a study on elephant dung decay rate estimation. The Williamson and Usongo (1995) survey was conducted mainly in the northern sector of the DFR. For comparison, we analysed our study

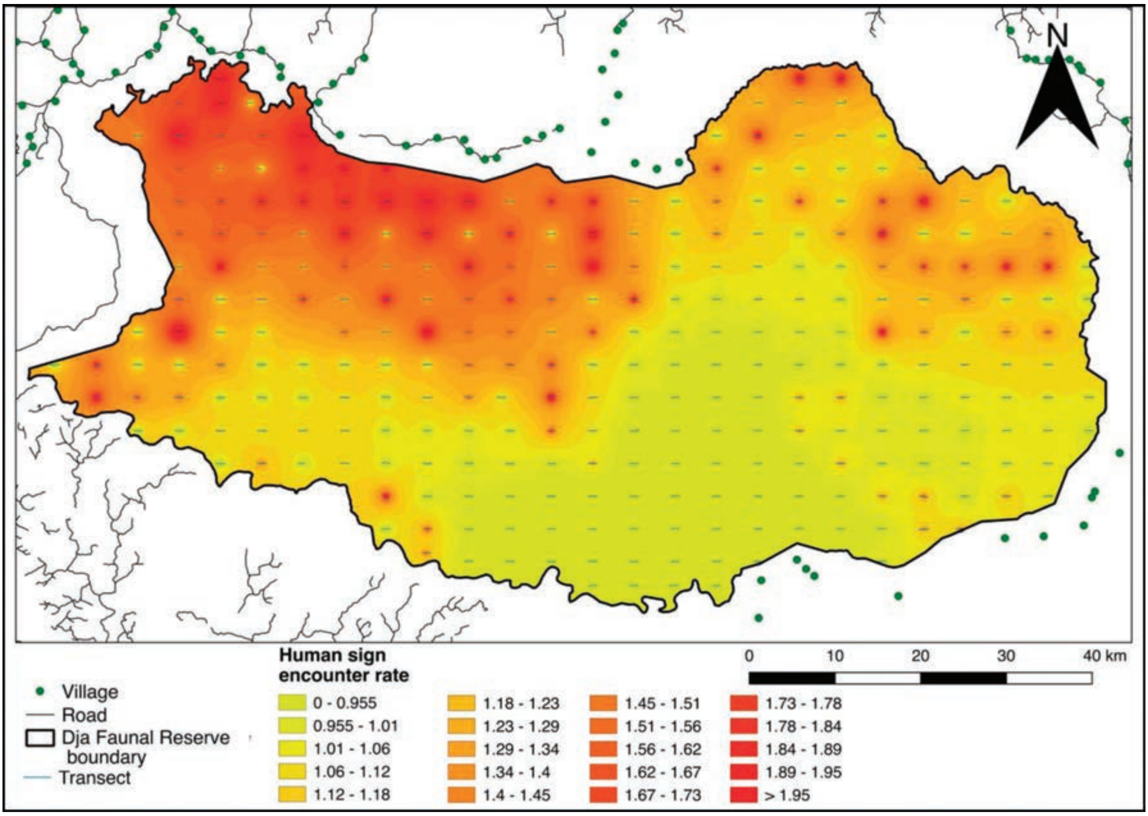


Figure 5. Distribution of signs of human activity (signs/km) within the Dja Faunal Reserve, Cameroon. Locations of signs of human activity encounters along transects and recces are also shown.

transects that were located in the 1995 survey area. Forest elephants in the sampled area have declined from an estimated 0.56 individuals/km^2 (95% CI: 0.33–0.96) in 1995 (Williamson and Usongo 1995) to 0.17 individuals/km^2 (95% CI: 0.10–0.31) in the current survey (a decrease of ~70%). However, for a wide-ranging species, such comparisons over longer time spans should be cautiously interpreted.

When compared to other national parks in Cameroon and northwest Central Africa (Table 1), the DFR currently has a low density of forest elephants (0.042 individuals/km^2), comparable to heavily impacted PAs, such as Korup National Park (0.04 individuals/km^2) (Kupsch et al. 2014). Minkébé NP in Gabon, approximately 100 km to the south of the DFR, has been reported to have lost an estimated 78% to 81% of forest elephant over the last decade (2004 to 2014) (Poulsen et al. 2017). Poulsen and colleagues (2017) estimate that in 2004 there was a population of circa 32,851 forest elephants (a density of 3.29 individuals/km^2) in the park compared to just circa 7,370 in 2014 (a density of 0.74 individuals/km^2) based on dung surveys. Minkébé NP (9,973 km^2) is approximately 90% larger than the DFR (5,260 km^2).

Drivers of declines

This catastrophic decline documented in forest elephants is most likely to be due to poaching for the illegal trade in ivory, with two recent ivory seizures of more than 100 tusks each from the town of Djoum just south of the DFR highlighting the continuing intensity of poaching activity[1]. There has been an intensification of illegal wildlife trade-related poaching in recent years throughout the region (Maisels et al. 2013, Abernethy et al. 2013, N'Goran et al. 2017). Regular movements of elephants into and out of the DFR have also been disrupted as roads surround the northern,

[1]https://www.zsl.org/conservation/news/anti-trafficking-officials-in-cameroon-seize-more-than-100-elephant-tusks

Table 1. Forest elephant population density estimates from recent surveys in national parks of Cameroon and northwest Central Africa.

Country	Site and survey	Forest elephant density estimate (individuals/km^2)
Cameroon	DFR 2018 (this study)	0.04 (95% CI: 0.03–0.06)
Cameroon	DFR 2015 (MINFOF and IUCN 2015)	0.08 (95% CI: 0.06–0.10)
Cameroon	DFR–northern sector only 1995 (Williamson and Usongo 1995)	0.56 (95% CI: 0.33–0.96)
Cameroon	DFR–northern sector only (this study with area corresponding to Williamson and Usongo 1995)	0.17 (95% CI: 0.10–0.31)
Cameroon	Lobéké NP (Nzooh et al. 2016a)	0.47 (95% CI: 0.31–0.73)
Cameroon	Nki NP (Nzooh et al. 2016b)	0.18 (95% CI: 0.11–0.29)
Cameroon	Boumba Bek NP (Nzooh et al. 2016b)	0.06 (95% CI: 0.03–0.09)
Cameroon	Campo Ma'an NP (Nzooh et al. 2016c)	0.12 (95% CI: 0.09–0.15)
Cameroon	Korup NP (Kupsch et al. 2014)	0.04 (95% CI: 0.02–0.07)
Cameroon	Mount Cameroon NP (Eno-Nku et al. 2013)	0.27 (95% CI: 0.17–0.45)
Republic of Congo	Noubalé-Ndoki NP (Stokes et al. 2010)	0.55 (95% CI: 0.40–0.75)
Gabon	Minkébé NP (Poulson et al. 2017)	0.74 (95% CI: 0.55–1.00)
Gabon	Lopé NP (Bezangoye and Maisels 2010)	0.92 (95% CI: 0.44–1.41)

western, and some parts of southern and eastern boundaries of the DFR, and increasing settlement which break the connections of contiguous forests to other forested landscapes. Forest elephants are known to avoid crossing unprotected roads in the Congo Basin, and a concern is that, with increasing infrastructure, forest elephants will adopt a 'siege' behavioural response (Blake et al. 2005). The increasing isolation of the DFR's elephant population may be creating negative demographic consequences, which also result in declining numbers. For example, smaller numbers can diminish genetic viability, reduce the demographic resilience of isolated populations, increase competition for food, and cause the breakdown of normal social cohesion within populations (Wittemyer et al. 2007, Blake et al. 2005). The species' ecological role in seed dispersal and maintaining forest clearings would also most likely have diminished (Theuerkauf et al. 2000). Expanding agriculture along the boundaries of the DFR also increases human-elephant conflicts, which may result in elephant injury and mortality. The only contiguous forest corridor that remains is in the south-eastern corner (fig. 1). This corridor needs to be maintained to ensure gene flow across the greater TRIDOM (Tri-National Dja-Odzala-Minkébé transborder forest), which connects DFR with protected areas such as Ngoyla Wildlife Reserve and Nki NP in Cameroon, and Minkébé NP in Gabon and Odzala NP in the Republic of Congo. If further development and settlement along an old logging track in the south-east corner of the DFR occurs as planned, this will also effectively isolate larger vertebrates.

Human activity within the DFR remains pervasive (MINFOF and IUCN 2015). Human signs were found throughout the DFR in this survey with the highest frequency of human signs encountered in the northwest of the DFR (fig. 5). While not all the signs of human activity are directly attributable to hunting or poaching, for example, machete marks and forest camps are also made by ranger patrols and researchers, we presume that areas that contain generally higher encounter rates of human sign, are likely to be experiencing greater hunting or poaching pressure than areas with lower encounter rates of all measured human sign. The frequent presence of humans across a large proportion of the DFR may also be pushing elephants away from key resources, such as swamps, bais, and fruiting trees, with associated stress on populations.

Common drivers of elephant density found by a number of studies include human population density, hunting intensity, weak law enforcement, poor governance, distance to roads and settlements, and proximity to infrastructure (Blom 2005, Blake et al. 2007, Maisels et al. 2013). In this study, areas containing the highest levels of human activity/signs of activity, being closer to significant infrastructure (Hydromekin Dam and Sud-Cameroun Hévéa rubber plantation) and associated human settlements, had the lowest encounter rates of forest elephant dung. The exception to this was around Bouamir Research Station located in the core of the north-west region, but the near permanent presence of ecoguards and visiting researchers may deter poachers and provide a functional refugia protecting them from hunting within this heavily impacted area of the DFR (Farfán 2019).

A proposed standard monitoring protocol for forest elephant of the DFR

Protected area managers should continue to adhere to best practice methods for distance sampling surveys (Hedges 2012). The distance sampling analysis used here with data collected through systematic line transects designed to achieve a desired coefficient of variation in estimates are recommended to periodically assess forest elephant population size and distribution, and trends in these population state variables. The DFR survey will be repeated in 2021. If populations continue to decline, then the survey effort (in transect length) required to achieve a set coefficient of variation would make transect sampling prohibitively inefficient within the DFR.

Conclusion

The documented decline in the elephant population (and great apes, Bruce et al. 2018) is placing significant risk on the Dja Faunal Reserve's World Heritage Site status being downgraded by UNESCO. The Cameroon Government is strengthening mitigating measures through the 2020–2025 Reserve Management Plan. Elephants continue to mostly persevere in the northern part of the DFR where local communities have exerted their traditional rights to collect non-timber forest products and to small-scale subsistence hunting. The DFR Conservation Service has initiated a community partnership agreement on sustainable access to forest resources and to date, these elephant refugia have also been receiving greater law enforcement both in terms of routine patrol coverage and rapid response following alerts from local communities. The southern part of the DFR is much more vulnerable to organised wildlife criminal gangs (OCG) especially from the southern elephant trafficking hub around the town of Djoum, which does not fall within traditional community areas. The presence of traditional subsistence hunters in the northern sector of the DFR may provide a disincentive to OCGs to operate there, compared to the more remote south where they can hunt with relative impunity. The DFR management is implementing a community surveillance network and increasing SMART based patrolling especially along the southern boundary of the DFR with its many exit roads. With improved security and appropriate engagement with local communities and private sector in the region, it is hoped that the remaining elephant population will start to expand across the Biosphere Reserve and numbers gradually increase. The Dja Biosphere Reserve is an integral component of TRIDOM transborder forest which covers 178,000 km^2, or 10% of the Congo Basin rainforest. It offers one of the last remaining opportunities for the long-term conservation of the forest elephant, great apes and other threatened species in the region.

Acknowledgements

We thank the government of the Republic of Cameroon and the Ministry of Forests and Fauna (MINFOF) for their continuing support of this effort as part of their overall programme to protect and manage Cameroon's wildlife. We thank the European Union for supporting this survey through the *Programme de Conservation et*

Utilisation Rationale des Ecosystemes Forestiers en Afrique Centrale 6 (ECOFAC6) project. We thank the late Conservator Hilaire Ndinga of the Dja Biosphere Reserve for his strong support of this study and his collegiality, he will be greatly missed. We thank the Chef d'Antenne of each sector for their on-going support. We thank Zacharie Nzooh Dongmo and Kouamé Paul N'Goran from WWF, Leonard Usongo from IUCN, and Fiona Maisels from WCS for advice on the survey methodology. We thank members of the field teams for all of their contributions to the survey and overcoming adverse conditions. We also sincerely thank Dr Philip Beacon for reviewing the manuscript prior to submission.

References

Abernethy KA, Coad L, Taylor G, Lee ME and Maisels F. 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of Royal Society* B 368 (1625).

Bezangoye A. and Maisels F. 2010. Great ape and human impact monitoring in the Lopé-Waka Exceptional Priority Area, Gabon. Part, 1, pp. 62.

Blake S, Strindberg S, Boudjan P, Makombo C, Bila-Isia I, et al. 2007. Forest elephant crisis in the Congo Basin. *PLOS Biology* 5:945–953.

Blake S. 2005. Central African Forests: Final Report on Population Surveys (2003–2004). WCS for the CITES/MIKE (Monitoring the Illegal Killing of Elephants) program. Wildlife Conservation Society, New York. pp. 122.

Blanc J. 2008. *Loxodonta africana*. The IUCN Red List of Threatened Species 2008: e.T12392A3339343. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T12392A3339343.en. [Downloaded 19 May 2020].

Blom A, Van Zalinge R, Heitkönig IM and Prins HH. 2005. Factors influencing the distribution of large mammals within a protected central African forest. *Oryx*, 39 (4) pp. 381–388.

Brittain S. 2013. A rapid assessment of the status of the status and distribution of *Loxodonta cyclotis* in South East Cameroon. MSc thesis. https://www.iccs.org.uk/wp-content/thesis/consci/2013/Brittain.pdf [Accessed 20 July 2020].

Bruce T, Ndjassi C, Fowler A, Ndimbe M, Fankem O, Mbobda RBT, Kobla A, Puemo FAW, Amin R, Wacher T, Grange-Chamfray S and Olson D. 2018. Faunal inventory of the Dja Faunal Reserve, Cameroon—2018. Unpublished Report. Ministry of Forests and Fauna (MINFOF), Zoological Society of London–Cameroon Country Programme, African Wildlife Foundation, Yaoundé, Cameroon, pp. 62.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL and Thomas L. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford.

Djuikouo MNK, Doucet JL, Nguembou CK, Lewis SL and Sonké B. 2010. Diversity and above ground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. *African Journal of Ecology* 48(4):1053–1063.

Djuikouo MNK, Doucet JL, Nguembou CK, Lewis SL and Sonké B. 2010. Diversity and above ground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. *African Journal of Ecology*, 48(4), pp. 1053–1063.

Eno-Nku M. 2013. Large mammal surveys of the Mt. Cameroon National Park, SW Region. WWF CCPO Coastal Forest Programme, Limbe, Cameroon pp. 27.

Farfán MA, Aliaga-Samanez A, Olivero J, Williams D, Dupain J, Guian Z and Fa JE. 2019. Spatial modelling for predicting potential wildlife distributions and human impacts in the Dja Forest Reserve, Cameroon. *Biological Conservation* 230, pp. 104–112.

Fowler A. 2019. Holistic approaches to protecting a pangolin stronghold in Central Africa', in Challender DW, Nash HC and Waterman C. (eds.) *Pangolins: Science, Society and Conservation*. Academic Press, pp. 427–439.

Hedges S. 2012. *Monitoring elephant populations and assessing threats*. Universities Press, India, pp. 346.

Kupsch D, Serge BK, Waltert M, Chia NB, Brice BCG, Abdoulaye D and Kalagan D. 2014. Biodiversity, carbon stock and market value assessment for the SGSOC project area, Southwest region, Cameroon, pp. 46.

Maisels F, Strindberg S, Blake S, Wittemyer G, Hart J, Williamson EA, Aba'a R, Abitsi G, Ambahe RD, Amsini F and Bakabana PC. 2013. Devastating decline of forest elephants in Central Africa. *PLOS ONE* 8 (3).

MINFOF and IUCN 2015. Caractérisation de la population de grands et moyens mammifères dans la Reserve de Faune du Dja: Potentiel et menaces. Ministry of Forests and Wildlife, IUCN, Yaoundé, Cameroon, pp. 31.

Muchaal PK and Ngandjui G. 1999. Impact of village hunting on wildlife populations in the western Dja Reserve, Cameroon. *Conservation Biology* 13 (2), pp. 385–396.

Ngatcha L. 2019. Contribution a la preservation de la biodiversite par la mise on oeuvre des activites generatrices de revenus (AGRs) au profit des populations riveraines de la reserve de la biosphere du Dja. Memoire presente en vue de l'obtention du Diplome de Master Professional en Sciences Forestieres. Universite de Yaounde´ 1, Cameroon.

N'Goran KP, Nzooh Dongmo ZL and Le-Duc yeno S. 2017. Summary report on WWF biomonitoring activities in FY15 and FY16: status of elephant and great apes in Central Africa priority sites. Annual Technical Report. WWF Regional Office for Africa–Yaoundé hub, Yaoundé, pp. 34.

Nzooh Dongmo ZL, N'Goran KP, Ekodeck H, Kobla S, Sombambo M, Famegni S and Mengamenya A. 2016a. Les populations de grands et moyens mammifères dans le segment lobéké du paysage tri-national de la sangha. Rapport Technique MINFOF-WWF, pp. 103.

Nzooh Dongmo ZL, N'Goran KP, Etoga G, Belinga JP, Fouda E, Dandjouma M and Dongmo P. 2016b. Les populations de grandes et moyens mammifères dans le segment Cameroun du paysage TRIDOM (forêt de Ngoyla-Mintom, et PN Boumba Bek et PN Nki et leurs zones périphériques). WWF CCPO-MINFOF, Yaounde, Cameroon. pp. 101.

Nzooh Dongmo ZL, N'Goran KP, Fondja C and Nkono J. 2016c. Evaluation de la dynamique des populations de grands et moyens mammiferes dand le domaine forestier permanent de l'unite technique operationnelle Campo Ma'an. pp. 103.

Poulsen JR, Koerner SE, Moore S, Medjibe VP, Blake S, Clark CJ, Akou ME, Fay M, Meier A, Okouyi J and Rosin C. 2017. Poaching empties critical Central African wilderness of forest elephants. *Current Biology* 27(4), pp. 134–135.

Stokes EJ, Strindberg S, Bakabana PC, Elkan PW, Iyenguet FC and Madzoké B. 2010. Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. *PLOS ONE* 5(4):e10294. https://doi.org/10.1371/journal.pone.0010294.

Thouless CR, Dublin HT, Blanc JJ, Skinner DP, Daniel TE, et al. 2016. African elephant status report 2016: an update from the African elephant database. Occasional Paper Series of the IUCN Species Survival Commission, No. 60 IUCN / SSC Africa Elephant Specialist Group. IUCN, Gland, Switzerland. vi + 309pp. Available: https://portals.iucn.org/library/node/46878. [Accessed June 30 2020].

Tchamba MN. 1992. Defecation by the African forest elephant (*Loxodonta africana cyclotis*) in the Santchou Reserve, Cameroon. *Mammalia* 56, pp. 155–158.

Theuerkauf J, Waitkuwait W, Guiro Y, Ellenberg H and Porembski S. 2000. Diet of forest elephants and their role in seed dispersal in the Bossematie Forest Reserve, Ivory Coast. *Mammalia* 64. 10.1515/mamm.2000.64.4.447.

Turkalo AK, Wrege PH and Wittemyer G. 2017. Slow intrinsic growth rate in forest elephants indicates recovery from poaching will require decades. *Journal of Applied Ecology* 54(1), pp. 153–159.

UNEP, CITES, IUCN and TRAFFIC. Nellemann C, Formo RK, Blanc J, Skinner D, Milliken T, De Meulenaer T. (Eds). *Elephants in the Dust*, A Rapid Response Assessment by UNEP: GRID-Arendal, Birkeland Trykkeri AS, Norway.

UNESCO 2018. Dja Faunal Reserve. Available at https://whc.unesco.org/en/list/407/ [Accessed 9 Aug. 2018].

Williamson L and Usongo L. 1995. Recensement des populations de primates et inventaires des grands mammifères. II Recensement des éléphants, gorilles et chimpanzés dans la Réserve de Faune du Dja (Cameroun). Rapport technique. Projet Ecofac, Agreco. pp. 47.

Wittemyer G, Getz WM, Vollrath F and Douglas-Hamilton I. 2007. Social dominance, seasonal movements, and spatial segregation in the African elephant: A contribution to conservation behavior. *Behavioral Ecology and Sociobiology* 61:1919–1931.

Assessing the Status of Great Apes in the Dja Faunal Reserve Using Distance Sampling and Camera-trapping

Rajan Amin[1], Oliver Fankem[2], Oum Ndjock Gilbert[3], Tom Bruce[2], Malenoh Sewuh Ndimbe[2], Anne Stephanie Kobla[2], David Olson[2] and Andrew Fowler[2]

[1]*Zoological Society of London, Regent's Park, London, UK*
[2]*Zoological Society of London – Cameroon, Yaoundé, Cameroon*
[3]*Ministry of Forestry and Wildlife, Yaoundé, Cameroon*

Abstract: Central chimpanzee (*Pan troglodytes troglodytes*) and western lowland gorilla (*Gorilla gorilla gorilla)* populations are rapidly declining due to habitat loss, poaching, and disease epidemics. We estimate the abundance and distribution of both species in the 5,260-km² Dja Faunal Reserve, a World Heritage Site in Cameroon. We compare with previous site estimates and with other great ape population estimates from the region. We also document illegal activities in the reserve. A total of 298.2 km of line transects (283) were completed using the standing-crop nest counts method, with a further 1,681.4 km of recces recording human signs. We estimated a chimpanzee nest mean decay rate of 95.4 days (SE = 4.45) and a combined great ape nest mean decay rate of 96.6 days (SE = 2.87). Gorilla population estimates of 0.38 (95% CI = 0.28–0.53) individuals/km² and 2,004 (95% CI = 1,447–2,774) individuals confirmed a significant decline since the 1995 survey in the north-central part of the reserve (a 57% decline for the area) and the reserve-wide survey in 2015 (a 70% decline). The population was also much lower than in most other protected areas in the region. The chimpanzee population with an estimated 0.53 (95% CI = 0.38–0.73) individuals/km² and 2,785 (95% CI = 2,020–3,839) individuals also revealed a marked decline of 34% and 23% compared to the 1995 and 2015 surveys, respectively. Human activity occurred throughout, with the highest levels encountered in the northwest of the reserve. Occupancy estimates from four 40 camera-trap grid surveys showed great apes persisting mainly in the north-eastern part of the reserve where Cameroon's Ministry of Forestry and Wildlife (MINFOF) is considering a community support partnership agreement on sustainable access to forest resources, along with community surveillance networks. The reserve management is also increasing law-enforcement patrols across the reserve. Our findings also inform conservation strategies for great apes across the TRIDOM landscape across Cameroon, Gabon and the Republic of Congo.

Key Words: *Pan troglodytes troglodytes*, *Gorilla gorilla gorilla*, abundance, density, distribution, Dja Biosphere Reserve

---

Introduction

Central African populations of great apes are in serious decline (IUCN 2014). The central chimpanzee *Pan troglodytes troglodytes* is listed as Endangered on the IUCN Red List (Humle *et al*. 2016) and the western lowland gorilla *Gorilla gorilla gorilla* is classified as Critically Endangered (Maisels *et al*. 2018). The major threats to great apes are the direct and synergystic effects of poaching, habitat loss, and disease (Ebola, in particular) (Strindberg *et al*. 2018).

Reliable estimates of population size, density, and distribution, and trends in these at regional and local scales are required by governments and protected area managers to take informed management action. An adequate understanding of the anthropogenic and ecological factors that influence the distribution of these species within their environment is also vital for adapative mangement strategies (Stokes *et al*. 2010; Strindberg *et al*. 2018). Estimates of the regional great ape population are useful for monitoring overall status and trends (Kühl *et al*. 2008; N'Goran *et al*. 2017). Conservation landscapes (that is, a network of protected areas (PAs) separated and surrounded by alternative land use) provide an effective framework for conservation planning and actions (Gardner *et al*. 2007; Stokes *et al*. 2010). Keeping track of great ape populations in individual PAs is needed to assess their efficacy as source populations and refugia (Stokes *et al*. 2010; N'Goran *et al*. 2017). Regular surveys can provide early warning signs of precipitous declines (Stokes *et al*. 2010). In Minkébé National Park (NP), Gabon, for example, great ape populations declined by about 98% in 1998–2000 compared to pre-1994 estimates, likely due to Ebola outbreaks (Huijbregts *et al*. 2003).

Here we assess the 2018 status of the central chimpanzee and western lowland gorilla (along with forest elephants, Amin *et al*. 2020) in the Dja Faunal Reserve (DFR) in south-east Cameroon, a World Heritage Site (UNESCO 2022; the DFR and its buffer zone constitute the Dja Biosphere Reserve). The DFR's extant megafauna is considered one of the reserve's Outstanding Universal Values (UNESCO 2022). Our main objective was to to assess the status of great apes in the DFR in order to provide baseline data for the adaptive management of the reserve and the TRIDOM landscape (across Cameroon, Gabon and the Republic of Congo).

Methods

Study area

The DFR is the largest protected area (5,260 km²) in Cameroon (3°08'5"N, 13°00'00"E, Fig. 1). Approximately 80% of the DFR is bordered by the Dja River (S, W, and N), which forms a natural barrier and provides some limited protection, although crossing in canoes is common. The biosphere reserve outside the formal DFR largely comprises Forestry Management Units (FMUs), settlements, and community forests. There is also a 450-km² rubber plantation and a hydroelectric dam on the Dja River in the western buffer zone, both adjacent to the DFR boundary (Fig. 1). There are no recent reliable estimates of the human population surrounding the DFR. Estimates suggest 19,500 village inhabitants in the buffer zone and a further 30,000 in the wider area directly surrounding this zone (Fowler 2019; Ngatcha 2019). Expanding settlements and transport corridors to the south and east of the DFR are rapidly clearing natural forest and may soon result in isolation of the DFR (Global Forest Watch 2022).

The DFR is a relatively flat plateau of round-topped hills and ranges at elevations of 600–800 m asl (MINFOF and IUCN 2015). The topography is mainly shallow valleys on either side of a ridgeline that cuts through the DFR east to west (MINFOF and IUCN 2015). Swamp habitat is common on the floor of valleys. Tributaries throughout the DFR flow into the Dja River (UNESCO 2022; MINFOF and IUCN 2015). The three major forest types in the DFR are terra firma mixed-species forest, mono-dominant forest, where *Gilbertiodendron dewevrei* is the most abundant species, and periodically flooded forest (Djuikouo *et al*. 2010). The DFR supports a rich, medium-to-large mammal fauna. In addition to the two species of great apes (central chimpanzee and western lowland gorilla), the biosphere reserve is an important landscape for the Critically Endangered African forest elephant (*Loxodonta cyclotis*). The DFR has a diverse community of forest ungulates and three threatened pangolins, namely the black-bellied pangolin (*Phataginus tetradactyla*): Vulnerable, the white-bellied pangolin (*Phataginus tricuspis*): Endangered, and the giant pangolin (*Smutsia gigantea*): Endangered.

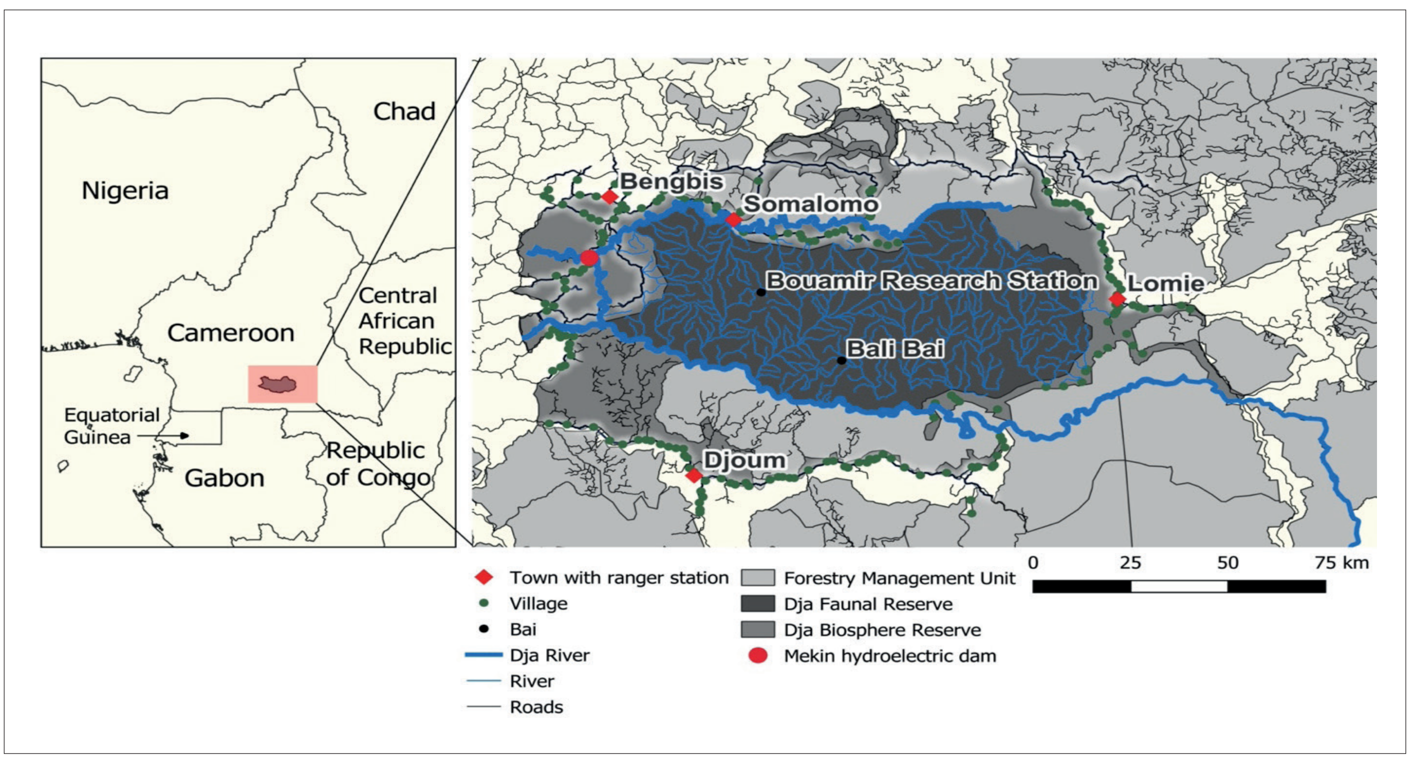


Figure 1. Location of the Dja Faunal Reserve, Cameroon.

There are four main seasons: the long rains (August–November); the longer dry season (November–March); the short rains (March–May); and a shorter dry season (June–July) (MINFOF and IUCN 2015). In the dry season there is, on average, <100 mm of rainfall out of the mean annual rainfall of approximately 1,570 mm (UNESCO 2022). The mean annual temperature is 23.5°C–24.5°C. The maximum temperature is reached in February and the minimum in July (MINFOF and IUCN 2015).

Poaching in and around the DFR is largely through non-traditional means, such as guns and wire snares. Much of the poaching supplies the commercial and illegal wildlife trade (UNESCO 2022). Other significant threats to biodiversity around the DFR include logging, agricultural clearance for subsistence crops and commercial crops such as pineapple, loss of the last remaining large forested corridor to the Ngoyla-Mintom forest block if the south-eastern road is developed, rubber plantations (for example, Sud-Cameroun Hévéa) and the associated demands for bushmeat, and the ecological impacts of existing (the Hydro Mekin) and planned hydroelectric dams (MINFOF and IUCN 2015; UNESCO 2022).

Cameroon's Ministry of Forestry and Wildlife (MINFOF) is responsible for the management of the DFR and the Dja Biosphere Reserve. The DFR has been divided into four management sectors with a base responsible for each sector in the nearest town: Lomié (East Sector), Djoum (South Sector), Meyomessala (West Sector), and Somalomo (North Sector).

Estimating great ape population densities and abundance

Central chimpanzee and western lowland gorilla population densities and abundances were estimated with distance sampling carried out through nest-based transect surveys (White and Edwards 2000), as part of a megafauna inventory. We used a standardized survey protocol to provide robust estimates for monitoring changes in the populations over the long-term (Kühl *et al*. 2008).

Line transect surveys

We first estimated the total length of transect we would need to achieve a desired precision in the density estimates for the great apes. We used the following equation (Buckland *et al.* 2001) and data from a previous transect survey (MINFOF and IUCN 2015).

$$L = (b \div \{cv_t(\widehat{D})\}^2).(L_o \div n_o),$$

where L = estimate of total transect-line length to be surveyed to achieve target coefficient of variation; b = dispersion factor (set to a default value of 3 as per Buckland *et al*. 2011); cv_t = target coefficient of variation of density estimate $\widehat{D}$; L_o = total length of all transects (from previous survey); and n_o = total number of observations on all transects (from previous survey). We estimated that 286 km of transects were needed to achieve a 10% coefficient of variation (based on the 2015 survey comprising 612 km of transects; MINFOF and IUCN 2015).

The survey, therefore, consisted of 286 one-km transects systematically positioned with orientation east to west to align transects along potential great ape density gradients, as the majority of watercourses in the DFR run north–south (Fig. 2). We conducted the survey at the end of the dry

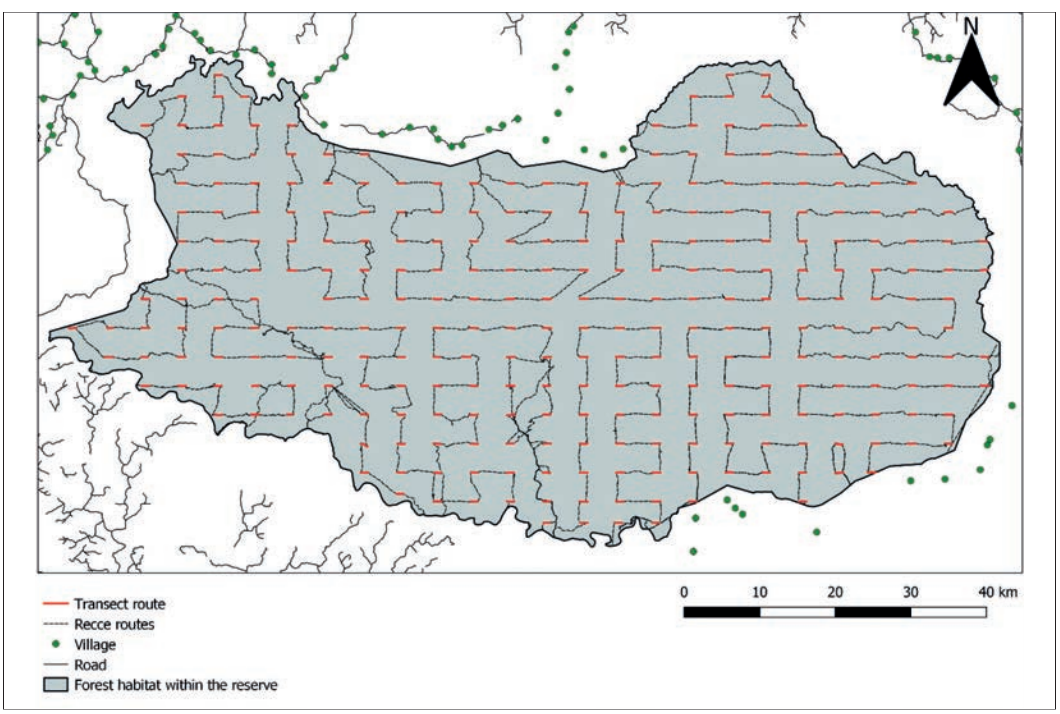


Figure 2. Locations of line transects and the associated routes between them (recces), systematically covering the entire Dja Faunal Reserve, Cameroon.

season between 4 April 2018 and 3 June 2018 using eight teams. Each team had two observers, one looking up for great ape nests, while the other looking at ground level for great ape nests, as well as human sign and other signs on the ground, such as elephant dung. Each team had two data recorders as well as four porters who walked at a distance behind the team and were responsible for carrying supplies and camping equipment.

The observers were trained in identifying and aging great ape nests. Nest-aging categories were based on the system proposed by Tutin and Fernandez (1984) and Kühl *et al.* (2008), namely: New: <24 hours old, with fresh faeces or urine under the nest; Fresh: vegetation green or not wilted (up to a week old); Recent: vegetation dry and changing colour (up to two weeks old); Old: vegetation dead, but nest still intact (>2 weeks); Decayed: nest beginning to disintegrate, holes visible in structure.

We used the approach of Kühl *et al.* (2008) to record nests. Great apes tend to build nests in groups. Once a great ape nest was detected from the transect, an area with a radius of 50 m was searched around the nest for other nests of the same age class. If another nest of the same age was found within 50 m, the search would begin again from that point. When no more nests within 50 m were found, the search was ended and perpendicular distances to each individual nest from the transect line were measured to the nearest cm and recorded along with the nest age category. Gorilla and chimpanzee nests were distinguished based on nest characteristics, shed hair, feces, odor and tracks. However, there is always a possibility that some of the tree nests were misassigned to the nest-builder.

Estimation of great ape nest decay rates

The standing-crop nest-count method used in this study, where all nests encountered were recorded in a distance-sampling framework, requires a nest production rate and a nest decay rate to convert nest density to population density of weaned apes (Kühl *et al*. 2008). Between April 2018 and September 2018, 119 fresh great ape nests were located and carefully marked across the study area. At the end of the study, the marked nests were checked to see which had disappeared and which were still visible. The data on state of the nests and time since nest construction were analyzed using logistic regression, with distribution left-truncated at $x = 0$ and rescaled, in R software package (R Development Core Team 2019; Laing *et al*. 2003) to estimate central chimpanzee and western lowland gorilla nest mean decay rates and their variance. For the production rate, we used 1.09 great ape nests per day (Morgan *et al*. 2006).

Recording human activity

The survey also recorded sign of human activity, both along line transects and during the approximately 3.8 km walk (hereafter, recce) between transects. Types of human sign recorded were trails, snares, signs of passage, machete cuts, shelters and camps, firearms and ammunition, timber exploitation, direct encounters with people, and gunshots heard. Camps were defined as any structure used for sleeping within the forest evident from cleared ground and the presence of a fire pit or structures. However, as a caveat, it is impossible to differentiate poacher's trails and cuts from those of ecoguards and NGO work within the DFR.

When combined with the information on the distribution of a species, human activity data can provide insights into the role of hunting pressure and human disturbance in diminishing wildlife populations. This also provides baseline data against which the effectiveness of management activities can be measured.

Transect and recce data management

All data were recorded using the Spatial Monitoring and Reporting Tool – Ecological Records (SMART-ER https://smartconservationtools.org) on Cedar Personal Digital Assistants (PDAs) and also in notebooks so as to have duplicate copies of the data. A Global Positioning System (GPS) point with date and time was also taken for each observation and recorded in the notebook.

The data were exported from the PDA units into a SMART desktop application. We checked all data entries in SMART against their paper counterparts to ensure that they were consistent with each other. We then exported the clean data in SMART into Excel and converted the data into a suitable format for analysis in *Distance 7.2* (Thomas *et al*. 2010; http://distancesampling.org/distance). We did not group nests so as to avoid potential bias in group size estimates due to the possibility of not all nests in a group being found and with ground nests likely to decay faster. This, however, may lead to some underestimate of variance. We considered models of the detection function with the half-normal, hazard-rate, and uniform key functions with cosine, simple polynomial, and Hermite polynomial adjustment terms for each species and for the combined great ape line-transect data. Adjustment terms were constrained, where necessary, to ensure the detection function was monotonically decreasing. We selected among candidate models by comparing AIC (Akaike Information Criterion) values. We also checked for model fit to the data using the Kolmogorov-Smirnov test provided by *Distance*. All maps were produced using the Quantum Geographic Information System (QGIS Development Team 2019).

Estimating occupancy

We used camera-trap data from standardized grids deployed across the management sectors of DFR to assess the distribution of central chimpanzees and western lowland gorillas. The camera-trap surveys were conducted to provide replicable baseline information on medium-to-large mammal species, including great apes, that occur in the DFR.

Camera-trap surveys

Four camera-trap grids were setup in the North (management) Sector between January 2018 and May 2018 (38 camera-traps); East Sector between January 2018 and May 2018 (39 camera-traps); South Sector between August 2018 and December 2018 (39 camera-traps); and West Sector between October 2019 and February 2020 (35 camera-traps) (Fig. 3). The West Sector grid was deployed in 2019 due to limited resources in difficult conditions. Bushnell Trophy Aggressor Low Glow camera-traps (Bushnell Outdoor Products, Kansas, USA) were placed at each locality with a two-km spacing between each camera-trap (Ahumada *et al*. 2011). Each grid operated long enough to achieve at least 1,000 camera-trap days of sampling effort (O'Brien *et al*. 2003). Global Positioning System receivers were used to locate the grid points. A single camera was placed at a height of about 30 cm, as close to the grid sampling point as possible, with a consistent and unobstructed field of view to capture lateral full-body images of small to medium-sized mammals. The cameras were programmed to take three images per trigger.

We modeled the effect of 'management sector' on central chimpanzee and western lowland gorilla occurrence. We did not have complete and up-to-date datasets on potential indicators of hunting pressure or disturbance such as distance to villages to investigate in this study. We assumed detection probability was constant across the four camera-trap grids, which were deployed using a standardized protocol. We constructed a detection / non-detection history, using a five-day period as the sampling occasion, for each camera-trap site. We performed Bayesian occupancy analysis implemented in *JAGS 4.3.0* (Plummer 2003), accessed through *R 3.6.0* (R Code Development Team 2019), using the package *RJAGS 3-10* (Plummer 2014). We ran three Markov Chain Monte Carlo (MCMC) chains with 110,000 iterations, a burn-in of 10,000 and a thinning rate of 10. This combination of values ensured an adequate number of iterations to characterize the posterior distribution of the modeled occupancy estimate. We checked for chain convergence with trace plots and the Gelman-Rubin statistic (Gelman *et al*. 2004), R-hat, which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman and Hill 2006). We assessed model fit using Freeman-Tukey discrepancy (Kery and Schaub 2012). We calculated the P value, i.e., the probability of obtaining a discrepancy at least as large as the observed discrepancy if the model fits the data. Values near 0.5 indicate a good fit; values above 0.9 or below 0.1, a poor fit.

Results

We traversed 283 transects, totaling 298.2 km. Two transects had to be abandoned due to flooding. One was abandoned as part of it was in a settlement. Recces covered a distance of 1,681.4 km (Fig. 2). We recorded 276 central chimpanzee nests and 138 western lowland gorilla nests suitable for distance analysis. However, as noted in

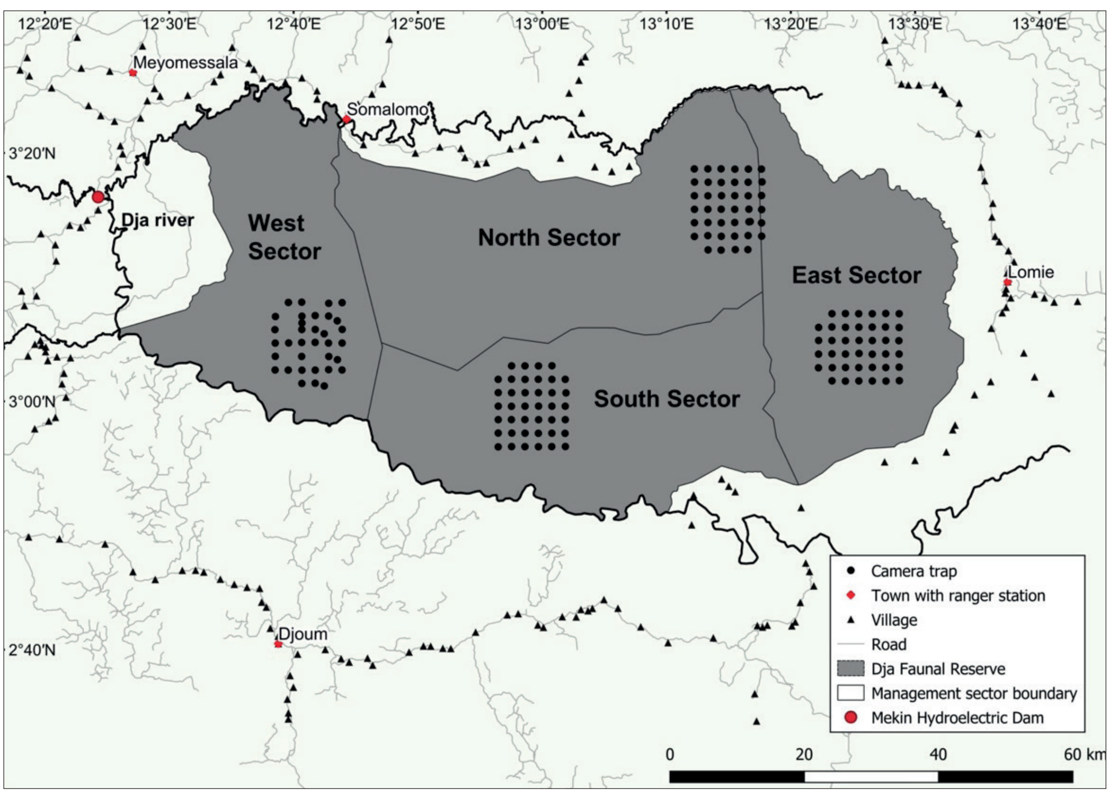


Figure 3. Location of camera-trap grids in the North, East, South and West Management Sectors in the Dja Faunal Reserve, Cameroon.

the methods, there is a possibility that some of the tree nests were misassigned to the nest-builder.

Density and abundance

We estimated a central chimpanzee nest mean decay rate of 95.4 days (SE = 4.45, 95% CI = 86.67–104.13). There were insufficient western lowland gorilla samples to estimate a nest decay rate, so we estimated the combined great ape nest mean decay rate at 96.6 days (SE = 2.87, 95% CI = 90.97–102.23).

Exploratory analyses revealed fewer detections close to the line (0–3m) than expected for the central chimpanzee. This was most likely due to observers missing nests on trees above their heads. We, therefore, analyzed this data using left truncation at 3 m with rescaling. The hazard-rate model with no adjustments minimized AIC for the rescaled central chimpanzee data right truncated to 10 m (172 observations). The Kolmogorov-Smirnov goodness of fit P value (0.63) indicated a good fit. The central chimpanzee nest density estimate was 55.04 (95% CI = 40.44–74.91) nests/km² and the average detection probability was 0.52 (95% CI = 0.43–0.63) (Fig. 4). Effective strip width was 5.24 (95% CI = 4.34–6.33) m. The central chimpanzee density was estimated as 0.53 (CV = 16.45%; 95% CI = 0.38–0.73) individuals/km² with a population estimate of 2,785 (95% CI = 2,020–3,839) individuals.

The half-normal model minimized AIC for the western lowland gorilla line transect data truncated to 12 m (127 observations). The Kolmogorov-Smirnov goodness of fit P value was 0.58. Western lowland gorilla nest density estimate was 40.1 (95% CI = 29.1–55.23) nests/km² and detection probability was 0.44 (95% CI = 0.39–0.5) (Fig. 5). Effective strip width was 5.31 (95% CI = 4.69–6.01) m. Western lowland gorilla density was estimated as 0.38 (CV = 16.66%; 95% CI = 0.28–0.53) individuals/km² with a population estimate of 2,004 (95% CI = 1,447–2,774) individuals.

The hazard model minimized AIC for the combined great ape line transect data truncated to 10 m (297 observations). The Kolmogorov-Smirnov goodness of fit P value was 0.15. Combined great ape nest density estimate was 96.57 (95% CI = 75.81–123.01) nests/km² and detection probability was 0.52 (95% CI = 0.45–0.6). Effective strip width was 5.16 (95% CI = 4.47–5.95) m. Great ape density was estimated as 0.92 (CV = 12.72%; 95% CI = 0.72–1.18) individuals/km² with a population estimate of 4,825 (95% CI = 3,672–6,188) individuals.

Occupancy

The total sampling effort was 14,082 camera-trap days: 3,647 trap days in the North Sector; 3,787 trap days in the East Sector; 3,689 trap days in the South Sector; and 2,959 trap days in the West Sector. Thirteen camera-traps failed to function (<30 days). Western lowland gorilla occupancy (ψ) was significantly higher in the North Sector (Fig. 6, posterior probability: ψ North Sector > ψ East Sector = 1; ψ North Sector > ψ South Sector = 1; ψ North Sector > ψ West Sector = 1). The estimated detection probability was 0.06 (95% CI = 0.04-0.08). Central chimpanzee occupancy was also significantly higher in the North Sector (posterior probability: ψ North Sector > ψ East Sector = 1; ψ North Sector > ψ South Sector = 0.95; ψ North Sector > yWest Sector = 0.83). The estimated detection probability for the central chimpanzee was 0.09 (95% CI = 0.08-0.11).

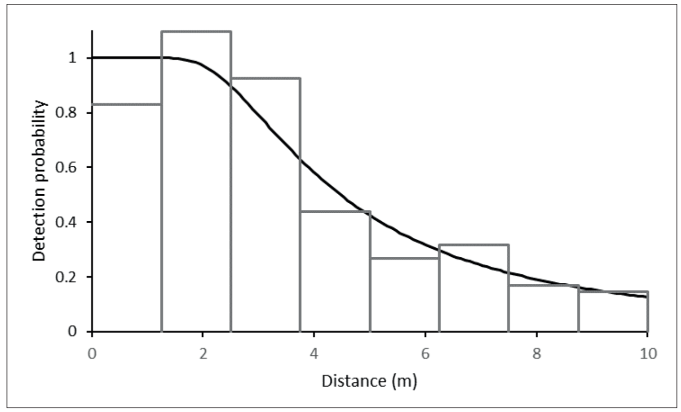


Figure 4. Hazard-rate detection function fit to the perpendicular distances of central chimpanzee nests from the line transect in the Dja Faunal Reserve, Cameroon (2018). The histograms of the observed distances are also shown.

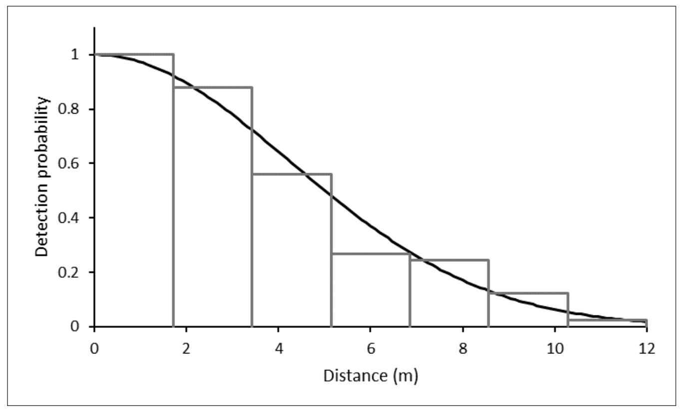


Figure 5. Half-normal detection function fit to the perpendicular distances of western lowland gorilla nests from the line transect in the Dja Faunal Reserve, Cameroon (2018). The histograms of the observed distances are also shown.

Human activity

A total of 359 human signs were encountered on the transects and 1,309 signs on recces resulting in an overall encounter rate of 0.84 sign/km. The most prevalent signs encountered were established trails (0.27/km), machete cuts (0.17/km), and signs of passage, such as marked trees and bent sticks (0.15/km). Among the signs directly attributable only to poaching, the most prevalent was spent firearm ammunition (0.11/km), followed by snares (0.06/km). The distribution of human signs encountered on recces and transects is shown as an encounter rate (signs/km) density contour map (Fig. 7).

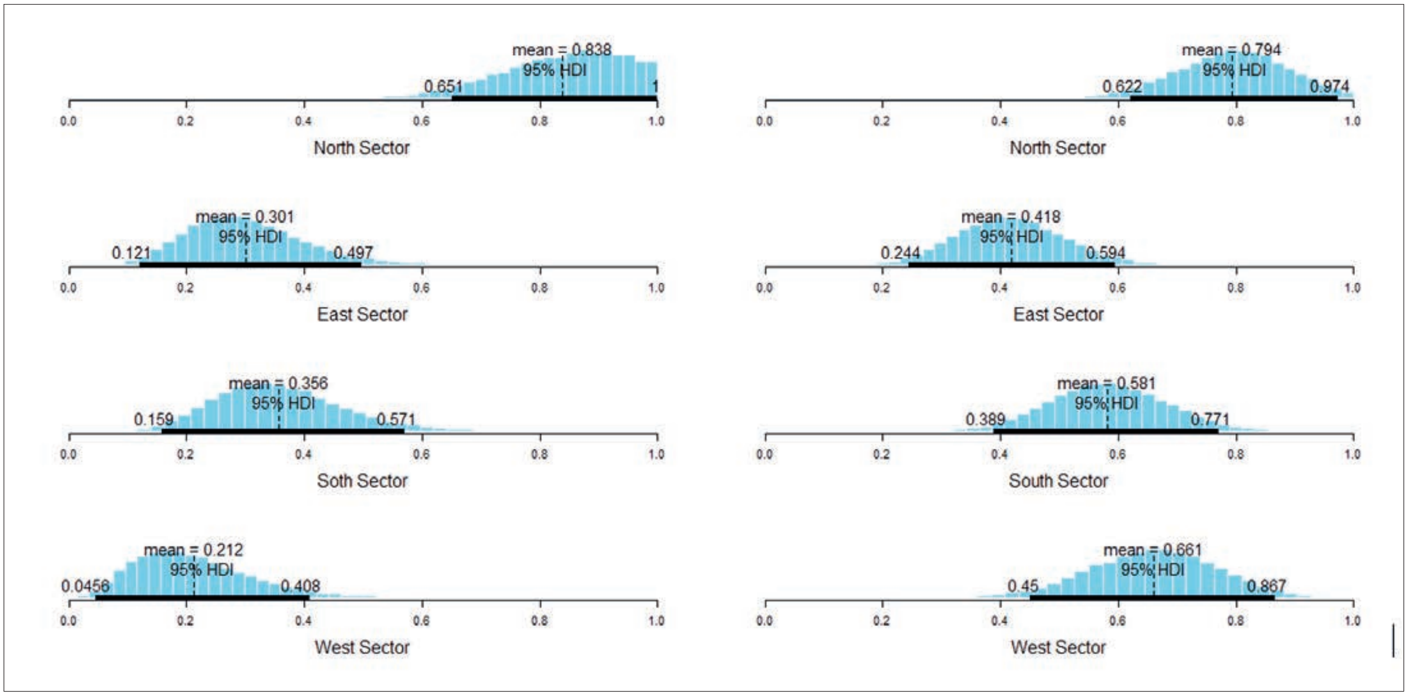


Figure 6. Western lowland gorilla (left) and central chimpanzee (right) occupancy posterior distributions for North, East, South, West management sectors, Dja Faunal Reserve, Cameroon. The 95% highest posterior density "credible" interval (HDI), the Bayesian equivalent to 95% confidence interval, are also shown.

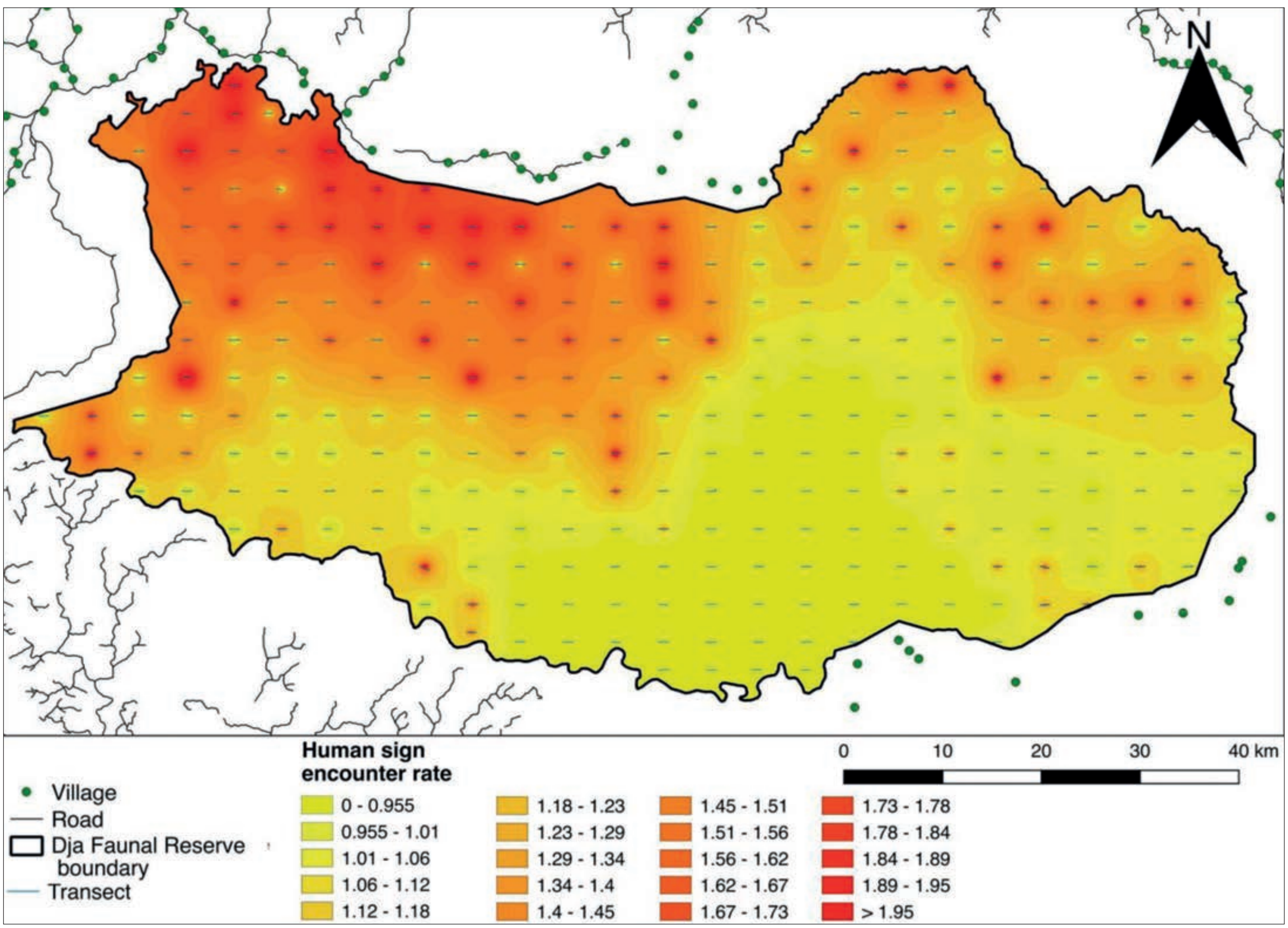


Figure 7. Distribution of signs of human activity (signs/km) within the Dja Faunal Reserve, Cameroon.

Discussion

This reserve-wide survey confirms that great ape populations within the DFR have diminished markedly over recent years in comparison to two earlier surveys by Williamson and Usongo (1995) and MINFOF and IUCN (2015) (Table 1). The Williamson and Usongo (1995) survey was conducted mainly in the north-central part of the reserve. For comparison, we analyzed our study transects that were located in the 1995 survey area. Central chimpanzees in the sampled area have declined by ~34%, and the western lowland gorillas by ~57% (Table 1). Compared to the 2015 inventory, the western lowland gorilla also showed the greater decline in estimated density, with more than a threefold decrease (Table 1). Survey methodology differences could, however, be magnifying the apparently sharp decline. Gorillas are thought to be less susceptible to anthropogenic impacts than chimpanzees when appropriate management is applied (Strindberg *et al*. 2018). An Ebola outbreak causing the major decline in western lowland gorillas in the DFR is not supported, as there have been no reports of rangers finding large numbers of dead animals and the impact of the disease would be expected to cause a similar decline in the central chimpanzee population. Western lowland gorilla numbers in the DFR are low compared to those in other protected areas of the region. The density of western lowland gorillas reported in Noubalé-Ndoki National Park, for example, is approximately three times higher (Table 1), and densities as high as 5.4 individuals/km² have been reported in Odzala National Park in the Republic of Congo (Bermejo 1999). More recent surveys in the nearby Mengame Gorilla Sanctuary (Kom-Mengame Wildlife Complex) and the Goualougo Triangle reported densities of 2.53 individuals/km² (Halford *et al.* 2003) and 1.28 individuals/km² (Sanz *et al*. 2007), respectively. Densities of 1.61 and 0.95 have also been reported from Boumba Bek National Park and Nki National Park in Cameroon, respectively (Nzooh *et al*. 2016b).

The DFR has the second highest reported density of central chimpanzees in Cameroon (Table 1), yet this is approximately half the density reported in Noubalé-Ndoki National Park, Republic of the Congo (Stokes *et al*. 2010). We are not able to conclude whether this difference represents ecological differences in forest composition or historic and current human activities such as hunting and other forest-based resource use between the two sites.

Drivers of declines

Human activity within the DFR remains pervasive (MINFOF and IUCN 2015). Human signs were found throughout the DFR in this survey with the highest frequency of human signs encountered in the northwest of the DFR. When compared to the 2015 inventory (MINFOF and IUCN 2015), the pattern is broadly similar with the northwest of the reserve experiencing the highest intensity of human activity. The main difference between the 2015 and 2018

Table 1. Central chimpanzee and western lowland gorilla population density estimates from recent surveys in protected areas of Cameroon and northwest Central Africa.

Country	Site and survey	Central chimpanzee density estimate (individuals/km²)	Western lowland gorilla density estimate (individuals/km²)
Cameroon	DFR 2018 (this study)	0.53 (95% CI = 0.38–0.73)	0.38 (95% CI = 0.28–0.53)
Cameroon	DFR 2015 (MINFOF and IUCN 2015)	0.69 (95% CI = 0.52–0.91)	1.26 (95% CI = 0.95–1.67)
Cameroon	DFR – north-central area 1995 (Williamson and Usongo 1995)	0.79 (95% CI = 0.6–1.14)	1.71 (95% CI = 1.02–2.86)
Cameroon	DFR – north-central area only (this study with area corresponding to Williamson and Usongo 1995)	0.52 (95% CI = 0.3–0.89)	0.74 (95% CI = 0.4–1.38)
Cameroon	Lobéké NP (Nzooh *et al*. 2016a)	0.29 (95% CI = 0.18–0.46)	1 (95% CI = 0.64–1.56)
Cameroon	Nki NP (Nzooh *et al*. 2016b)	0.16 (95% CI = 0.09–0.26)	0.95 (95% CI = 0.62–1.44)
Cameroon	Boumba Bek NP (Nzooh *et al*. 2016b)	0.24 (95% CI = 0.15–0.39)	1.61 (95% CI = 1.41–2.27)
Cameroon	Campo Ma'an NP (Nzooh *et al*. 2016c)	0.26 (95% CI = 0.20–0.35)	0.22 (95% CI = 0.14–0.33)
Cameroon	Korup NP (Kupsch *et al*. 2014)	0.13 (95% CI = 0.07–0.24) **Pan troglodytes ellioti*	Not detected
Cameroon	Mount Cameroon NP (Eno-Nku *et al*. 2013)	0.67 (95% CI = 0.41–1.11)	Not detected
Republic of Congo	Noubalé-Ndoki NP (Stokes *et al*. 2010)	1.03 (95% CI = 0.61–1.71)	1.02 (95% CI = 0.59–1.77)

surveys is what appears to be a reduction in human signs in the South Sector. This is most likely due to the establishment of a permanent river ecoguard post in proximity to Bali Bai (see Fig. 1). There also appears to be increased human signs around the research station at Bouamir, which is most likely due to an increase in station activities. While not all the signs of human activity are directly attributable to hunting or poaching, for example, machete marks and forest camps are also made by ranger patrols and researchers, we presume that areas that contain generally higher encounter rates of human sign are likely to be experiencing greater hunting or poaching pressure than areas with lower encounter rates of all measured human sign. The frequent presence of humans across a large proportion of the DFR may also be pushing great apes away from key resources, such as swamps and bais (forest clearings), with associated stress on the population.

Interaction between human impacts and wildlife distributions has been modeled at a variety of scales in the Congo Basin. In general, the distance to roads and human densities provides a reliable predictor of great ape distributions, with increasing densities of the species with distance from anthropogenic infrastructure and settlements (Strindberg *et al*. 2018). The same general pattern was found in this survey. The area containing the most human activity/signs of activity was closer to significant infrastructure, such as the Hydromekin Dam and the Sud-Cameroun Hévéa rubber plantation and associated human settlements. These areas had the lowest encounter rates of great ape nests.

A proposed standard monitoring protocol for great apes of the DFR

Protected area managers should continue to adhere to best practice methods for distance sampling surveys (Kühl *et al.* 2008). The distance sampling analysis used here, with data collected through systematic line transects designed to achieve a desired coefficient of variation, are recommended to periodically assess great ape population size and trends. Estimated survey effort to achieve a desired precision in the population estimates should also account for the uncertainty in the nest production and decay rate estimates, one of the reasons for the slightly higher CV compared to the desired CV in this study. The use of individual nests instead of nest groups, as used in this study, is also recommended to avoid potential bias in density estimates. If species detections become few then the central chimpanzee and western lowland gorilla observations can be combined and analyzed using multiple covariate distance sampling with species as a covariate to estimate density of each species. The DFR survey is planned to be repeated in 2021. If populations continue to decline, then the survey effort (in transect length) required to achieve a set coefficient of variation would make transect sampling prohibitively inefficient within the DFR. Camera-trap surveys provide an alternative approach to assessing population trends (discussed below).

Indirect nest surveys should yield unbiased estimates of density and abundance for monitoring trends in population status if implemented carefully to address sources of sampling error, such as variation in skills among those doing the surveys and differential detectability of nests in different habitats. The largest source of error when calculating density estimates, however, is the estimate of nest decay rate. Nest decay rate can vary substantially both within and between areas due to several factors, including rainfall, altitude, nest height, exposure, soil pH, and nest tree species (Kühl *et al*. 2008), and now due to climate change (Bessone *et al*. 2021). This means that survey specific nest decay rate estimates are necesssary.

Occupancy model estimates derived from camera-trap data offer an alternative rigorous measure for monitoring trends in great ape status as they are corrected by detection probability (i.e., the likelihood that a species was detected when present) (MacKenzie *et al*. 2006). Heterogeneity in site use and detection can be incorporated into the modeling. Occupancy data also has the advantage of being relatively easy to collect in a standardized format, and the use of camera-traps is particularly suited to this approach as they can be set up to operate constantly over the survey period. The use of modeled occupancy for monitoring the status of wildlife populations has become popular for a range of taxa (O'Connell *et al*. 2011). The use of distance sampling with camera-traps for estimating population densities of medium-to-large terrestrial mammals is also being developed and implemented (Howe *et al*. 2017; Amin *et al*. 2022). Whilst this approach has been tested for chimpanzees with camera-traps placed intentionally within the home range of one fully known group (Cappelle *et al*. 2019), further validation of the method needs to be carried out in populations of both chimpanzees and gorillas where group structures and home ranges are less well understood to enable effective monitoring of trends in great ape populations.

The documented decline in the great ape population (and forest elephants, Amin *et al*. 2020) is a contributory factor to UNESCO's possible downgrading of the World Heritage status of the DFR (https://whc.unesco.org/en/decisions/7889). The Cameroon Government is strengthening conservation measures as outlined in the 2020–2025 Dja Faunal Reserve Management Plan, which addresses many of the concerns raised by UNESCO concerning the management of the reserve. Great apes are currently most abundant in the north-eastern part of the DFR where local communities have exerted their traditional rights to collect non-timber forest products and to undertake small-scale subsistence hunting. The DFR Conservation Service is considering a community partnership agreement on sustainable access to forest resources and, to date, these great ape refugia have also been receiving greater management attention, both in terms of routine patrol coverage and rapid ranger response following alerts from local communities. The southern part of the DFR is much more vulnerable to organized wildlife crime gangs (OCGs), especially from the southern wildlife trafficking hub around the town of Djoum, which does not fall within traditional community areas (Poulsen *et al.* 2017). The presence of traditional subsistence hunters in the northern part of the DFR may provide a disincentive to OCGs to operate there compared to the more remote south where they can poach with relative impunity. The DFR management is implementing a community surveillance network and increasing law-enforcement patrols, especially along the southern boundary of the DFR with its many exit routes.

With improved security and appropriate engagement with local communities and the private sector in the region, it is hoped that the remaining great ape population will start to expand across the biosphere reserve and numbers gradually increase. The Dja Biosphere Reserve is an integral component of the TRIDOM transborder landscape which covers 178,000 km², roughly 10% of the Central African forest. It offers one of the last remaining opportunities for the long-term conservation of great apes, forest elephant, and other threatened species in the region. To prevent the increasing isolation of populations of large mammals, it is recommended that management plans for protected areas such as the Dja Biosphere Reserve in the TRIDOM landscape, incorporate zones outside and between the protected areas, such as private sector logging concessions and commercial plantations. Landscape level, transboundary planning is required to maintain existing wildlife corridors. Existing and future survey results, based on line-transects and camera-traps, should be used to identify areas used by great apes and other large mammals for travel within the landscape. These results should be incorporated into wildlife management plans and land-use plans for the region, such as the existing TRIDOM landscape agreement between Cameroon, Gabon and the Republic of Congo. Law enforcement strategies and community engagement activities in the landscape should be developed and strengthened.

Acknowledgments

We thank the government of the Republic of Cameroon and the Ministry of Forestry and Wildlife (MINFOF) for their continuing support of this effort as part of their overall program to protect and manage Cameroon's wildlife. We thank the European Union for supporting this survey through the Programme de Conservation et Utilisation Rationale des Ecosystemes Forestiers en Afrique Centrale 6 (ECOFAC6) project. We are most grateful to the late Conservator Hilaire Ndinga of the Dja Biosphere Reserve for his strong support of this study and his collegiality; he is greatly missed. We also thank the Chef d'Antenne of each sector for their ongoing support, and Zacharie Nzooh Dongmo and Kouamé Paul N'Goran from WWF, Leonard Usongo from IUCN, and Fiona Maisels from WCS for advice on the line transect survey methodology. Members of the field teams provided invaluable contributions to the survey and stalwart fortitude and commitment to the mission in the face of adverse conditions. We also sincerely thank Samantha Strindberg for reviewing a draft of the manuscript and Professor Steve Buckland for his advice.

Literature Cited

Ahumada, J. A. *et al.* 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Phil. Trans. Roy. Soc. Lond., Biol. Sci.* 366(1578): 2703–2711. doi.org/10.1098/rstb.2011.0115

Amin, R., O. Fankem, O. N. Gilbert, T. Bruce, C. Ndjassi, D. Olson and A. Fowler. 2020. The status of the forest elephant in the world heritage Dja Faunal Reserve, Cameroon. *Pachyderm* 61: 78-89.

Amin, R., H. Klair, T. Wacher, C. Ndjassi, A. Fowler, D. Olson and T. Bruce. 2022. Estimating forest antelope population densities using distance sampling with camera traps. *Oryx* 56(9): 345–351. doi:10.1017/S0030605320001209.

Bessone, M., L. Booto, A. R. Santos, H. Kuhl and B. Fruth. 2021. No time to rest: how the effects of climate change on nest decay threaten the conservation of apes in the wild. *PLoS One* 16(6): e0252527. doi.org/10.1371/journal.pone.0252527

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK.

Cappelle, N., M. L. Després-Einspenner, E. J. Howe, C. Boesch and H. S. Kühl. 2019. Validating camera trap distance sampling for chimpanzees. *Am. J. Primatol.* 81(3): e22962.

Djuikouo, M. N. K., J. L. Doucet, C. K. Nguembou, S. L. Lewis and B. Sonké. 2010. Diversity and aboveground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. *Afr. J. Ecol.* 48(4): 1053–1063.

Eno-Nku, M. 2013. Large mammal surveys of the Mt. Cameroon National Park, SW Region. WWF CCPO Coastal Forest Programme, Limbe, Cameroon.

Fowler, A. 2019. Holistic approaches to protecting a pangolin stronghold in Central Africa. In *Pangolins: Science, Society and Conservation*, D. W. Challender, H. C. Nash and C. Waterman (eds.), pp.427–439. Academic Press, New York.

Gardner, T. A., T. Caro, E. B. Fitzherbert, T. Banda and P. Lalbhai. 2007. Conservation value of multiple-use areas in East Africa. *Conserv. Biol.* 21(6): 1516–1525.

Gelman, A., J. B. Carlin., H. S. Stern and D. B. Rubin. 2004. *Bayesian Data Analysis*. Chapman and Hall/CRC, London.

Gelman, A. and J. Hill. 2006. *Data Analysis Using Regression and Multilevel Hierarchical Models*. Cambridge University Press, Cambridge, UK.

Global Forest Watch. 2022. Forest cover online map. URL:<https://www.globalforestwatch.org/

map/?map=eyJjZW50ZXIiOnsibGF0IjoyLjY4MjA1N-zA4ODQ5Nzg2OCwibG5nIjoxMi43NzYzNDM1MzAyMzIzOTZ9LCJ6b29tIjo4LjA1ODMwMzA3MzA4NzAxNiwiZGF0YXNldHMiOlt7ImRhdGFzZXQiOi-J3ZHBhLXByb3RlY3RlZC1hcmVhcyIsIm9wYWN-pdHkiOjEsInZpc2liaWxpdHkiOnR>. Accessed 13 March 2021.

Howe, E. J., S. T. Buckland, M. L. Despres-Einspenner and H. S. Kühl. 2017. Distance sampling with camera traps. *Methods Ecol. Evol.* 8: 1558–1565.

Huijbregts, B., P. De Wachter, L. S. N. Obiang and M. E. Akou. 2003. Ebola and the decline of gorilla *Gorilla gorilla* and chimpanzee *Pan troglodytes* populations in Minkébé Forest, north-eastern Gabon. *Oryx* 37(4): 437–443.

Humle, T., F. Maisels, J. F. Oates, A. Plumptre and E. A. Williamson. 2016. *Pan troglodytes* (errata version published in 2018). The IUCN Red List of Threatened Species 2016: e.T15933A129038584. Accessed 13 March 2021.

IUCN. 2014. *Regional Action Plan for the Conservation of Western Lowland Gorillas and Central Chimpanzees 2015–2025*. IUCN SSC Primate Specialist Group, Gland, Switzerland. 56pp. URL: <http://www.primate-sg.org/WEA2014.pdf>.

Kéry, M. and M. Schaub. 2012. *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*. Academic Press, New York.

Kühl, H., F. Maisels, M. Ancrenaz and E. A. Williamson (eds). 2008. *Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations*. IUCN, Gland, Switzerland. URL: <https://portals.iucn.org/library/efiles/documents/ssc-op-036.pdf>

Kupsch, D., B. K. Serge, M. Waltert, N. B. Chia, B. C. G. Brice, D. Abdoulaye and D. Kalagan. 2014. Biodiversity, carbon stock and market value assessment for the SGSOC project area, Southwest region, Cameroon. URL: <https://www.researchgate.net/publication/262077035_Biodiversity_carbon_stock_and_market_value_assessment_for_the_SGSOC_project_area_Southwest_region_Cameroon>.

Laing, S. E., S. T. Buckland, R. W. Burn, D. Lambie and A. Amphlett. 2003. Dung and nest surveys: estimating decay rates. *J. Appl. Ecol.* 40: 1102–1111.

MacKenzie, D. I, J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey and J. E. Hines. 2006. *Occupancy Estimation and Modelling*. Elsevier, Amsterdam.

Maisels, F., S. Strindberg, T. Breuer, D. Greer, K. Jeffery and E. Stokes. 2018. *Gorilla gorilla* ssp. *gorilla* (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2018: e.T9406A136251508. Accessed 13 March 2021.

MINFOF and IUCN. 2015. Caractérisation de la population de grands et moyens mammifères dans la Reserve de Faune du Dja : Potentiel et menaces. Ministry of Forestry and Wildlife, IUCN, Yaoundé, Cameroon.

Morgan, D., C. Sanz, J. R. Onononga and S. Strindberg. 2006. Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. *Int. J. Primatol.* 27: 147–179.

Ngatcha, L. 2019. Contribution a la preservation de la biodiversite par la mise on oeuvre des activites generatrices de revenus (AGRs) au profit des populations riveraines de la reserve de la biosphere du Dja. Memoire presente en vue de l'obtention du Diplome de Master Professional en Sciences Forestieres. Universite de Yaounde´ 1, Cameroon.

N'Goran, K. P., Z. L. Nzooh Dongmo and S. Le-Duc Yeno. 2017. Status of Elephant and Great Apes in Central Africa Priority Sites. Annual Technical Report. WWF Regional Office for Africa - Yaoundé hub, Yaoundé. URL: <https://d80g3k8vowjyp.cloudfront.net/downloads/The_status_of_Forest_Elephant_and_Great_Apes_in_Central_Africa_priority_sites.pdf>.

Nzooh Dongmo, Z. L., K. P. N'Goran, H. Ekodeck, S. Kobla, M. Sombambo, S. Famegni and A. Mengamenya. 2016a. Les populations de grands et moyens mammifères dans le segment lobéké du paysage tri-national de la sangha. Rapport Technique MINFOF-WWF, Yaounde, Cameroon.

Nzooh Dongmo, Z. L, K. P. N'Goran, G. Etoga, J. P. Belinga, E. Fouda, M. Dandjouma and P. Dongmo. 2016b. Les populations de grandes et moyens mammifères dans le segment Cameroun du paysage TRIDOM (forêt de Ngoyla-Mintom, et PN Boumba Bek et PN Nki et leurs zones périphériques). WWF CCPO-MINFOF, Yaounde, Cameroon.

Nzooh Dongmo, Z. L., K. P. N'Goran, C. Fondja and J. Nkono. 2016c. Evaluation de la dynamique des populations de grands et moyens mammiferes dand le domaine forestier permanent de l'unite technique operationnelle Campo Ma'an.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, K. Hornik, F. Leisch & A. Zeileis (eds.). Vienna, Austria. URL: <https://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf>.

Plummer, M. 2014. RJAGS: Bayesian graphical models using MCMC. R package version 3-10.

Poulsen, J. R., S. E. Koerner, S, Moore, V. P. Medjibe, S. Blake, C. J. Clark, M. E. Akou, M. Fay, A. Meier, J. Okouyi and C. Rosin. 2017. Poaching empties critical Central African wilderness of forest elephants. *Curr. Biol.* 27(4): 134–135.

O'Brien, T. G., M. F. Kinnaird and H. T. Wibisono. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Anim. Conserv.* 6(2): 131–139. doi.org/10.1017/S1367943003003172

O'Connell, A. F., J. D. Nichols and U. Karanth. 2011. *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, New York.

QGIS Development Team. 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project. URL: <http://qgis.osgeo.org>.

R Development Core Team. 2019. R: A language and environment for statistical computing. Foundation for Statistical Computing. Vienna, Austria. URL: <http://www.R-project.org>.

Sanz, C., D. Morgan, S. Strindberg and J. R. Onononga. 2007. Distinguishing between the nests of sympatric chimpanzees and gorillas. *J. Appl. Ecol.* 44(2): 263–272.

Stokes, E. J., S. Strindberg, P. C. Bakabana, P. W. Elkan, F. C. Iyenguet, B. Madzoké, G. A. Malanda, B. Mowawa, C. Moukoumbou, F. K. Ouakabadio and H. J. Rainey. 2010. Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. *PLoS One* 5(4): e10294. doi.org/10.1371/journal.pone.0010294

Strindberg, S. *et al*. 2018. Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. *Sci. Adv.* 4(4): eaar2964. doi.org/10.1126/sciadv.aar2964

Thomas. L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* (47): 5–14. doi: 10.1111/j.1365-2664.2009.01737.x

Tutin, C. E. and M. Fernandez. 1984. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *Am. J. Primatol.* 6(4): 313–336.

UNESCO 2022 World Heritage List. Available at https://whc.unesco.org/en/list/407/ Accessed 4 March 2022. URL: <https://whc.unesco.org/en/decisions/7889>.

White, L. J. T. and A. Edwards (eds.). 2000. *Conservation Research in the African Rain Forests: A Technical Handbook*. Wildlife Conservation Society, New York. URL: <https://www.researchgate.net/publication/277813627_Conservation_Research_in_the_African_Rain_Forest_A_Technical_Handbook>.

Williamson, L. and L. Usongo. 1995. Recensement des populations de primates et inventaires des grands mammifères. II Recensement des éléphants, gorilles et chimpanzés dans la Réserve de Faune du Dja (Cameroun). Rapport technique. Projet Ecofac, Agreco, Brussels.

Authors' addresses:
Rajan Amin, Zoological Society of London, Regent's Park, London NW1 4RY, UK; **Oliver Fankem**, **Tom Bruce**, **Malenoh Sewuh Ndimbe**, **Anne Stephanie Kobla**, **David Olson**, **Andrew Fowler**, Zoological Society of London – Cameroon, Yaoundé, Cameroon; and **Oum Ndjock Gilbert**, Ministry of Forestry and Wildlife, Yaoundé, Cameroon.

Corresponding author: Rajan Amin
email: raj.amin@zsl.org

Received for publication: 11 October 2021
Revised: 9 March 2022

Original Study

Rajan Amin*, Tim Wacher, Oliver Fankem, Tom Bruce, Oum Ndjock Gilbert, Malenoh Sewuh Ndimbe and Andrew Fowler

Giant pangolin and white-bellied pangolin observations from a World Heritage site

https://doi.org/10.1515/mammalia-2021-0173
Received November 10, 2021; accepted December 20, 2022; published online January 24, 2023

Abstract: Pangolins are one of the most threatened mammal groups, as a result of habitat loss and exploitation for their meat, scales, and other body parts. However, there is a lack of quantitative data on pangolin populations; their behaviour and ecology make them challenging to survey. We undertook systematic camera-trap surveys of the 5260 km^2 World Heritage Dja Faunal Reserve, Cameroon, sampling 305 sites in eight grids over 28,277 camera-trap days. We recorded 768 images of giant pangolin in 99 independent detections at 57 sites (RAI = 0.35), and 2282 images in 355 detections (RAI = 1.26) of white-bellied pangolin at 137 sites. Ground-dwelling giant pangolins were largely confined to the core of the Reserve. Semi-arboreal white-bellied pangolins were predominantly distributed in the northeast, east and south of the Reserve. Lower occupancy in the west and northwest could partly be due to pressures from human settlements around the Hydromekin Dam and Sud-Cameroun Hévéa rubber plantation. Our study suggests that at the ground-level the two species do not spatially segregate, and both were active throughout the night. We found high diel activity overlap, although there was a significant difference in activity peak times. There was also evidence of white-bellied pangolin possibly exhibiting fine-scale behavioural avoidance of giant pangolin.

***Corresponding author: Rajan Amin**, Zoological Society of London, Regents Park, London NW1 4RY, UK, E-mail: raj.amin@zsl.org. https://orcid.org/0000-0003-0797-3836
Tim Wacher, Zoological Society of London, Regents Park, London NW1 4RY, UK, E-mail: tim.wacher@zsl.org
Oliver Fankem, Tom Bruce, Malenoh Sewuh Ndimbe and Andrew Fowler, Zoological Society of London – Cameroon, Yaoundé, Cameroon, E-mail: oliverfankem@globalconservation.org (O. Fankem), tom.bruce@my.jcu.edu.au (T. Bruce), malenohsewuh@gmail.com (M.S. Ndimbe), andrew.fowler@zsl.org (A. Fowler)
Oum Ndjock Gilbert, Ministry of Forestry and Wildlife, Yaoundé, Cameroon, E-mail: ndjockoum@yahoo.fr

Keywords: camera-trap; conservation; Dja Faunal Reserve; occupancy; pangolin; relative abundance index.

1 Introduction

Pangolins (Pholidota: Manidae) are among the most globally threatened mammal groups. All eight extant species, four in sub-Saharan Africa and four in Asia, are listed as globally threatened on the IUCN Red List of Threatened Species (IUCN 2019). The most significant threat to pangolins is overexploitation. In Cameroon, this mainly involves the meat and some use of scales locally, but also a very large illegal international trade involving belief-based demand for pangolin scales elsewhere (Harvey-Carroll et al. 2022; Ichu 2019; Ingram et al. 2018; Ingram et al. 2019a; Nguyen et al. 2021). Despite high levels of exploitation, both historic and contemporary, there is a lack of quantitative data on pangolin populations. In addition, the behaviour and ecology of the species make them challenging to survey.

The Dja Faunal Reserve is the largest protected area in Cameroon (5260 km^2; Figure 1). The Reserve, a World Heritage Site, has high levels of both flora and fauna diversity, with 107 known mammal species (UNESCO 2022). Three species of pangolin occur in the Reserve, black-bellied pangolin (*Phataginus tetradactyla* Linnaeus, 1766, average body weight 2.79 kg), white-bellied pangolin (*Phataginus tricuspis* Rafinesque, 1821, average body weight 1.54 kg) and the giant pangolin (*Smutsia gigantea* Illiger, 1815, average body weight 33 kg). *P. tetradactyla* is listed as Vulnerable on the IUCN Red List (Ingram et al. 2019b), while *P. tricuspis* and *S. gigantea* are both listed as Endangered (Nixon et al. 2019; Pietersen et al. 2019). As a result of their cryptic behaviour, there is limited knowledge of the general ecology of all pangolin species (Wilcox et al. 2019). Both giant pangolin and white-bellied pangolin are thought to be predominantly solitary and nocturnal, with occasional records of diurnal activity (Hoffmann et al. 2020; Jansen et al. 2020; Khwaja et al. 2019). Pangolins are

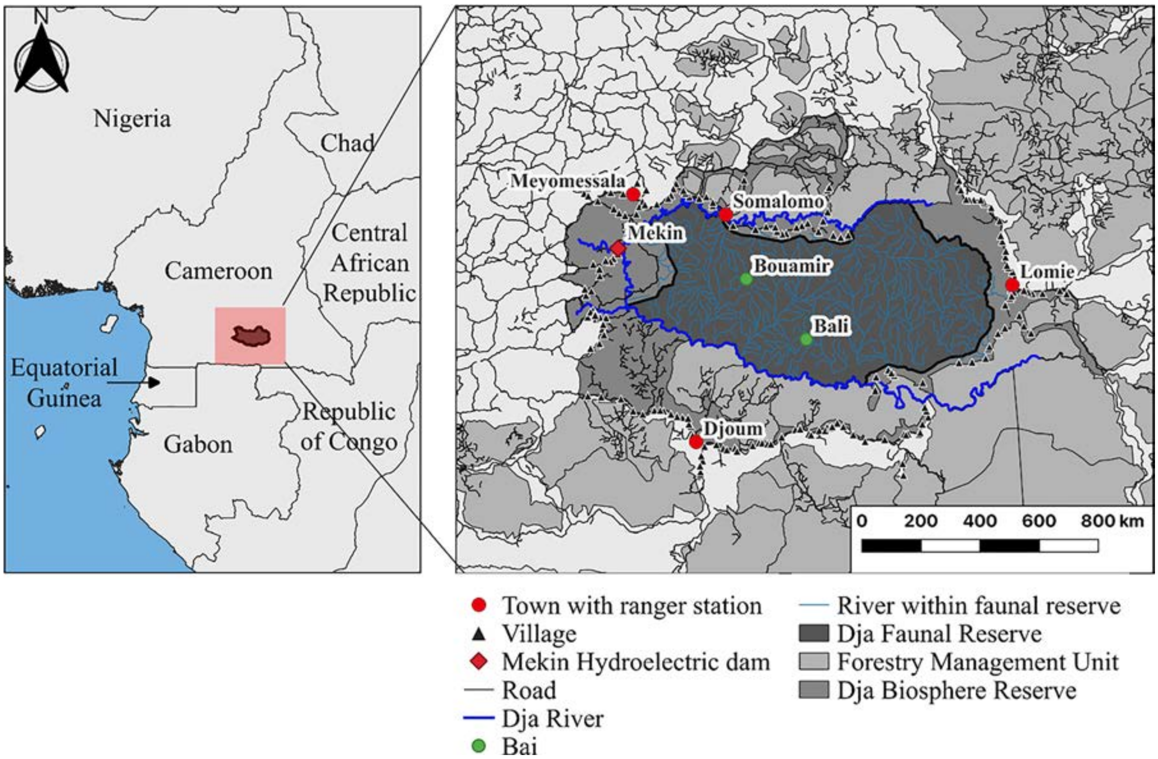


Figure 1: Location of the Dja Faunal Reserve, Cameroon.

myrmecophagous, locating their prey using a keen sense of smell and then breaking open the nests using their front limbs and claws to access the ants and termites (Kingdon and Hoffmann 2013). Both species are mainly found in forest habitats near swamps and water courses. However, white-bellied pangolins are thought to be more tolerant of disturbed forest habitats and have been found in plantations, whereas giant pangolins can persist in grasslands with high rainfall (Jansen et al. 2020; Kingdon and Hoffmann 2013).

The main objective of our study was to provide replicable baseline information on all medium to large terrestrial mammal species occurring in the Reserve through systematic, ground-based, camera-trap grids deployed at eight locations across the Reserve between 2016 and 2020. In this paper, we provide much needed information on the occurrence and distribution of the ground-dwelling, fossorial giant pangolin and the semi-arboreal white-bellied pangolin, to help develop effective conservation interventions and allow assessment of conservation progress through future monitoring using a standardised methodology. This camera-trap study obtained no information on the strictly arboreal, black-bellied pangolin.

2 Materials and methods

2.1 Study area

The Dja Faunal Reserve is a relatively flat plateau of round-topped hills and ranges in altitude from 600–800 m asl (MINFOF and IUCN 2015). The topography is mainly shallow valleys on either side of a ridgeline that cuts through the Reserve east to west. Swamp habitat is common on the floor of valleys, particular in the southern part of Reserve which has greater elevational variation. Tributaries throughout the Reserve flow into the Dja River (MINFOF and IUCN 2015, UNESCO 2022). The mean annual rainfall is c. 1600 mm (UNESCO 2022). The Reserve faces many pressures. Both illegal subsistence and commercial hunting occur within the Reserve (Epanda et al. 2019). Other significant threats in and around the Reserve include logging, agricultural clearance for subsistence crops and commercial crops such as pineapple, loss of the last remaining large forested corridor to the Ngoyla-Mintom forest block if the south-eastern road is developed, rubber plantations (e.g. Sud-Cameroun Hévéa), and the ecological impacts of existing (the Hydro Mekin) and planned hydroelectric dams (MINFOF and IUCN 2015; UNESCO 2022).

Cameroon's Ministry of Forestry and Wildlife (MINFOF) is responsible for the management of the Dja Faunal Reserve and the Biosphere Reserve. The Faunal Reserve has been divided into four management sectors with a base responsible for each sector in the nearest town: Lomié (East Sector), Djoum (South Sector), Meyomessala (West Sector), and Somalomo (North Sector).

Table 1: Survey effort, eight camera-trap grids deployed across the Dja Faunal Reserve between November 2015 and November 2020.

Management sector	Grid name	Operational period	Number of cameras	Camera days
North sector (Secteur Nord)	NS2016	14/11/2015–06/05/2016	41	3725
South sector (Secteur Sud)	SS2017	04/04/2017–26/07/2017	40	3371
North sector (Secteur Nord)	NS2018	22/01/2018–08/05/2018	38	3647
East sector (Secteur Est)	ES2018	27/01/2018–17/05/2018	39	3787
South sector (Secteur Sud)	SS2018	15/08/2018–11/12/2018	39	3689
North sector (Secteur Nord)	NS2019	30/04/2019–17/09/2019	37	3421
West sector (Secteur Ouest)	WS2020	04/10/2019–09/02/2020	35	2959
East sector (Secteur Est)	ES2020	13/05/2020–05/11/2020	36	3678

2.2 Survey design and camera deployment

We set up eight camera-trap grids (35–41 camera sampling points per grid, Table 1), with 2 km camera spacing, across the four management sectors of the Reserve (Figure 2). Each grid operated long enough to achieve at least 1000 camera-trap days of sampling effort (Table 1, O'Brien et al. 2003).

We used three camera models (Bushnell Trophy Aggressor (Bushnell Outdoor Products, Kansas, USA), Reconyx HC500 (RECONYX Inc., Wisconsin, USA) and Cuddeback Long Range IR E2 (Cuddeback, Wisconsin, USA)) across the eight camera-trap grids. Global Positioning System receivers were used to navigate to the grid sampling points. We placed a single camera (= a camera station) at a height of about 30 cm as close to the grid sampling point as possible, with a consistent and unobstructed field of view. The cameras were programmed to take three images per trigger.

2.3 Data analysis

We used *Exiv2* software (Huggel 2012) to extract EXIF information from each photograph (image name, date and time) into an *Excel* spreadsheet (Microsoft Office Professional Plus 2010). We identified animals in the photographs to species where possible, or to lowest taxonomic level discernible in unclear images. Based on head and body size and shape, hindlimbs and tail length (Kingdon 1971), the two African forest pangolin species (Figure 3) are distinguishable in camera-trap images. We analysed the resulting data with the *CTAP* camera-trap data analysis software (Amin and Wacher 2017) and the R statistical package (R Development Core Team 2019).

2.3.1 Relative abundance: We calculated the trap rate as a relative abundance index (RAI) for each species in each camera-trap grid as the total number of "independent detections" divided by the number of days cameras were operational $\times$ 100. We defined an "independent detection" as any sequence of images for a given species occurring after an interval of >= 60 min from the previous trigger (three-image sequence) of that species (Amin et al. 2015). Sixty minutes was used as adult giant pangolins were observed following one another in this survey and 60 min can therefore be regarded as a conservative measure of independence. Species trap rate provides an index of relative abundance with the assumption that species trigger cameras in relation to their density, all other factors being equal (Rovero and Marshall 2009). Trap rate provides a comparative index within species and habitat when a standardised protocol is used for the surveys, including consistent positioning and management of cameras to help ensure similar detection probabilities.

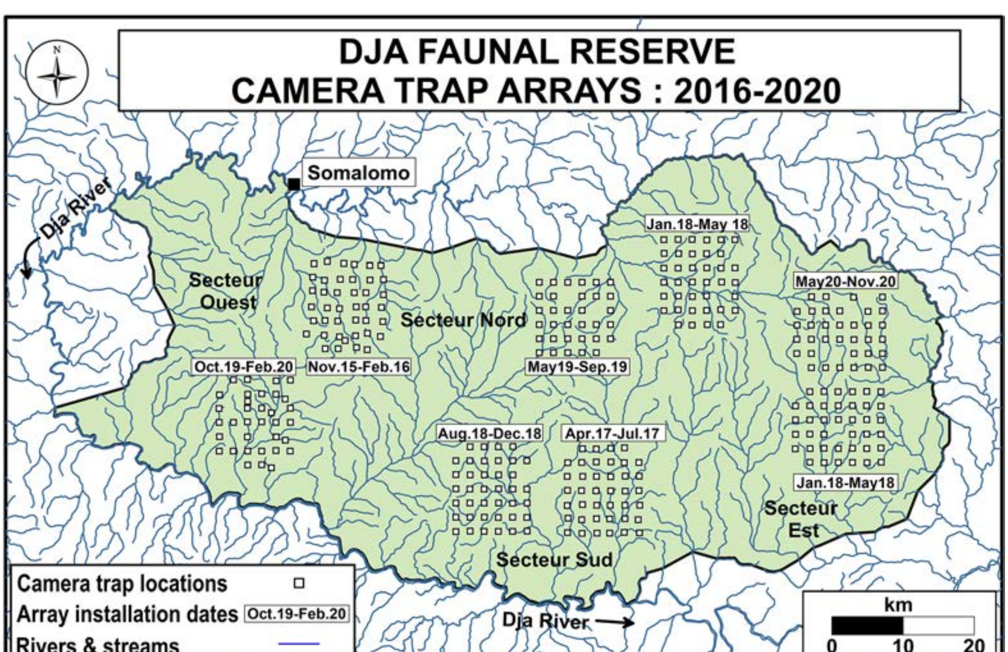


Figure 2: Location of the eight camera-trap grids deployed in the Dja Faunal Reserve, Cameroon.

Figure 3: Camera-trap images of giant pangolin (left) and white-bellied pangolin (right), Dja Faunal Reserve, Cameroon. In contrast to the white-bellied pangolin in camera-trap images, the giant pangolin is characterized by a elongated muzzle, stout body, short and stumpy hindlegs, a tail shorter than head and body length, the outside of fore- and hindlimbs covered with scales.

2.3.2 Spatial distribution: We used occupancy modelling (MacKenzie et al. 2006) to estimate the probability of site use for each species within each survey grid and in each management sector. We didn't have complete and up-to-date datasets on potential indicators of hunting pressure such as illegal activities recorded during patrols or distances to relevant features to investigate in this study (O'Brien et al. 2020; Pfeifer et al. 2017; Rovero et al. 2017). We didn't incorporate ecological covariates as tributaries occur throughout the Reserve (Figure 1), and the habitat within the Reserve is mainly mixed species rainforest with swamp habitats across a small altitudinal range.

We constructed a detection/non-detection history, using a five-day period as the sampling occasion, for each camera-trap station. For occupancy analysis at management sector, we used the whole survey dataset with different parameters for occupancy probability for each sector, but with no changes with time. Each camera-trap grid deployment was over a short time period so that an assumption of closure is reasonable. The two South Sector grids were deployed over consecutive years, and the North and East Sector grids over a three-year period, whilst a single grid was deployed in the West Sector. We expect seasonal effects on species presence to be minimal as limited observations suggest that the home-ranges are likely to be small (Kingdon and Hoffmann 2013). We also accounted for individual grids in estimating probability of detection when the species is present. We performed Bayesian occupancy analysis implemented in *JAGS 4.3.0* (Plummer 2003), accessed through *R 3.6.0* (R Development Core Team 2019), using the package *RJAGS 3–10* (Plummer 2014). We ran three Markov chain Monte Carlo (MCMC) chains with 110,000 iterations, a burn-in of 10,000 and a thinning rate of 10. This combination of values ensured an adequate number of iterations to characterise the posterior distribution of the modelled occupancy estimate. We checked for chain convergence with trace plots and the Gelman-Rubin statistic (Gelman et al. 2004), R-hat, which compares between and within chain variation. R-hat values below 1.1 indicate convergence (Gelman and Hill 2006). We assessed model fit using Freeman-Tukey discrepancy (Kery and Schaub 2012). We calculated the *P*-value, i.e., the probability of obtaining a discrepancy at least as large as the observed discrepancy if the model fits the data. Values near 0.5 indicate a good fit; values above 0.9 or below 0.1, a poor fit.

We also applied two-species occupancy modelling to test if the presence of the larger giant pangolin affected probability of occupancy of the much smaller white-bellied pangolin (Richmond et al. 2010).

2.3.3 Temporal interaction: We constructed diel activity patterns for the two species using the time of detection on the camera trap photographs. For the white-bellied pangolin, the activity pattern represented the species ground activities (Ingram et al. 2019c).

We estimated temporal overlap between the two species in the *overlap* package (version 0.3.2) in R software (Ridout and Linkie 2009). The Δ4 overlap coefficient, which is recommended for sample sizes >75, was calculated (Meredith and Ridout 2014; Ridout and Linkie 2009). The values of the Δ4 overlap coefficient range from 0 (no overlap) to 1 (complete overlap). The estimate 95% confidence intervals were obtained from 10,000 bootstrap samples. We followed Monterroso et al. (2014) and defined low overlap when Δ4 was <0.5, moderate when Δ4 was between 0.5 and 0.75, and high overlap when Δ4 was >0.75. We also performed the Watson-wheeler test using the *circular R* package (version 0.4–94) to compare the species activity patterns.

2.3.4 Fine-scale behavioural interactions: To assess fine-scale behavioural adaptations, we calculated time-to-encounters, in decimal days, between consecutive WBP-WBP 'white-bellied pangolin-white-bellied pangolin', GP-GP 'giant pangolin-giant pangolin', WBP-GP 'white-bellied pangolin-giant pangolin' and GP-WBP 'giant pangolin-white-bellied pangolin' capture events. We fitted a linear mixed-effects model with cross factors 'capture 1' as the initial capture either white-bellied pangolin or giant pangolin, and 'capture 2' the subsequent capture as either white-bellied pangolin or giant pangolin in R statistical package *lme4* (version 1.1–26, Bates et al. 2015). Camera location was added as a random-effect (Harmsen et al. 2009). The model 'time-to-encounter' response variable was log10-transformed to approximate a normal distribution of the residuals and equal variances. We calculated the differences between model predicted time-to-encounters for (1) GP-WBP and WBP-WBP events, and (2) WBP-GP and GP-GP events, and the 95% confidence intervals of the differences using a bootstrap.

3 Results

The surveys accumulated a total of 28,277 camera-trap days over eight grids (305 camera-trap sampling points, Table 1), with the minimum of 1000 camera trap days per grid fulfilled

Table 2: Giant pangolin: number of images and number of camera sites detected (in brackets), relative abundance index (number of independent detections per trap day times 100), and modelled occupancy estimates with 95% confidence interval (in brackets) recorded in eight camera-trap grids deployed across the Dja Faunal Reserve, 2016–2020.

Camera-trap grid	Number of images (number of sites detected)	Relative abundance index (number of independent detections)	Modelled occupancy (95% CI)
NS2016	72 (7)	0.3 (11)	0.51 (0.19–0.92)
NS2018	203 (8)	0.47 (17)	0.32 (0.13–0.55)
NS2019	89 (5)	0.35 (12)	0.33 (0.09–0.69)
ES2018	13 (3)	0.08 (3)	?
ES2020	34 (4)	0.16 (6)	?
SS2017	176 (14)	0.86 (29)	0.61 (0.35–0.92)
SS2018	128 (12)	0.43 (16)	0.63 (0.35–0.98)
WS2019	53 (4)	0.17 (5)	?

'?' indicates insufficient detections to model occupancy.

(mean 93/camera). Fifteen cameras, out of 305 cameras, failed to return any data by loss or camera malfunction.

3.1 Giant pangolin

We recorded 768 images in 99 independent detections of giant pangolin at 57 camera sites. Two events of two giant pangolins following one another were captured during this survey. This species was most frequently recorded in the South Sector (RAI = 0.64). The East and West Sectors had much fewer giant pangolin detections (East Sector RAI = 0.12, West Sector RAI = 0.17, Table 2). The RAI (0.37) in the North Sector was about half that of the South Sector.

The occupancy model parameters all converged (Rhat<1.1) and the models fitted well to the data ($P \sim 0.5$). There were insufficient detections to model occupancy for the East and West Sector grids (Table 2). At the management sector level, giant pangolin occupancy was significantly higher in the South Sector than the North Sector (posterior probability = 0.99), East Sector (posterior probability = 1) or the West Sector (posterior probability = 0.99) (Figures 4 and 5). The North Sector had higher giant pangolin occupancy than the East Sector (posterior probability = 0.96) and the West Sector (posterior probability = 0.8). The detection probability across all sectors was 0.04 (95% CI = 0.03–0.06).

3.2 White-bellied pangolin

There were 2282 images recorded in 355 independent detections of white-bellied pangolin at 137 camera sites (Table 3). Only single adults were recorded. The East Sector had the highest RAI (2.26) followed by the South Sector (1.15) and North Sector (0.82). The West Sector had the lowest RAI (0.54).

The occupancy models converged (Rhat < 1.1) and fitted well to the data ($P \sim 0.5$). White-bellied pangolin occupancy was significantly higher in the East Sector than the North Sector (posterior probability = 1), South Sector (posterior probability = 0.98) or West Sector (posterior probability = 1) (Figure 6, Table 3). The West Sector had significantly lower occupancy than the North Sector (posterior probability = 0.96) and South

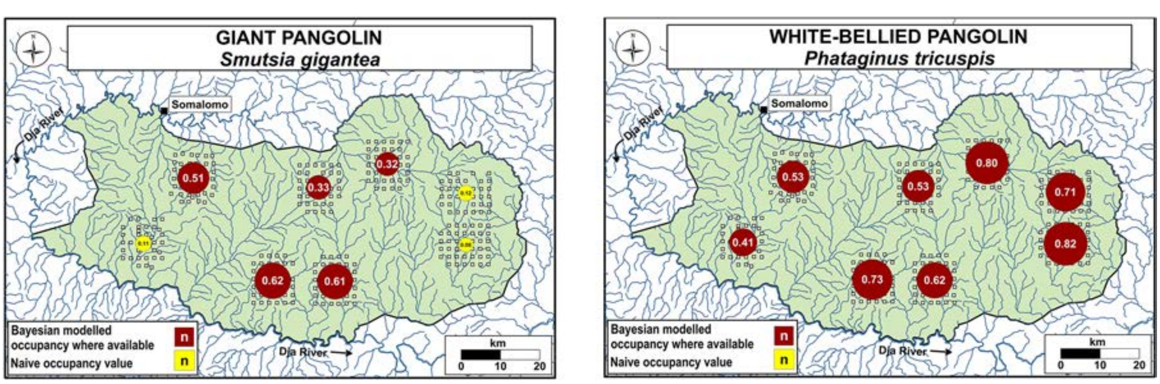


Figure 4: Giant pangolin (left) and white-bellied pangolin (right) occupancy map. Dja Faunal Reserve.

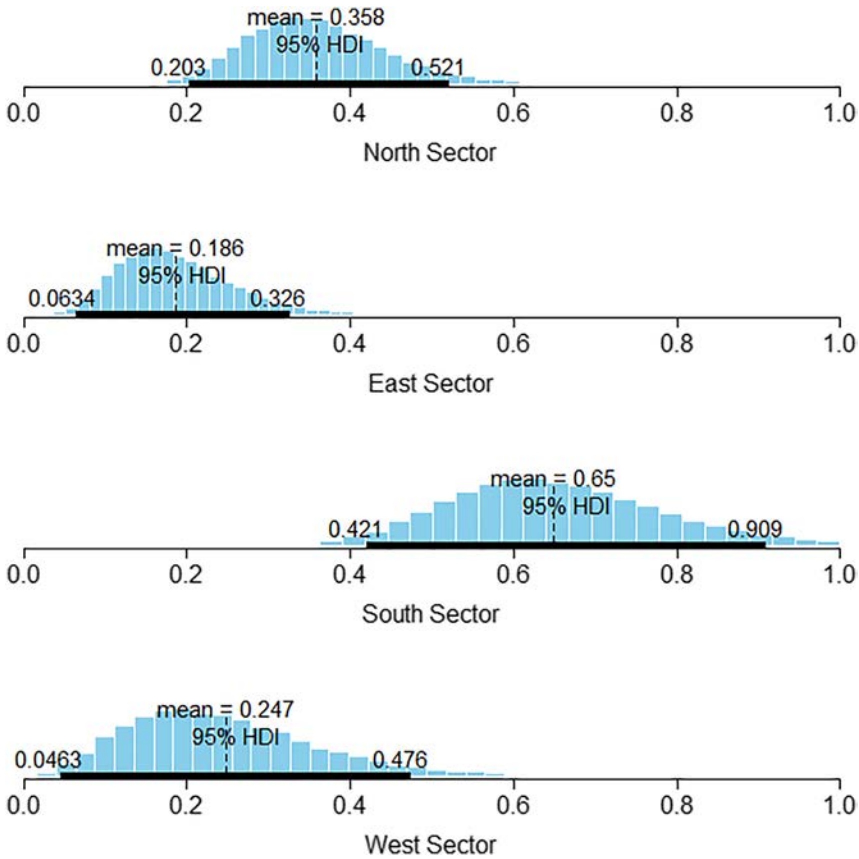


Figure 5: Giant pangolin occupancy posterior distributions for the North, East, South and West management sectors, Dja Faunal Reserve, Cameroon. The 95% highest posterior density "credible" interval (HDI), the Bayesian equivalent to 95% confidence interval, are also shown.

Table 3: White-bellied pangolin: number of images and number of camera sites detected (in brackets), relative abundance index (number of independent detections per trap day times 100), and modelled occupancy estimates with 95% confidence interval (in brackets) recorded in eight camera-trap grids deployed across the Dja Faunal Reserve, 2016–2020.

Camera-trap grid	Number of images (number of sites detected)	Relative abundance index (number of independent detections)	Modelled occupancy (95% CI)
NS2016	174 (12)	0.78 (29)	0.53 (0.27–0.82)
NS2018	207 (21)	1.18 (43)	0.8 (0.59–1)
NS2019	155 (12)	0.79 (17)	0.53 (0.3–0.79)
ES2018	1002 (30)	2.93 (111)	0.82 (0.68–0.95)
ES2020	309 (19)	1.58 (58)	0.71 (0.5–0.92)
SS2017	81 (14)	0.92 (31)	0.62 (0.36–0.93)
SS2018	253 (22)	1.36 (50)	0.73 (0.53–0.95)
WS2019	101 (7)	0.54 (16)	0.42 (0.25–0.7)

'?' indicates insufficient detections to model occupancy.

Sector (posterior probability = 0.99). The detection probability across all sectors was 0.08 (95% CI = 0.07–0.09).

There were 107 camera-trap sites where only white-bellied pangolins were detected, 27 sites where only giant pangolins were detected, and 30 sites where both species were detected. White-bellied pangolin occupancy was unaffected by the presence of giant pangolins. The average probability of white-bellied occupancy was 0.72 (95% CI = 0.55–0.84) when giant pangolins were present, and 0.78 (95% CI = 0.3–0.97) when they were absent.

3.3 Temporal interactions

The giant pangolin was predominantly nocturnal with peak of activity around midnight. The white-bellied pangolin was also mainly nocturnal with pre-dawn and after-dusk peaks

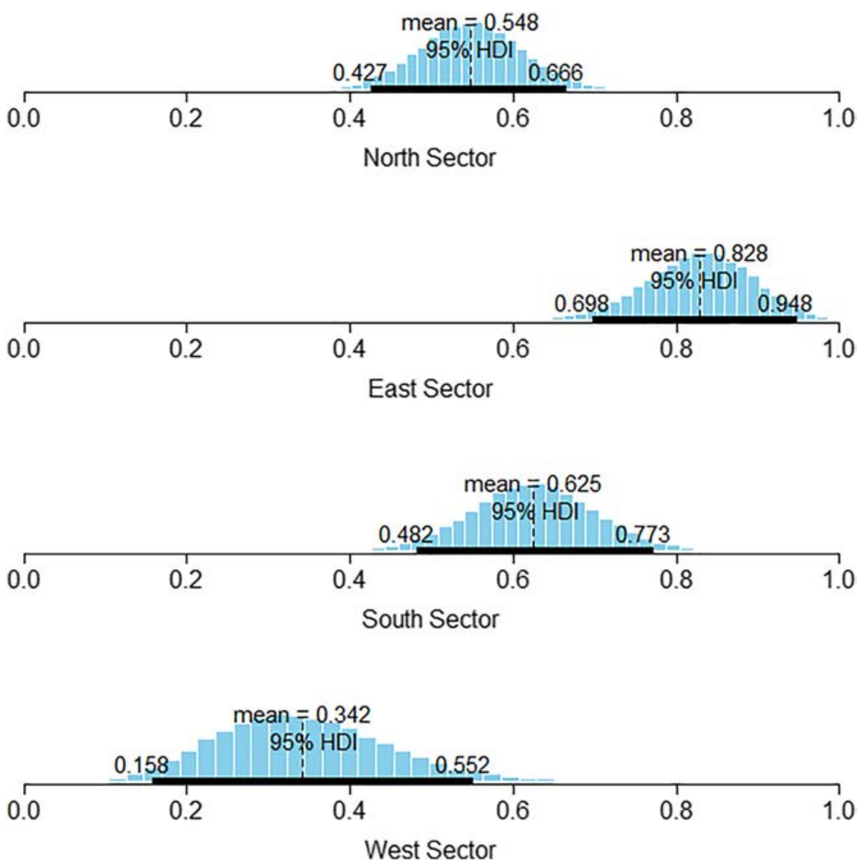


Figure 6: White-bellied pangolin occupancy posterior distributions for the North, East, South and West management sectors, Dja Faunal Reserve, Cameroon. The 95% highest posterior density "credible" interval (HDI), the Bayesian equivalent to 95% confidence interval, are also shown.

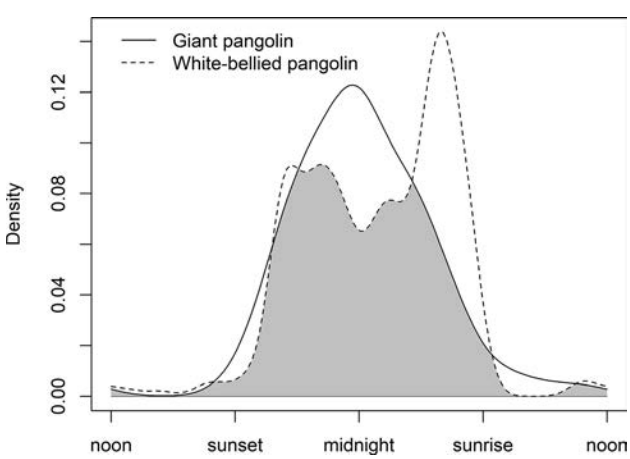


Figure 7: Overlap (grey area) in diel activity patterns between giant pangolin and white-bellied pangolin.

of ground activity. It was also intermittently active on the ground during daytime (Figure 7). Temporal overlap between giant pangolin and white-bellied pangolin was high (0.78; 95% CI: 0.69–0.85), however there was a significant difference in activity peak times (P = 0.0005).

3.4 Fine-scale behavioural interactions

The number of intraspecific and interspecific photo-capture events were 198 (WBP-WBP), 28 (WBP-GP), 21 (GP-WBP) and 30 (GP-GP). Our model revealed the time-to-encounters (decimal days in log10 scale) between giant pangolin and white-bellied pangolin (1.03) were significantly longer than those between consecutive same-species captures, white-bellied pangolin-white-bellied pangolin (0.78). The predicted difference between interspecific and intraspecific time-to-encounter events were (1) GP-WBP and WBP-WBP (0.25, 95% CI: −0.09–0.62, P = 0.04) and (2) WBP-GP and GP-GP (−0.07, 95% CI: −0.54–0.35, P = 0.85).

4 Discussion and conclusion

There is a dearth of quantitative data on the African forest pangolins and our extensive ground-based camera-trap study has provided important insights into the occurrence, spatial distribution and temporal ecology of two species of pangolins detected in the World Heritage Reserve.

The ground dwelling giant pangolin is largely confined to the core of the Reserve. There are extensive swamps, providing suitable habitat to the species, in the southern part the Reserve (Hoffmann et al. 2020). Along the Reserve's southern boundary, the Dja River forms a natural barrier providing some protection from developed areas to the south, in conjunction with a permanent ecoguard river post being present on the Reserve side of the river. In the North Sector, the presence of a long-term research station permanently manned by rangers, provides a deterrence to poaching, and a community surveillance network has also been established in the sector. There is potentially greater pressure in the eastern and western part of the Reserve. Adjacent to the eastern boundary is a 276 km^2 buffer zone and two towns (Lomié and Mindourou) inhabited by over 30,000 people according to 2005 Cameroon population census (https://www.citypopulation.de/en/cameroon/admin/). Historically, indigenous people and local communities were very close to the Reserve forests and were sustainably utilizing the forests (Leclerc 2012). With the gazettement of the Reserve, the communities have reluctantly respected the limit of the Reserve and over time with increased human population and the cost of bushmeat and pangolin scales, the impact of the towns and villages seems to have increased. On the western edge of the Reserve, there is significant infrastructure (Hydromekin Dam and Sud-Cameroun Hévéa rubber plantation) and associated human settlements. Increased infrastructure development has been demonstrated to cause a proliferation in the demand for bushmeat, along with easier access to the forests due to the associated roads (Poulsen et al. 2009). It is therefore not unreasonable to assume that the development occurring in the eastern and western sectors could be negatively affecting the giant pangolin locally (Rainforest Foundation UK 2021).

The white-bellied pangolin is predominantly distributed in the northeast, east and south of the Reserve. Compared to the giant pangolin, it is more disturbance tolerant and is known to occur in anthropogenically disturbed habitats such as plantations or abandoned farms (Jansen et al. 2020; Khwaja et al. 2019). Its semi-arboreal habits may provide some protection against hunting with snares and other ground-based devices, but this does not prevent poaching using torches and firearms. Furthermore, when threatened, white bellied pangolins often roll into a ball as their primary defence; this behaviour is inappropriate for evading human hunters and allows hunters to capture a significant number by hand. In contrast, the giant pangolin with its large body tends to leave marks on the ground, which could easily lead hunters to its burrows. Also, the distributions could be linked to the fact that hunters prefer to hunt larger-bodied species (Jerozolimski and Peres 2003), and body size has been found to correlate with threat status in some hunted species (Isaac and Cowlishaw 2004).

There was no evidence that giant pangolin affected the spatial distribution of white-bellied pangolins. However, our findings suggest that there could be temporal separation between the two species. Despite both being nocturnal giant pangolin were much more active early in the night compared to white-bellied pangolin, which were significantly more active later in the night closer to dawn. The main caveat is that white-bellied pangolin will only be detected by ground-based cameras when they come to ground level. Previous studies have shown via radio tracking, that their activity is highly variable dependent on the season, but much of their preferred prey is present at ground level (Pages 1975), raising the possibility they could be segregating their spatial activity within the vertical niche to maximise their ability to acquire ants/termites.

Monitoring trends: One of the main difficulties associated with developing effective conservation interventions for pangolins is assessing change in their status and identifying associated drivers. There are no population estimates available for the giant pangolin and only a single site density estimate is documented for the white-bellied pangolin (0.84 individuals/km^2, Lama Forest Reserve, Benin, Akpona et al. 2008). Currently, it is not possible to identify individual pangolins using natural marks, such as the scale pattern, for estimating density using capture-recapture methods. Methods for estimating population densities using camera traps without or with partial individual recognition are being developed and implemented (Amin et al. 2021; Augustine et al. 2018; Howe et al. 2017; Rowcliffe et al. 2008; Stevenson et al. 2018; Willcox et al. 2019). Modelled occupancy estimates, as presented in this study, offer an alternative measure for monitoring trends in species status as they are corrected by detection probability (i.e., the likelihood that a species was detected when present) (MacKenzie et al. 2006). Although not performed in this study due to lack of suitable data, occupancy modelling can also help in the identification and testing of the significance of predictors of species occurrence, such as distance from roads and settlements, logging operations, and hunting intensities.

Surveying the strictly arboreal and particularly elusive, black-bellied pangolin is more challenging. Targeted arboreal camera-trap surveys and focussing on features such as fallen trees have the potential to confirm species presence (Simo et al. 2020) and to estimate occupancy (Bowler et al. 2017) and may also provide insight into their activity and ecology.

In conclusion, we recommend, surveys are conducted on a periodic basis using a standardised methodology to assess the status of pangolins and other threatened species in the Dja Faunal Reserve. Future camera-trap surveys could also attempt to implement distance sampling to obtain population size estimates. It would also be useful to incorporate accurate data on potential predictors of species occurrence in occupancy modelling to help guide adaptive management decisions.

Research ethics: Our research did not include handling of wild animals. It was based on remote sensing using camera traps and approval for conducting the study was obtained from the Cameroon Ministry of Forests and Fauna.

Acknowledgements: We thank the Cameroon Ministry of Forests and Fauna and the late Conservator Hilaire Ndinga of the Dja Faunal Reserve for support, and the Ministry ecoguards and local porters who accompanied the survey teams in the field. We also thank David Olson, Hannah Klair and Constant Ndjassi for their input in the initial stages of the surveys.

Author contributions: All the authors have accepted responsibility for the entire content of this submitted manuscript and approved submission.

Research funding: None declared.

Conflict of interest statement: The authors declare no conflicts of interest regarding this article.

References

Akpona, H.A., Djagoun, C.A.M.S., and Sinsin, B. (2008). Ecology and ethnozoology of the three-cusped pangolin *Manis tricuspis* (Mammalia, Pholidota) in the Lama forest reserve, Benin. Mammalia 72: 198–202.

Amin, R. and Wacher, T. (2017). A new comprehensive package for the management and analysis of camera trap data for monitoring antelopes and other wild species. GNUSLETTER 34: 21–23.

Amin, R., Andanje, S.A., Ogwonka, B., Ali, A.H., Bowkett, A.E., Omar, M., and Wacher, T. (2015). The northern coastal forests of Kenya are nationally and globally important for the conservation of Aders' duiker *Cephalophus adersi* and other antelope species. Biodivers. Conserv. 24: 641–658.

Amin, R., Klair, H., Wacher, T., Ndjassi, C., Fowler, A., Olson, D., and Bruce, T. (2021). Estimating forest antelope population densities using distance sampling with camera traps. Oryx 56: 345–351.

Augustine, B.C., Royle, J.A., Kelly, M.J., Satter, C.B., Alonso, R.S., Boydston, E.E., and Crooks, K.R. (2018). Spatial capture-recapture with partial identity: an application to camera traps. Ann. Appl. Stat. 12: 67–95.

Bates, D., Mächler, M., Bolker, B.M., and Walker, S.C. (2015). Fitting linear mixed –effects models using lme4. J. Stat. Software 67: 1–48.

Bowler, M.T., Tobler, M.W., Endress, B.A., Gilmore, M.P., and Anderson, M.J. (2017). Estimating mammalian species richness and occupancy in tropical forest canopies with arboreal camera traps. Remote. Sens. Ecol. Conserv. 3: 146–157.

Epanda, M.A., Fotsing, A.J.M., Bacha, T., Frynta, D., Lens, L., Tchouamo, I.R., and Jef, D. (2019). Linking local people's perception of wildlife and conservation to livelihood and poaching alleviation: a case study of the Dja biosphere reserve, Cameroon. Acta Oecol. 97: 42–48.

Gelman, A. and Hill, J. (2006). *Data analysis using regression and multilevel/ hierarchical models*. Cambridge University Press, Cambridge.

Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. (2004). *Bayesian data analysis*. Chapman and Hall/CRC.

Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E.T., and Doncaster, C.P. (2009). Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a neotropical forest. J. Mammal. 90: 612–620.

Harvey-Carroll, J., Simo, F.T., Sonn-Juul, T., Tsafack, J.P., Aka'a, S.J., Tarla, F.N., Fowler, A., and Ingram, D.J. (2022). Continued availability and sale of pangolins in a major urban bushmeat market in Cameroon despite national bans and the COVID-19 outbreak. Afr. J. Ecol. 00: 1–7.

Hoffmann, M., Nixon, S., Alempijevic, D., Ayebare, S., Bruce, T., Davenport, T.R., Hart, J., Hart, T., Hega, M., Maisels, F., et al. (2020). Giant pangolin *Smutsia gigantea* (illiger, 1815). In: *Pangolins*. Academic Press, pp. 157–173.

Howe, E.J., Buckland, S.T., Després-Einspenner, M.L., and Kühl, H.S. (2017). Distance sampling with camera traps. Methods Ecol. Evol. 8: 1558–1565.

Huggel, A. (2012). *Exiv2 software tool*, Available at: http://www.exiv2.org/ index.html (Accessed 16 May 2012).

Ichu, I.G. (2019). *Status of pangolin trade in Cameroon and between Cameroon and destination countries*. TRAFFIC, Yaoundé, Cameroon, Cambridge.

Ingram, D.J., Coad, L., Abernethy, K.A., Maisels, F., Stokes, E.J., Bobo, K.S., Breuer, T., Gandiwa, E., Ghiurghi, A., Greengrass, E., et al. (2018). Assessing africa-wide pangolin exploitation by scaling local data. Conservation Letters 11: e12389.

Ingram, D.J., Cronin, D.T., Challender, D.W., Venditti, D.M., and Gonder, M.K. (2019a). Characterising trafficking and trade of pangolins in the Gulf of Guinea. Glob. Ecol. Conserv. 17: e00576.

Ingram, D.J., Shirley, M.H., Pietersen, D., Ichu, I.G., Sodeinde, O., Moumbolou, C., Hoffmann, M., Gudehus, M., and Challender, D. (2019b). *Phataginus tetradactyla. The IUCN Red List of Threatened Species 2019: e.T12766A123586126* (Accessed 06 Sep 2022).

Ingram, D.J., Willcox, D., and Challender, D.W. (2019c). Evaluation of the application of methods used to detect and monitor selected mammalian taxa to pangolin monitoring. Glob. Ecol. Conserv. 18: e00632.

Isaac, N.J.B. and Cowlishaw, G. (2004). How species respond to multiple extinction threats. Proc. Biol. Sci. 271: 1135–1141.

IUCN (2019). *The IUCN red list of threatened species*, Version 2018-2, 17 January 2019. Available at: http://www.iucnredlist.org.

Jansen, R., Sodeinde, O., Soewu, D., Pietersen, D.W., Alempijevic, D., and Ingram, D.J. (2020). White-bellied pangolin *Phataginus tricuspis* (rafinesque, 1820). In: *Pangolins*. Academic Press, pp. 139–156.

Jerozolimski, A. and Peres, C.A. (2003). Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. Biol. Conserv. 111: 415–425.

Kery, M. and Schaub, M. (2012). *Bayesian population analysis using WinBUGS - a hierarchical perspective*. Academic Press.

Khwaja, H., Buchan, C., Wearn, O.R., Bahaa-el-din, L., Bantlin, D., Bernard, H., Bitariho, R., Bohm, T., Borah, J., Brodie, J., et al. (2019). Pangolins in global camera trap data: implications for ecological monitoring. Glob. Ecol. Conserv. 20: e00769.

Kingdon, J. (1971). *East African mammals. An atlas of evolution in Africa. Volume I: primates, hyraxes, pangolins, protoungulates, sirenians*. Academic Press, London, pp. 446.

Kingdon, J., and Hoffmann, M. (Eds.), (2013). *Mammals of Africa. Volume V: carnivores, pangolins, equids and rhinoceroses*. Bloomsbury Publishing, London.

Leclerc, C. (2012). *L'adoption de l'agriculture chez les Pygmees baka du Cameroun. Dynamique sociale et continuite structurale*. Editions de la Maison des sciences de l'homme, Editions Quae, Versailles.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E. (2006). *Occupancy estimation and modelling*. Elsevier, Amsterdam.

Meredith, M. and Ridout, M. (2014). *Overview of the overlap package*, Available at: https://cran.cs.wwu.edu/web/packages/overlap/vignettes/overlap.pdf.

MINFOF and IUCN (2015). *Caractérisation de la population de grands et moyens mammifères dans la Reserve de Faune du Dja : Potentiel et menaces*. Ministry of Forestry and Wildlife, IUCN, Yaoundé, Cameroon.

Monterroso, P., Alves, P.C., and Ferreras, P. (2014). Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behav. Ecol. Sociobiol 68: 1403–1417.

Nguyen, L.B., Fossung, E.E., Affana Nkoa, C., and Humle, T. (2021). Understanding consumer demand for bushmeat in urban centers of Cameroon with a focus on pangolin species. Conserv. Sci. Pract 3: e419.

Nixon, S., Pietersen, D., Challender, D., Hoffmann, M., Godwill Ichu, I., Bruce, T., Ingram, D.J., Matthews, N., and Shirley, M.H. (2019). *Smutsia gigantea. The IUCN Red List of Threatened Species 2019: e.T12762A123584478* (Accessed 22 February 2022).

O'Brien, T.G., Kinnaird, M.F., and Wibisono, H.T. (2003). Crouching tigers, hidden prey: sumatran tiger and prey populations in a tropical forest landscape. Anim. Conserv. 6: 131–139.

O'Brien, T.G., Ahumada, J., Akampurila, E., Beaudrot, L., Boekee, K., Brncic, T., Hickey, J., Jansen, P.A., Kayijamahe, C., Moore, J., et al. (2020). Camera trapping reveals trends in forest duiker populations in African National Parks. Remote. Sens. Ecol. Conserv. 6: 168–180.

Pages, E. (1975). Etude éco-éthologique de Manis tricuspis par radio-tracking. Mammalia 39: 613–641.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., et al. (2017). Creation of forest edges has a global impact on forest vertebrates. Nature 551: 187–191.

Pietersen, D., Moumbolou, C., Ingram, D.J., Soewu, D., Jansen, R., Sodeinde, O., Keboy Mov Linkey Iflankoy, C., Challender, D., and Shirley, M.H. (2019). *Phataginus tricuspis. The IUCN Red List of Threatened Species 2019: e.T12767A123586469* (Accessed 22 February 2022).

Plummer, M. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik, K., Leisch, F., and Zeileis, A. (Eds.), *Proceedings of the 3rd international workshop on distributed statistical computing Vienna*. Austria, Available at: https://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf.

Plummer, M. (2014). *RJAGS: Bayesian graphical models using MCMC*. R package version 3–10.

Poulsen, J.R., Clark, C.J., Mavah, G., and Elkan, P.W. (2009). Bushmeat supply and consumption in a tropical logging concession in northern Congo. Conserv. Biol. 23: 1597–1608.

R Development Core Team (2019). *R: a language and environment for statistical computing*. Foundation for Statistical Computing, Vienna, Austria, Available at: http://www.R-project.org.

Rainforest Foundation UK (2021). *Roads to Ruin: the emerging impacts of infrastructure development in Congo Basin forests*, Available at: https://www.rainforestfoundationuk.org/media.ashx/infrastructure-report (Accessed 18 September 2022).

Richmond, O.M.W., Hines, J.E., and Beissinger, S.R. (2010). Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. Ecol. Appl. 20: 2036–2046.

Ridout, M.S. and Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14: 322–337.

Rovero, F. and Marshall, A.R. (2009). Camera trapping photographic rate as an index of density in forest ungulates. J. Appl. Ecol. 46: 1011–1017.

Rovero, F., Owen, N., Jones, T., Canteri, E., Iemma, A., and Tattoni, C. (2017). Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses. Biodivers. Conserv. 26: 1103–1119.

Rowcliffe, J.M., Field, J., Turvey, S.T., and Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. J. Appl. Ecol. 45: 1228–1236.

Simo, F., Fopa, G.D., Kekeunou, S., Ichu, I.G., Esong Ebong, L., Olson, D., and Ingram, D.J. (2020). Using local ecological knowledge to improve the effectiveness of detecting white-bellied pangolins (Phataginus tricuspis) using camera traps: a case study from Deng-Deng National Park, Cameroon. Afr. J. Ecol. 54: 879–884.

Stevenson, B.C., Borchers, D.L., and Fewster, R.M. (2018). Cluster capture-recapture to account for identification uncertainty on aerial surveys of animal populations. Biometrics 75: 326–336.

UNESCO (2022). *World heritage list*, Available at: https://whc.unesco.org/en/list/407/ (Accessed 4 March 2022).

Willcox, D., Nash, H.C., Trageser, S., Kim, H.J., Hywood, L., Connelly, E., Ichu, G.I., Nyumu, J.K., Moumbolou, C.L.M., Ingram, D.J., et al. (2019). Evaluating methods for detecting and monitoring pangolin (Pholidata: Manidae) populations. Global Ecology and Conservation 17: e00539.

Original Study

Rajan Amin*, Tim Wacher, Oliver Fankem, Oum Ndjock Gilbert, Malenoh Sewuh Ndimbe and Andrew Fowler

Status and ecology of forest ungulates in the Dja Faunal Reserve, Cameroon

https://doi.org/10.1515/mammalia-2021-0175
Received November 10, 2021; accepted March 10, 2022;
published online May 11, 2022

Abstract: Ungulates have undergone major declines in Central and West African forests as a result of bushmeat trade and habitat loss. Monitoring forest ungulate status is a critical conservation need. We undertook a systematic camera-trap survey of the 5260 km^2 Dja Faunal Reserve, Cameroon's largest protected area. We deployed cameras at 305 sites in eight grids across the reserve over 28,277 camera-trap days. We recorded 30,601 independent detections of 12 species of forest ungulate. The blue and Peters' duikers were the most abundant, accounting for 82% of all ungulate detections, both with occupancy >85% in all survey grids. The black-fronted duiker was relatively widespread but rare. The white-bellied duiker and water chevrotain were found mostly in the southern part of the reserve. There were very few detections of sitatunga, forest buffalo and bongo. Our results suggest ecological partitioning among the more abundant duikers based on activity pattern and body size. The reserve faces many pressures including illegal subsistence and commercial hunting. Community surveillance and partnerships, with improved law enforcement are among measures being implemented by the Cameroon government to enhance security and ensure retention of the reserve's World Heritage status.

Keywords: camera-trap; conservation; duiker; forest antelopes; occupancy; threatened species.

***Corresponding author: Rajan Amin**, Zoological Society of London, Regents Park, London NW1 4RY, UK, E-mail: raj.amin@zsl.org. https://orcid.org/0000-0003-0797-3836
Tim Wacher, Zoological Society of London, Regents Park, London, UK
Oliver Fankem, Malenoh Sewuh Ndimbe and Andrew Fowler, Zoological Society of London – Cameroon, Yaoundé, Cameroon
Oum Ndjock Gilbert, Ministry of Forestry and Wildlife, Yaoundé, Cameroon

1 Introduction

Antelopes and other artiodactyl species constitute a significant component of forest and woodland ecosystems both in terms of biomass (White 1994) and ecological services (Feer 1995). Many of these ungulate species are increasingly threatened by habitat loss and hunting (East 1999; Kingdon and Hoffmann 2013). They are primary targets for the trade in bushmeat (Fa et al. 2005; Wilkie and Carpenter 1999; Wilson 2001) and as a result have undergone major local and regional declines (e.g. O'Brien et al. 2019; van Vliet et al. 2007), while remaining an important source of protein for human populations. Therefore, monitoring the status of forest ungulates is a critical conservation need.

The 5260 km^2 Dja Faunal Reserve (DFR) is Cameroon's largest protected area (Figure 1). The reserve is a World Heritage Site (UNESCO 2018; the DFR and its buffer zone constitute the Dja Biosphere Reserve), with its extant megafauna considered one of the reserve's Outstanding Universal Values (UNESCO 2018). The DFR harbours exceptional biodiversity and provides one of the last strongholds for several globally threatened species including the African forest elephant (*Loxodonta cyclotis* Matschie, 1900) and western lowland gorilla (*Gorilla gorilla gorilla* Savage & Wyman, 1847), both Critically Endangered, and the Endangered central chimpanzee (*Pan troglodytes troglodytes* Blumenbach, 1775). The reserve has three Vulnerable species of pangolins; black-bellied pangolin (*Phataginus tetradactyla* Linnaeus, 1766), white-bellied pangolin (*Phataginus tricuspis* Rafinesque, 1821), and giant pangolin (*Smutsia gigantea* Illiger, 1815), and a diverse community of forest ungulates which are primary targets for trade in bushmeat.

Within and around the DFR, illegal hunting is occurring largely through non-traditional means, such as guns and wire snares, with the products supplying the commercial and illegal wildlife trade as well as augmenting local food supplies (Bruce et al. 2018; UNESCO 2018). Other significant threats to biodiversity are numerous. These include logging, agricultural clearance for subsistence crops and commercial crops such as pineapple, loss of the last remaining large forested corridor to a proposed road development in the

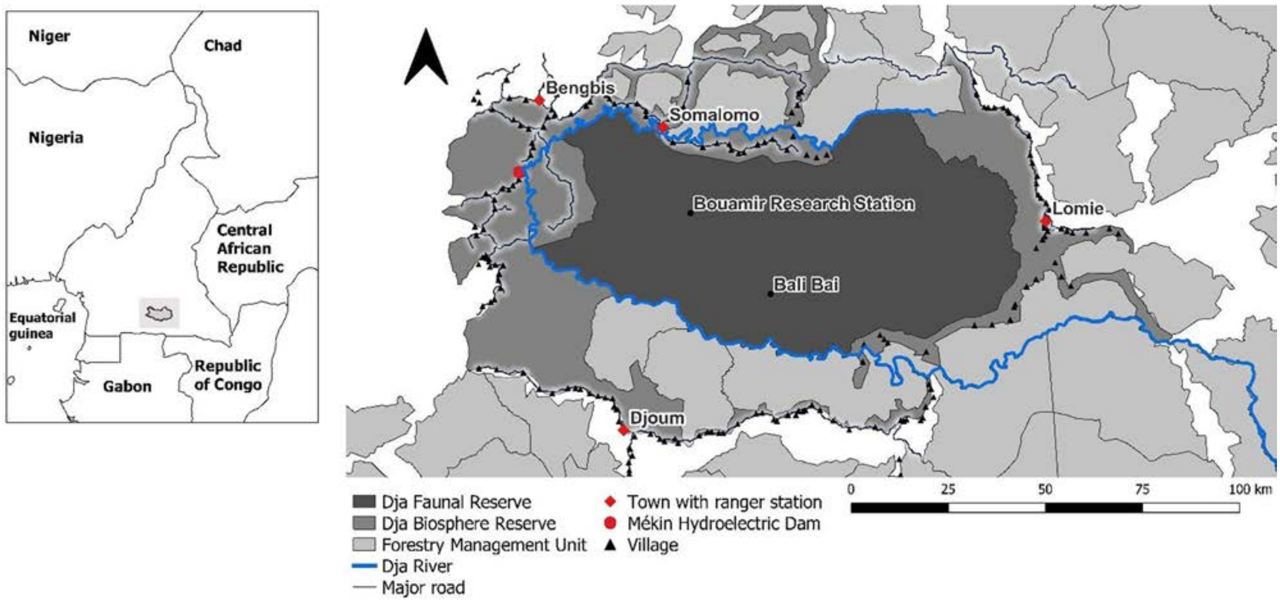


Figure 1: Location of the Dja Faunal Reserve, Cameroon.

south-east, rubber plantations (e.g. Sud-Cameroun Hévéa), and the ecological impacts of existing (the Hydro Mekin) and planned hydroelectric dams (MINFOF and IUCN 2015; Muchaal and Ngandjui 1999).

Previous surveys and inventories of ungulate fauna, particularly forest antelopes, of DFR, and Central and West Africa more broadly, have been based on line-transect sampling, (Bruce et al. 2018; MINFOF and IUCN 2015). However, forest ungulates are difficult to monitor using transect methods based on direct sightings or signs as many species are solitary, nocturnal, shy, spend long periods concealed in dense vegetation, and the spoor and droppings are mostly not identifiable to species with confidence (Croes et al. 2007; Jost Robinson et al. 2017; Rovero and Marshall 2004; van Vliet et al. 2008).

The main objective of our study was to provide replicable baseline information on all medium to large terrestrial mammal species occurring in the DFR, through systematic camera-trap grids of 35–41 cameras each (Table 1) deployed at eight locations across the reserve between 2016–2020. In this paper, we provide new information on the status and distribution of forest antelopes and other ungulate species in the DFR using this data set. Our research represents the first major study of the full ungulate community in one of the most important sites for antelope conservation in Central and West Africa and provides insights and baselines which will allow assessment of conservation progress through future monitoring using the same standardised methodology.

2 Materials and methods

Study area: The DFR is a relatively flat plateau of round-topped hills and ranges in altitude from 600–800 m asl (MINFOF and IUCN 2015). The topography is mainly shallow valleys on either side of a ridgeline that cuts through the DFR east to west (MINFOF and IUCN 2015).

Table 1: Survey effort, eight camera-trap grids deployed in the Dja Faunal Reserve between November 2015 and November 2020.

Management sector	Grid name	Operational period	Number of cameras	Camera days
North Sector (secteur nord)	NS2016	14/11/2015–06/05/2016	41	3725
South Sector (secteur sud)	SS2017	04/04/2017–26/07/2017	40	3371
North Sector (secteur nord)	NS2018	22/01/2018–08/05/2018	38	3647
East Sector (secteur est)	ES2018	27/01/2018–17/05/2018	39	3787
South Sector (secteur sud)	SS2018	15/08/2018–11/12/2018	39	3689
North Sector (secteur nord)	NS2019	30/04/2019–17/09/2019	37	3421
West Sector (secteur ouest)	WS2020	04/10/2019–09/02/2020	35	2959
East Sector (secteur est)	ES2020	13/05/2020–05/11/2020	36	3678

Swamp habitat is common on the floor of valleys, particular in the southern part of reserve which has greater elevational variation. Tributaries throughout the DFR flow into the Dja River (MINFOF and IUCN 2015, UNESCO 2018). Three major forest types occur within the reserve: terra firma forest; monodominant forest (*Gilbertiodendron* sp.), and seasonally inundated forests (Djuikouo et al. 2010). There are four main seasons: the long rains (August–November); the dry season (November–March); the short rains (March–May); and a shorter dry season (June–July), though some rain falls in all months of the year (MINFOF and IUCN 2015). During the dry season there is on average <100 mm of rainfall out of the mean annual rainfall of approximately 1570 mm (UNESCO 2018). The mean annual temperature is 24 °C, varying between 18 °C in the coolest month (July) and 30 °C in the warmest month (February) (MINFOF and IUCN 2015).

Cameroon's Ministry of Forests and Fauna (MINFOF) is responsible for the management of the DFR and the Biosphere Reserve. The DFR has been divided into four management sectors with a base responsible for each sector in the nearest town: Lomié (East Sector), Djoum (South Sector), Meyomessala (West Sector), and Somalomo (North Sector).

Survey design and camera deployment: We setup eight camera-trap grids, with 2 km camera spacing, across the four management sectors of the reserve (Table 1 and Figure 2). Each grid operated long enough to achieve at least 1000 camera-trap days of sampling effort (O'Brien et al. 2003).

We used three camera models (Bushnell Trophy Aggressor (Bushnell Outdoor Products, Kansas, USA), Reconyx HC500 (RECONYX Inc., Wisconsin, USA) and Cuddeback Long Range IR E2 (Cuddeback, Wisconsin, USA)) across the eight camera-trap grids. Global Positioning System receivers were used to locate the grid points on the survey map. We placed a single camera at a height of about 30 cm as close to the grid sampling point as possible, with a consistent and unobstructed field of view. The cameras were programmed to take three images per trigger.

Data analysis: We used Exiv2 software (Huggel 2012) to extract EXIF information from each photograph (image name, date and time) into an Excel spreadsheet (Microsoft Office Professional Plus 2010). We identified animals in the photographs to species where possible, or to lowest taxonomic level discernible in unclear images. We analysed the resulting data with the 'CTAP' camera-trap data analysis software (Amin and Wacher 2017) and the R statistical package (R Development Core Team 2019).

We calculated the trap rate (as a relative abundance index – RAI) for each species and for each sampling grid as the total number of "independent detections" divided by the number of days cameras were operational × 100. We defined an "independent detection" as any sequence of images for a given species occurring after an interval of ≥60 min from the previous trigger (three-image sequence) of that species (Amin et al. 2015).

We used occupancy modelling (MacKenzie et al. 2006) to estimate the probability of site use for each species within each survey grid and in each management sector. We constructed a detection/non-detection history, using a five-day period as the sampling occasion, for each camera-trap site. For occupancy analysis at management sector level, we used the whole survey dataset, grouped into grids. Data

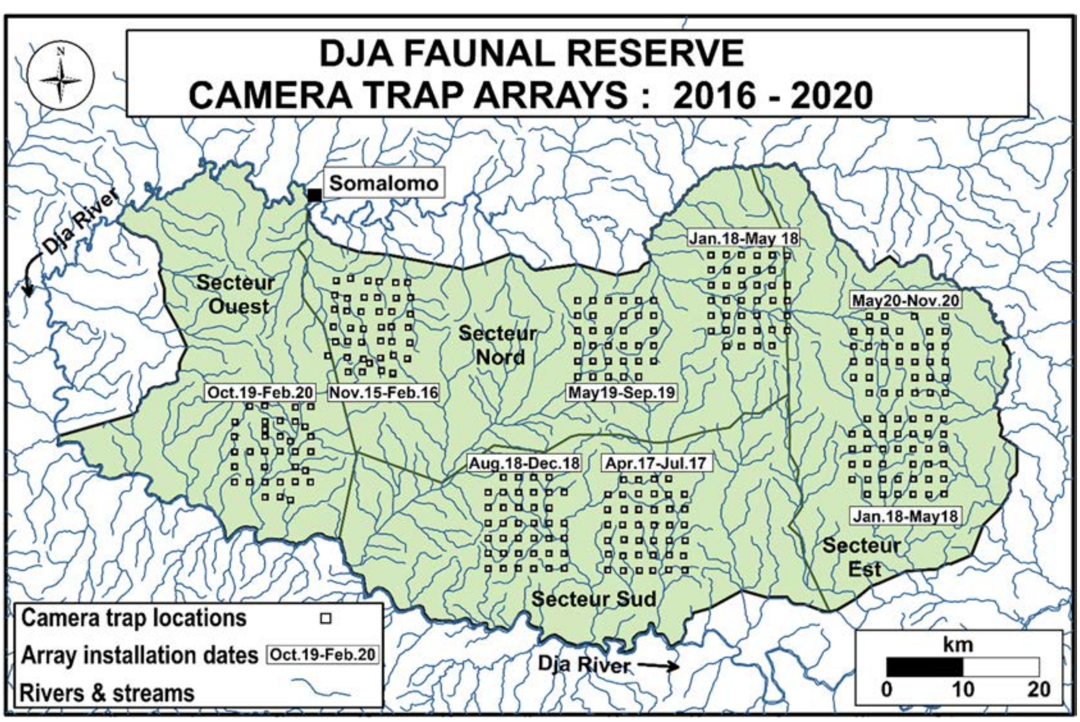


Figure 2: Location of camera-trap survey grids, and operational dates [label format month.year (start)–month.year (end)], in Dja Faunal Reserve, 2016–2020.

collection at each camera site was carried out in a short time so that an assumption of closure is reasonable, and we assume that occupancy for each species is plausibly constant over the period of the study. We expect seasonal effects on species presence and activity to be minimal. We also accounted for individual grids in estimating detection probability. We performed Bayesian occupancy analysis implemented in *JAGS 4.3.0* (Plummer 2003), accessed through *R 3.6.0* (R Code Development Team 2019), using the package *RJAGS 3-10* (Plummer 2014). We ran three Markov chain Monte Carlo (MCMC) chains with 110,000 iterations, a burn-in of 10,000 and a thinning rate of 10. This combination of values ensured an adequate number of iterations to characterise the posterior distribution of the modelled occupancy estimate. We checked for chain convergence with trace plots and the Gelman-Rubin statistic (Gelman et al. 2004), *R*-hat, which compares between and within chain variation. *R*-hat values below 1.1 indicate convergence (Gelman and Hill 2006). We assessed model fit using Freeman-Tukey discrepancy (Kery and Schaub 2012). We calculated the *p* value, i.e., the probability of obtaining a discrepancy at least as large as the observed discrepancy if the model fits the data. Values near 0.5 indicate a good fit; values above 0.9 or below 0.1, a poor fit.

We constructed circadian (24 h) activity patterns for species from the time of detections. In addition to comparing occupancy results between management sectors, we mapped modelled occupancy estimate for each species at each camera sampling grid to aid in assessing species distribution.

3 Results

The surveys accumulated a total of 28,277 camera-trap days over eight grids (305 camera-trap sampling points), and the minimum of 1000 camera-trap days was achieved at all grids (mean 93 days/camera). Fifteen cameras failed to return any data.

There were 30,601 independent detections of 12 species of forest ungulates (Table 2). Overall, blue duiker (*Philantomba monticola* Thunberg, 1789) was the most frequently recorded forest ungulate (Figure 3, 46.4% of detections, RAI = 50.25) across the DFR. Peters' duiker (*Cephalophus callipygus* Peters, 1876) also had a significantly higher RAI (=38.75) than the other two sympatric medium-large duikers, bay duiker (*Cephalophus dorsalis* Gray, 1846, RAI = 6.86) and yellow-backed duiker (*Cephalophus silvicultor* Afzelius, 1815, RAI = 3.48). The white-bellied duiker (*Cephalophus leucogaster* Gray, 1873, RAI = 1.6) and the black-fronted duiker (*Cephalophus nigrifrons* Gray, 1871, RAI = 0.47) were the least encountered duiker species (Figure 3). The sitatunga (*Tragelaphus spekii* Speke, 1863), forest buffalo (*Syncerus caffer nanus* Sparrman, 1779) and lowland bongo (*Tragelaphus eurycerus* Ogilby, 1837) had less than 30 independent detections (RAI≤0.1). Together, blue duiker and Peters' duiker accounted for 82% of the total forest ungulate detections.

Species distribution: The blue duiker and Peters' duiker were distributed throughout the reserve with occupancy approaching 1 (Figure 4, Table 3). The nocturnal bay duiker and yellow-backed duiker also occurred in all grids but with lower occupancy in the East and West Sectors (posterior probability = 0.83–1, Table 3). Bay duiker occupancy was also higher in the North Sector compared to South Sector (posterior probability = 0.8–1). The white-bellied duiker and water chevrotain (*Hyemoschus aquaticus* Ogilby, 1841) showed

Table 2: Number of images and number of sites detected (in brackets) for 12 forest ungulate species recorded in eight camera grids deployed across the Dja Faunal Reserve.

Species	Number of images (number of sites detected)							
	NS2016 camera grid	NS2018 camera grid	NS2019 camera grid	ES2018 camera grid	ES2020 camera grid	SS2017 camera grid	SS2018 camera grid	WS2019 camera grid
Bay duiker	2909 (31)	3194 (30)	8648 (26)	342 (12)	1170 (20)	2270 (31)	3388 (24)	2067 (13)
Black-fronted duiker	897 (4)	19 (1)	59 (4)	91 (5)	230 (3)	110 (5)	0 (0)	48 (2)
Blue duiker	30,611 (30)	25,254 (38)	20,001 (34)	7592 (35)	5639 (27)	11,466(35)	16,692(35)	28,755 (32)
Peters' duiker	8468 (30)	13,157 (38)	24,680 (31)	5641 (33)	5189 (27)	27,703 (36)	27,002 (38)	7411 (28)
Yellow-backed duiker	2088 (28)	2773 (20)	2694 (26)	941 (20)	843 (16)	1462 (29)	1819(30)	274 (11)
White-bellied duiker	0 (0)	135 (5)	1105 (13)	42 (4)	100 (6)	1385 (24)	1681 (26)	142 (6)
Bates' pygmy antelope	140 (6)	105 (6)	35 (3)	325 (7)	17 (4)	43 (9)	32 (6)	30 (1)
Bongo	21 (2)	0 (0)	0 (0)	0 (0)	0 (0)	17 (2)	9 (1)	0 (0)
Sitatunga	70 (5)	177 (4)	15 (1)	15 (1)	18 (2)	25 (2)	0 (0)	15 (1)
Forest buffalo	117 (2)	0 (0)	0 (0)	0 (0)	0 (0)	9 (1)	0 (0)	0 (0)
Water chevrotain	126 (2)	690 (4)	330 (3)	47 (1)	0 (0)	1510 (14)	1218 (11)	208 (2)
Red river hog	4507 (20)	993 (12)	3189 (22)	1545 (18)	734 (10)	13,059 (31)	2395 (22)	2359 (17)

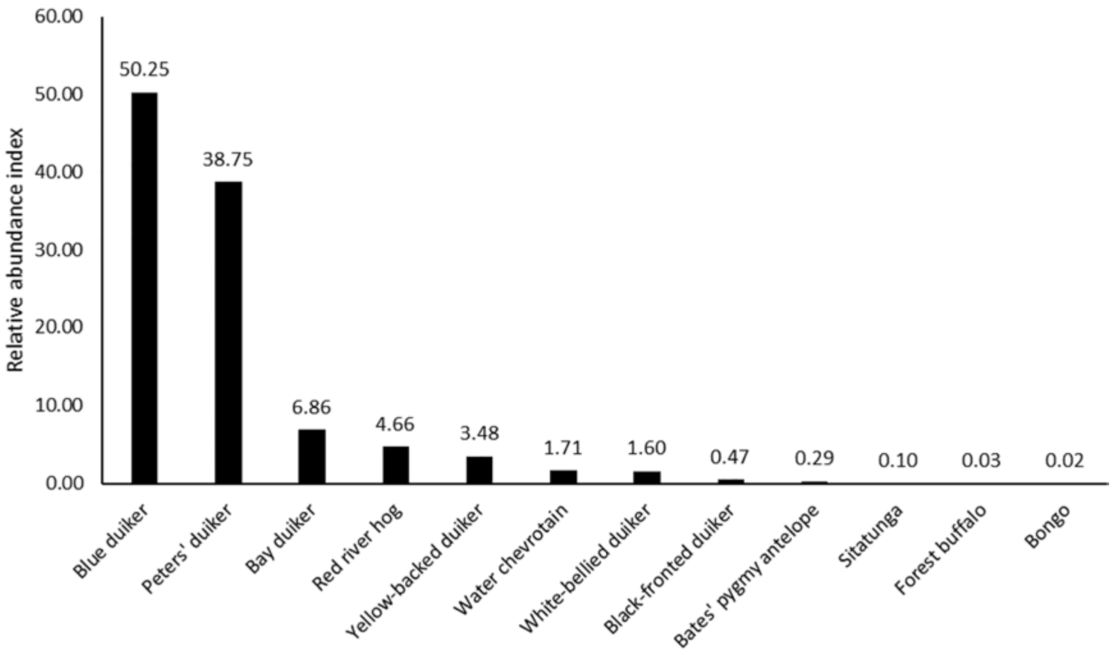


Figure 3: Relative abundance indices for 12 ungulate species recorded in the Dja Faunal Reserve, Cameroon, camera-trap study 2016–2020.

significantly higher occupancy in the South Sector (posterior probability = 1). The black-fronted duiker, Bates' pygmy antelope (*Neotragus batesi* de Winton, 1903), and Sitatunga had low occupancy values throughout the reserve. Red river hog was widely distributed in the DFR. The bongo was only recorded at five sites, two in the western part of the North Sector and three sites in the South Sector. Similarly, the forest buffalo was recorded at two sites in the western part of the North Sector and one site in the eastern part of the South Sector.

Species activity pattern: Comparison of the four duiker species with the highest occupancy across the eight camera-trap grids revealed the two medium-sized (and similarly sized) species, Peter's duiker and bay duiker, were active in different time periods (Figure 4). The diurnal Peter's duiker shared day-time activity with the much smaller blue duiker, while the nocturnal bay duiker was active in the same general period as mainly used by the much larger yellow-backed duiker.

Within this broader pattern, blue duiker and Peters' duiker and perhaps yellow-backed duiker and bay duiker showed a tendency to crepuscular peaks of activity close to dawn and dusk. The less frequently recorded and smaller species showed less obvious indications of temporal partitioning. The black-fronted duiker showed a predominantly diurnal activity pattern with intermittent nocturnal activity while the similar sized white-bellied duiker was also diurnal with some degree of crepuscular behaviour. Bates' pygmy antelope was active throughout day and night with low peaks around dawn and dusk. The two Tragelaphine antelopes, sitatunga (recorded at 16 camera sites) and bongo (recorded at only five camera sites) both showed primarily nocturnal behaviour.

Among the other ungulates, water chevrotain was mostly active at night with sporadic periods of activity during the day. Forest buffalo records also occurred both night and day but were too few to infer any consistent pattern. The red river hogs were active throughout the 24 h cycle, though at higher rates at night than during the day.

4 Discussion and conclusion

Our extensive camera-trap study provides important insights into the status and ecology of 12 forest ungulate species occurring in the World Heritage DFR. We focus on ungulates because as a group they include some of the species heavily targeted by hunters engaged in the bushmeat trade in the region (Fa et al. 2005). The DFR retains an intact community of forest ungulates. The blue duiker is the most abundantly recorded species with occupancy 90% or more in all parts of the surveyed area. It is usually found to be the most abundant species in ungulate communities where it occurs, and it has been suggested that it is relatively resilient under high hunting pressure due to flexibility in habitat, capacity to live at high density with relatively high fecundity (Kingdon and Hoffmann 2013; Mockrin 2008; van Vliet and Nasi 2019). Peters' duiker is

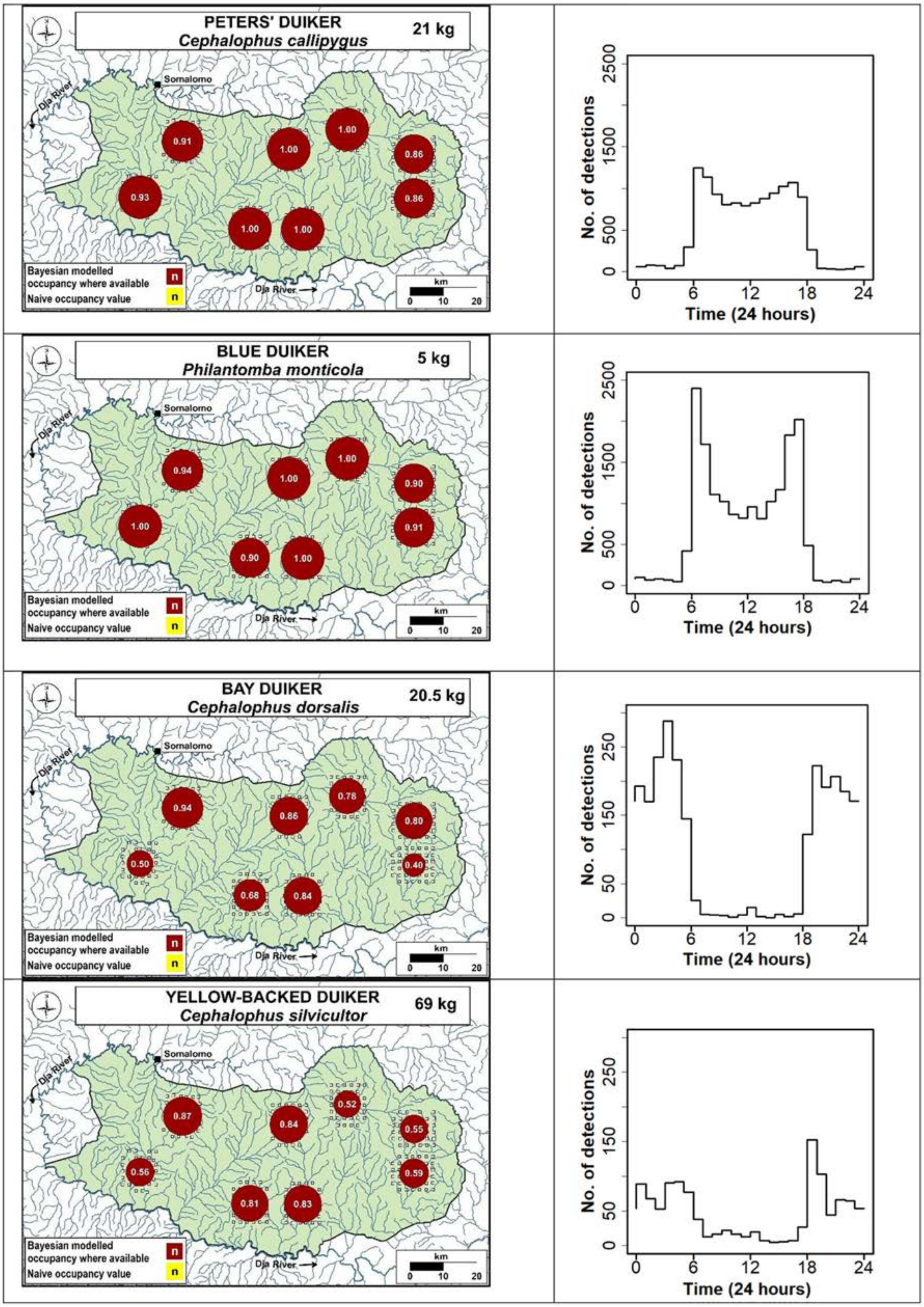


Figure 4: Occupancy by camera-trap grid (left) and 24 h activity patterns (right) for Peters' duiker and blue duiker; bay duiker and yellow-backed duiker; black-fronted duiker and white-bellied duiker; sitatunga and bongo; Bates' pygmy antelope and forest buffalo; water chevrotain and red river hog, Dja Forest Faunal Reserve, Cameroon. Note *y*-axis scales for activity patterns.

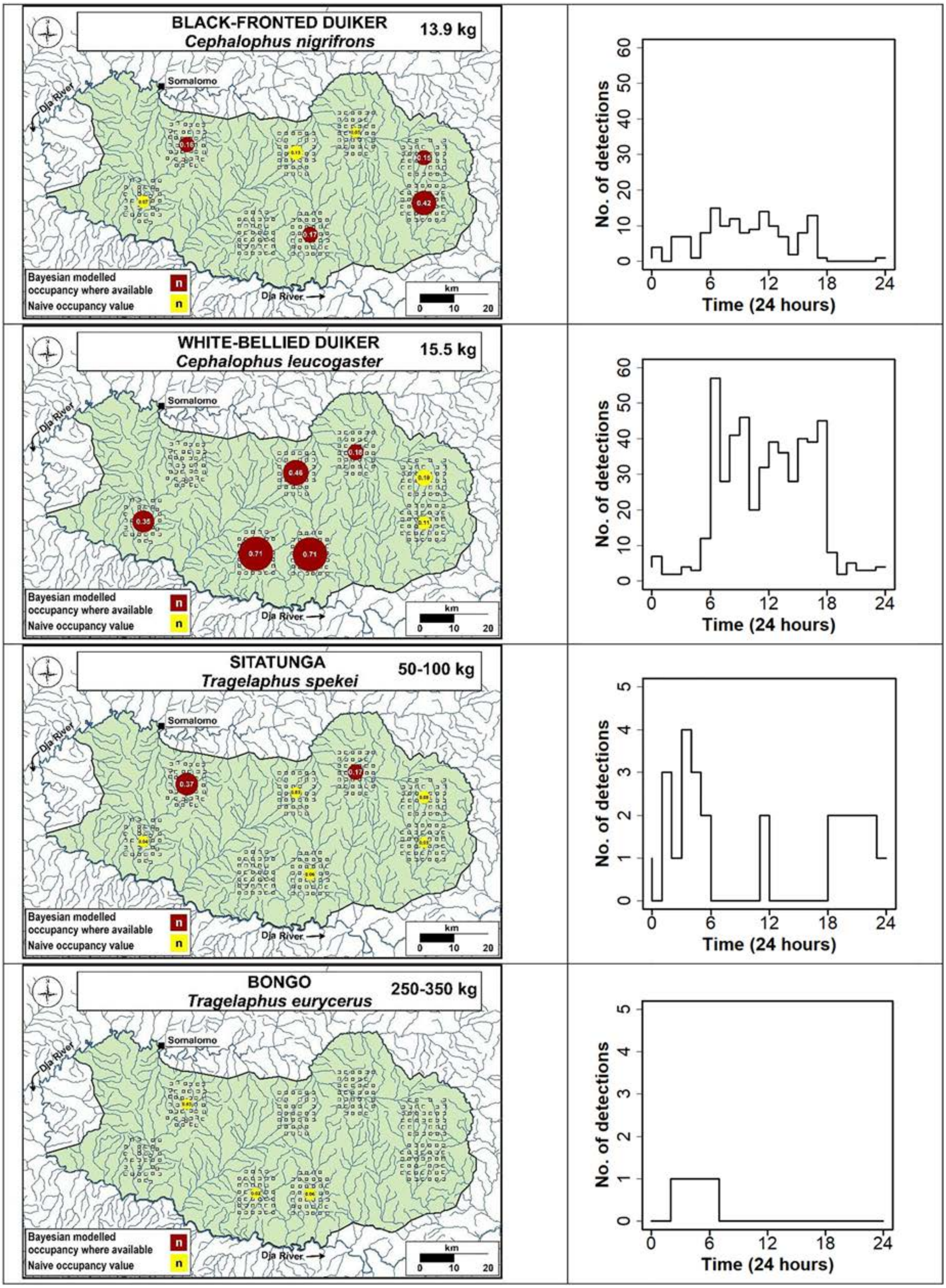


Figure 4: Continued.

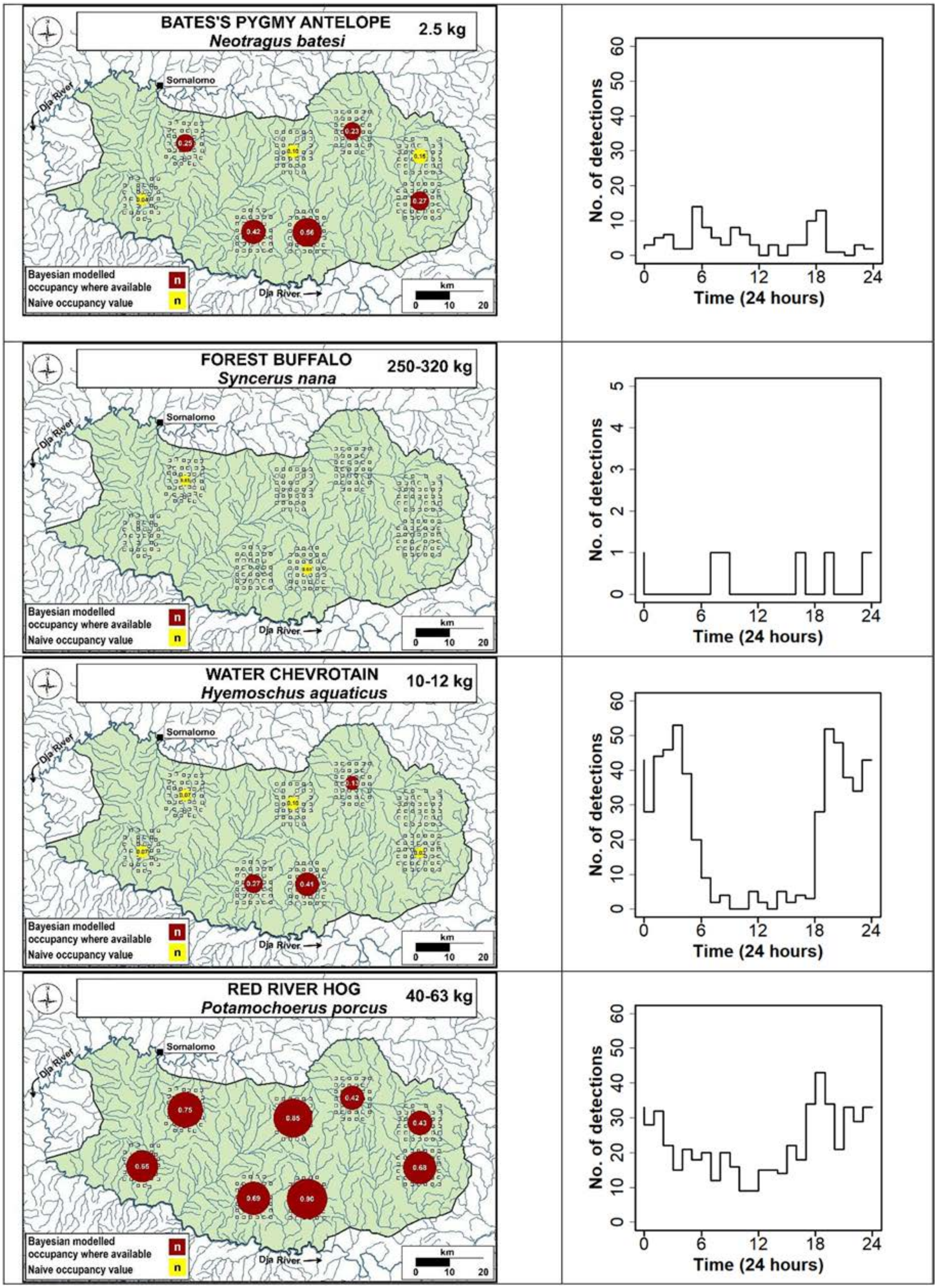


Figure 4: Continued.

Table 3: Forest ungulate species modelled occupancy estimates with 95% credible intervals (in brackets) for the North, East, South and West management sectors, Dja Faunal Reserve, Cameroon, 2016–2020.

Species	North Sector	East Sector	South Sector	West Sector
Bay duiker	0.911 (0.846–0.971)	0.647 (0.458–0.835)	0.755 (0.65–0.856)	0.486 (0.307–0.671)
Black-fronted duiker	0.151 (0.065–0.249)	0.201 (0.084–0.328)	0.103 (0.002–0.361)	–
Blue duiker	0.977 (0.946–0.999)	0.921 (0.85–0.983)	0.955 (0.905–0.995)	0.945 (0.86–1)
Peters' duiker	0.967 (0.929–0.996)	0.861 (0.77–0.948)	0.985 (0.956–1)	0.931 (0.828–1)
Yellow-backed duiker	0.816 (0.717–0.916)	0.568 (0.425–0.71)	0.857 (0.77–0.936)	0.554 (0.274–0.871)
White-bellied duiker	0.286 (0.148–0.424)	–	0.71 (0.594–0.821)	0.348 (0.112–0.616)
Bates' pygmy antelope	0.212 (0.111–0.322)	0.331 (0.15–0.544)	0.459 (0.185–0.808)	–
Water chevrotain	0.104 (0.044–0.17)	0.041 (0–0.099)	0.331 (0.221–0.445)	0.097 (0.011–0.2)
Sitatunga	0.201 (0.072–0.344)	–	0.017 (0–0.05)	–
Red river hog	0.763 (0.621–0.901)	0.534 (0.337–0.753)	0.815 (0.69–0.94)	0.665 (0.419–0.929)

Lowland bongo and forest buffalo had insufficient data to model occupancy. '–' indicates estimate had very wide 95% credible interval.

also relatively abundant and well-distributed in the reserve, a pattern also seen in several undisturbed forests in Central and West Africa (Kingdon and Hoffmann 2013; Nakashima et al. 2013; O'Brien et al. 2019). The mainly nocturnal bay duiker and yellow-backed duiker are less abundant but still readily detected and widespread. The black-fronted duiker was found to be relatively rare despite extensive swamp habitat on the floor of reserve's valleys. The white-bellied duiker is poorly known across its range, and in DFR it was found most frequently in the southern part of the reserve. Water chevrotain shows a similar distribution, occurring mostly in the South Sector with its more extensive swamp habitat. The species may have disappeared from much of their historic range in Central and West Africa (Hart 2013) and these results indicate that the DFR remains an important protected area for chevrotain. The lowland bongo appears to be very rare, detected in only five sampling sites across the reserve. The status of the lowland bongo in Central and West Africa remains uncertain with populations fragmented and declining in many areas (East 1999; Elkan and Smith 2013). Camera-traps offer an effective approach for assessing the status of this elusive, mostly nocturnal and yet wide-ranging species in dense forest habitat (Amin et al. 2016). In the DFR, bongo would benefit from a camera-trap study targeted on use of forest clearings, which should also provide further insight on sitatunga, forest buffalo and other important species such as forest elephant and western lowland gorilla.

The study has also highlighted the role of continuous 24 h multi-species monitoring uniquely achievable with camera-traps in helping elucidate patterns of ecological partitioning among closely related species. The results suggest some partitioning patterns among the more widespread and abundant duikers based on activity pattern and body size, with the most frequent species pair of similar size active at different times, and the more frequently detected species active simultaneously being of different sizes. Previous study comparing activity pattern in two sympatric diurnal duikers (5 kg *P. monticola* sharing habitat with the 11–12 kg *C. natalensis*) conform to the extent that these two species also differ in body size (Bowland and Perrin 1995). A more focused approach stratifying camera deployment to compare habitat use among rarer antelopes would provide further insight on forest ungulate community ecology.

Bushmeat studies in the region have shown that forest ungulates constitute the highest proportion of catches in terms of numbers and weight (Fa et al. 2005; Martin et al. 2020; Nasi et al. 2011). Large-bodied animals with low reproductive rates are the most vulnerable to hunting and therefore, the first to be extirpated from hunting forests (Nasi et al. 2008; O'Brien et al. 2019; van Vliet et al. 2008). There is now evidence that hunting in southeast Cameroon has resulted in an increase of the proportion of blue duikers killed in snare traps and a decline in the proportion of red duikers (*Cephalophus* spp.), with the white-bellied duiker and black-fronted duiker rarely caught (Duda et al. 2017; Jeanmart 1998; Kamgaing et al. 2019; Martin et al. 2020; Yasuoka et al. 2015). A recent study of wild meat hunting by 10 Baka villages along the Djoum-Mintom road, south of the DFR and Dja River found that 42% of ungulates caught in 1946 hunting trips (by 121 hunters) were blue duiker, followed by bay duiker (23%) and Peters' duiker (16%) (Martin et al. 2020). The inverse relationship in the frequencies of Peter's duiker and Bay duiker in camera trapping results compared to the reported hunting outcomes is notable. More detailed investigation of hunting methods and exact hunting areas would help explain this. The remaining 19% of the hunted ungulate catch was of seven species and undetermined duikers. There were no bongo and forest buffalo catches, and white bellied duiker (three catches) and black fronted duiker (23 catches) were the least caught duiker species. It may be that the white-bellied duiker and black fronted duiker are naturally less abundant in the region.

The Cameroon Government is strengthening conservation measures as outlined in the 2020–2025 Dja Faunal Reserve Management Plan. In the North Sector, the DFR Conservation Service is considering a community partnership agreement on sustainable access to forest resources. The DFR management is also implementing a community surveillance network and increasing law-enforcement patrols, especially along the southern boundary of the DFR with its many exit routes. Patrol strategies are increasingly targeted towards zones of high human activity and areas where wildlife are vulnerable, for example around bais. With improved security and appropriate engagement with local communities and the private sector in the region, it is hoped that the DFR will maintain its World Heritage status. The Dja Biosphere Reserve is an integral component of the TRIDOM transborder forest which covers 178,000 km^2, roughly 10% of the Central African forest. It offers one of the last remaining opportunities for the long-term conservation of great apes, forest elephant, a community of forest ungulates and other threatened species in the region.

Research ethics: Our research did not include handling of wild animals. It was based on remote sensing using camera-traps and approval for conducting the study was obtained from the Cameroon Ministry of Forests and Fauna.

Acknowledgements: We thank the Cameroon Ministry of Forests and Fauna and the late Conservator Hilaire Ndinga of the Dja Faunal Reserve for support, and the Ministry ecoguards and local porters who accompanied the survey teams in the field. We also thank Tom Bruce, David Olson, Hannah Klair and Constant Ndjassi for their input in the initial stages of the surveys.

Author contributions: All the authors have accepted responsibility for the entire content of this submitted manuscript and approved submission.

Research funding: None declared.

Conflict of interest statement: The authors declare no conflicts of interest regarding this article.

References

Amin, R., Andanje, S.A., Ogwonka, B., Ali, A.H., Bowkett, A.E., Omar, M., and Wacher, T. (2015). The northern coastal forests of Kenya are nationally and globally important for the conservation of Aders' duiker *Cephalophus adersi* and other antelope species. Biodivers. Conserv. 24: 641–658.

Amin, R., Bowkett, A., and Wacher, T. (2016). The use of camera trapping to monitor threatened forest antelope species. In: Bro-Jørgensen, J. and Mallon, D.P. (Eds.), Antelope conservation: from diagnosis to action, 1st ed. John Wiley & Sons, London, pp. 190–216.

Amin, R. and Wacher, T. (2017). A new comprehensive package for the management and analysis of camera trap data for monitoring antelopes and other wild species. Gnusletter 34: 21–23.

Bowland, A.E. and Perrin, M.R. (1995). Temporal and spatial patterns in blue duikers *Philantomba monticola* and red duikers *Cephalophus natalensis*. J. Zool. 237: 487–498.

Bruce, T., Ndjassi, C., Fowler, A., Ndimbe, M., Fankem, O., Tabue Mbobda, R.B., Kobla, A., Wabo Puemo, F.A., Amin, R., Wacher, T., et al. (2018). *Faunal inventory of the Dja Faunal Reserve, Cameroon – 2018*. Unpublished Report. Ministry of Forestry and Wildlife (MINFOF), Zoological Society of London – Cameroon Country Programme, African Wildlife Foundation, Yaoundé, Cameroon.

Croes, B.M., Laurance, W.F., Lahm, S.A., Tchignoumba, L., Alonso, A., Lee, M.E., Campbell, P., and Buij, R. (2007). The influence of hunting on antipredator behavior in Central African monkeys and duikers. Biotropica 39: 257–263.

Djuikouo, M.N.K., Doucet, J.L., Nguembou, C.K., Lewis, S.L., and Sonké, B. (2010). Diversity and above ground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. Afr. J. Ecol. 48: 1053–1063.

Duda, R., Gallois, S., and Reyes-Garcia, V. (2017). Hunting techniques, wildlife offtake and market integration. A perspective from individual variations among the Baka (Cameroon). Afr. Stud. Monogr. 38: 97–118.

East, R. (1999). *African antelope database 1998. Occasional paper of the IUCN species survival commission no. 21*. IUCN, Gland and Cambridge, pp. x + 434.

Elkan, P.W. and Smith, J.L.D. (2013). Tragelaphus eurycerus Bongo. In: Kingdon, J. and Hoffmann, M. (Eds.), *Mammals of Africa: volume VI: pigs, hippopotamuses, chevrotain, giraffes, deer and bovids*. Bloomsbury Publishing, London, pp. 179–185.

Fa, J.E., Ryan, S.F., and Bell, D.J. (2005). Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. Biol. Conserv. 121: 167–176.

Feer, F. (1995). Seed dispersal in African forest ruminants. J. Trop. Ecol. 11: 683–689.

Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. (2004). Bayesian data analysis. Chapman and Hall/CRC, New York.

Gelman, A. and Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*. Cambridge: Cambridge University Press.

Hart, J.A. (2013). Hyemoschus aquaticus water chevrotain. In: Kingdon, J. and Hoffmann, M. (Eds.), *Mammals of Africa: volume VI: pigs, hippopotamuses, chevrotain, giraffes, deer and bovids*. Bloomsbury Publishing, London, pp. 88–92.

Huggel, A. (2012). Exiv2 software tool, Available at: <http://www.exiv2.org/index.html> (Accessed 16 May 2012).

Jeanmart, P. (1998). Tentative d'Élaboration d'un Plan de Gestion de la Chasse Villageoise dans la Réserve de Faune du Dja. Projet ECOFAC-Composante Cameroun. Groupement AGRECO- G.E.I.E. - BDPA-SCETAGRI - SECA - CIRAD FORET, Bruxelles.

Jost Robinson, C.A., Zollner, P.A., and Kpanou, J.B. (2017). Night and day: evaluating transect methodologies to monitor duikers in the Dzanga-Sangha Protected Areas, Central African Republic. Afr. J. Ecol. 55: 222–232.

Kamgaing, T.O.W., Dzefack, Z.C.B., and Yasuoka, H. (2019). Declining ungulate populations in an African rainforest: evidence from local knowledge, ecological surveys and bushmeat records. Front. Ecol. Evol 7: 249.

Kery, M. and Schaub, M. (2012). Bayesian population analysis using WinBUGS – a hierarchical perspective. Academic Press, Cambridge, Massachusetts.

Kingdon, J. and Hoffmann, M. (Eds.) (2013). *Mammals of Africa. Volume VI: pigs, hippopotamuses, chevrotain, giraffes, deer and bovids*. Bloomsbury Publishing, London.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E. (2006). *Occupancy estimation and modelling*. Elsevier, Amsterdam.

Martin, A.E., Ros Brull, G., Funk, S.M., Luiselli, L., Okale, R., and Fa, J.E. (2020). Wild meat hunting and use by sedentarised Baka Pygmies in Southeastern Cameroon. PeerJ 8: e9906.

MINFOF and IUCN (2015). Caractérisation de la population de grands et moyens mammifères dans la reserve de faune du Dja: potentiel et menaces. Ministry of Forestry and Wildlife, IUCN, Yaoundé, Cameroon.

Mockrin, M.H. (2008). *The spatial structure and sustainability of subsistence wildlife harvesting in Kabo, Congo*, Ph.D. thesis. New York, USA, Columbia University.

Muchaal, P.K. and Ngandjui, G. (1999). Impact of village hunting on wildlife populations in the Western Dja Reserve, Cameroon. Conserv. Biol. 13: 385–396.

Nakashima, O., Inoue, E., and Akomo-Okoue, E. (2013). Population density and habitat preferences of forest duikers in Moukalaba-Doudou National Park, Gabon. Afr. Zool. 48: 395–399.

Nasi, R., Brown, D., Wilkie, D., Bennett, E., Tutin, C., van Tol, G., and Christophersen, T. (2008). *Conservation and use of wildlife-based resources: the bushmeat crisis*. Secretariat of the Convention on Biological Diversity, Montreal, and Center for International Forestry Research (CIFOR), Bogor. Technical Series no. 33, 50. Available at: https://www.cbd.int/doc/publications/cbd-ts-33-en.pdf.

Nasi, R., Taber, A., and Van Vliet, N. (2011). Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. Int. For. Rev. 13: 355–368.

O’Brien, T.G., Ahumada, J., Akampurila, E., Beaudrot, L., Boekee, K., Brncic, T., Hickey, J., Jansen, P.A., Kayijamahe, C., Moore, J., et al. (2019). Camera trapping reveals trends in forest duiker populations in African National Parks. Remote Sens. Ecol. Conserv 6: 168–180.

O’Brien, T.G., Kinnaird, M.F., and Wibisono, H.T. (2003). Crouching tigers, hidden prey: sumatran tiger and prey populations in a tropical forest landscape. Anim. Conserv. 6: 131–139.

Plummer, M. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik, K. Leisch, F. and Zeileis A. (Eds), *Proceedings of the 3rd international workshop on distributed statistical computing*. Vienna, Austria. https://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf.

Plummer, M. (2014). *RJAGS: Bayesian graphical models using MCMC. R package version 3-10*.

R Development Core Team. (2019). *R: a language and environment for statistical computing*. Foundation for Statistical Computing, Vienna, Austria, Available at: <http://www.R-project.org>.

Rovero, F. and Marshall, A.R. (2004). Estimating the abundance of forest antelopes by line transect techniques: a case from the Udzungwa Mountains of Tanzania. Trop. Zool. 17: 267–277.

UNESCO. (2018). Dja Faunal Reserve, Available at: <whc.unesco.org/en/list/407> (Accessed 9 August 2018).

van Vliet, N. and Nasi, R. (2019). What do we know about the life-history traits of widely hunted tropical mammals? Oryx 53: 670–676.

van Vliet, N., Nasi, R., Emmons, L., Feer, F., Mbazza, P. and Bourgarel, M. (2007). Evidence for the local depletion of bay duiker *Cephalophus dorsalis*, within the Ipassa Man and Biosphere Reserve, North-East Gabon. Afr. J. Ecol. 45: 440–443.

van Vliet, N., Zundel, S., Miquel, C., Taberlet, P., and Nasi, R. (2008). Distinguishing dung from blue, red and yellow-backed duikers through non-invasive genetic techniques. Afr. J. Ecol. 46: 411–417.

White, L.J.T. (1994). Biomass of rain forest mammals in the Lopé Reserve, Gabon. J. Anim. Ecol. 63: 499–512.

Wilkie, D. and Carpenter, J. (1999). Bushmeat hunting in the congo basin. Biodivers. Conserv. 8: 927–955.

Wilson, V.J. (2001). *Duikers of Africa: masters of the African forest floor. A study of duikers, hunting, people and bushmeat.* Chipangali Wildlife Trust, Bulawayo, Zimbabwe, p. 798, Reprinted in 2005 by Zimbi Books, Pretoria, South Africa, Available at: <www.zimbibooks.com>.

Yasuoka, H., Hirai, M., Kamgaing, T.O.W., Dzefack, Z.C.B., Kamdoum, E.C., and Bobo, K.S. (2015). Changes in the composition of hunting catches in southeastern Cameroon: a promising approach for collaborative wildlife management between ecologists and local hunters. Ecol. Soc. 20: Article 25.

Estimating forest antelope population densities using distance sampling with camera traps

RAJAN AMIN, HANNAH KLAIR, TIM WACHER, CONSTANT NDJASSI
ANDREW FOWLER, DAVID OLSON and TOM BRUCE

Abstract Traditional transect survey methods for forest antelopes often underestimate density for common species and do not provide sufficient data for rarer species. The use of camera trapping as a survey tool for medium and large terrestrial mammals has become increasingly common, especially in forest habitats. Here, we applied the distance sampling method to images generated from camera-trap surveys in Dja Faunal Reserve, Cameroon, and used an estimate of the proportion of time animals are active to correct for negative bias in the density estimates from the 24-hour camera-trap survey datasets. We also used multiple covariate distance sampling with body weight as a covariate to estimate detection probabilities and densities of rarer species. These methods provide an effective tool for monitoring the status of individual species or a community of forest antelope species, information urgently needed for conservation planning and action.

Keywords Abundance, antelope, camera trap, Cameroon, Central Africa, distance sampling, Dja Faunal Reserve, forest

Introduction

Antelopes and other artiodactyl species constitute a significant component of forest and woodland ecosystems both in terms of biomass (White, 1994) and ecological services (Feer, 1995). Many species are increasingly threatened by habitat loss and hunting for bushmeat (East, 1998). Forest antelopes are primary targets for the trade in bushmeat (Wilkie & Carpenter, 1999; Fa et al., 2005) and have undergone major local and regional declines as a result (e.g. van Vliet et al., 2007). Therefore, monitoring the status of forest antelopes is a critical conservation need. However, forest antelopes are difficult to monitor using traditional methods based on direct sightings or signs as many species are solitary, nocturnal, shy, spend long periods concealed in dense vegetation, and the spoor and droppings are difficult to identify to species level with confidence (Rovero & Marshall, 2004; Croes et al., 2007; van Vliet et al., 2008; Jost Robinson et al., 2017). DNA-based amplification of species-specific mitochondrial DNA fragments from droppings is possible, but time-consuming, expensive, and largely impractical with currently available analysis techniques (e.g. Breuer & Breuer-Ndoundou Hockemba, 2012; Bowkett et al., 2013; Bourgeois et al., 2019). Here, we present a method based on distance sampling with images from camera traps to obtain density estimates of forest antelopes. We demonstrate its use for monitoring the status of threatened forest antelopes in the Dja Faunal Reserve, southern Cameroon.

Study area

The Dja Faunal Reserve is the largest protected area in Cameroon (5,260 km^2; Fig. 1). The Reserve, a World Heritage Site, has high levels of both flora and fauna diversity, with 107 known mammal species (UNESCO, 2018). Ten species of forest antelopes occur in the Reserve, from the largest (the Near Threatened bongo *Tragelaphus eurycerus*) to one of the smallest (Bates pygmy antelope *Neotragus batesi*) (Table 1). All these antelope species are hunted for bushmeat. Other threatened species include the Critically Endangered western lowland gorilla *Gorilla gorilla gorilla* and African forest elephant *Loxodonta cyclotis*, and the Endangered central chimpanzee *Pan troglodytes troglodytes* (Bruce et al., 2017, 2018). Dja Faunal Reserve comprises round-topped hills of 600–800 m altitude, with valleys on either side of a central east–west ridgeline (MINFOF & IUCN, 2015). The predominant habitat within the Reserve is mixed species rainforest with swamp habitats and some periodically flooded forest patches in valley areas. Mean total annual rainfall is c. 1,600 mm. The Reserve faces many pressures. The surrounding human population is increasing and industries, such as logging, rubber extraction, hydropower, and mining are proliferating, resulting in increased demand for bushmeat. Both illegal subsistence and commercial hunting occur within the Reserve.

Methods

Distance sampling with camera-trap images

We applied the distance sampling method of Howe et al. (2017), who processed video sequences, adapted here for

RAJAN AMIN (Corresponding author, orcid.org/0000-0003-0797-3836), HANNAH KLAIR and TIM WACHER (orcid.org/0000-0002-5552-7577) Zoological Society of London, Regents Park, London NW1 4RY, UK
E-mail raj.amin@zsl.org

CONSTANT NDJASSI, ANDREW FOWLER and TOM BRUCE (orcid.org/0000-0001-6958-1657) Zoological Society of London, Cameroon Office, Yaoundé, Cameroon

DAVID OLSON WWF–Hong Kong, Kwai Chung, Hong Kong

Received 16 July 2020. Revision requested 7 August 2020.
Accepted 15 October 2020.

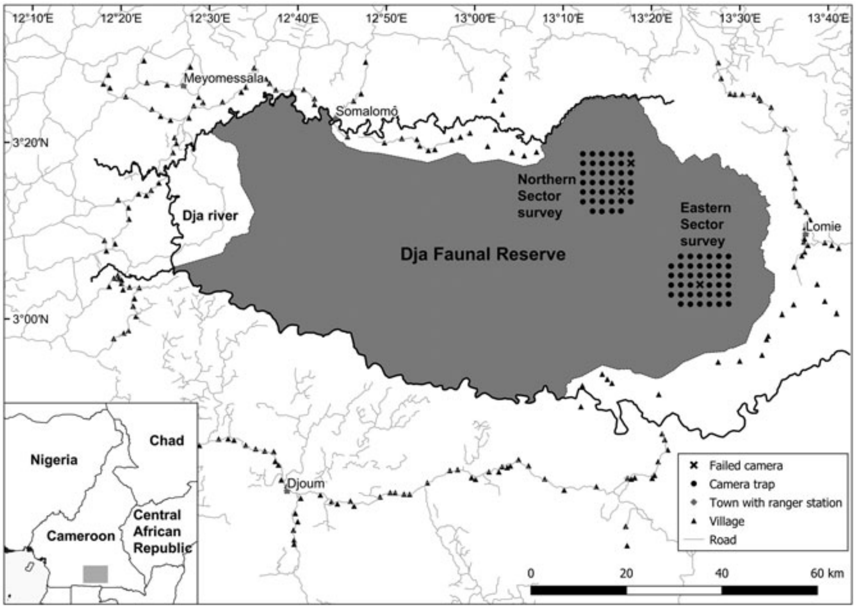


FIG. 1 Location of the two grids, each containing 40 camera traps, deployed in the northern and eastern sectors of Dja Faunal Reserve, Cameroon.

TABLE 1 The 10 forest antelope species detected by camera traps in the northern and eastern sectors of Dja Faunal Reserve, Cameroon (Fig. 1), with the species' IUCN Red List status, mean body weights (from Kingdon & Hoffmann, 2013), and details of detections.

Species	IUCN Red List status (trend)[1]	Mean body weight (kg)	Number of camera placements with detections (number of camera triggers)	
			Northern	Eastern
Peters' duiker *Cephalophus callipygus*	LC (decreasing)	19.6	30 (3,239)	33 (1,795)
Bay duiker *Cephalophus dorsalis*	NT (decreasing)	19.0	31 (751)	12 (86)
Bates pygmy antelope *Neotragus batesi*	LC (unknown)	2.2	6 (21)	7 (111)
White-bellied duiker *Cephalophus leucogaster*	NT (decreasing)	15.5	5 (47)	4 (14)
Black-fronted duiker *Cephalophus nigrifrons*	LC (decreasing)	13.8	4 (23)	5 (30)
Yellow-backed duiker *Cephalophus silvicultor*	NT (decreasing)	66.5	28 (540)	20 (287)
Water chevrotain *Hyemoschus aquaticus*	LC (decreasing)	12.1	3 (8)	1 (17)
Blue duiker *Philantomba monticola*	LC (decreasing)	4.8	30 (6,521)	35 (2,296)
Bongo *Tragelaphus eurycerus*	NT (decreasing)	229.0	2 (7)	0 (0)
Sitatunga *Tragelaphus spekii*	LC (decreasing)	45.0	5 (23)	1 (5)

[1]LC, Least Concern; NT, Near Threatened.

actively triggered still images (see below) from camera-trap surveys, and used estimates of the overall proportion of time animals are active, and thus available for detection, to correct for negative biases in density estimates from 24-hour datasets. We used multiple covariate distance sampling to estimate detection probabilities and densities from the combined dataset of multiple species to provide improved density estimates for species with fewer observations.

Each deployed camera in a survey is treated as a point transect. The cameras were programmed to record a set number of still images at a fixed time interval between images when triggered and with a short latent period t_q between triggers. The temporal effort for each camera is then equal to the camera operation period T divided by the time period between two consecutive triggers T_t. This represents the maximum possible number of triggers. The time period between successive triggers should be sufficiently short so that an animal is unlikely to pass completely through without being detected by the camera (Howe et al., 2017, used 2 s as a snapshot). The spatial coverage is the fraction of a circle covered by a camera, which is given by the horizontal angle of view (field of view) divided by 360 degrees (two radians). The overall sampling effort at a camera is the temporal effort multiplied by the spatial coverage.

Observations of the species of interest were taken from the first image of each trigger when it was detected by the camera. The standard assumptions of distance sampling hold (Buckland et al., 2001; Howe et al., 2017): (1) animals at the sampling point are detected with certainty, (2) animals are detected at their initial location, prior to any movement,

(3) distances are measured accurately, and (4) sampling points are placed independently of animal locations. The first assumption could be violated by animals passing beneath the camera field of view, failure to identify the species because only part of the animal is visible, and possibly the delay between the time the sensor is activated and the time the first image is recorded. The violation of the first assumption may be detectable during exploratory data analysis in the form of fewer than expected detections close to the sampling point, and bias can be avoided via left-truncation in which these detections are excluded from the analysis. To avoid violating the second and third assumptions, the distance to the animal in only the first image in a trigger sequence is included in the analysis. To assign animals in images accurately to distance intervals, reference images are taken at camera deployment, recording horizontal distances and angles from the camera using a measuring tape and a pole (see below for details). Systematic or random camera-trap survey designs are consistent with the assumption that sampling points are placed independently of animal locations. Cameras are not intentionally placed to target habitat features known to be either preferred or avoided by the animals of interest (Howe et al., 2017).

A significant advantage of camera traps is that they operate 24 hours per day and record data on multiple species. However, data on rarer species may be insufficient to fit detection functions to obtain reliable density estimates. Multiple covariate distance sampling allows probability of detection to be modelled as a function of additional covariates; in this study we used (1) species as a factor and (2) species body weight as a continuous variable (Marques et al., 2007). Additionally, the overall proportion of time a species is active can be estimated directly from the camera-trap data by fitting a circular kernel distribution, thus allowing the complete 24-hour data to be used.

Density estimate of forest antelopes

We used point transect distance sampling methods to estimate the densities of forest antelope species in the Dja Faunal Reserve. We deployed a systematic grid of 40 Bushnell Trophy Aggressor Low Glow cameras (Bushnell Outdoor Products, Overland Park, USA) at 2 km spacing during 22 January–8 May 2018 in the northern sector and from 27 January–17 May 2018 in the eastern sector of the Reserve (Fig. 1). This design was consistent with the assumption that sampling points are placed independently of animal locations. A single camera was placed at a height of c. 30 cm as close to the grid sampling point as possible, with a consistent and unobstructed field of view. The cameras were programmed to take three images per trigger, with a 2 s delay before the camera could be triggered again. This resulted in a 5 s time interval between consecutive triggers, to minimize the chance that an animal could pass without being detected by the camera. We also expect any bias in the density estimate as a result of this issue to be small. The camera field of view was 35 degrees.

During installation of each camera, we took reference images with a 1-m pole placed at distances of 1, 1.5, 2, 3, 4, 5 and 6 m from the camera at 0 degrees and at 15 degrees either side of the centre of the field of view. Distance reference points were then identified from the reference images and superimposed on all subsequent survey images using the marker tool of *EpiPen Basic* (Tank Studios, Edinburgh, UK). We assigned the nearest animal in the first image of a trigger to the appropriate distance band (0–2, 2–3, 3–4, 4–5, 5–6, $>$ 6 m) based on the position of its feet relative to the reference marker points.

We excluded data recorded on day of camera deployment or retrieval, to allow animals to become accustomed to the cameras in their environment, the smell of humans to dissipate, and to avoid any influence on the data as a result of disturbing animals while approaching a camera to recover it. We fitted point transect models in *Distance 7.0* (Thomas et al., 2010). Firstly, we performed conventional distance sampling analyses for each species with sufficient detections, to compare densities between the northern and eastern sectors using sector as the stratum. We considered models of the detection function for the combined data from the two camera grids with the half-normal, hazard rate, and uniform key functions with up to five cosine, simple polynomial and Hermite polynomial adjustment terms. Adjustment terms were constrained, where necessary, to ensure the detection function was monotonically decreasing. We selected among candidate models of the detection function by comparing AIC values, acknowledging the potential for overfitting as many observations were not independent (Howe et al., 2017). Secondly, we analysed the combined forest antelope species dataset and the two sectors using the multiple covariate distance sampling engine in *Distance*, to obtain density estimates for the rarer species with fewer detections. We assumed species body weight influences the scale of the detection function but not its shape, and we used both global and separate estimation of the species detection function.

We fitted a circular kernel distribution to individual species activity pattern using the *activity* package (Rowcliffe et al., 2014) in *R 4.0.2* (R Development Core Team, 2020). We subsequently divided the density estimates with estimates of the proportion of time species are active. We assumed that all individuals in the sampled population are active at the peak of the daily activity cycle.

Results

We recorded all 10 species of forest antelopes known to be present in Dja Faunal Reserve (Table 1). All animals were active when detected. The blue duiker *Philantomba monticola* was the most frequently recorded forest antelope (Table 1). The bongo, sitatunga *Tragelaphus spekii* and water

  doi:10.1017/S0030605320001209

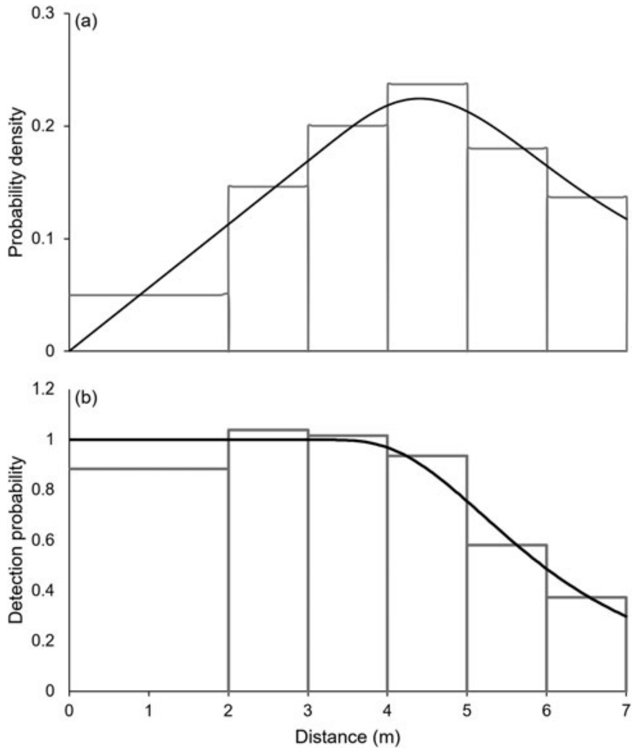


FIG. 2 Probability density function of (a) observed distances and (b) detection probability as a function of distance from hazard-rate point transect model fitted with multiple covariate distance sampling of antelope species in Dja Faunal Reserve.

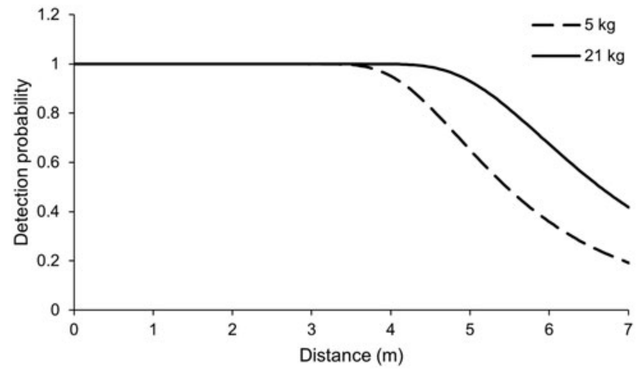


FIG. 3 Detection probabilities for antelopes of 5 and 21 kg body weight as a function of distance from hazard-rate point transect model fitted with multiple covariate distance sampling in Dja Faunal Reserve.

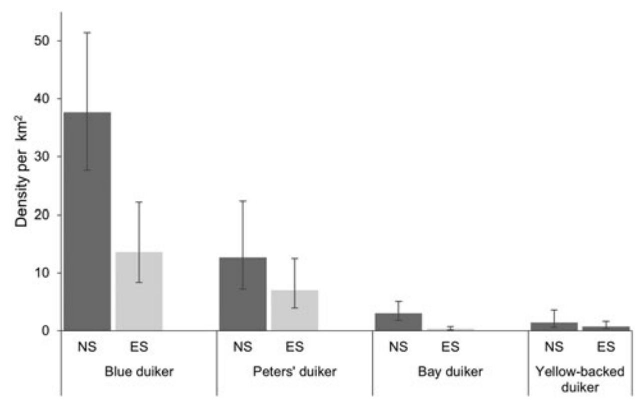


FIG. 4 Between-grid comparison of density estimates with 95% confidence intervals (using conventional distance sampling) for bay duiker *Cephalophus dorsalis*, blue duiker *Philantomba monticola*, Peters' duiker *Cephalophus callipygus* and yellow-backed duiker *Cephalophus silvicultor* in the northern sector (NS) and eastern sector (ES) of Dja Faunal Reserve.

chevrotain *Hyemoschus aquaticus* were detected < 30 times across both camera-trap grids and were therefore not included in the data analysis. Encounter rates were highly variable among locations for the other seven species and did not exhibit an obvious spatial pattern. There was no evidence of spatial autocorrelation (Moran's I $P > 0.05$).

Exploratory analyses revealed no evidence of a paucity of observations at 0–2 m from the cameras or issues with variation in visibility distances between cameras. The hazard rate model with no adjustments terms minimized AIC for both the conventional distance sampling and the multiple covariate distance sampling analyses (Figs 2 & 3).

Density estimates for the bay duiker *Cephalophus dorsalis*, blue duiker, Peters' duiker *Cephalophus callipygus*, and yellow-backed duiker *Cephalophus silvicultor* were higher in the northern than the eastern sector. The differences were statistically significant for bay duiker and blue duiker, based on the Wald test ($P < 0.05$) (Fig. 4).

Overall, blue duiker was the most abundant forest antelope. Peters' duiker had a significantly higher estimated density than Bates pygmy antelope, bay duiker, black-fronted duiker *Cephalophus nigrifrons*, white-bellied duiker *Cephalophus leucogaster*, and yellow-backed duiker. Bates pygmy antelope, black fronted duiker and white-bellied duiker had densities of < 1 individual per km^2. Proportion of time species were active was 0.15–0.32 (Table 2). Detection probability ranged from 0.62 (Bates pygmy antelope) to 1 (yellow-backed duiker) (Table 2).

Discussion

In this study, we have shown that camera-trap distance sampling can be an effective method for monitoring the densities and therefore population status of a community of forest antelopes, information urgently needed for conservation planning and action. Data from period of peak activity for most species was insufficient to fit detection models. We therefore used the whole 24-hour dataset by correcting for bias using an estimate of the proportion of time animals are active. We further applied multiple covariate distance sampling on the combined species dataset with body weight as a covariate to estimate densities for rarer species.

Line transect sampling using direct sightings or signs (including DNA based methods) for estimating density of

TABLE 2 Estimates of proportion of time active during 24 hours and multiple covariate distance sampling model outputs (estimates of density and detection probability, and effective detection radius) for seven forest antelope species in Dja Faunal Reserve.

Species	Proportion of time active	Density estimate, individuals per km^2 (95% CI)	Detection probability estimate (95% CI)	Effective detection radius (m)
Bates pygmy antelope	0.20	0.53 (0.20–1.45)	0.63 (0.56–0.70)	5.54
Bay duiker	0.32	1.54 (0.95–2.52)	0.82 (0.80–0.85)	6.36
Black-fronted duiker	0.23	0.15 (0.06–0.38)	0.75 (0.66–0.86)	6.08
Blue duiker	0.26	26.06 (19.52–34.79)	0.65 (0.64–0.66)	5.66
Peters' duiker	0.32	9.30 (6.13–14.12)	0.83 (0.82–0.84)	6.38
White-bellied duiker	0.15	0.25 (0.10–0.60)	0.80 (0.71–0.89)	6.25
Yellow-backed duiker	0.26	1.56 (0.82–2.96)	1.00	7.00

TABLE 3 Density estimates of blue duiker obtained in Central Africa using line transect sightings and dung count surveys.

Site	Density, individuals per km^2 (95% CI)	CV (%)	Method	Source
Cross River National Park, Nigeria	15.5 (7.8–30.9)	Not reported	Sightings	Jimoh et al. (2011)
Bouma Bek National Park, Cameroon	6.9 (4.4–10.7)	21.5	Dung	Kamgaing et al. (2018)
Bouma Bek National Park, Cameroon	3.5 (1.9–6.6)	31.6	Sightings (daytime)	Kamgaing et al. (2018)
Bouma Bek National Park, Cameroon	59.8 (46.3–77.4)	12.8	Sightings (night-time)	Kamgaing et al. (2018)
Moukalaba-Doudou National Park, Gabon	16.4 (11.4–23.6)	Not reported	Sightings (daytime)	Nakashima et al. (2013)
Korup National Park, Cameroon	1.5	107.3	Dung	Viquerat et al. (2012)
Korup National Park, Cameroon	8.3	45.3	Sightings (daytime)	Viquerat et al. (2012)
Korup National Park, Cameroon	6.8	53.1	Sightings (night-time)	Viquerat et al. (2012)

forest antelopes has severe limitations in terms of reliability, and/or cost and effort (Rovero & Marshall, 2004; Lwanaga, 2006; Waltert et al., 2006; Rovero & Marshall, 2009; Elenga et al., 2020). Despite the high initial set-up costs of camera-trap surveys, there are multiple advantages in terms of reliability of data gathered, long-term cost efficiency, and the large number of species that can be surveyed using a single technique (Amin et al., 2018). Our line transect surveys cost c. EUR 38,000 in the Dja Faunal Reserve compared to EUR 15,300 for a camera-trapping grid of 40 cameras, including costs of buying cameras and accessories, deployment and retrieval, training and analysis. Seven such camera-trap grids would be required to adequately cover Dja Faunal Reserve. Each subsequent grid would cost c. EUR 8,700, including the costs of replacing damaged cameras, assuming five replacements are required per deployment. In terms of application in the field, it is less labour intensive to train surveyors to deploy camera traps than to train them in line transect skills. For example, during this study a 5-day training session was adequate for setting up cameras. This training enabled five teams, each comprising two trained personnel, to deploy the camera-trap grids. During the analysis phase uncertain species identifications can be independently validated by experts, which increases the confidence of the estimates generated using this method (Amin et al., 2016). There is the potential for camera-trap distance sampling to be used to obtain density estimates for other species of conservation concern such as elephants, great apes and pangolins (Cappelle et al., 2019).

Comparing density estimates with other sites is challenging because of the paucity of data on forest antelope populations. This problem is further compounded by a lack of standardization of monitoring methods such as daytime transects and night-time transects using spotlights, and reporting (Waltert et al., 2006; Kamgaing et al., 2018; O'Brien et al., 2019). Several studies have only been able to estimate abundance of generic red duiker species because species often cannot be distinguished in brief glimpses in the field (Yasouka, 2006; Nakashima et al., 2013; Kamgaing et al., 2018). This means that only estimates of the common diurnal blue duiker populations can be confidently compared between our study and studies that have used line transect methods in Central Africa (Table 3). The combined northern and eastern sector blue duiker population density estimate of 26.06 individuals per km^2 (95% CI 19.52–34.79) is comparable to estimates from less disturbed parks of Gabon and higher than for some protected areas where there is extensive hunting, such as Korup National Park in Cameroon (Table 3).

Our study revealed that the eastern sector of the Dja Faunal Reserve has significantly lower densities of forest antelopes than the northern sector. This is probably a result of the many roads and trails leading into the eastern sector (it is the only part of the Reserve not surrounded by the Dja

  doi:10.1017/S0030605320001209

River). Declines in forest antelope populations associated with hunting pressure have been documented in other parts of Central Africa (Remis, 2000; Remis & Kpanou, 2011; Garande-Vega et al., 2016). It is unlikely that the differences in forest antelope density between the two camera-trap grids was primarily a result of habitat differences, as blue and red duiker species reach high densities in logged forests and disturbed habitat when poaching is limited (van Vilet & Nasi, 2008; Clark et al., 2009; Poulsen et al., 2011). Given the relatively intact nature of Dja Faunal Reserve, we would expect consistent densities of duikers between the sectors in the absence of hunting. Therefore, it is not unreasonable to hypothesize that anthropogenic impacts are affecting the density and distribution of forest antelopes, particularly duikers, within the Reserve.

Given that forest antelopes comprise a large proportion of the biomass and volume of bushmeat removed from Central African forests for local consumption and trade, they are important for the food security of an increasing human population. The lack of historical census data and increasing consumer demand could result in declines of these forest species going undetected. The development of tools such as applied in this study to monitor the status of forest antelopes effectively will help in informing much needed conservation efforts. Well-designed camera-trap surveys can help in the identification and testing of the significance of predictors of antelope abundance, such as distance from roads and settlements, logging operations, and hunting intensities, and these techniques are likely to be applicable in forest habitats on all continents.

Acknowledgements We thank Professor Steve Buckland for his advice, the Cameroon Ministry of Forests and Fauna and the late Conservator Hilaire Ndinga of the Dja Faunal Reserve for support, and the Ministry ecoguards and local porters who accompanied the survey teams in the field.

Author contributions Study design: RA, TB, TW, DO, AF, CN; fieldwork: TB, CN; camera-trap data image processing, species identification: TB, CN, HK; data analysis: RA; writing: RA, TW, HK, DO, AF, TB.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards.

References

Amin, R., Bowkett, A.E. & Wacher, T. (2016) The use of camera-traps to monitor forest antelope species. In *Antelope Conservation: From Diagnosis to Action* (eds J. Bro-Jørgensen & D.P. Mallon), pp. 190–216. John Wiley & Sons, Ltd, Hoboken, USA.

Amin, R., Wacher, T., Bowkett, A.E., Ogwoka, B., Morris, M. & Agwanda, B.R. (2018) Africa's forgotten forests: the conservation value of Kenya's northern coastal forests for large mammals. *Journal of East African Natural History*, 107, 41.

Bourgeois, S., Senn, H., Kaden, J., Bunnefeld, N., Cusack, J., Jeffery, K.J. et al. (2019) Improving cost-efficiency of non-invasive genotyping using fecal samples: new tools for elephant species. *PLOS ONE*, 14, e0210811.

Bowkett, A.E., Jones, T., Laizzer, R.L., Plowman, A.B. & Stevens, J.R. (2013) Can molecular data validate morphometric identification of faecal pellets in Tanzanian forest antelope species? *Conservation Genetics Resources*, 5, 1095–1100.

Breuer, T. & Breuer-Ndoundou Hockemba, M. (2012) Intrasite variation in the ability to detect tropical forest mammals. *African Journal of Ecology*, 50, 335–342.

Bruce, T., Amin, R., Wacher, T., Fankem, O., Ndjassi, C., Ngo Bata, M. et al. (2018) Using camera trap data to characterise terrestrial larger-bodied mammal communities in different management sectors of the Dja Faunal Reserve, Cameroon. *African Journal of Ecology*, 56, 759–776.

Bruce, T., Wacher, T., Ndinga, H., Bidjoka, V., Meyong, F., Ngo Bata, M. & Olson, D. (2017) *Camera-Trap Survey for Larger Terrestrial Wildlife in the Dja Biosphere Reserve, Cameroon*. Zoological Society of London & Cameroon Ministry of Forests and Wildlife, Yaoundé, Cameroon.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling*. Oxford University Press, Oxford, UK.

Cappelle, N., Després-Einspenner, M.L., Howe, E.J., Boesch, C. & Kühl, H.S. (2019) Validating camera trap distance sampling for chimpanzees. *American Journal of Primatology*, 81, 1–9.

Clark, C.J., Poulsen, J.R., Malonga, R. & Elkan, P.W. (2009) Logging concessions can extend the conservation estate for Central African tropical forests. *Conservation Biology*, 23, 1281–1293.

Croes, B.M., Laurance, W.F., Lahm, S.A., Tchignoumba, L., Alonso, A., Lee, M.E. et al. (2007) The influence of hunting on antipredator behavior in Central African monkeys and duikers. *Biotropica*, 39, 257–263.

East, R. (1998) *African Antelope Database 1998*. IUCN/SSC Antelope Specialist Group., Gland, Switzerland and Cambridge, UK.

Elenga, G., Bonenfant, C. & Péron, G. (2020) Distance sampling of duikers in the rainforest: dealing with transect avoidance. *PLOS ONE*, 15, p.e0240049.

Fa, J.E., Ryan, S.F. & Bell, D.J. (2005) Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. *Biological Conservation*, 121, 167–176.

Feer, F. (1995) Seed dispersal in African forest ruminants. *Journal of Tropical Ecology*, 11, 683–689.

Grande-Vega, M., Farfán, M.Á., Ondo, A. & Fa, J.E. (2016) Decline in hunter offtake of blue duikers in Bioko Island, Equatorial Guinea. *African Journal of Ecology*, 54, 49–58.

Howe, E.J., Buckland, S.T., Després-Einspenner, M.L. & Kühl, H.S. (2017) Distance sampling with camera traps. *Methods in Ecology and Evolution*, 8, 1558–1565.

Jimoh, S.O., Ikyaagba, E.T., Alarape, A.A., Adeyemi, A.A. & Waltert, M. (2011) Preliminary information on the density and distribution of duikers in the Oban sector of Cross River National Park, Nigeria. In *Tropentag 2011: Conference on International Research on Food Security, Natural Resource Management and Rural Development*. 5–7 October 2011, University of Bonn, Bonn, Germany.

Jost Robinson, C.A., Zollner, P.A. & Kpanou, J.B. (2017) Night and day: evaluating transect methodologies to monitor duikers in the Dzanga-Sangha Protected Areas, Central African Republic. *African Journal of Ecology*, 55, 222–232.

Kamgaing, T.O.W., Bobo, K.S., Djekda, D., Azobou, K.B.V., Hamadjida, B.R., Balangounde, M.Y. et al. (2018) Population density estimates of forest duikers (*Philantomba monticola* &

Cephalophus spp.) differ greatly between survey methods. *African Journal of Ecology*, 56, 908–916.

Kingdon, J. & Hoffmann, M. (eds) (2013) *Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids. Mammals of Africa*. Bloomsbury, London, UK.

Lwanga, J.S. (2006) The influence of forest variation and possible effects of poaching on duiker abundance at Ngogo, Kibale National Park, Uganda. *African Journal of Ecology*, 44, 209–218.

Marques, T.A., Thomas, L., Fancy, S.G. & Buckland, S.T. (2007) Improving estimates of bird density using multiple covariate distance sampling. *The Auk*, 124, 1229–1243.

MINFOF (Ministry of Forests and Fauna) & IUCN (2015) *Caractérisation de la Population de Grands et Moyens Mammifères dans la Reserve de Faune du Dja: Potentiel et Menaces*. MINFOF & IUCN, Yaoundé, Cameroon.

Nakashima, Y., Inoue, E. & Akomo-Okoue, E.-F. (2013) Population density and habitat preferences of forest duikers in Moukalaba-Doudou National Park, Gabon. *African Zoology*, 48, 395–399.

O'Brien, T.G., Ahumada, J., Akampurila, E., Beaudrot, L., Boekee, K., Brncic, T. et al. (2019) Camera trapping reveals trends in forest duiker populations in African National Parks. *Remote Sensing in Ecology and Conservation*, 168–180.

Poulsen, J.R., Clark, C.J. & Bolker, B.M. (2011) Decoupling the effects of logging and hunting on an afrotropical animal community. *Ecological Applications*, 21, 1819–1836.

R Development Core Team (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for statistical computing, Vienna, Austria.

Remis, M.J. (2000) Preliminary assessment of the impacts of human activities on gorillas *Gorilla gorilla gorilla* and other wildlife at Dzanga-Sangha Reserve, Central African Republic. *Oryx*, 34, 56–65.

Remis, M.J. & Kpanou, J.B. (2011) Primate and ungulate abundance in response to multi-use zoning and human extractive activities in a Central African Reserve. *African Journal of Ecology*, 49, 70–80.

Rovero, F. & Marshall, A.R. (2004) Estimating the abundance of forest antelopes by line transect techniques: a case from the Udzungwa Mountains of Tanzania. *Tropical Zoology*, 17, 267–277.

Rovero, F. & Marshall, A.R. (2009) Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, 46, 1011–1017.

Rowcliffe, J.M., Kays, R., Kranstauber, B., Carbone, C. & Jansen, P.A. (2014) Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5, 1170–1179.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L. et al. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, 5–14.

UNESCO (2018) *Dja Faunal Reserve*. whc.unesco.org/en/list/407 [accessed 9 August 2018].

van Vliet, N. & Nasi, R. (2008) Mammal distribution in a Central African logging concession area. *Biodiversity and Conservation*, 17, 1241–1249.

van Vliet, N., Nasi, R., Emmons, L., Feer, F., Mbazza, P. & Bourgarel, M. (2007) Evidence for the local depletion of bay duiker *Cephalophus dorsalis*, within the Ipassa Man and Biosphere Reserve, north-east Gabon. *African Journal of Ecology*, 45, 440–443.

van Vliet, N., Zundel, S., Miquel, C., Taberlet, P. & Nasi, R. (2008) Distinguishing dung from blue, red and yellow-backed duikers through noninvasive genetic techniques. *African Journal of Ecology*, 46, 411–417.

Viquerat, S.M.A., Bobo, K.S., Mller, M., Kiffner, C. & Waltert, M. (2012) Estimating forest duiker (Cephalophinae) density in korup national park: a case study on the performance of three line transect methods. *African Journal of Wildlife Research*, 42, 1–10.

Waltert, M., Heber, S., Riedelbauch, S., Lien, J.L. & Mühlenberg, M. (2006) Estimates of blue duiker (*Cephalophus monticola*) densities from diurnal and nocturnal line transects in the Korup region, south-western Cameroon. *African Journal of Ecology*, 44, 290–292.

White, L.J.T. (1994) Biomass of rain forest mammals in the Lopé Reserve, Gabon. *Journal of Animal Ecology*, 63, 499–512.

Wilkie, D. & Carpenter, J. (1999) Bushmeat hunting in the Congo Basin. *Biodiversity and Conservation*, 8, 927–955.

Yasuoka, H. (2006) The sustainability of duiker (*Cephalophus* spp.) hunting for the baka hunter-gatherers in southeastern Cameroon. *African Study Monographs*, 33, 95–120.

TOM BRUCE[1*], CONSTANT NDJASSI[1], MATTHEW LEBRETON[2], TIM WACHER[3], ANDREW FOWLER[1], ROGER BRUNO TABUE MBOBDA[4] AND DAVID OLSON[1]

African golden cat and leopard persist in the Dja Faunal Reserve, Cameroon

Both leopard *Panthera pardus pardus* and African golden cat *Caracal aurata* occur throughout the Congo Basin and coastal forests of Central Africa. However, there remains a paucity of documented occurrences of these species within the region. Here, we document both species in the Dja Faunal Reserve DFR, Cameroon from images captured in a camera-trap survey. This represents the first confirmed occurrence of leopard for 18 years and the first documentation of African golden cat within the reserve.

The African golden cat, hereafter, referred to as 'golden cat', is Africa's only forest-dependent felid (Ray & Butyinski 2013). The species is elusive and thought to be very rare throughout its range (Ray & Butyinski 2013). In contrast, the leopard is the most abundant and widespread felid in Africa (Hunter et al. 2013). Both are classified as Vulnerable under IUCN Red List criteria (Bahaa-el-Din et al 2015a, Stein et al. 2016) and listed as "Class A", the highest protection status for wildlife under Cameroon legislation (Loi 94/01 1994).

The Dja Faunal Reserve is a 5,260 km² area of contiguous semi-deciduous lowland for-est located in southern-central Cameroon, ranging in altitude from 600–800 m above sea level (MINFOF & IUCN 2015). A camera trap survey with the objective of monitoring medium-to-large terrestrial mammal (>0.5 kg) populations, was conducted in the South-ern Sector of the DFR from 6th April–29th July 2017, encompassing both wet and dry seasons. Forty infrared Bushnell Aggressor camera-traps programmed to take three pictures per trigger with no delay, were placed at a height of ~30–45 cm on trees between 4–8 m from wildlife trails. Cameras were deployed for 100 days in a systematic grid centred on 3°00'09.5" N / 13°07'46.4" E with 2 km spacing between each camera (Fig. 1) for a total effort of 3,371 camera-trap days.

The most recent published record of leopard occurrence in the reserve was a record of an individual snared by hunters between December 1994 and January 1995 in the Western Sector of the reserve (Nganduji & Blanc 2000). Golden cat are mentioned anecdotally in reports and faunal lists (Wilme 2002), but the basis for these records are unclear. In the current survey, golden cat and leopard were detected in 19 and 28 independent photographic events respectively, each at 11 camera traps stations between 573–668 m above sea level (Supporting Online Material SOM Figure F1). Only three of the 11 camera traps photographed both leopard and golden cat. At one site a leopard was detected two days after installing a camera. At a different camera, golden cat was recorded the same day as the camera was deployed. Capture rates for both species were low, with a mean capture rate of 0.83 (± 0.17) and 0.58 (± 0.15) independent photographic events per trap 100 trap days for leopard and golden cat, respectively.

Neither species were detected in a previous camera-trap survey (November 2015 – May 2016) in the Northern Sector of the DFR (centred on 3°14'16.8" N / 12°48'03.1" E) using the same methodology and sample effort (Bruce et al. 2017), despite the survey areas being separated by approximately 32 km of contiguous forest. Bahaa-el-Din et al. (2015b) suggest golden cat and leopards are particularly sensitive to hunting with snares. No snares were found during camera deployment or retrieval in the Southern Sector, while snares were commonly found in the Northern Sector (O. Fankem pers comm.). Other disturbance-sensitive species, such as white-bellied duiker (*Cephalophus leucogaster*) (Hart 2013), which co-occurred on cameras with both felid species at 13 of 18 sites where they were present, were also only detected in the southern grid. This suggests that a difference in hunting pressure and human disturbance is acting at a fine spatial scale within the reserve. This is supported by both species displaying primarily crepuscular or diurnal activity patterns (Fig. 2), both species are thought to shift to more nocturnal activity patterns when hunting activity is high (Bahaa-el-din et al. 2015b, Henschel & Ray 2003).

As snares have a disproportionately strong effect on carnivore populations (Farris et al. 2015), it is important that increased efforts are undertaken to remove snares from the environment (Becker et al. 2013). If this area remains as a refuge for wildlife and free of the impacts of poaching, then there is the potential for the animals residing here to act as a source population for the more heavily impacted areas within the reserve (Naranjo & Bodmer 2007).

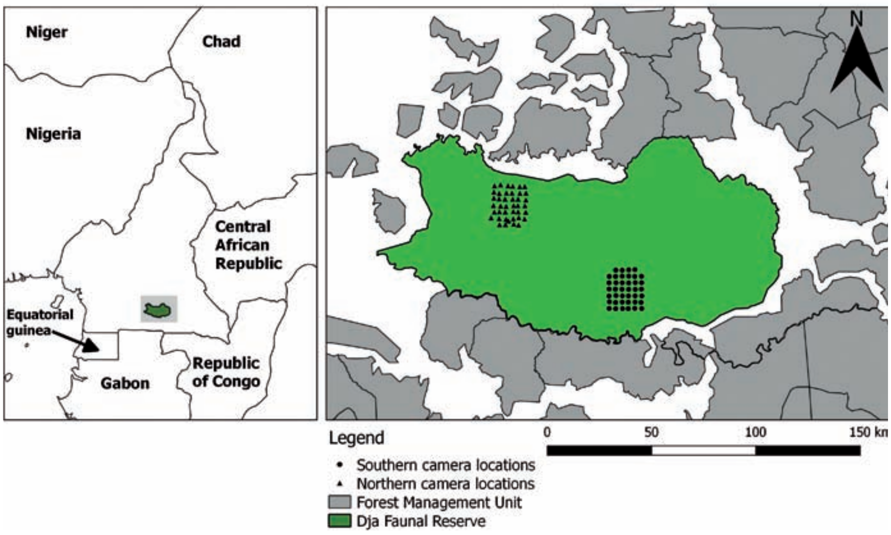


Fig. 1. Location of the two camera-trap grids in the southern and northern sectors of the Dja Faunal Reserve, Cameroon.

Acknowledgements

We thank the Government of the Republic of Cameroon, the Ministry of Forests and Wildlife, and DFR Conservator H Ndinga for their continuing support as part of their overall programme to protect Cameroon's wildlife. We thank the DFR ecoguards for their assistance in this study.

References

Bahaa-el-din L., Mills D., Hunter L. & Henschel P. 2015a. *Caracal aurata*. The IUCN Red List of Threatened Species 2015: e.T18306A50663128. http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T18306A50663128.en. Downloaded on 03 August 2018.

Bahaa-el-din L., Henschel P., Butynski T. M., Macdonald D. W., Mills D., Slotow R. & Hunter L. 2015b. The African golden cat *Caracal aurata*: Africa's least known felid. Mammal Review, 45, 1, 63–77.

Becker M., McRobb R., Watson F., Droge E., Kanyembo B., Murdoch J. & Kakumbi C. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. Biological Conservation, 158, 26–36.

Bruce T., Wacher T., Ndinga H., Bidjoka V., Meyong F., Ngo Bata M., Easton J., Fankem O., Elisee T., Taguieteu P. A. & Olson D. 2017. Camera-trap survey for larger terrestrial wildlife in the Dja Biosphere Reserve, Cameroon. Zoological Society of London (ZSL) & Ministry of Forests and Fauna (MINFOF), Yaoundé, Cameroon.

Farris Z. J., Golden C. D., Karpanty S., Murphy A., Stauffer D., Ratelolahy F., Andrianjakarivelo V., Holmes C. M. & Kelly M. J. 2015. Hunting, exotic carnivores, and habitat loss: anthropogenic effects on a native carnivore community, Madagascar. PloS one, 10, p.e0136456. 1–20.

Hart J. 2013. White-bellied duiker Cephalophus leucogaster. *In* Mammals of Africa. Volume VI. Hippopotamuses, Pigs, Deer, Giraffe and Bovids. Kingdon J & Hoffmann M. (Eds). Bloomsbury Publishing, London, United Kingdom, pp. 255–258.

Henschel P. & Ray J. 2003. Leopards in African rainforests: survey and monitoring techniques. Wildlife Conservation Society. 54 pp.

Hunter L.T.B., Henschel P. & Ray J. 2013. Leopard Panthera pardus. *In* Mammals of Africa. Volume V: Carnivora, Pangolins, Equids and Rhinoceroses. Kingdon J. & Hoffmann M. (Eds). Bloomsbury Publishing, London, United Kingdom. pp. 159–168.

Law n° 94/01 du 20 janvier 1994 portant régime des forêts, de la faune et de la pêche.

MINFOF & IUCN. 2015. Caractérisation de la population de grands et moyens mammifères dans la Reserve de Faune du Dja: Potentiel et menaces. Yaoundé, Cameroun.

Naranjo E. J. & Bodmer R. E. 2007. Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. Biological Conservation, 138, 412–420.

Ngandjui G. & Blanc C. P. 2000. Effects of hunting on mammalian (Mammalia) populations in the western sector of the Dja Reserve (Southern Cameroon). Game Wildlife Science 17, 93–113.

Ray, J. and Butynski, T. 2013. African golden cat *Profelis aurata*. *In* The Mammals of Africa. Volume V: Carnivores, Pangolins, Equids and Rhinoceroses. Kingdon J & Hoffmann M. (Eds). Bloomsbury Publishing, London, United Kingdom, pp. 168–173.

Stein A. B., Athreya V., Gerngross P., Balme G., Henschel P., Karanth U., Miquelle D., Rostro-Garcia S., Kamler J.F., Laguardia A., Khorozyan I. & Ghoddousi A. 2016. *Panthera pardus* (errata version published in 2016). The IUCN Red List of Threatened Species 2016: e.T15954A102421779.

Wilme L .2002. La reserve de faune du Dja: a la decouvert de la foret tropicale. ECOFAC. pp. 42–46.

Supporting Online Material SOM Figure F1 is available at www.catsg.org.

[1] Zoological Society of London – Cameroon, Yaoundé, Cameroon

[2] Congo Basin Institute, Yaoundé, Cameroon

[3] Zoological Society of London, Conservation Programmes, Africa Programme, Regent's Park, London, UK

[4] Ministry of Forestry and Wildlife, MINFOF, Dja Faunal Reserve, Yaoundé, Cameroon

*<Thomas.Bruce@zsl.org>

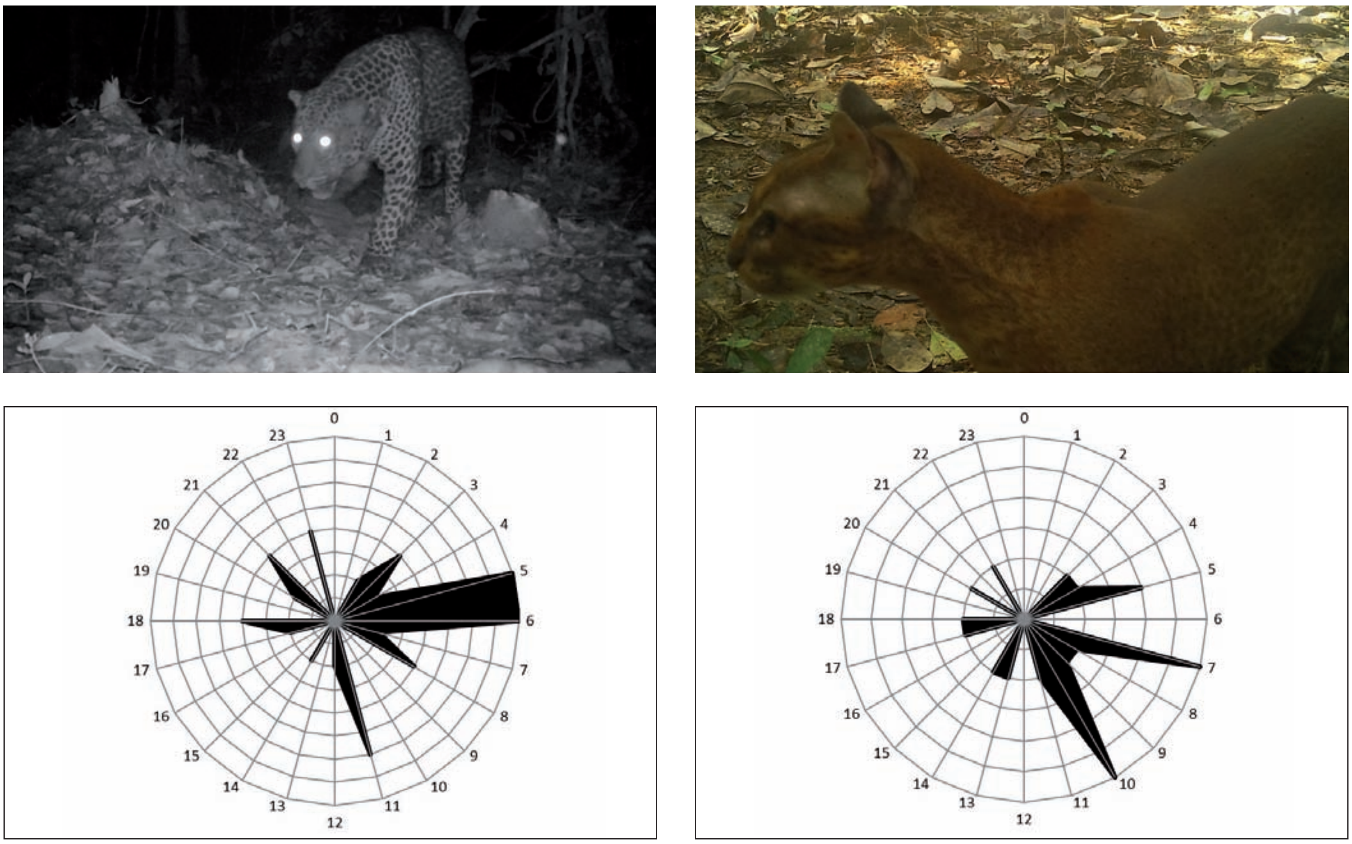


Fig. 2. Images and activity patterns of leopard (left) and golden cat (right) in the DFR. The radial plots are proportional with each circular line representing an increase of one event. Time is on the outer circle in 24 hour clock. Diurnal activity is between 07:00–18:00 h, nocturnal 19:00–06:00 h and crepuscular 18:00–17:00, h 06:00–07:00 h (Photos ZSL & MINFOF).

African Primates 12: 65-67 (2017)

Brief Communication:

Extending the Northeastern Distribution of Mandrills (*Mandrillus sphinx*) into the Dja Faunal Reserve, Cameroon

Madeleine Ngo Bata[1], Julian Easton[1], Oliver Fankem[1], Tim Wacher[2], Tom Bruce[1], Tchana Eliseé[1], Pierre Augustin Taguieteu[1], and David Olson[1]

[1]*Zoological Society of London - Cameroon, Yaoundé, Cameroon;*
[2]*Zoological Society of London - London, United Kingdom*

Mandrills (*Mandrillus sphinx*, Linnaeus, 1758) are restricted to forests of the Atlantic Equatorial Forests Ecoregion, eastern portions of the Northwestern Congolian Lowland Forest Ecoregion, and northern portions of the Western Congolian Forest-Savanna Mosaic Ecoregion of Central Africa (Olson *et al.* 2001; Oates & Butynski 2008). The species distribution is imperfectly known, especially the northeastern limits of its estimated range. Here we report on the presence of mandrills in the northwestern region of the Dja Faunal Reserve in south-central Cameroon, a protected area with no known published records for this species.

We found no published records after evaluating available surveys and faunal lists for the reserve (specifically, Bergmans 1994; Lejoly 1995; Williamson & Usongo 1995; Nzooh Dongmo 1999; MINFOF/IUCN 2015; GBIF 2016) and no reports through consultations with specialists who had worked within the reserve for several years (T. Smith, pers. comm. 2016). The current IUCN Red List description states mandrills are not known east of the Dja River (Oates & Butynski 2008).

This new locality documents the species in the northwest sector of the Dja Faunal Reserve (which lies entirely east of the Dja River) and extends the IUCN Red List primary range map approximately 20 km towards the northeast (Oates & Butynski 2008).

An array of 40 infrared-triggered trail cameras (Bushnell Trophy Cam Aggressor), each roughly 2 km apart in a square grid pattern, was in place for approximately 3,725 trap days for a wildlife survey in late 2015 and early 2016. All cameras were in primary tropical lowland rainforest. Two cameras (C11 at N3.2621 E12.83306 and C39 at N3.17567 E12.81618) photographed a single mature male mandrill on March 1, 2016 and April 9, 2016 (Figure 1). It is not known if they are different males or the same individual and if groups of mandrills, in addition to wandering males, also occur east of the Dja River. The two locations were 10.5 km apart. Each camera took six sequential images of each animal within six seconds (Figure 1).

Given the clear documentation of mandrills east of the Dja River presented here, we recommend the primary distribution for the species of Oates and Butynski (2008) and Abernethy and White (2013) be extended to encompass the new localities.

ACKNOWLEDGEMENTS

We are grateful for permission and collaboration on this project from the Ministère des Forêts et de la Faune (MINFOF), the Conservator of the Dja Faunal Reserve, the Ecoguards who assisted with camera placement, and retrieval, and the Government of the Republic of Cameroon. We thank E. Milnes for research assistance and F. Maisels and K. Abernethy for technical review. We thank two anonymous reviewers for their helpful contributions.

Correspondence to: Madeleine Ngo Bata, Zoological Society of London - Cameroon, Yaoundé, Cameroon; Phone: +237 676969242; E-mail: madeleine.bata@zsl.org.

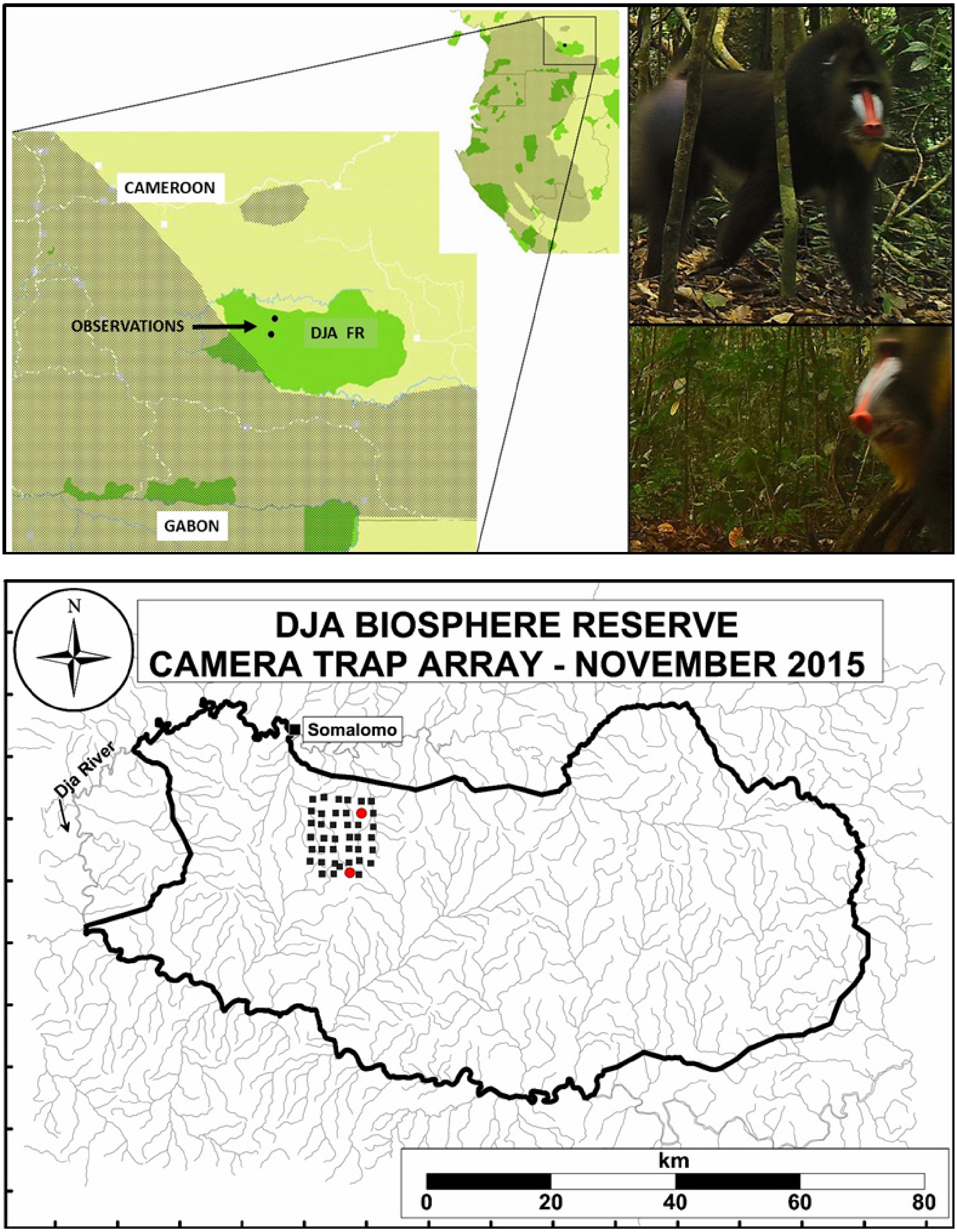


Figure 1. Male mandrills photographed by two infrared trail cameras in the Dja Faunal Reserve, Cameroon. The black dots on the range map show the approximate location of cameras that documented mandrills. The dark shade represents the IUCN Red List distribution of the mandrill and protected areas are shown in light shade. The disjunct range polygon to the north of the Dja Reserve is likely an error (F. Maisels & K. Abernethy, pers. comm. 2016; range map source: Oates & Butynski 2008). The lower map shows the approximate location of the camera trap grid used in the survey with the cameras that photographed mandrills shown in circles.

LITERATURE CITED

Abernethy, K.A. & L.J.T. White. 2013. *Mandrillus sphinx* Mandrill, In *Mammals of Africa: Primates*. Butynski, T., J. Kingdon, J. Kalina, eds. Bloomsbury, London, New Delhi, New York, Sydney. Pp. 192-196.

Bergmans, W. 1994. *Liste provisoire des Mammifères de la Réserve de faune du Dja et de sa périphérie. Rap. Comité Néerlandais pour l'UICN. IUCN,* Amsterdam, Netherlands.

GBIF. 2016. Global Biodiversity Information Facility. http://www.gbif.org/occurrence/search?TAXON_KEY=5219555&q=dja. Accessed on November 1, 2016.

Lejoly, J. 1995. *Biodiversité des ligneux sur le transect d'Alat Makay dans la réserve de faune du Dja (Cameroun). Rapport technique, Projet ECOFAC, AGRECO.* ECOFAC, Brussels.

MINFOF/IUCN. 2015. *Caractérisation de la population de grands et moyens mammifères dans la Reserve de Faune du Dja: Potentiel et menaces. MINFOF/IUCN,* Yaoundé, Cameroon.

Nzooh Dongmo, Z.L. 1999. *Dynamique de la faune sauvage et des activités anthropiques dans la Réserve de Biosphère du Dja et ses environs (Cameroun).* Volumes 1 & 2. MINEF–ECOFAC, Brussels.

Oates, J.F. & T.M. Butynski. 2008. *Mandrillus sphinx*. The IUCN Red List of Threatened Species 2008: e.T12754A3377579. http://dx.doi.org/10.2305/IUCN.UK2008.RLTS.T12754A3377579.en. Downloaded on 22 October 2016.

Olson, D., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, J.A. D'Amico, H.E. Strand, J.C. Morrison, C.J. Loucks, T.F. Allnutt, J.F. Lamoreux, T.H. Ricketts, I. Itoua, W.W. Wettengel, Y. Kura, P. Hedao, & K. Kassem. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51: 933-938.

Williamson, E. & L. Usongo. 1995. *Réserve de faune du Dja: recensement des populations de primates et inventaire des grands mammifères.* ECOFAC, Brussels.

Received: 3 December 2016
Accepted: 16 December 2016

Received: 14 May 2018 | Revised: 10 October 2018 | Accepted: 10 October 2018
DOI: 10.1111/aje.12574

SPECIAL SECTION: CAMERA TRAPPING IN AFRICA

WILEY African Journal of Ecology

Using camera trap data to characterise terrestrial larger-bodied mammal communities in different management sectors of the Dja Faunal Reserve, Cameroon

Tom Bruce[1] | Rajan Amin[2] | Tim Wacher[2] | Oliver Fankem[1] | Constant Ndjassi[1] | Madeleine Ngo Bata[1] | Andrew Fowler[1] | Hilaire Ndinga[3] | David Olson[1]

[1]Zoological Society of London – Cameroon, Yaoundé, Cameroon

[2]Global Conservation Programmes, Zoological Society of London, London, UK

[3]Ministry of Forests and Wildlife, MINFOF, Dja Faunal Reserve, Yaoundé, Cameroon

Correspondence
Tom Bruce, Zoological Society of London – Cameroon, Yaoundé, Cameroon.
Email: tom.bruce@my.jcu.edu.au

Funding information
US Fish and Wildlife Service (USFWS); African Elephant Conservation and IUCN SOS; Fondation Segré Pangolin Conservation Initiative

Abstract

Camera trap surveys can be useful in characterising terrestrial larger-bodied mammal communities in Central Africa forests. Two 40-trap, minimum of 100 days, survey grids conducted in the Dja Faunal Reserve of southern Cameroon showed differences in the mammal communities of two sites 32 km apart. Mammal richness, diversity, guild structure, body-size patterns and relative abundance of taxa were measured by trapping rates and occupancy of the two mammal communities. One of the survey sites was (a) less rich in terrestrial mammal species; (b) missing disturbance-sensitive felids and white-bellied duiker (*Cephalophus leucogaster*, subsp, *leucogaster*, Gray, 1873); (c) greater in abundance of some disturbance-tolerant species; and (d) lower in abundance of larger-bodied species. Several indicators suggest a higher hunting pressure at this site, and this may be a contributing factor to these differences.

Résumé

Les études avec pièges photographiques peuvent être utiles pour caractériser des communautés de grands mammifères terrestres dans les forêts d'Afrique centrale. Deux grilles de recherches de 40 pièges, sur un minimum de 100 jours, réalisées dans la Réserve de Faune du Dja, dans le sud du Cameroun, ont montré des différences dans des communautés de deux sites séparés l'un de l'autre de 32 km. La richesse en mammifères, la diversité, la structure des guildes, le schéma des tailles corporelles et l'abondance relative des taxons ont été mesuré d'après le taux de piégeage et l'occupation des deux communautés animales. Une des sites étudiés était (a) moins riche en espèces de mammifères terrestres; (b) dépourvu de tout félin sensible aux perturbations et de céphalophe à ventre blanc *Cephalophus leucogaster*, subsp. *leucogaster*, Gray, 1873; (c) plus peuplé de certaines espèces plus tolérantes vis-à-vis des perturbations; et (d) moins peuplé d'espèces de plus grande taille. Plusieurs indicateurs suggèrent une plus forte pression de la chasse sur ce site et cela pourrait être un facteur contribuant à cette différence.

KEYWORDS

camera trap, Cameroon, Dja Faunal Reserve, mammal, occupancy

1 | INTRODUCTION

Wildlife in Central African forests is under increasing pressure from habitat loss, habitat fragmentation, and intensive hunting for bushmeat and wildlife parts (Hansen, Stehman, & Potapov, 2010; Mallon et al., 2015; Mambeya et al., 2018; Potapov et al., 2012; Poulsen et al., 2017). Hunting is a daily occurrence in Central African villages (Abernethy, Coad, Taylor, Lee, & Maisels, 2013; Ziegler et al., 2016) and is an important factor contributing to the distribution of mammal species within protected areas (Muchaal & Ngandjui, 1999) and around settlements (Abrahams, Peres, & Costa, 2017). Bushmeat market surveys within Central Africa have demonstrated that mammals represent >90% of the carcasses sold (Fa et al., 2006). The motives behind hunting range from traditional subsistence and commercial hunting for bushmeat to targeting species for the illegal wildlife trade, such as great apes for body parts, forest elephant (*Loxodonta cyclotis*, Matschie, 1900) for ivory and pangolins for their scales (Craigie et al., 2010; Stiles, 2011).

Reduction and extirpation of mammal populations in Central African forests have cascading ecological impacts on forest ecosystems. In particular, the loss of top predators (Malhi, Adu-Bredu, Asare, Lewis, & Mayaux, 2013), key seed dispersers, including great apes and forest elephants (Blake, Deem, Mossimbo, Maisels, & Walsh, 2009), and landscape architects, such as elephants that keep clearings open in Central African forests (Maisels et al., 2013), can have long-term and far-reaching impacts on forest communities and processes (Abernethy et al., 2013; Laurance et al., 2012).

Understanding the interplay of patterns of hunting (for example, distribution, intensity, target species, frequency and hunting methods), a major driver of mammalian defaunation, and resultant impacts on the composition, structure, and distribution of medium- to larger-bodied terrestrial mammals in Central Africa forests can inform management actions (Abernethy et al., 2013; Bennett et al., 2007; Laurance et al., 2006; Nielsen, 2006; Seddon, Griffiths, Soorae, & Armstrong, 2014).

For example, can regular, effective patrolling by rangers maintain robust wildlife communities within “defended” zones when surrounding areas are experiencing higher levels of hunting? The answer will depend, in part, on the long-term reach of hunting impacts on mammal communities across forest landscapes. As larger-bodied mammals are usually more wide-ranging, occur at low densities and have long gestation periods, this makes them particularly vulnerable to extinction (Purvis, Gittleman, Cowlishaw, & Mace, 2000; Tucker, Ord, & Rogers, 2014), whereas species with smaller home ranges and higher densities, on average, may be more resilient as the minimum area needed to maintain viable populations is smaller. Thus, a refined understanding of the process of defaunation across forested Central African landscapes will help identify management actions and the scales at which they are most effective for slowing and reversing it (Bruce et al., 2017; Campbell, Kuehl, Diarrassouba, N’Goran, & Boesch, 2011; Redford, 1992).

Camera trap surveys are well-suited as a methodology to document the richness of faunas and understand diel activity patterns and habitat preferences of medium to large terrestrial mammal species in dense forests (Ahumada et al., 2011; Hedwig et al., 2018; Silveira, Jacomo, & Diniz-Filho, 2003; Tobler, Carrillo-Percastegui, Leite Pitman, Mares, & Powell, 2008). They provide a cost-effective, efficient, non-invasive and replicable survey method (Ahumada et al., 2011; Rovero & Marshall, 2009; Tobler et al., 2008). Importantly, they remove much of the human error and uncertainty associated with other survey types, such as distance sampling through line transects and interviews with the local populations (Ahumada, Hurtado, & Lizcano, 2013; Hedwig et al., 2018), that are often biased towards larger-bodied, diurnal species and fail to detect rare and elusive nocturnal species (Srbek-Araujo & Chiarello, 2005). The use of standardised camera trapping methods and classifying species into functional groups, such as by trophic category, life history, social structure and body size, allows mammal communities in different sites to be compared regardless of differences in species composition.

Here, we investigate if camera trap surveys can discern differences in community metrics of terrestrial larger-bodied mammal assemblages at different sites within the same Central African protected area. We examine metrics of richness, guild, body-size and relative abundance as measured by trapping rates and occupancy of the two mammal communities surveyed using a grid of camera traps at each site.

2 | MATERIALS AND METHODS

Camera trap surveys were conducted at two sites approximately 32 km apart (at their closest proximity) within the Dja Faunal Reserve (DFR) in southern Cameroon. Contiguous natural forest encompasses both sites and intervening and surrounding habitat.

2.1 | Study area

The DFR, the largest protected area in Cameroon, is approximately 5,260 km^2 (3°08′58.9″N, 13°00′00.1″E, Figure 1). The Dja River surrounds 80% of the reserve acting as a partial buffer to human encroachment and animal movement (Muchaal & Ngandjui, 1999). The topography within the reserve is made up of round-topped hills, between 600 and 800 masl, with valleys on either side of a central ridgeline that traverses the reserve east to west (MINFOF & IUCN, 2015). Swamps are prevalent in the tributaries feeding into the Dja River. Three major forest types occur within the reserve: terra firme forest (Sonké, 1998); monodominant forest (*Gilbertedendron* sp); and seasonally inundated forests (Djuikouo, Doucet, Nguembou, Lewis, & Sonké, 2010). There are four seasons: a long rainy season from August to November; the long dry season from November to March; a short rainy season from March to May; and the short dry season is between June and July. Average annual rainfall is *c.* 1,600 mm (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Commercial logging was limited and has now ceased. Only traditional hunting is allowed within the Dja Faunal (Biosphere) Reserve, and no fully protected Class A species can be taken (Republic of Cameroon, 1994). However,

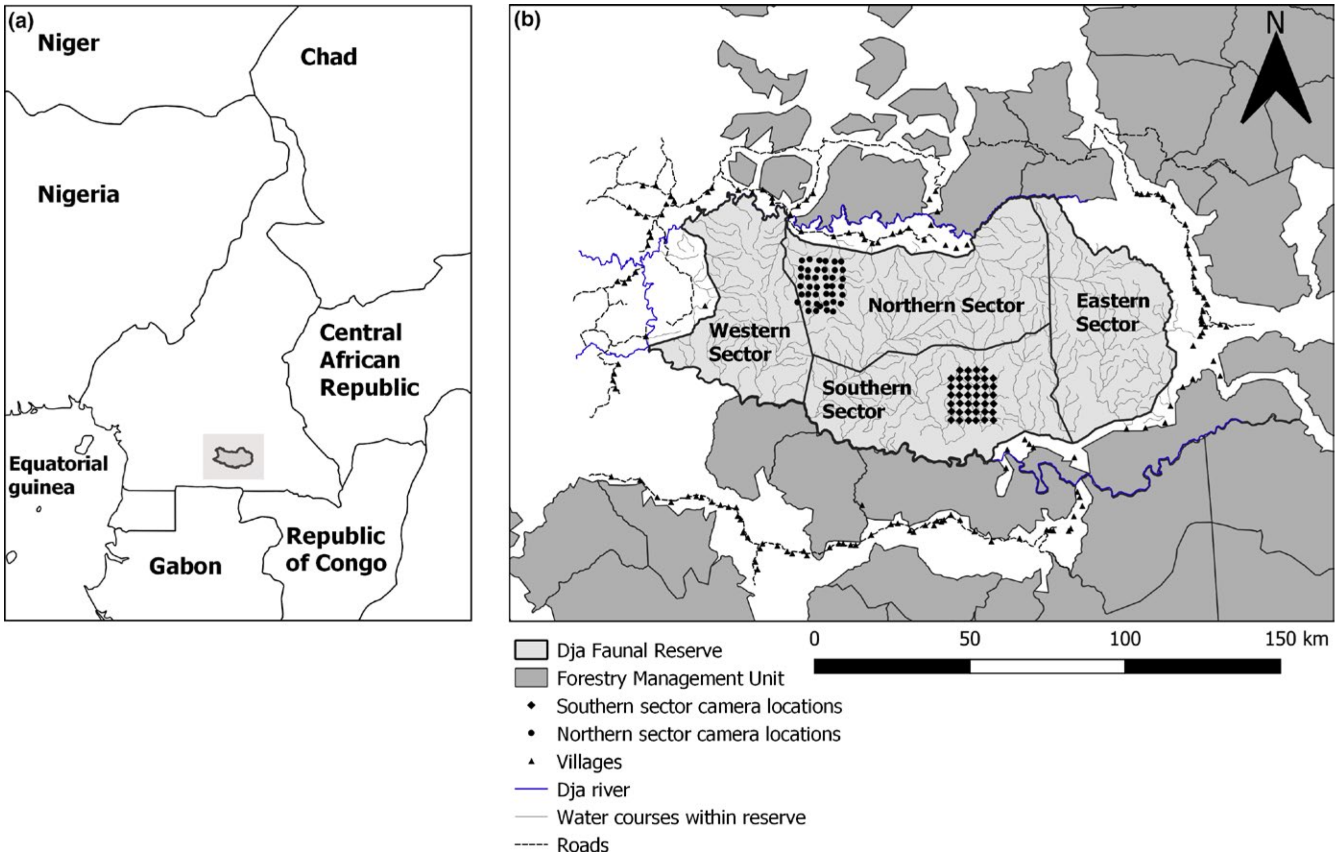


FIGURE 1 Location of the Dja Faunal Reserve, Cameroon (a) and the location of camera trap grids in the Northern and Southern sectors (b). Management sectors are in grey [Colour figure can be viewed at wileyonlinelibrary.com]

the human population around the reserve is increasing and industries, such as logging, rubber, hydropower and mining are proliferating, resulting in increased demand for bushmeat. Both illegal non-traditional subsistence and commercial hunting occur within the reserve.

2.2 | Northern and southern sector sites

We set up camera trap grids in the Northern (management) Sector (centred on 03°13'33''N, 12°48'18''E) between November 2015 and May 2016 and the Southern (management) Sector (02°59'37''N, 13°07'43''E) of the DFR between May and June 2017 (Figure 1). The camera trap grid within the Northern Sector was placed using the northern protected area boundary as an approximate baseline reference. The cameras were set over a range of *c.* 3.1 to *c.* 15.9 km from the boundary of the reserve with an average distance of 9.5 (*SE* ± 3.9) km from the boundary. Cameras were placed on average 12.3 (*SE* ± 3.8) km from the nearest settlements with a range of between *c.* 6 and 18.8 km. The Northern Sector of the Dja presents a generally higher and more uniform elevation (662–720 masl) than the Southern Sector (563–689 masl). Watercourses are sparser and swamp habitat less common within this management sector. Correspondingly, the northern camera trap stations were, on average, more distant from the nearest watercourse (*c.* 2.61 km) and only two northern cameras were placed in swamp habitat.

The cameras in the Southern Sector grid were placed on average 12.3 (*SE* ± 3.8) km over a range of *c.* 5.7–19 km from the reserve boundary and were between *c.* 7.7 and 22 km from the nearest human settlement with an average distance of 15.5 (*SE* ± 3.7) km. The topography within the southern camera trap grid is more complex with a greater elevational variation. The greater prevalence of lowland areas resulted in more swamp habitat (five cameras placed within 50 m of swamp habitats) and cameras being, on average, placed closer to watercourses (*c.* 0.6 km).

2.3 | camera trap surveys

Forty cameras were placed at each locality with a 2 km spacing between each camera (Ahumada et al., 2011) (Figure 1). Each grid operated long enough to achieve at least 1,000 camera trap days of sampling effort (O'Brien, Kinnaird, & Wibisono, 2003). We used Global Positioning System receivers to locate the grid points. A single camera was positioned 30–45 cm above ground level within 200 m of each point, aimed at a game trail that provided sufficient field of view to capture lateral full-body images of small to medium-sized mammals. Sites were selected based on the presence of a game trail (Amin et al., 2015) to maximise the probability of obtaining useful photographs (TEAM, 2008), and a suitable tree allowing the camera to be positioned facing either north or south to minimise the impacts of sunrise and sunset on camera performance.

We used three different camera models across the two grids (Bushnell Aggressor, Reconyx HC500, and Cuddeback Long range IR E2). Detection range was at least 25 m with either a two-second delay (Bushnell - 2015 Northern Sector survey) or one-second delay (Reconyx, Cuddeback and Bushnell - 2017 Southern Sector survey). Three consecutive images were taken per trigger. Low glow infrared flash lighting was used to minimise the risk of startling animals. The full list of settings for each camera can be found in Annex 1.

2.4 | Natural mammal fauna

The reserve is reported to contain 109 species of mammal of which 35 species are terrestrial and have a bodyweight >0.5 kg (Kingdon, 2015). Currently, the only baseline data for populations for these species within the reserve come from encounter rates from ranger patrols and distance sampling through line transect surveys (Dupain, Bombome, & Van Elsacker, 2003; MINFOF & IUCN, 2015; Williamson & Usongo, 1995).

2.5 | Assessment of differences in human activity

To assess the relative differences in human activity, including hunting, between the Northern and Southern Sector where the two sites were located, we evaluated trends from multiple sources. Evidence of human sign was recorded on 1-kilometre line transects during a full faunal inventory of the DFR (Bruce et al., 2018). Transects are often used to monitor the trends of human impacts in Central African forests (Kühl et al., 2008). There were a total of 86 and 76 transects, covering a distance of 91.6 and 80.7 km, completed in the Northern Sector and Southern Sector, respectively. Encounters of human sign between January 2016 and September 2017 by Ministry of Forests and Wildlife (MINFOF) ranger patrols, who record data using Spatial Monitoring And Reporting Tool devices, were also used (ZSL & MINFOF, 2017a, 2017b). A buffer of 2 km was set around each camera, and the sign within this area was converted into the amount of human sign per km^2. This buffer was used to counteract unequal survey effort within the sectors, possibly due to ecoguards being required to be present at a research station in the Northern Sector at the bottom of the camera trap grid.

Transects provide a more objective measure of hunting pressure as they use a standardised methodology and team composition compared to ranger patrols. Transects are not biased by following trails or other paths of least resistance that affects the probability of human sign being detected.

2.6 | Data analysis

We used Exiv2 software (Huggel, 2012) to extract EXIF information from each photograph (image name, date and time). Species of animal in the photographs were identified, when possible. These data were compiled in an Excel spreadsheet (Microsoft Office Professional Plus 2016, Version 1809) and analysed with software developed by at ZSL (Camera Trap Analysis Package [CTAP]) (Davey, Wacher, & Amin,2017).

We only considered terrestrial mammal species that have an estimated average mass greater than 0.5 kg (medium-to-large mammals) for the analyses because they are the main target group for camera traps placed at ground level. Smaller mammals induce sampling error through a reduced likelihood of detection by the camera trap's thermal sensor and accurate identification of small mammals to species level is difficult from camera traps set-up for medium-to-large mammals (Tobler et al., 2008).

We calculated rarified species accumulation curves and estimated the medium-to-large terrestrial mammal species richness for each sector using the ZSL CTAP tool.

We calculated Simpson's diversity index and Shannon–Weiner diversity index for each sector from species daily trap rates using package vegan in R statistical software (Oksanen, 2015). Simpson's diversity index is most sensitive to changes in more common highly abundant species, while Shannon–Weiner diversity index is most sensitive to changes in rare, less abundant species (Magurran, 2005).

We calculated the number of independent photographic events per 100 trap days as a relative abundance index (RAI) for each species. We defined an "event" as any sequence for a given species occurring after an interval of ≥60 min from the previous three-image sequence of that species to ensure that species events were independent (Amin et al., 2015; Tobler et al., 2008). The events were automatically screened by the ZSL CTAP software. We calculated the 95% confidence intervals using the bootstrap method (Efron & Tibshirani, 1994) and considered non-overlapping confidence intervals as indicative of a significant difference in RAI between management sectors. We assume that the camera trapping rates calculated as the RAI reflect actual relative abundance as in Rovero and Marshall (2009).

We used single-season occupancy analysis (MacKenzie et al., 2006), where assumptions and data quality allowed, to estimate the proportion of area occupied by a species, within each grid. Occupancy estimates were corrected by detection probability (i.e. the likelihood that a species was detected when present) and, therefore, provide a more rigorous index of abundance for both within and between species comparisons. This, however, is limited to species generating adequate data sets, where camera spacing is greater than the species home range, and occupancy is not confounded by changes in the home range (Efford & Dawson, 2012). For all the occupancy analyses, we generated 11, 10-day sampling occasions. This meant the Northern Sector data were truncated to match the number of occasions available for analysis in the Southern Sector. We tested for significant differences in species occupancy between the Northern and Southern sectors using the "Wald" parametric statistical test, as it is known to be an independent and robust measure of difference (Amin et al., 2015) with $p < 0.05$ considered to be significant.

We also modelled occupancy as a function of site covariates distance to the protected area boundary in kilometres (D) and management sector (M) using the "unmarked" (Fiske & Chandler, 2011) software package in R. We treated detection probability as a constant and evaluated all covariate combinations: ψ(.),*p*(.); ψ(D),*p*(.); ψ(M),*p*(.); ψ(D*M),*p*(.); ψ(D + M), *p*(.). For covariate analysis to compare the management sectors, we also implemented a Royle–Nichols model (2003) which takes into account the number of individuals at a site influencing detection probability and thus occupancy. The selection of Royle–Nichols model above a single-season model for a species would provide further support that species abundance was significantly different between the management sectors. We ranked models by Akaike's information criteria (AIC), and models that had a delta AIC of <2 were considered to be a competing model (Burnham & Anderson, 2002). The c-hat and chi-squared values to assess model dispersion were generated using the Mackenzie and Bailey (2004) goodness-of-fit test, which was conducted using 1,000 simulations for each model. Models with a c-hat >2 were rejected as they were regarded as overdispersed (Farris et al., 2015).

3 | RESULTS

We accumulated 3,725 operational camera trap days (mean 91 days/camera) in the Northern Sector and 3,371 operational camera trap days (mean 84 days/camera) in the Southern Sector. In the Northern Sector grid, ten cameras were lost or damaged by people or elephants, and some malfunctioned. The Southern Sector only had eight cameras fail due to the same issues, as well as to leopard damage. In total, 16 cameras were excluded from occupancy analysis, due to being operational for <80% of occasions.

3.1 | Relative assessment of human sign

Overall, human pressure as measured by human sign within the reserve was more abundant in the Northern Sector compared to the Southern Sector. Encounter rate of human sign on transects was 1.54/km in the Northern Sector, three times higher than 0.49/km in the Southern Sector. A similar pattern was observed in the data gathered by MINFOF rangers. The Northern Sector had a density of hunting sign of 0.87/km^2 within the area of the grid, including the 2 km buffer compared to 0.08/km^2 in the Southern Sector. Given that several signs measured are closely associated with hunting activity, such as snares and cartridges, we assume that hunting activity is, on average, higher in the Northern Sector than the Southern Sector.

3.2 | Species richness

A total of 26 medium-to-large terrestrial mammal species were photographed in the Northern Sector and 31 medium-to-large terrestrial mammal species in the Southern Sector (Table 1). We also recorded five arboreal mammal species that were not the target of this survey (Table 1). Four medium-to-large terrestrial mammal species expected to occur in the surveyed habitats according to available IUCN distribution maps and literature were not detected by the camera trap surveys in either sector (Table 1).

The species accumulation curves for medium-to-large terrestrial mammal species show more species detected per unit effort in the Southern Sector (Figure 2). The diversity indices were marginally lower in the Northern Sector (Simpsons = 0.72, Shannon–Weiner = 1.79), compared to the Southern Sector (Simpsons = 0.78, Shannon–Weiner = 2.08).

3.3 | Community structure

Community structure of mammals differed between the Northern Sector and Southern Sector sites (Figures 3 and 4), with more species being encountered for three out of the four guilds (herbivores, insectivores and carnivores) in the Southern Sector. The most frequently encountered guild in both sectors was herbivore (14 species in the Southern Sector and 13 in the Northern Sector), followed by omnivore (seven in both sectors), carnivore (six in the Southern Sector, four in the Northern Sector) and insectivore (three in the Southern Sector, two in the Northern Sector). Overall, across the guilds, trapping rates for lower body mass species were higher in the Northern Sector. A marked difference was the higher trapping rates of herbivores and omnivores with body mass >10 kg in the Southern Sector (Figure 4) compared to the Northern Sector (Figure 3).

3.4 | Forest antelopes

We recorded 4,495 independent photographic events of ten species of forest antelopes. The blue duiker (*Philantomba monticola*, Thunberg, 1789) was the most frequently encountered forest antelope species across both camera trap grids (RAI = 52.7) followed by Peters' duiker (*Cephalophus callipygus*, Peters, 1876) (RAI = 41.2) and Bay duiker (*Cephalophus dorsalis*, Gray, 1846) (RAI = 7.47). The rest of the forest antelopes were relatively infrequently encountered with a global trapping rate of less than five. The disturbance-sensitive white-bellied duiker (Hart, 2013b) was only encountered in the Southern Sector (RAI = 3.95 [lower 95% confidence limit (LCL) = 2.14, upper 95% confidence limit (UCL) = 6.11]). Trapping rates were significantly higher for Peter's duiker in the Southern Sector, displaying a fivefold increase between sectors (Table 1). Peter's duiker occupancy was also significantly higher in the Southern Sector compared to the Northern Sector (p = 0.02; Table 2). There were no significant differences in trapping rates between the two sectors for Bate's pygmy antelope (*Neotragus batesi*, de Winton, 1903), bay duiker, bongo (*Tragelaphus eurycerus*, Ogilbyi, 1837), sitatunga (*Tragelaphus spekii*, Speke, 1863) and black-fronted duiker (*Cephalophus nigrifrons*, Gray, 1871). Occupancy values for bay duiker, black-fronted duiker and Bate's pygmy antelope did not differ significantly between the sectors. There were insufficient detections of the other species to model occupancy.

TABLE 1 Mammal species predicted to be recorded in the Northern and Southern (management) sectors of Dja Faunal Reserve, Cameroon

Order	Species	IUCN Status	Habitat	Northern sector RAI (LCL–UCL)	Southern sector RAI (LCL–UCL)
Afrosoricida	Giant otter shrew (*Potamogale velox*, Du Chaillu, 1860)	LC	Wetland	Not detected	Not detected
Carnivora	African golden cat (*Profelis aurata*, Temminck, 1827)[a]	VU	Forest	Not detected	0.58 (0.27–0.91)
Carnivora	Leopard (*Panthera pardus*, Linnaeus, 1758)[a]	NT	Mixed	Not detected	0.83 (0.32–1.45)
Carnivora	Marsh mongoose (*Atilax paludinosus*, Cuvier, 1829)[a]	LC	Wetland	0.56 (0.33–0.82)[b]	0.09 (0–0.2)[b]
Carnivora	Black-legged mongoose (*Bdeogale nigripes*, Pucheran, 1855)[a]	LC	Forest	1.83 (0.79–3.14)	3.71 (2.63–4.84)
Carnivora	Cameroon cusimanse (*Crossarchus platycephalus*, Goldman, 1984)[a]	LC	Forest	1.83 (1.24–2.47)	0.83 (0.46–1.27)
Carnivora	Long-nosed mongoose (*Herpestes naso*, de Winton, 1901)[a]	LC	Forest	1.02 (0.53–1.60)	0.89 (0.09–2.27)
Carnivora	African palm civet (*Nandinia binotata*, Gray, 1830)[a]	LC	Forest	1.13 (0.71–1.6)	0.89 (0.52–1.3)
Carnivora	Servaline genet (*Genetta servalina*, Pucheran, 1855)[a]	LC	Forest	3.25 (2.39–4.16)	2.14 (1.42–2.95)
Carnivora	Large-spotted genet (*Genetta maculata*, Gray, 1830)	LC	Forest	Not detected	Not detected
Carnivora	Central African oyan (*Poiana richardsonii*, Thomson, 1842)c	LC	Forest	Not detected	0.03 (0.03–0.09)
Cetartiodactyla	Bates's pygmy antelope (*Neotragus batesi*, de Winton, 1903)[a]	LC	Forest	0.4 (0.11–0.78)	0.36 (0.15–0.59)
Cetartiodactyla	Forest buffalo (*Syncerus caffer*, Sparrman, subsp. *nanus*, 1779)[a]	EN	Forest	0.08 (0–0.24)	0.06 (0–0.19)
Cetartiodactyla	Peters' duiker (*Cephalophus callipygus*, Peters, 1876)[a]	LC	Forest	14.1 (8.38–20.71)[b]	71.46 (49.63–96.41)[b]
Cetartiodactyla	Bay duiker (*Cephalophus dorsalis*, Gray, 1846)[a]	LC	Forest	6.68 (4.4–9.35)	8.34 (4.92–12.28)
Cetartiodactyla	White-bellied duiker (*Cephalophus leucogaster, subsp. leucogaster*, Gray, 1873)	LC	Forest	Not detected	3.95 (2.14–6.11)
Cetartiodactyla	Black-fronted duiker (*Cephalophus nigrifrons*, Gray, 1871)[a]	LC	Forest	0.86 (0.03–2.46)	0.5 (0.06–1.14)
Cetartiodactyla	Yellow-backed duiker (*Cephalophus silvicultor*, Afzelius, 1815)[a]	LC	Forest	3.7 (2.25–5.54)	5.55 (3.54–7.94)
Cetartiodactyla	Blue duiker (*Philantomba monticola*, Thunberg, 1789)[a]	LC	Forest	61.64 (46.02–78.8)	42.98 (31.5–55.61)
Cetartiodactyla	Bongo (*Tragelaphus eurycerus*, Ogilbyi, 1837)[a]	NT	Forest	0.05 (0–0.14)	0.06 (0–0.15)
Cetartiodactyla	Sitatunga (*Tragelaphus spekii*, Speke, 1863)[a]	LC	Wetland	0.24 (0.05–0.48)	0.09 (0–0.24)
Cetartiodactyla	Red river hog (*Potamochoerus porcus*, Linnaeus, 1758)[a]	LC	Woodland	1.61 (1.02–2.28)[b]	7 (3.36–13.04)[b]
Cetartiodactyla	Giant forest hog (*Hylochoerus mein-ertzhageni*, Thomas, 1904)	LC	Forest	Not detected	Not detected
Cetartiodactyla	Water chevrotain (*Hyemoschus aquaticus*, Ogilby, 1841)[a]	LC	Forest	0.3 (0–0.75)[b]	4.6 (1.92–7.99)[b]

(Continues)

TABLE 1 (Continued)

Order	Species	IUCN Status	Habitat	Northern sector RAI (LCL–UCL)	Southern sector RAI (LCL–UCL)
Hyracoidea	Western tree hyrax (*Dendrohyrax dorsalis*, Fraser, 1855)	LC	Forest	Not detected	Detected
Pholidota	White-bellied pangolin (*Phataginus tricuspis*, Rafinesque, 1821)[a]	VU	Forest	0.62 (0.29–1)	0.8 (0.44–1.21)
Pholidota	Giant pangolin (*Smutsia gigantea*, Illiger, 1815)[a]	VU	Forest	0.27 (0.08–0.52)	0.68 (0.38–1.01)
Primates	Agile mangabey (*Cercocebus agilis*, Milne-Edwards, 1886)[a]	LC	Forest	0.35 (0.13–0.59)	4.48 (2.65–6.82)
Primates	Moustached guenon (*Cercopithecus cephus*, Linnaeus, 1758)[c]	LC	Forest	Detected	Not detected
Primates	Greater spot-nosed guenon (*Cercopithecus nictitans*, Linnaeus, 1766)[c]	LC	Forest	Detected	Detected
Primates	Black colobus (*Colobus satanas*, Waterhouse, 1838)[c]	VU	Forest	Not detected	Detected
Primates	Galago sp.c	-		Detected	Not detected
Primates	Mandrill (*Mandrillus sphinx*, Linnaeus, 1758)[a]	VU	Forest	0.05 (0–0.13)	0.06 (0–0.19)
Primates	Western lowland gorilla (*Gorilla gorilla*, Savage, subsp. *gorilla*, 1847)[a]	CR	Forest	0.16 (0.03–0.31)	0.44 (0.2–0.73)
Primates	Central chimpanzee (*Pan troglodytes*, Blumenbach, subsp. *troglodytes*, 1799)[a]	EN	Forest	1.61 (0.77–2.9)[b]	4.57 (3.14–6.17)[b]
Proboscidea	Forest elephant (*Loxodonta cyclotis*, Matschie, 1900)[a]	VU	Mixed	0.86 (0.46–1.35)	1.9 (0.86–3.29)
Rodentia	African brush-tailed porcupine (*Atherurus africanus*, Gray, 1842)[a]	LC	Forest	17.53 (11.42–24.46)	7.62 (4.64–11.45)
Rodentia	Emin's pouched rat (*Cricetomys emini*, Wroughton, 1910)[a]	LC	Forest	32 (23.58–41.41)[b]	7.56 (3.41–14.65)[b]
Rodentia	Greater cane rat (*Thryonomys swinderianus*, Temminck, 1827)	LC	Wetland	Not detected	Not detected
Rodentia	Lady Burton's rope squirrel (*Funisciurus isabella*, Gray, 1862)[c]	LC	Forest	Detected	Detected
Rodentia	Fire-footed rope squirrel (*Funisciurus pyrropus*, Cuvier, 1833)[c]	LC	Forest	Detected	Detected
Rodentia	African giant squirrel (*Protoxerus stangeri*, Waterhouse, 1842)[c]	LC	Forest	Detected	Detected
Tubulidentata	Aardvark (*Orycteropus afer*, Pallas, 1766)[a]	LC	Mixed	Not detected	0.09 (0.05–0.19)

Notes. For each sector and species that was detected, we present the mean and 95% confidence limits (in brackets) of the number of independent photographic events per trap day times 100. Trapping rates were only calculated for medium-to-large terrestrial mammals due to inconsistent detection probabilities with other species.
IUCN status: critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC).
[a]Indicates a species that was included in the rarefaction analysis according to the definition give in the data analysis section of the methods. [b]Indicates that the RAI confidence intervals do not overlap and can be considered significantly different. [c]Signifies an arboreal species.

3.5 | Carnivore

The carnivore community differed in RAI and structure between the two sectors. Felids were not detected at all in the Northern Sector, but both leopard (*Panthera pardus*, Linneaus, 1758) and golden cat (*Profelis aurata*, Temminck, 1827) were present in the Southern Sector (Table 1). Among the Herpestidae, black-legged mongoose (*Bdeogale nigripes*, Pucheran, 1855) showed a significantly higher occupancy (p = >0.01) in the Southern Sector, but trapping rates lacked significant difference (RAI = 3.71, [LCL = 2.63, UCL = 4.84]) compared to the Northern Sector (RAI = 1.83, [LCL = 0.79, UCL = 3.14]). Marsh mongoose (*Atilax paludinosus*, Cuvier, 1829) had significantly higher

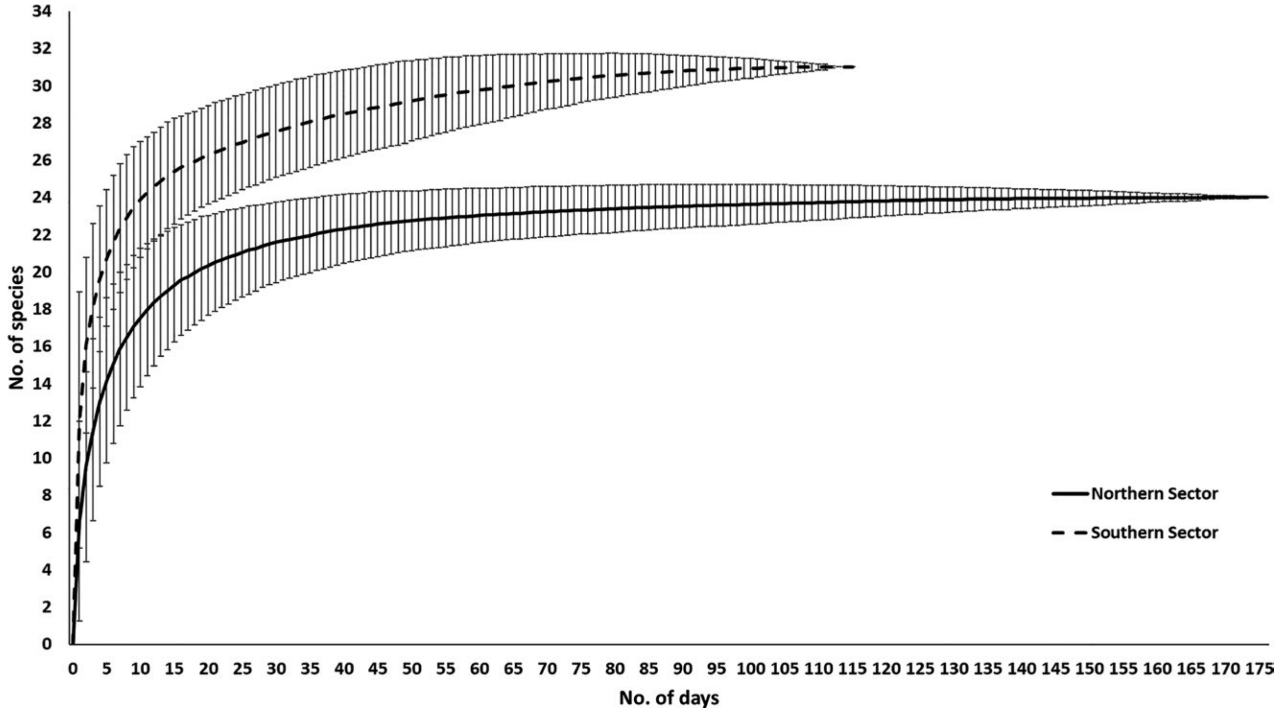


FIGURE 2 Rarefied species accumulation curves for medium-to-large terrestrial mammals in the Northern and Southern sectors of Dja Faunal Reserve, Cameroon

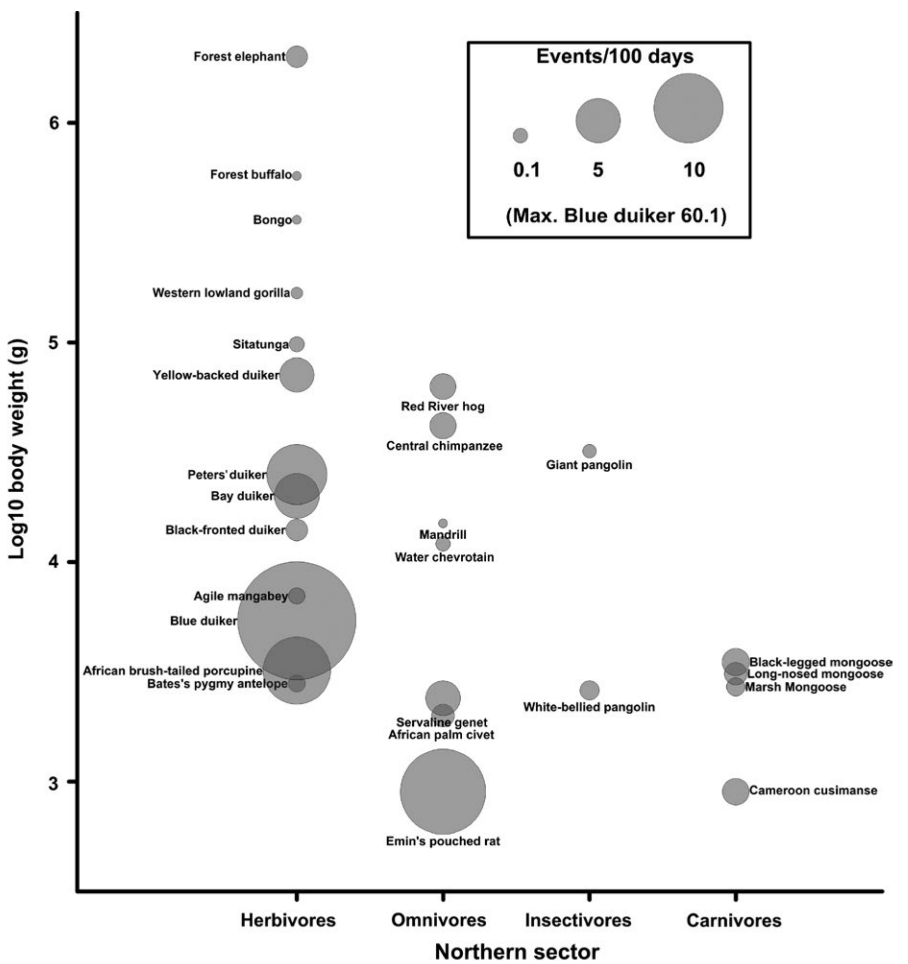


FIGURE 3 Distribution of medium-to-large terrestrial mammal species in the Northern Sector of the Dja Faunal Reserve, Cameroon, on the basis of body size and trophic category. Each circle represents a species in functional space. Size of the circle proportional to the trapping rate for that species

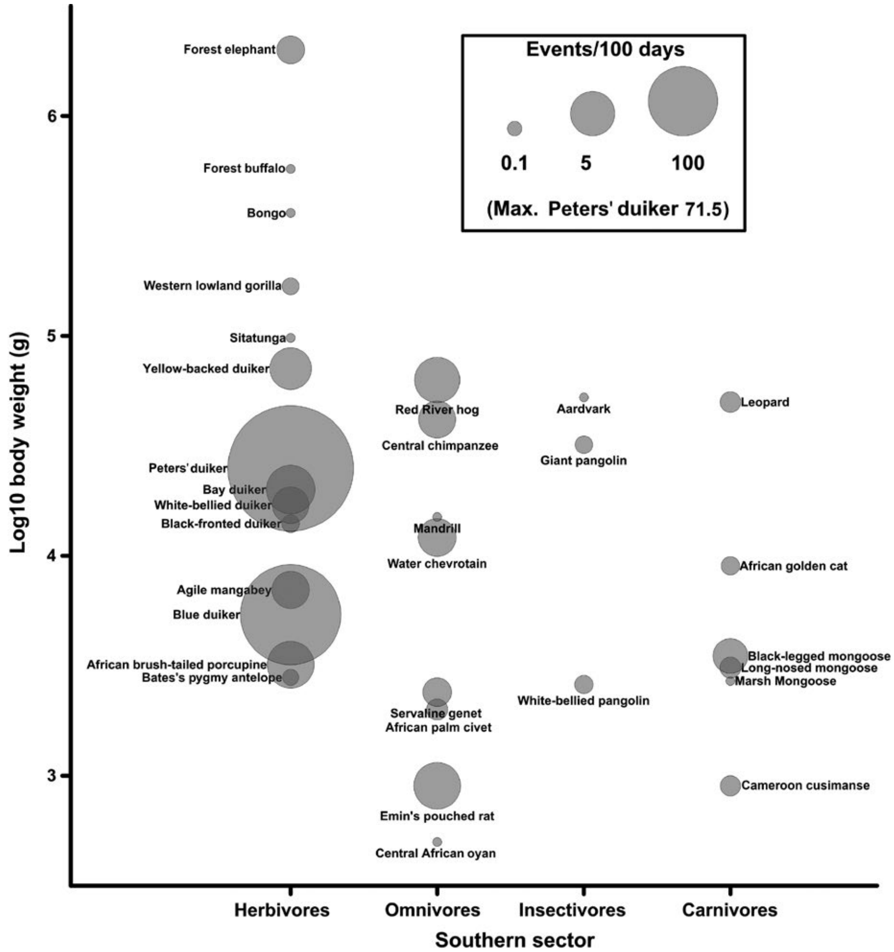


FIGURE 4 Distribution of medium-to-large terrestrial mammal species in the Southern Sector of the Dja Faunal Reserve, Cameroon, on the basis of body size and trophic category. Each circle represents a species in functional space. Size of the circle proportional to the trapping rate for that species

trapping rate in the Northern Sector (Table 1) but lacked sufficient detections to reliably calculate occupancy. Abundance of Cameroon cusimanse (*Crossarchus platycephalus*, Goldman, 1984) did not differ significantly between the two sectors (Northern Sector RAI = 1.83, [LCL = 1.24, UCL = 2.47, $\psi = 0.75$], Southern Sector RAI = 0.83, [LCL = 0.46, UCL = 1.27], $\psi = 0.56$, $p = 0.28$).

3.6 | Elephants, great apes and giant pangolin (illegal wildlife trade targets)

Among the terrestrial mammals targeted by the illegal wildlife trade, specifically, central chimpanzee (*Pan troglodytes*, Blumenbach, subsp, *troglodytes*, 1799), western lowland gorilla, (*Gorilla gorilla*, Savage, subsp, *gorilla*, 1847) forest elephant, giant pangolin (*Smutsia gigantea*, Illiger, 1815) and white-bellied pangolin (*Phataginus tricuspis*, Rafinesque, 1821), only central chimpanzee displayed a significant difference in RAI between the management sectors (Northern Sector RAI = 1.61 [LCL = 0.77, UCL = 2.9], Southern Sector RAI = 4.57 [LCL = 3.14, UCL = 6.17]). However, there was no significant difference in mean occupancy between the two sectors ($p = 0.74$). Giant pangolin displayed the greatest difference with a threefold increase in RAI from 0.27 [LCL = 0.08, UCL = 0.52] in the Northern Sector to 0.68 [LCL = 0.38, UCL = 1.01] in the Southern Sector, but this was not significant due to the overlapping confidence limits. The RAIs and, where appropriate, occupancy of forest elephant, western lowland gorilla and white-bellied pangolin were not significantly higher in the Southern Sector compared to the Northern Sector (Tables 1,2 and 1,2).

3.7 | Other bushmeat-targeted species

Emin's pouched rat (*Cricetomys emini*, Wroughton, 1910) was more abundant as measured by both occupancy ($p \geq 0.01$) and trap rates in the Northern Sector compared to the Southern Sector (Table 1). African brush-tailed porcupine (*Atherurus africanus*, Gray, 1842) did not have significant differences in RAI between the management sectors, but occupancy was significantly higher in the Northern Sector ($p \geq 0.04$). In comparison, the larger-bodied red river hog (*Potamochoerus porcus*, Linneaus, 1758) was more frequently encountered, as measured by both species abundance metrics, in the Southern Sector (RAI = 7 [LCL = 3.36, UCL = 13.04], $\psi = 0.91$) compared to the Northern Sector (RAI = 1.61 [LCL = 1.02, UCL = 2.28], $\psi = 0.65$, ($p = 0.04$).

3.8 | Species occupancy with covariates

There was a total of 15 species that had sufficient detections to model occupancy with interacting site covariates (distance to park boundary

TABLE 2 Null mean occupancy (ψ) and detection (p) probabilities with standard error presented in brackets for the Northern Sector and Southern Sector

Species	Northern sector (ψ)	Northern sector (p)	Southern sector (ψ)	Southern sector (p)	Model	Beta—Parameter chosen	Lower 95% beta	Upper 95% beta	C-hat value	Chi-squarep value
Certiodactyla										
Bates's pygmy antelope	0.22 (0.1)	0.15 (0.06)	[0.26]	–	Null	–	–	–	–	–
Bay duiker	0.91 (0.06)	0.4 (0.03)	0.87 (0.06)	0.4 (0.03)	D.RN	lam(DistanceSTD)	0.006356808	0.4333565	0.93	0.25
Black-fronted duiker	0.1 (0.06)	0.36 (0.1)	0.15 (0.06)	0.25 (0.08)	Null	–	–	–	–	–
Blue duiker	0.97 (0.03)	0.82 (0.02)	1 (0)	1 (0)	D.RN	lam(DistanceSTD)	0.02013549	0.3637492	0.21	0.24
Peters' duiker	0.83 (0.07)[a]	0.56 (0.03)	1 (0)[a]	1 (0)	D*S.RN	lam(DistanceSTD:sectorSouthern)	−0.7435528	0.03659243	0.004	0.3
Water chevrotain	[0.07]	–	0.4 (0.08)	0.45 (0.05)	–	–	–	–	–	–
White-bellied duiker	–	–	0.72 (0.08)	0.31 (0.03)	Null	–	–	–	–	–
Yellow-backed duiker	0.84 (0.08)	0.27 (0.03)	0.86 (0.07)	0.39 (0.03)	D*S.RN	lam(DistanceSTD:sectorSouthern)	0.1088372	1.0251104	0.69	0.21
Red river hog	0.65 (0.11)[a]	0.21 (0.03)	0.91 (0.06)[a]	0.33 (0.03)	D*S.RN	lam(DistanceSTD:sectorSouthern)	−1.2560347	−0.1352547	0.27	0.44
Proboscidae										
Forest elephant	0.67 (0.15)	0.14 (0.04)	0.63 (0.13)	0.14 (0.04)	Null	–	–	–	–	–
Primates										
Central chimpanzee	0.77 (0.14)	0.15 (0.04)	0.82 (0.07)	0.35 (0.03)	S.RN	lam(sectorSouthern)	0.3736869	1.4429314	0.3	0.39
Western lowland gorilla	[0.07]	–	0.45 (0.17)	0.1 (0.04)	Null	–	–	–	–	–
Philodota										
Giant pangolin	[0.2]	–	0.61 (0.16)	0.11 (0.04)	Null	–	–	–	–	–
White-bellied pangolin	0.45 (0.16)	0.12 (0.05)	0.63 (0.17)	0.11 (0.03)	D*S.occu	psi(DistanceSTD:sectorSouthern)	−48.425115	−1.910401	0.22	0.6
Rodentia										
African brush-tailed porcupine	0.98 (0.03)[a]	0.57 (0.03)	0.84 (0.06)[a]	0.42 (0.03)	D*S.RN	lam(DistanceSTD:sectorSouthern)	−1.0008123	−0.1586108	0.42	0.71
Emin's pouched rat	1 (0)[a]	1 (0)	0.79 (0.07)[a]	0.38 (0.03)	D*S.RN	lam(DistanceSTD:sectorSouthern)	−0.95574568	−0.1390762	0.21	0.75
Carnivora										

(Continues)

TABLE 2 (Continued)

Species	Northern sector (*ψ*)	Northern sector (*p*)	Southern sector (*ψ*)	Southern sector (*p*)	Model	Beta–Parameter chosen	Lower 95% beta	Upper 95% beta	C-hat value	Chi-squarep value
African golden cat	-	-	0.41 (0.13)	0.13 (0.04)	Null	-	-	-	-	-
African palm civet	[0.47]	-	0.73 (0.17)	0.12 (0.03)	D.Occu	psi(DistanceSTD)	−8.177158	Inf	1.97	0.08
Black-legged mongoose	0.47 (0.1)[a]	0.25 (0.04)	0.82 (0.08)[a]	0.31 (0.03)	S.RN	lam(sectorSouthern)	0.2802663	1.4627420	0.11	0.58
Cameroon cusimanse	0.75 (0.09)	0.27 (0.04)	0.56 (0.15)	0.12 (0.04)	S.RN	lam(sectorSouthern)	−1.808131	−0.5098939	0.05	0.73
Long-nosed mongoose	0.55 (0.12)[a]	0.2 (0.04)	0.15 (0.06)[a]	0.27 (0.07)	Null	-	-	-	-	-
Servaline genet	0.92 (0.06)	0.35 (0.03)	0.8 (0.09)	0.2 (0.03)	D*S.RN	lam(DistanceSTD:sectorSouthern)	−0.9202819	0.03582157	0.5	0.26

Notes. Naïve occupancy values are presented in square brackets for species with a detection probability <0.1. The optimum model chosen by Akaike's information criteria for each species generating sufficient occupancy values in both sectors, with the Beta parameter and it is respective lower and upper 95% confidence limits is shown and the associated c-hat and chi-squared *p* value.
D: distance to boundary; S: management sector; RN: Royle–Nichols model; Occu: Mckenzie single-season occupancy mode; *: synergistic interaction.
[a]Indicates a significant difference in occupancy between sectors as measured by the Wald test statistic.

and management sector; Table 2). Forest elephant, black-fronted duiker and long-nosed mongoose (*Herpestes naso*, de Winton, 1901) lacked a model that had an AIC difference of >2; therefore, the covariate models were not significantly different to the null model for these species. Eleven of 15 species had a Royle–Nichols model selected as the lowest AIC value, suggesting a difference in the number of individuals was significantly influencing detection probabilities and, therefore, occupancy.

Royle–Nichols models accounted for occupancy being significantly higher in differing management sectors, with no interaction of distance to the protected area boundary for three species. Cameroon cusimanse had higher occupancy in the Northern Sector. In contrast, central chimpanzee and black-legged mongoose had significantly lower occupancy within the Northern Sector compared to the Southern Sector (Figure 5).

African brush-tailed porcupine, Emin's pouched rat and servaline genet (*Genetta servalina*, Pucheran, 1855) had a synergistic Royle–Nichols model selected as the most supported. The probability of site occupancy slightly increased with distance to the boundary and was overall higher in the Northern Sector, but declined with distance to the boundary in the Southern Sector (Figure 6). Both Peters' duiker and red river hog also displayed this pattern of occupancy, but had a much greater increase in occupancy in the Northern Sector and had higher occupancy overall in the Southern Sector (Figure 6). In contrast, yellow-backed duiker (*Cephalophus silvicultor*, Afezilus, 1815) was the only species to demonstrate an increase in occupancy with distance to the boundary in the Southern Sector, while declining in the Northern Sector. However, similar to other larger species, occupancy was higher in the Southern Sector (Figure 6).

With regard to the remaining duiker species modelled, a Royle–Nichols model with distance to the protected area boundary was identified as the most appropriate. The probability of a site being occupied by blue duiker and bay duiker increased with distance to the boundary with no discernible difference between management sectors in the model (Figure 7).

White-bellied pangolin had a single-season occupancy model selected, suggesting differences in abundance between the management sectors did not affect detection probabilities. The probability of a site being occupied by white-bellied pangolin increased in the Northern Sector and declined in the Southern Sector with increasing distance to the boundary (Figure 8).

Seven species were detected only in one sector or lacked sufficient detections in one sector to reliably model occupancy across both management sectors. Therefore, only the effect of distance to the boundary could be modelled. These were African golden cat, western lowland gorilla, white-bellied duiker, giant pangolin, African palm civet (*Nandinia binotata*, Gray, 1830), Bates's pygmy antelope and water chevrotain (*Hymeoschus aquaticus*, Ogilby, 1841). African palm civet was the only species to have distance to the boundary selected as the optimum model to explain occupancy, as occupancy increased with distance from the boundary of the protected area (Table 2). All the remaining species had the null model selected as the optimum model according to AIC criteria (Table 2). However, distance to the boundary was within <2 AIC for these species, suggesting that a significant

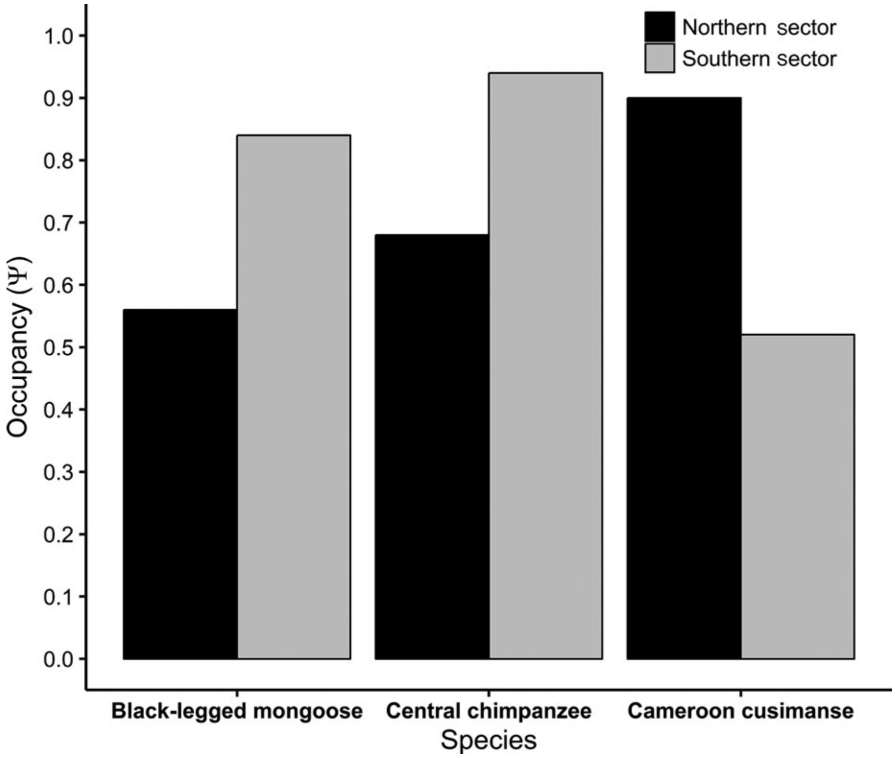


FIGURE 5 Change in the probability of occupancy for black-legged mongoose, central chimpanzee and Cameroon cusimanse with management sector according to a Royle–Nichols model

relationship with distance to the boundary could be influencing occupancy. In the Southern Sector, the occupancy increased with distance to the boundary for western lowland gorilla and giant pangolin, but decreased for African golden cat, white-bellied duiker and water chevrotain. In the Northern Sector, occupancy increased with distance to the boundary for Bates's pygmy antelope.

4 | DISCUSSION

The comparison of the two surveys confirms that standard camera trap surveys and derived metrics of presence/absence, trapping rates and occupancy can discern confident differences in ground-dwelling mammal communities in Central African forests.

4.1 | Camera trap surveys for documenting species

The comparative efficacy of camera traps for surveying medium to large ground-dwelling mammals in the DFR is indicated by observation rates and verifiability of records, especially of elusive, smaller and nocturnal species. For example, the direct encounter rate recorded by rangers on patrol throughout the entire reserve over a nine-month period is much lower than the combined number of independent photographic events in both management sectors (ZSL & MINFOF, 2017b) even for relatively large, conspicuous species, such as forest elephant (96 photographic events compared to 29 direct encounters) and central chimpanzee (204 independent photographic events compared to 23 direct encounters). Methodologies, such as camera trapping, therefore, provide important baseline data that, when repeated through time using a standardised protocol, can allow at least trends in relative abundance indices to be monitored.

4.2 | Camera trap surveys for comparing assemblages among sites

Despite being separated by only *c.* 32 km, the mammal communities between the two camera trap grids displayed marked differences. This was the case even though both grids had low Shannon–Weiner and Simpsons diversity indices due to the dominance of three or four species in each camera trap grid. Significant differences among the sites were observed for the trapping rates of species of different sizes between sectors. Smaller-bodied species within the herbivore and omnivore guilds were more prevalent within the Northern Sector (Figure 2). Trapping rates and occupancy values for small carnivores are also lower in the Southern Sector. This could be due to the difficulty of identifying morphologically similar species, such as marsh mongoose and long-nosed mongoose (Bahaa-el-din et al., 2013; Ray, 1997), in infrared imagery with single cameras. There were more unidentifiable mongoose events that were classified to a family level—66/224 in the Southern Sector compared to 29/156 in the Northern Sector of all combined mongoose events.

4.3 | The potential impact of seasonality on estimates derived from camera traps

Due to logistical and financial constraints, the surveys could not be run in the same season. This has the potential to affect trapping

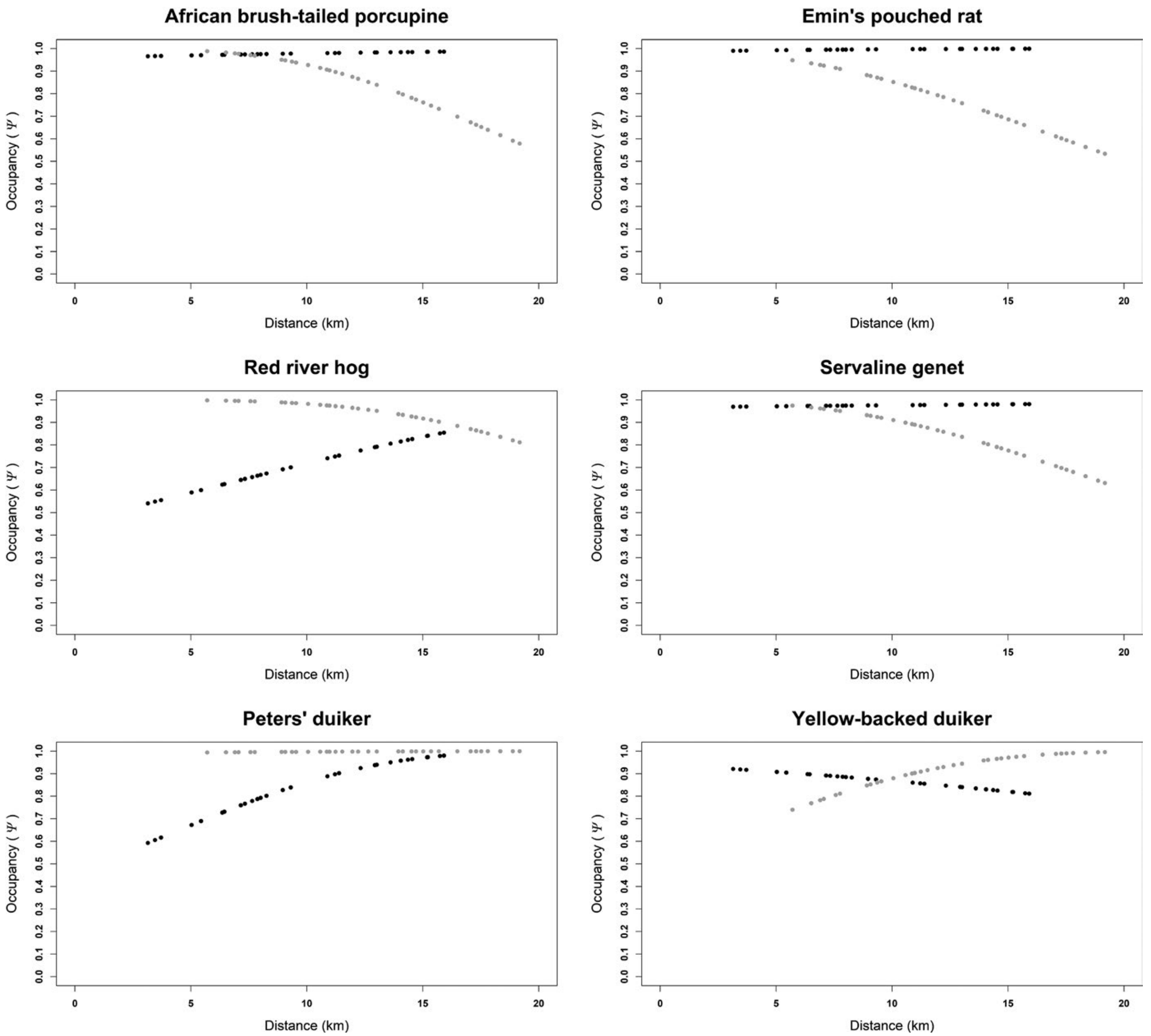


FIGURE 6 Change in the probability of occupancy for African brush-tailed porcupine, Emin's pouched rat, red river hog, servaline genet, Peters' duiker and yellow-backed duiker with management sector and distance to the boundary in kilometres according to a Royle–Nichols model. Grey circles represent the Southern Sector and black circles the Northern Sector

rates and occupancy for species with larger home ranges, because when species are wide-ranging, occupancy can prove ineffective for measuring relative abundance. Forest elephants (Blake, 2002) and great apes are known to display seasonal shifts in their habitat usage over great distances in response to increased fruit availability and precipitation (Head, Robbins, Mundry, Makaga, & Boesch, 2012). This could also influence other gregarious species, such as red river hog, that are also thought to occasionally display similar aggregations and movements in response to masting events (Leslie & Huffman, 2015). However, as both red river hog and chimpanzee had significantly higher RAI and higher occupancy with variable detection probability according to the number of individuals incorporated, this supports the possibility that these species are favouring the Southern Sector. If managers are able to establish whether wide-ranging species are predictably moving to known areas within the reserve, they can respond in a manner that provides enhanced protection to vulnerable wildlife populations in concentration areas. As most species in this survey likely have a smaller home range than the inter-trap distance and display fixed territories, it can be regarded as appropriate to compare occupancy values, as the extent of overlap of territories within the two surveys are unlikely to change in such a way as to affect the results. Future studies would benefit from trying to match camera trap surveys seasonally to try and clarify the issue of seasonal shifts in habitat usage within the DFR.

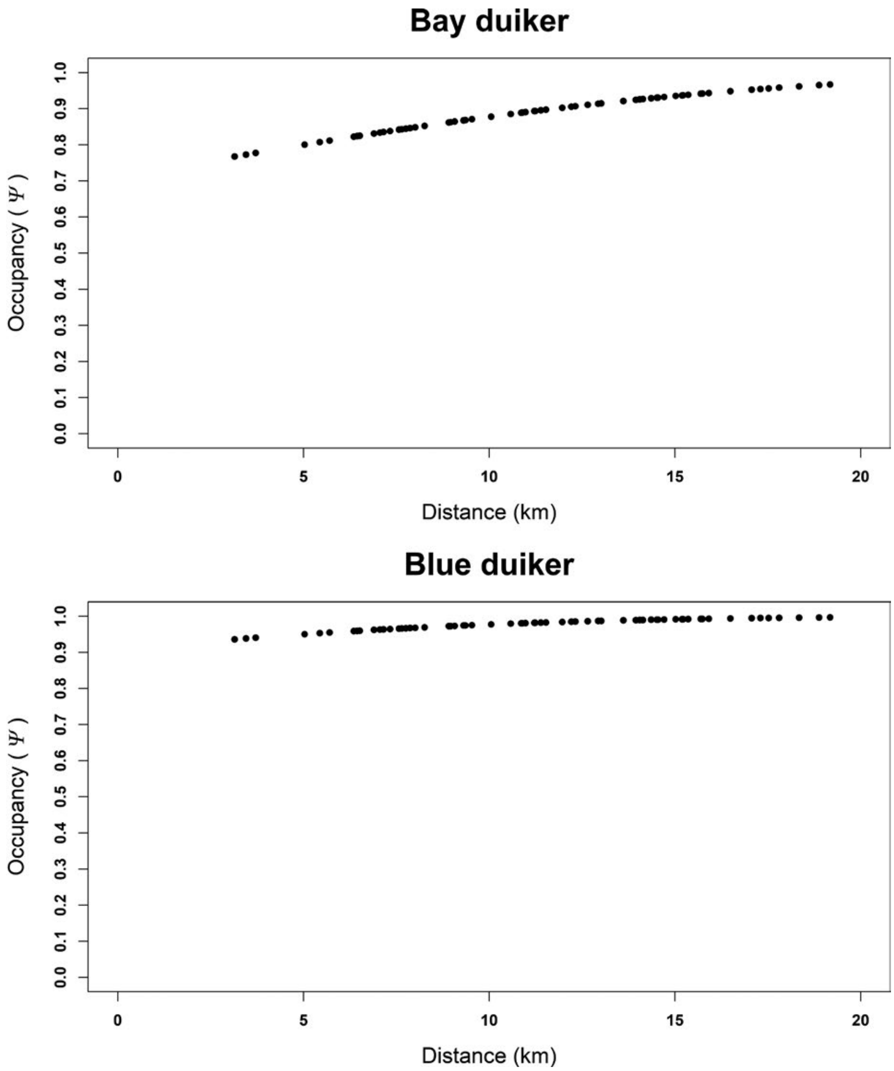


FIGURE 7 Change in the probability of occupancy for blue duiker and bay duiker with distance to the boundary in kilometres across both management sectors according to a Royle–Nichols model. Grey circles represent the Southern Sector and black circles the Northern Sector

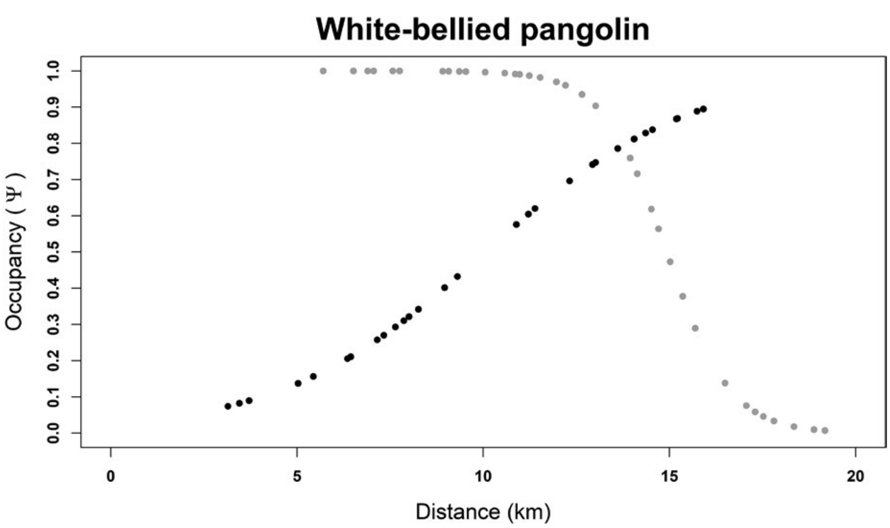


FIGURE 8 Change in the probability of occupancy for white-bellied pangolin with management sector and distance to the boundary in kilometres according to a Mackenzie occupancy model. Grey circles represent the Southern Sector and black circles the Northern Sector

4.4 | Camera trap surveys for measuring the impacts of hunting on mammal communities

The spatial scale at which mammal communities are affected by, and how populations respond to, anthropogenic pressures, such as bushmeat hunting, is difficult to empirically measure (Laurance et al., 2006). This is especially true for mammals residing within tropical forests where gathering consistent and meaningful population- and community-level metrics is challenging (Ahumada et al., 2013). Population density of tropical mammals can vary greatly due to heterogeneity present within the environment. For example, forest elephants have different distributions and aggregations in wet and dry seasons in Nouabalé-*Ndoki* National Park which is partially dependent on spatio-temporal patterns of fruiting trees across the landscape (Blake, 2002).

Whether the differences observed among the two sites surveyed here are attributable to different levels of hunting pressure remains to be confirmed. There are, however, indications that hunting pressure and its impacts on mammal faunas are greater in the Northern Sector than in the Southern Sector. The effects of hunting pressure on mammalian declines in Central African forests are well documented. The pattern, in general, is the largest-bodied species, frugivores, and those with high hunter or black market value (Abernethy et al., 2013; Cardillo et al., 2005; Fa, Olivero, Farfán, Márquez, Duarte, et al., 2014a; Fa, Olivero, Farfán, Márquez, Vargas, et al., 2014b; Peres & Palacios, 2007) are the first species to show noticeable decline. In this study, the significant decline in the relative abundance for frugivores, such as Peters' duiker and species with high hunter value, like the red river hog, under increased hunting pressure in the Northern Sector, is reported in other surveys (Abernethy et al., 2013). This is also reflected in the differences observed in this study in biomass in the different guilds of each mammal community. The mammal community within the Northern Sector shows indications of a community that is disturbed and is experiencing elevated hunting pressure. These are higher (camera) trapping rates for smaller-bodied species, such as Emin's pouched rat, and significantly fewer encounters of larger-bodied mammals that are targets of the bushmeat trade, such as Peters' duiker and red river hog (Fa, Ryan, & Bell, 2005; Jerozolimski & Peres, 2003). Additional indicators are the absence in the surveys of larger carnivores in the Northern Sector, such as golden cat and leopard, which are sensitive to snaring (Bahaa-el-din et al., 2015), and significantly reduced abundance metrics for disturbance-sensitive species, such as black-legged mongoose and water chevrotain (Hart, 2013a). The absence of white-bellied duiker in the Northern Sector also suggests elevated human disturbance as this species has been reported as very sensitive to even minor perturbation within the environment (Hart, 2013b). In comparison, the Southern Sector contained indicator fauna, such as the white-bellied duiker, and had higher trapping rates for larger-bodied species.

We suspect the differences observed are most likely due to lower human disturbance in the Southern Sector. The teams deploying and recovering the cameras in the Southern Sector covered 238 km and encountered few signs of human perturbation (T. Bruce *pers. obs.*), whereas human sign was commonly encountered by the teams in the Northern Sector. This perceived difference is reflected in the 2017 and 2018 density of hunting sign within each camera trap grid as detected through MINFOF ranger patrols (ZSL & MINFOF, 2017a, 2017b) and through the 2018 Distance Sampling inventory for the DFR (Bruce et al., 2018). Higher numbers of hunting sign in the Northern Sector would be consistent with an elevated hunting pressure in that area.

4.5 | Protection of refugia from hunting

Though inferences made for wide-ranging species, such as forest elephants and great apes, using camera traps are difficult, the fact that trapping rates were higher in more challenging terrain with assumed lower hunting pressure could be indicative of complex habitat providing some level of protection from hunting. Elephant is known to retreat when they are disturbed to terrain that is more difficult to access by humans (Hedges, 2012). Thus, within larger protected areas, certain zones may act as refugia for wildlife populations (Campbell et al., 2011). This can be due to a range of factors, such as remote and difficult terrain for poachers (Attum, 2007; Hedges, 2012) or the regular presence of field researchers and rangers (Campbell et al., 2011). The significance of these refugia for larger protected areas is that the populations of wildlife residing within them, if adequately protected, may provide source populations to allow recolonisation of other areas of the reserve (Naranjo & Bodmer, 2007). Therefore, if adequate protection can be provided to relatively small, but important areas of large reserves, this may provide tropical forests with a better chance of being ecologically resilient to ongoing and increasing human perturbation. Well-designed camera trap surveys may provide data on the status of wildlife populations at relatively fine spatial resolutions so as to identify functional refugia with greater confidence.

ACKNOWLEDGEMENTS

We appreciate the ongoing support of Cameroon's Ministry of Forests and Wildlife (MINFOF) and the opportunity to contribute to biodiversity conservation throughout the country. In particular, we would like to thank the Chef d'Antenne Serge Jacob Meye for his ongoing support of conservation research within the protected area. We appreciate the stalwart efforts of MINFOF ecoguards and local porters who accompanied the survey teams in the field. We would also like to thank the United States Fish and Wildlife Service (USFWS)—African Elephant Conservation and IUCN SOS—Fondation Segré Pangolin Conservation Initiative for supporting this work.

ORCID

Tom Bruce http://orcid.org/0000-0001-6958-1657

REFERENCES

Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E., & Maisels, F. (2013). Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of the Royal Society of London: Biological Sciences*, *368*(1625), 20120303. https://doi.org/10.1098/rstb.2012.0303

Abrahams, M. I., Peres, C. A., & Costa, H. C. (2017). Measuring local depletion of terrestrial game vertebrates by central-place hunters in rural Amazonia. *PLoS ONE*, *12*(10), e0186653. https://doi.org/10.1371/journal.pone.0186653

Ahumada, J. A., Hurtado, J., & Lizcano, D. (2013). Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: A tool for conservation. *PLoS ONE*, *8*(9), e73707. https://doi.org/10.1371/journal.pone.0073707

Ahumada, J. A., Silva, C. E., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., … Sheil, D. (2011). Community structure and diversity of tropical forest mammals: Data from a global camera trap network. *Philosophical Transactions of the Royal Society of London: Biological Sciences*, *366*(1578), 2703–2711. https://doi.org/10.1098/rstb.2011.0115

Amin, R., Andanje, S. A., Ogwonka, B., Ali, A. H., Bowkett, A. E., Omar, M., & Wacher, T. (2015). The northern coastal forests of Kenya are nationally and globally important for the conservation of Aders' duiker Cephalophus adersi and other antelope species. *Biodiversity and Conservation*, *24*(3), 641–658. https://doi.org/10.1007/s10531-014-0842-z

Attum, O. (2007). Can landscape use be among the factors that potentially make some ungulates species more difficult to conserve? *Journal of Arid Environments*, *69*(3), 410–419.

Bahaa-el-din, L., Henschel, P., Aba'a, R., Abernethy, K., Bohm, T., Bout, N., … Lee, M. (2013). Notes on the distribution and status of small carnivores in Gabon. *Small Carnivore Conservation*, *48*, 19–29.

Bahaa-el-din, L., Henschel, P., Butynski, T. M., Macdonald, D. W., Mills, D., Slotow, R., & Hunter, L. (2015). The African golden cat Caracal aurata: Africa's least-known felid. *Mammal Review*, *45*(1), 63–77.

Bennett, E. L., Blencowe, E., Brandon, K., Brown, D., Burn, R. W., Cowlishaw, G., … Robinson, J. G. (2007). Hunting for consensus: Reconciling bushmeat harvest, conservation, and development policy in West and Central Africa. *Conservation Biology*, *21*(3), 884–887. https://doi.org/10.1111/j.1523-1739.2006.00595.x

Blake, S., Deem, S. L., Mossimbo, E., Maisels, F., & Walsh, P. (2009). Forest elephants: Tree planters of the Congo. *Biotropica*, *41*(4), 459–468. https://doi.org/10.1111/j.1744-7429.2009.00512.x

Blake, S. (2002). The ecology of forest elephant distribution and its implications for conservation. Doctoral dissertation. University of Edinburgh.

Bruce, T., Ndjassi, C., Fowler, A., Ndimbe, M., Fankem, O., Tabue, R., … Olson, D. (2018). *Faunal inventory of the Dja Faunal Reserve, Cameroon*. Yaoundé, Cameroon: Ministry of Forests and Wildlife (MINFOF), Zoological Society of London – Cameroon Country Programme, African Wildlife Foundation.

Bruce, T., Wacher, T., Ndinga, H., Bidjoka, V., Meyong, F., Ngo Bata, M., & Olson, D. (2017). *camera trap survey for larger terrestrial wildlife in the Dja Biosphere Reserve, Cameroon*. Yaoundé, Cameroon: Zoological Society of London (ZSL) & Cameroon Ministry of Forests and Wildlife (MINFOF).

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference*. New York , NY: Springer.

Campbell, G., Kuehl, H., Diarrassouba, A., N'Goran, P. K., & Boesch, C. (2011). Long-term research sites as refugia for threatened and over-harvested species. *Biology Letters*, *7*(5), 723–726. https://doi.org/10.1098/rsbl.2011.0155

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R., Sechrest, W., … Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, *309*(5738), 1239–1241. https://doi.org/10.1126/science.1116030

Craigie, I. D., Baillie, J. E., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, *143*(9), 2221–2228. https://doi.org/10.1016/j.biocon.2010.06.007

Davey, K., Wacher, T., & Amin, R. (2017). *Analysis tool for camera-trap survey, data, [Computer software]*. Zoological Society of London. Retrieved fromhttps://www.zsl.org/zsl-camera-trap-data-management-and-analysis-package

Djuikouo, M. N. K., Doucet, J. L., Nguembou, C. K., Lewis, S. L., & Sonké, B. (2010). Diversity and aboveground biomass in three tropical forest types in the Dja Biosphere Reserve. *Cameroon. African Journal of Ecology*, *48*(4), 1053–1063. https://doi.org/10.1111/j.1365-2028.2010.01212.x

Dupain, J., Bombome, K., & Van Elsacker, L. (2003). Les chimpanzés et les gorilles de la réserve de faune du Dja. *Canopée*, *24*, 14–15.

Efford, M. G., & Dawson, D. K. (2012). Occupancy in continuous habitat. *Ecosphere*, *3*(4), 1–15. https://doi.org/10.1890/ES11-00308.1

Efron, B., & Tibshirani, R. J. (1994). *An introduction to the bootstrap*. Washington, DC: CRC Press.

Fa, J. E., Olivero, J., Farfán, M. Á., Márquez, A. L., Duarte, J., Nackoney, J., … Macdonald, D. W. (2014a). Correlates of bushmeat in markets and depletion of wildlife. *Conservation Biology*, *29*(3), 805–815.

Fa, J. E., Olivero, J., Farfán, M. Á., Márquez, A. L., Vargas, J. M., Real, R., & Nasi, R. (2014b). Integrating sustainable hunting in biodiversity protection in Central Africa: Hot spots, weak spots, and strong spots. *PLoS ONE*, *9*(11), e112367.

Fa, J. E., Ryan, S. F., & Bell, D. J. (2005). Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. *Biological Conservation*, *121*(2), 167–176. https://doi.org/10.1016/j.biocon.2004.04.016

Fa, J. E., Seymour, S., Dupain, J. E. F., Amin, R., Albrechtsen, L., & Macdonald, D. (2006). Getting to grips with the magnitude of exploitation: Bushmeat in the Cross-Sanaga rivers region. *Nigeria and Cameroon. Biological Conservation*, *129*(4), 497–510. https://doi.org/10.1016/j.biocon.2005.11.031

Farris, Z. J., Boone, H. M., Karpanty, S., Murphy, A., Ratelolahy, F., Andrianjakarivelo, V., & Kelly, M. J. (2015). Feral cats and the fitoaty: First population assessment of the black forest cat in Madagascar's rainforests. *Journal of Mammalogy*, *97*(2), 518–525.

Fiske, I., & Chandler, R. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, *43*(10), 1–23.

Hansen, M. C., Stehman, S. V., & Potapov, P. V. (2010). Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences*, *107*(19), 8650–8655. https://doi.org/10.1073/pnas.0912668107

Hart, J. (2013a). Water chevrotain Hymemoschus aquaticus. In J. Kingdon & M. Hoffmann (Eds.), *Mammals of Africa, VI. Hippopotamuses, pigs, deer, giraffe and bovids* (pp. 88–92). London, UK: Bloomsbury.

Hart, J. (2013b). White-bellied duiker Cephalophus leucogaster. In J. Kingdon & M. Hoffmann (Eds.), *Mammals of Africa, VI. Hippopotamuses, pigs, deer, giraffe and bovids* (pp. 255–258). London, UK: Bloomsbury.

Head, J. S., Robbins, M. M., Mundry, R., Makaga, L., & Boesch, C. (2012). Remote video-camera traps measure habitat use and competitive exclusion among sympatric chimpanzee, gorilla and elephant in Loango National Park, Gabon. *Journal of Tropical Ecology*, *28*(06), 571–583. https://doi.org/10.1017/S0266467412000612

Hedges, S. (2012). *Monitoring elephant populations and assessing threats*. Himayatnagar, Telangana: Universities Press.

Hedwig, D., Kienast, I., Bonnet, M., Curran, B. K., Courage, A., Boesch, C., … King, T. (2018). A camera trap assessment of the forest mammal community within the transitional savannah-forest mosaic of the Batéké Plateau National Park, Gabon. *African Journal of Ecology*, *56*(4), 777–790. https://doi.org/10.1111/aje.12497

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Huggel, A. (2012). Exiv2 software tool. [Computer software]. Retrieved from https://www.exiv2.org/index.html

Jerozolimski, A., & Peres, C. A. (2003). Bringing home the biggest bacon: A cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. *Biological Conservation*, *111*(3), 415–425. https://doi.org/10.1016/S0006-3207(02)00310-5

Kingdon, J. (2015). *The Kingdon field guide to African mammals*. London, UK: Bloomsbury Publishing.

Kühl, H., F. Maisels, M. Ancrenaz, & E. A. Williamson (Eds.) (2008). *Best practice guidelines for surveys and monitoring of great ape populations*. Gland, Switzerland: IUCN.

Laurance, W. F., Croes, B. M., Tchignoumba, L., Lahm, S. A., Alonso, A., Lee, M. E., … Ondzeano, C. (2006). Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, *20*(4), 1251–1261. https://doi.org/10.1111/j.1523-1739.2006.00420.x

Laurance, W. F., Useche, D. C., Rendeiro, J., Kalka, M., Bradshaw, C. J., Sloan, S. P., … Arroyo-Rodriguez, V. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, *489*(7415), 290. https://doi.org/10.1038/nature11318

Leslie, D. M., & Huffman, B. A. (2015). *Potamochoerus porcus* (Artiodactyla: Suidae). *Mammalian Species*, *47*, 15–31.

MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, *9*, 300–318. https://doi.org/10.1198/108571104X3361

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2006). *Occupancy estimation and modelling*. Burlington, MA: Academic Press.

Magurran, A. E. (2005). Species abundance distributions: Pattern or process? *Functional Ecology*, *19*(1), 177–181. https://doi.org/10.1111/j.0269-8463.2005.00930.x

Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E. A., … Warren, Y. (2013). Devastating decline of forest elephants in Central Africa. *PLoS ONE*, *8*(3), e59469. https://doi.org/10.1371/journal.pone.0059469

Malhi, Y., Adu-Bredu, S., Asare, R. A., Lewis, S. L., & Mayaux, P. (2013). African rainforests: Past, present and future. *Philosophical Transactions of the Royal Society of London: Biological Sciences*, *368*(1625), 20120312.

Mallon, D. P., Hoffmann, M., Grainger, M. J., Hibert, F., VanVliet, N., & McGowan, P. J. K. (2015). An IUCN situation analysis of terrestrial and freshwater fauna in West and Central Africa. Occasional paper of the IUCN species survival commission, (54).

Mambeya, M. M., Baker, F., Momboua, B. R., Koumba Pambo, A. F., Hega, M., Okouyi Okouyi, V. J., … Abernethy, K. (2018). The emergence of a commercial trade in pangolins from Gabon. *African Journal of Ecology*, *56*(3), 601–609. https://doi.org/10.1111/aje.12507

MINFOF & IUCN (2015). Caractérisation de la population de grands et moyens mammifères dans la Reserve de Faune du Dja: Potentiel et menaces. Yaoundé, Cameroun.

Muchaal, P. K., & Ngandjui, G. (1999). Impact of village hunting on wildlife populations in the western Dja Reserve. *Cameroon. Conservation Biology*, *13*(2), 385–396. https://doi.org/10.1046/j.1523-1739.1999.013002385.x

Naranjo, E. J., & Bodmer, R. E. (2007). Source–sink systems and conservation of hunted ungulates in the Lacandon Forest. *Mexico. Biological Conservation*, *138*(3–4), 412–420. https://doi.org/10.1016/j.biocon.2007.05.010

Nielsen, M. R. (2006). Importance, cause and effect of bushmeat hunting in the Udzungwa Mountains, Tanzania: Implications for community based wildlife management. *Biological Conservation*, *128*(4), 509–516. https://doi.org/10.1016/j.biocon.2005.10.017

O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, *6*(2), 131–139. https://doi.org/10.1017/S1367943003003172

Oksanen, J. (2015). Vegan: an introduction to ordination, Vol. *8*, (p. 19). Retrieved from https://cran.r-project.org/web/packages/vegan/vignettes/introvegan.pdf

Peres, C. A., & Palacios, E. (2007). Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal-mediated seed dispersal. *Biotropica*, *39*(3), 304–315. https://doi.org/10.1111/j.1744-7429.2007.00272.x

Potapov, P. V., Turubanova, S. A., Hansen, M. C., Adusei, B., Broich, M., Altstatt, A., … Justice, C. O. (2012). Quantifying forest cover loss in Democratic Republic of the Congo, 2000–2010, with Landsat ETM+ data. *Remote Sensing of Environment*, *122*, 106–116. https://doi.org/10.1016/j.rse.2011.08.027

Poulsen, J. R., Koerner, S. E., Moore, S., Medjibe, V. P., Blake, S., Clark, C. J., … Rosin, C. (2017). Poaching empties critical Central African wilderness of forest elephants. *Current Biology*, *27*(4), 134–R135. https://doi.org/10.1016/j.cub.2017.01.023

Purvis, A., Gittleman, J. l., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1456), 1947–1952. https://doi.org/10.1098/rspb.2000.1234

Ray, J. (1997). Comparative ecology of two African forest mongooses, Herpestes naso and Atilax paludinosus. *African Journal of Ecology*, *35*(3), 237–253. https://doi.org/10.1111/j.1365-2028.1997.08689086.x

Redford, K. H. (1992). The empty forest. *BioScience*, *42*(6), 412–422. https://doi.org/10.2307/1311860

Republic of Cameroon (1994). Law no 94/01 du 20 janvier 1994 portant régime des forêts, de la faune et de la pêche. Republic of Cameroon.

Rovero, F., & Marshall, A. R. (2009). Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, *46*(5), 1011–1017. https://doi.org/10.1111/j.1365-2664.2009.01705.x

Royle, J. A., & Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology*, *84*(3), 777–790. https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2

Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, *345*(6195), 406–412. https://doi.org/10.1126/science.1251818

Silveira, L., Jacomo, A. T., & Diniz-Filho, J. A. F. (2003). Camera trap, line transect census and track surveys: A comparative evaluation. *Biological Conservation*, *114*(3), 351–355. https://doi.org/10.1016/S0006-3207(03)00063-6

Sonké, B. (1998). Etudes floristiques et structurales des forêts de la Réserve de Faune du Dja (Cameroun). Laboratoire de Botanique Systématique et de Phytosociologie, Université Libre de Bruxelles (ULB).

Srbek-Araujo, A. C., & Chiarello, A. G. (2005). Is camera trapping an efficient method for surveying mammals in Neotropical forests? A case study in south-eastern Brazil. *Journal of Tropical Ecology*, *21*(1), 121–125. https://doi.org/10.1017/S0266467404001956

Stiles, D. (2011). Elephant meat and ivory trade in Central Africa. *Pachyderm*, *50*, 26–36.

TEAM Network (2008). Terrestrial vertebrate protocol implementation manual, v. 3.0 (p. 56). Washington DC: Tropical Ecology, Assessment and Monitoring Network, Center for Applied Biodiversity Science, Conservation International.

Tobler, M. W., Carrillo-Percastegui, S. E., Leite Pitman, R., Mares, R., & Powell, G. (2008). An evaluation of camera traps for inventorying large-and medium-sized terrestrial rainforest mammals. *Animal Conservation*, *11*(3), 169–178. https://doi.org/10.1111/j.1469-1795.2008.00169.x

Tucker, M. A., Ord, T. J., & Rogers, T. L. (2014). Evolutionary predictors of mammalian home range size: Body mass, diet and the environment. *Global Ecology and Biogeography*, *23*(10), 1105–1114. https://doi.org/10.1111/geb.12194

Williamson, L., & Usongo, L. (1995). Recensement des populations de primates et inventaire des grands mammifères. Recensement des éléphants, gorilles et chimpanzés: réserve de faune du Dja-Cameroun. Projet Ecofac-Composante Cameroun.

Ziegler, S., Fa, J. E., Wohlfart, C., Streit, B., Jacob, S., & Wegmann, M. (2016). Mapping bushmeat hunting pressure in Central Africa. *Biotropica*, *48*(3), 405–412. https://doi.org/10.1111/btp.12286

ZSL & MINFOF (2017a). *Rapport de patrouilles SMART - Réserve de Biosphère du Dja au Cameroun, (Du 1 janvier 2016 au 31 décembre 2016)*. Unpublished report, Zoological Society of London.

ZSL & MINFOF (2017b). *Rapport de patrouilles SMART - Réserve de Biosphère du Dja au Cameroun, (Du 1 janvier 2017 au 30 septembre 2017)*. Unpublished report, Zoological Society of London.

How to cite this article: Bruce T, Amin R, Wacher T, et al. Using camera trap data to characterise terrestrial larger-bodied mammal communities in different management sectors of the Dja Faunal Reserve, Cameroon. *Afr J Ecol*. 2018;56:759–776. https://doi.org/10.1111/aje.12574

Short Communication

Tropical Conservation Science
Volume 11: 1–5
© The Author(s) 2018
Reprints and permissions:
sagepub.com/journalsPermissions.nav
DOI: 10.1177/1940082917749224
journals.sagepub.com/home/trc
SAGE

Locating Giant Ground Pangolins (*Smutsia gigantea*) Using Camera Traps on Burrows in the Dja Biosphere Reserve, Cameroon

Tom Bruce[1], Romeo Kamta[2,3], Roger Bruno Tabue Mbobda[4], Stephane Talla Kanto[4], Djibrilla Djibrilla[4], Ituka Moses[4], Vincent Deblauwe[2,5,6], Kevin Njabo[2,5], Matthew LeBreton[2], Constant Ndjassi[1], Chris Barichievy[7,8], and David Olson[1]

Abstract

Giant ground pangolins (*Smutsia gigantea*) are poorly known and difficult to study due to their nocturnal and burrowing habits. Here, we test the efficacy of using camera traps on potentially active burrows identified by local Ba'Aka guides to rapidly locate giant ground pangolins in the wild for subsequent observation and tagging for telemetry studies. We deployed nine cameras on potential giant ground pangolin burrows in the Dja Biosphere Reserve, Cameroon. One camera photographed an adult male giant ground pangolin using a burrow within 2 days of camera deployment. The pangolin used the same burrow several times over a 25-day period and possible scent-marking behavior was recorded.

Keywords

Smutsia gigantea, burrow, giant pangolin, Dja Biosphere Reserve, Cameroon

Introduction

The giant ground pangolins (*Smutsia gigantea* [Illiger, 1815]) of African lowland forests and savanna gallery forests remain one of the planet's least studied animals (Kingdon, Hoffmann, & Hoyt, 2013). What little information there is describes an animal that is largely nocturnal, burrowing, and primarily restricted to remote areas where hunting pressure is low. The steep rise in demand for pangolin scales driven by traditional remedies in Asia has greatly increased black market prices and is now driving intensive commercial hunting of all pangolin species in Africa (Challender & Hywood, 2012; Cheng, Zing, & Bonebrake, 2017). Giant ground pangolins are coveted by illegal wildlife traffickers for their large scales and by hunters for bushmeat (Ingram et al., 2017; Waterman, Pietersen, Hywood, Rankin, & Soewu, 2014).

Kingdon et al. (2013) warn that, "the large size, slow reproductive rate and terrestrial habits make the giant ground pangolins vulnerable to over exploitation, and that more research is required to address the currently inadequate conservation situation of the species" (p. 399). Understanding resource and area requirements for *S. gigantea* is essential for conservation management. This can be achieved through generating baseline natural history information and in developing and testing spatial habitat use models that can predict the species' potential

[1]Zoological Society of London—Cameroon, Yaoundé, Cameroon
[2]Congo Basin Institute, Yaoundé, Cameroon
[3]University of Dschang, Dschang, Cameroon
[4]Ministry of Forestry and Wildlife, MINFOF, Dja Faunal Reserve, Yaoundé, Cameroon
[5]Center for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles, CA, USA
[6]International Institute of Tropical Agriculture, Yaoundé, Cameroon
[7]Zoological Society of London, Conservation Programmes, Regent's Park, London, UK
[8]Institute for Communities and Wildlife in Africa, University of Cape Town, Rondebosch, South Africa

Received 3 November 2017; Revised 29 November 2017; Accepted 29 November 2017

Corresponding Author:
Tom Bruce, Zoological Society of London—Cameroon, Yaoundé, Cameroon.
Email: Thomas.Bruce@zsl.org

range and habitat use. Knowledge gained from such models can inform conservation-relevant estimates of home range size and variation, overlap of home ranges among individuals, population densities (and range of variation) within major habitat types, and minimum area requirements for maintaining viable populations of giant ground pangolins in different habitats or regions and under different hunting pressure regimes—presently no data or estimates exist for any of these for this pangolin species.

A spatial habitat use model would be derived, in part, from quantified habitat covariates combined with a species' activity model that can inform how the animals engage with their habitat. However, gathering data to support this is challenging due to the species' largely nocturnal and reclusive habits. Encounter rates of giant ground pangolins from previous studies are low (e.g. 0.22 [0.08 SE] independent photographic events/100 days; Bruce et al., 2017]). These traits make direct observational studies to understand how it utilizes its habitat difficult as it is not easy to find or to relocate the animal. An understanding of the habitat requirements and activity patterns, as well as natural history observations, will need to be augmented with remotely sensed data, such as telemetry and camera-trap studies. Giant ground pangolins have never been tagged or tracked to date, though other pangolin species have (Nebo & Rankin, 2011; Pagés, 1975; Pietersen, McKechnie, & Jansen, 2014; Sun, Lin, Lai, & Pei, 2015). Temminck's ground pangolin (*Smutsia temminckii* [Smuts, 1832]) habitat use has been studied by following animals that have radio transmitters attached and remotely sensed information collected through GPS receivers (Pietersen et al., 2014). However, simply finding a giant ground pangolin to attach a tracking device to begin such research can be difficult given their apparent rarity and furtive habits. For these reasons, we tested a field survey method to cost-effectively locate a giant ground pangolin in order to deploy a tracking tag by a research team. As camera traps have been used previously to document elusive species (Whitworth, Braunholtz, Huarcaya, MacLeod, & Beirne, 2016), we placed camera traps on potential pangolin burrows identified by local Ba'Aka guides to test if it was possible to locate an active burrow within 2 to 3 weeks. We also assessed the feasibility of using camera traps for longer term surveillance of active burrows to learn more about the natural history of giant ground pangolins.

Methods

Study Area

The camera-trap burrow survey was conducted in south central Cameroon in the 526,000 ha Dja Biosphere Reserve (DBR; Figure 1). The reserve is among the largest protected areas in Cameroon and surrounded by community forests, forestry management units, and rural roads and settlements. Nine camera traps were placed on nine possible pangolin burrows (see below for selection criteria) in the vicinity of the Congo Basin Institute's Bouamir Research Station in the DBR (3°11′27″N, 12°48′41″E; 650 m–800 m elevation) situated

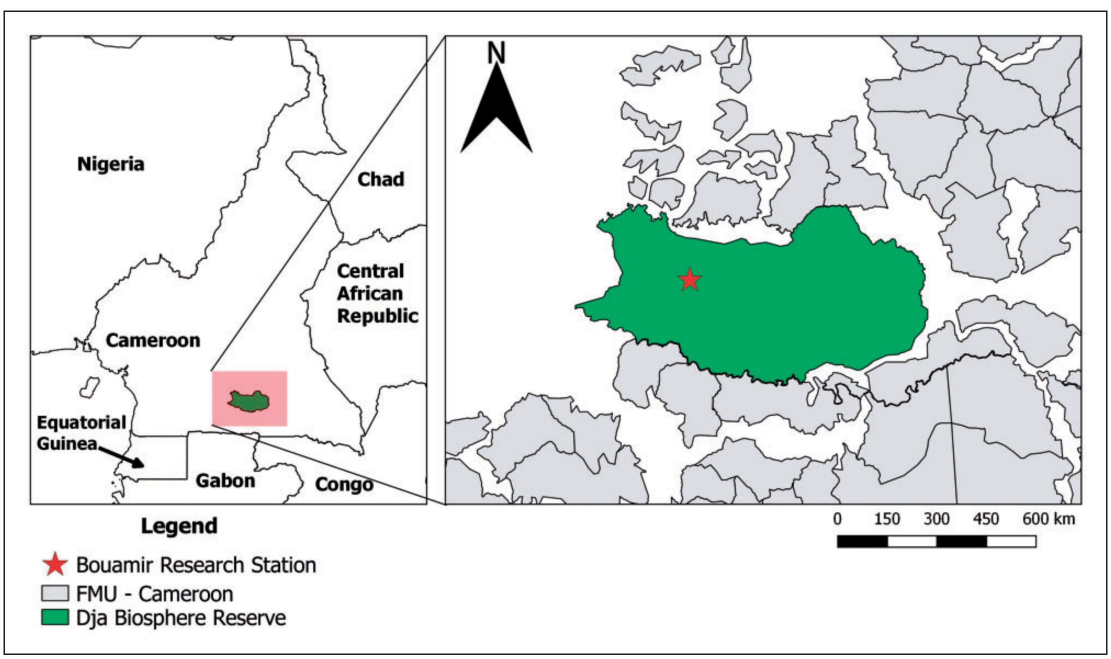


Figure 1. Location of Bouamir Research station in the Dja Biosphere Reserve (DBR), Cameroon. FMU are surrounding forestry management units.

in the western portion of the Northern Sector (Figure 1). Semideciduous lowland forest is the dominant habitat. Low areas support *Raphia* and *Uapaca* swamps. Annual rainfall is ca. 1,600 mm with two wet (September maximum) and two dry (December to January and July) seasons (Laclavére, 1980). The forests surrounding the research station have never been commercially logged or farmed and are approximately 16 km from the nearest village or road. Giant pangolins are fully protected in Cameroon (Ministry of Forests and Wildlife [MINFOF], 2017). However, poaching for bushmeat and the illegal trade in elephant ivory, great apes, and pangolin scales is increasing within the DBR (MINFOF and International Union for the Conservation of Nature [IUCN], 2015), though populations of many species of wildlife (giant ground pangolins remain unassessed) in the immediate vicinity of the research station appear to have remained stable over the past decade (Chen, Garcia, Kameni, & Roswall, 2017).

Burrows

Two experienced forest guides who work with the Bouamir Field Station identified nine potentially active burrows. Burrows were identified based on diameter, location, and the presence of scratch marks on surrounding ground and roots. All the burrows were within 2.5 km of the Bouamir Field Station. We made the reasonable assumption that burrows used by giant ground pangolins have to be relatively large to accommodate an adult pangolin. Burrows that ranged in diameter from 30 cm to 60 cm were, therefore, selected for monitoring by camera traps. Giant ground pangolins are reported to be commonly associated with swamps, though they are reported to forage in diverse habitats (Kingdon, Hoffman, and Hoyt, 2013). Six out of eight localities discovered by local guides were within 100 m of swamp habitat. In addition to distance to swamp, we recorded covariate data about burrows, such as diameter breast height (dbh) of associated trees, if present, aspect, slope, and canopy cover. Several burrows had entrances at the base of trees and roots. Some trees had multiple entrances that may lead to a single interconnected burrow.

Camera Traps

Cuddeback Long Range IR E2 camera traps were set on trees 3 to 5 m from the burrows. The cameras were strapped to trees roughly 30 to 50 cm above the ground. The cameras were set to take ambient light photos and videos in the day and infrared photos and video at night. The first cameras were installed on June 29, 2017, and the last on July 4, 2017. The cameras were not checked until retrieval on either July 27, 2017, or July 28, 2017. The cameras were active between 23 and 29 days.

Results

One camera trap out of nine at eight localities (two burrow entrances were associated with a single tree) photographed a pangolin at a burrow in this survey (Figure 2). The burrow was adjacent to a tree located on a northeast facing slope at the edge of a swamp. The tree had multiple burrow entrances around its trunk and roots, and cameras were placed to capture

Figure 2. Giant pangolin photographed by camera trap leaving a burrow at Bouamir Research Station in the Dja Biosphere Reserve, Cameroon.

images of the two largest burrow entrances. The active burrow (30 cm in diameter) was located under extended roots, and the tree diameter at 1.3 m (dbh) was 152 cm. Another camera on a 60-cm diameter burrow located directly on the other side of the large root on the same tree produced overexposed images, and we could not tell if a pangolin was active there. At the active burrow, we photographed at least one single, adult male—testicles are clearly discerned in several images and video—giant ground pangolin entering and exiting the burrow multiple times. The camera was placed on June 30, 2017, and retrieved on July 25, 2017, and was thus active for 25 nights. The pangolin visited this burrow on July 1 at 7:55 p.m. (2 days after camera set-up; the pangolin appears to be departing the burrow, though in this case and the others that follow, it may have been simply investigating the burrow and not residing there), July 7 at 7:55 a.m. (the pangolin is assumed to be departing the burrow), July 8 at 10:17 p.m. (possibly departing, possibly scent-marking), July 18 at 11:55 p.m. (possibly returning), July 20 at 11:21 p.m. (possibly returning, possibly scent-marking), July 21 at 6:38 p.m. (possibly departing), July 21 at 6:42 p.m. (possibly returning), and July 22 at 1:25 a.m. (possibly returning). All the activities of the giant ground pangolin recorded at the burrow occurred at night. We cannot be certain if the pangolin was staying inside the burrow or simply investigating it. As there were several burrow entrances greater than 30 cm in diameter on the same tree and these were not effectively monitored, one cannot surmise any further on the activity patterns of the giant ground pangolin photographed at Camera 56 as it may have been able to exit and enter the burrow complex from another burrow entrance. The giant ground pangolin was observed in the videos to be actively sniffing the tree root on several occasions and appears to scent mark twice by prominently pressing its anal glands to the top of the root (Zoological Society of London [ZSL], Congo Basin Institute [CBI], and MINFOF, 2017).

Discussion

Our observations indicate that camera traps placed on potentially active burrows (i.e., burrows where pangolins are residing in them or are investigating them on a regular basis) can potentially detect animal presence within 2 days of placement. Identifying candidate burrows may be facilitated through the assistance of indigenous guides with knowledge of pangolin signs and habits. Based on this limited data set, we can profile an active giant ground pangolin's burrow as being at least 30 cm in diameter, it may possibly be located under roots that appear to have the moss and lichens on the upper surface abraded by passage of the pangolin and may have scent-marking sign. This latter feature may mean that trained dogs may potentially be useful in finding active burrows. Multiple burrow entrances may be present.

This survey further confirms that giant ground pangolins are active at night. However, several anecdotal reports (Gabon, J. Bailie, personal communication, 24 November 2016) of animals encountered in the day (Mbam et Djerem National Park, Cameroon, I Goodwill, personal communication, August 2017; Lopé NP, Gabon. K. Abernethy, personal communication, July 2017) indicate that giant ground pangolins may be active in the day as well. This is not without precedent as white-bellied pangolins (*Phataginus tricuspis* [Rafinesque, 1821]), black-bellied pangolins (*P. tetradactyla* [Linnaeus, 1766]) and Temminck's ground pangolins are known to be active in the day (Pietersen et al., 2014). The presence of multiple burrow entrances around the active pangolin burrow prohibits any confident conclusions about the activity patterns of giant ground pangolins, such as how long they remain in burrows, when they enter and exit, on average, and whether they use multiple burrows. It is also not known if giant ground pangolin share burrows with other individuals, either together or at different times, though recent camera-trap surveys in the same protected area have twice captured two adult animals walking one after another. The current understanding is that giant ground pangolins are solitary (Kingdon et al., 2013).

Camera 56 also photographed Emin's pouched rat (*Cricetomys emini* [Wroughton, 1910]) and African brush-tailed porcupine (*Atherurus africanus* [Gray, 1942]) going in and out of the active giant ground pangolin burrow on the same evening, and the porcupine was photographed within 15 min following giant ground pangolin activity. This suggests that the burrow may be complex below ground with multiple chambers or, alternatively, burrow residents have high tolerance for one another. It remains unknown which animals dig the burrows in the DBR, though. Aardvarks (*Orycteropus afer* [Pallas, 1766]) are active burrowers and have recently been recorded in the Reserve. *Smutsia temminckii* is known to utilize aardvark burrows (Pietersen, McKechnie, and Jansen, 2014).

Implications for Conservation

For any researcher intent on learning more about giant ground pangolins, camera traps on potential burrows offer a cost-effective means of locating and observing the animals as they use single or multiple burrows. Researchers hoping to place a tag on an animal to learn more about its activity patterns and habitat requirements may potentially use this survey technique to rapidly locate an animal for tag placement. If active burrows can be identified through physical characteristics, camera trapping or eDNA sampling could help develop a habitat/predictive model for active burrows and could be used to build a picture of local giant pangolin populations. Gaining a better understanding of giant pangolin natural history could help to characterize and identify viable refugia for this threatened species and shed light on its vulnerability to exploitation, and help inform conservation management of the species.

Acknowledgments

The authors would like to thank the government of the Republic of Cameroon and the Ministry of Forests and Wildlife for their continuing support of this effort as part of their overall program to protect and manage Cameroon's wildlife. The authors would also like to thank Conservator H Ndinga of the Dja Faunal Reserve and the Chef d'Antenne SJ Meye for their ongoing support of conservation research within the protected area. The authors thank T Smith of the Congo Basin Institute and the University of California, Los Angeles for his guidance and ongoing support of this research. The authors greatly appreciate the assistance of A David, S Augustin, and M Mebengue, the Ba'Aka guides who work with the Congo Basin Institute's Bouamir Research Station, and who shared their knowledge and ably identified candidate giant pangolin burrows. The authors thank Cuddeback (Non Typical, Inc) for their contributions towards making camera traps affordable for our wildlife research work. The authors also thank C Waterman, T Smith, P De Ornellas, T Wacher, and C Ransom for review of earlier drafts. We thank Dan Challender and an anonymous reviewer for their reviews of the final manuscript. We thank R Sennett Day, S Winteringham, and J Ridley for assistance with the giant ground pangolin videos.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

Supplementary material

Supplementary material is available for this article online.

References

Bruce, T., Wacher, T., Ndinga, H., Bidjoka, V., Meyong, F., Ngo Bata, M., . . . Olson, D. (2017). *Camera-trap survey for larger terrestrial wildlife in the Dja Biosphere Reserve, Cameroon*. Yaoundé, Cameroon: Zoological Society of London (ZSL) & Cameroon Ministry of Forests and Wildlife (MINFOF).

Challender, D. W. S., & Hywood, L. (2012). African pangolins under increased pressure from poaching and intercontinental trade. *TRAFFIC Bulletin*, *24*, 53–55.

Chen, E., Garcia, J., Kameni, M., & Roswall, T. (2017). *Interdecadal alterations in frugivore abundance and diversity in a Congo Basin tropical rainforest: The Bouamir story* (Unpublished report). Yaoundé, Cameroon: Congo Basin Institute.

Cheng, W., Zing, S., & Bonebrake, T. C. (2017). Recent pangolin seizures in China reveal priority areas for intervention. *Conservation Letters*. Advance online publication. doi:10.1111/conl.12339.

Ingram, D. J., Coad, L., Abernethy, K. A., Maisels, F., Stokes, E. J., Bobo, K. S., . . . Scharlemann, J. P. W. (2017). Assessing Africa-wide pangolin exploitation by scaling local data. *Conservation Letters*. Advance online publication. doi:10.1111/conl.12389.

Kingdon, J. S., Hoffmann, M., & Hoyt, R. (2013). *Smutsia gigantea* Giant Ground Pangolin. In: J. S. Kingdon, & M. Hoffmann (Eds.). *The mammals of Africa. Volume 5: Carnivores, pangolins, equids, rhinoceroses* (pp. 396–399). London, England: Bloomsbury Publishing.

Laclavére, G. (Ed.). (1980). *Atlas of the United Republic of Cameroon*. Paris, France: Editions Jeune Afrique.

Ministry of Forests and Wildlife [MINFOF]. (2017). *Lettre Circulaire No 0007/LC/MINFOF/DFAP/SDVEF du 11 JAN 2017: Relative a l'Exportation du Perroquet Gris a Queue Rouge et du Pangolin.* Yaoundé, Cameroon: Cameroon Ministry of Forests and Wildlife.

MINFOF & International Union for the Conservation of Nature [IUCN] (2015) *Caractérisation de la population de grands et moyens mammifères dans la Reserve de Faune du Dja: Potentiel et menaces*. Yaoundé, Cameroon: IUCN.

Nebo, B., & Rankin, P. (2011.) Tagging Okulunu with a GPS/GSM unit. *Pangolin Research Mundulea: Pangolin survival strategies in dry-land Savannahs: A pilot study in Namibia.* Retrieved from http://pangolins-namibia.blogspot.com/2010/12/tagging-okulunu-with-gps-combination.html.

Pagés, E. (1975). Etude éco-éthologique de *Manis tricuspis* par radio-tracking. *Mammalia*, *39*, 613–641.

Pietersen, D. W., McKechnie, A. E., & Jansen, R. (2014). Home range, habitat selection and activity patterns of an arid zone population of ground pangolins, *Smutsia temminckii*. *Africa Zoology*, *49*, 365–276.

Sun, C-M., Lin, J-S., Lai, C-Y., & Pei, K. J-C. (2015). *Home range, density, habitat preference and modelling of pangolins* (Manis p. pentadactyla) *in southeastern Taiwan*. Presentation at the 1st International Conference on Pangolin Conservation, Trade and Rehabilitation, Mabula Lodge, South Africa, October 12–15, 2016.

Waterman, C., Pietersen, D., Hywood, L., Rankin, P., & Soewu, D. (2014). *Smutsia gigantea*. *The IUCN Red List of Threatened Species 2014*: e.T12762A45222061. Retrieved from http://dx.doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12762A45222061.en.

Whitworth, A., Braunholtz, L. D., Huarcaya, R. P., MacLeod, R., & Beirne, C. (2016). Out on a limb: Arboreal camera traps as an emerging methodology for inventorying elusive rainforest mammals. *Tropical Conservation Science*, *9*, 675–698.

Zoological Society of London, Congo Basin Institute, & MINFOF. (2017). Giant pangolin video from Bouamir Research Station, Dja Biosphere Reserve, Cameroon. Video clips can be viewed at: https://youtu.be/7oiqZDQf-G8; https://youtu.be/vaLpunbjAHo; https://youtu.be/vdXelgj5PlM.