Status of terrestrial mammals in the Yangambi Landscape, Democratic Republic of the Congo

Nathalie van Vliet, Simón Quintero, Jonas Muhindo, Jonas Nyumu
Paolo Omar Cerutti, Robert Nasi and Francesco Rovero

Abstract In this study we provide the first comprehensive camera-trap assessment of terrestrial mammals in the Yangambi landscape, comprising the Yangambi Biosphere Reserve and a logging concession in the Democratic Republic of the Congo. The terrestrial mammal community in this area exhibits lower occupancy and species richness compared to other conservation areas in the Congo Basin. The community is dominated by four species: Emin's pouched rat *Cricetomys emini* (1.3 kg), African brush-tailed porcupine *Atherurus africanus* (2.8 kg), blue duiker *Philantomba monticola* (5 kg) and bay duiker *Cephalophus dorsalis* (12 kg), which are known to be highly resilient. Large ungulates and medium-sized carnivores have particularly low abundances. Our study also confirmed the presence of four species categorized as threatened on the IUCN Red List: the chimpanzee *Pan troglodytes*, giant ground pangolin *Smutsia gigantea*, black-bellied pangolin *Phataginus tetradactyla* and white-bellied pangolin *Phataginus tricuspis*. Our findings highlight the need to consider wildlife conservation at the landscape level, including the logging concession, where species showed higher occupancy levels compared to the Biosphere Reserve, and highlighting the need for planning infrastructure construction and developing mitigation schemes, reducing forest degradation from logging and developing permanent cash crop agriculture. Landscape-level conservation will only be possible if a collaborative management model steered by local communities is developed with the participation of all constituencies.

Keywords Biosphere reserve, camera traps, Congo Basin rainforest, data augmentation, dynamic community model, logging concession, terrestrial mammals, Yangambi

Nathalie van Vliet (Corresponding author, orcid.org/0000-0002-2741-2801, nathalievanvliet@yahoo.com) and Robert Nasi (orcid.org/0000-0001-9739-3135) Center for International Forestry Research (CIFOR), Jalan CIFOR Situ Gede, Bogor Barat 16115, Indonesia

Simón Quintero* (orcid.org/0000-0001-7489-4009) CIFOR, Bogotá, Colombia

Jonas Muhindo, Jonas Nyumu and Paolo Omar Cerutti (orcid.org/0000-0002-7745-3863) CIFOR, Kisangani, Democratic Republic of the Congo

Francesco Rovero (orcid.org/0000-0001-6688-1494) Department of Biology, University of Florence, Sesto Fiorentino, Italy

*Also at: Centro de Estudios Socioecológicos y Cambio Global, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá D.C., Colombia

The supplementary material for this article is available at doi.org/10.1017/S0030605322001569.

Introduction

Wildlife population assessments make a central scientific contribution to the conservation and management of wildlife, but the prohibitive costs associated with surveys (e.g. equipment and the deployment of teams over large and remote areas) have often limited the capacity to generate critical information on the status and trends of terrestrial mammals (Forrester et al., 2017). Advancements in the technology of camera traps have not only helped to lower these costs but also established such technology as a core tool for ecologists and conservationists (Rowcliffe, 2017; Rovero & Kays, 2021), as attested by the large number of published research studies that have used camera traps over the last 2 decades (Wearn & Glover-Kapfer, 2019).

Although the use of camera traps has expanded globally, there is a disproportionate lack of published camera trap-based research from Central Africa, with the exception of Gabon, and particularly outside strictly protected areas (Agha et al., 2018). In the Democratic Republic of the Congo, the largest Central African country, there has been an increase in camera-trap assessments since 2020 (Bessone et al., 2020; Alempijevic et al., 2021; Mencia et al., 2021; van der Hoek et al., 2023), but there has been only one published study looking at the terrestrial mammal community as a whole, within Nkuba Conservation Area (van der Hoek et al., 2023).

Wildlife assessments in this region are needed from a management perspective because mammals play a significant role in the subsistence of people and unsustainable hunting is driving declines (Maxwell et al., 2016; Coad et al., 2019). Offtake rates for Central Africa could be 1.6–11.8 million t of meat per year (Fa et al., 2016) and the main vertebrate group targeted by hunting are terrestrial mammals (Ripple et al., 2016). In this context, it is unclear how terrestrial mammal populations can be managed sustainably to support both people and wildlife. However, without a baseline from which to assess the status of terrestrial mammal populations, it is unlikely that any management interventions will be appropriate.

In this study, we used camera traps to assess the terrestrial mammal community in the Yangambi landscape in the Democratic Republic of the Congo. The study area

encompasses the Yangambi Biosphere Reserve, the neighbouring logging concession, and customary land of the Turumbu tribe. Because of a lack of human and financial resources, the Yangambi Biosphere Reserve has never been managed since its creation in 1976, its borders have always been contested (Koy et al., 2019) and its terrestrial mammals have not been assessed. Food security is poor in the region (Nowak et al., 2019) and wildmeat contributes significantly to household food security and nutrition (van Vliet et al., 2019). The forests around Yangambi provide 103–145 t of wildmeat per year to the local informal and official markets (van Vliet et al., 2019). The only available information on wildlife in the Yangambi landscape is based on the knowledge of hunters (van Vliet et al., 2018), and this information suggests that most species are now seen less frequently than 30 years ago and that a few species have disappeared locally (e.g. the African savannah elephant *Loxodonta africana*).

We therefore conducted a comprehensive assessment of the terrestrial mammals of the Yangambi landscape using camera traps. We assessed relative abundance, community composition, population dynamic parameters (occupancy, persistence and colonization) and activity patterns for the most abundant species. We suggest management options for the sustainable hunting of native species throughout the landscape, which could benefit the relationship between local people and nature.

Study area

The Yangambi landscape lies in the north-east of the Democratic Republic of the Congo, in Tshopo Province (Fig. 1). This landscape is characterized by a superposition of land tenures of the Yangambi Biosphere Reserve created in 1976, the customary land of the Turumbu ethnic group and a neighbouring logging concession. Given its protection status, our focus is the Yangambi Biosphere Reserve but we have also included the portion of the neighbouring logging concession that borders the Reserve to the north and overlaps with Ngazi Forest Reserve, a geographical entity with contested legal status. We refer to this area of overlap between the legally established logging concession, Ngazi Forest Reserve and the customary land of Weko (a Turumbu village) as 'Ngazi'. The climate of the area is marked by two dry seasons (December–March and June–July) that alternate with two rainy seasons (April–May and August–November). The landscape is covered by old secondary forests, semideciduous dense forests, young secondary forests and dense evergreen forests. The human population in the Yangambi landscape is c. 141,600 inhabitants (data from Yangambi Registry Office, 2016) and includes the city of Yangambi, which grew from a research campus during colonial times, and villages in the Turumbu and Bamanga sectors.

Methods

Data collection

Mapping the area   We carried out a participatory mapping exercise of the Yangambi landscape with small groups of hunters from 10 villages. On a large flipchart on which we had previously indicated the main road, the villages surrounding the Reserve, and the Congo and Aruwimi Rivers, we asked hunters to spatialize other landscape features such as hunting trails, hunting/fishing camps, river crossing points, marshy areas, logging roads and artisanal mining camps. Then, with guidance and permission from village leaders and to calibrate the map scale, we walked each trail with a GPS on track mode, marking the positions of the various features. The resulting map provided information for planning the deployment of cameras and key landscape information for occupancy modelling.

Survey design and camera-trap deployment   The objectives of the camera-trap survey were to assess relative abundance, species composition, demographic variables and activity patterns for selected species. We used systematic randomized sampling over a 4.2 × 4.2 km grid (to ensure independence between observations) covering the Yangambi Biosphere Reserve and Ngazi. Based on the mean size of home ranges for most medium-sized mammal species in our study area (duikers, rodents, the red river hog *Potamochoerus porcus*, small monkeys, small carnivores, the okapi *Okapia johnstoni*), we assumed site independency.

There were 71 survey sites in two blocks, covering almost the entire area: 32 in Ngazi and 39 in Yangambi (Fig. 1). Camera trapping occurred in both blocks for nearly 2 months each year during 2018–2021. The survey season varied between years and blocks but in general covered both rainy and dry seasons during August–January.

We positioned cameras in the same location every year, choosing locations to maximize detection probabilities. At each camera station, we cleared the field of vision by removing large leaves and any other major obstacles in front of the camera. We secured the cameras to trees (30–40 cm above the ground) and locked them to prevent theft. We did not use bait. After placing each camera, the team recorded the camera identification number, date, time, location coordinates, orientation of the camera, name of the researcher and any other information that we deemed important.

Data analysis

Identification of species   We identified terrestrial mammals based on the visible features captured on photographs and confirmed species identity following Kingdon & Hoffmann (2013). Photographs of unidentified species were excluded
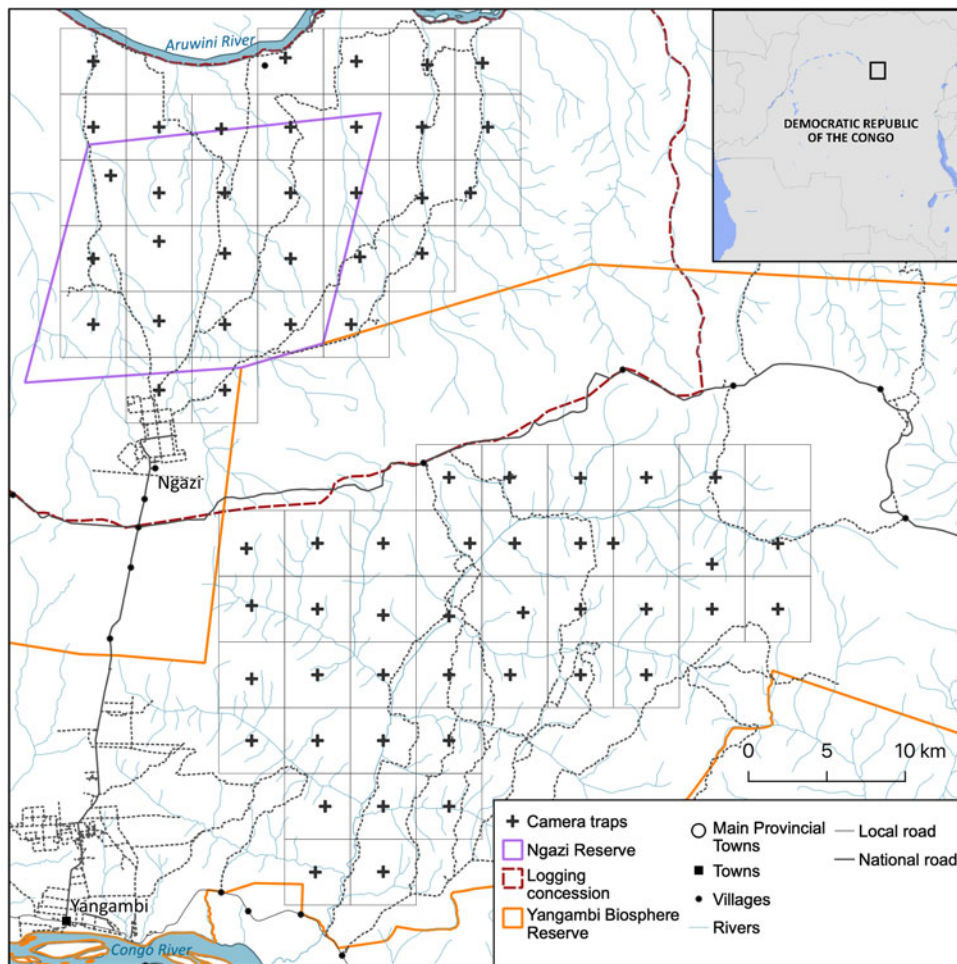
Fig. 1 The study area in the Democratic Republic of the Congo, comprising Ngazi Forest Reserve and the Yangambi Biosphere Reserve, with the general location of the 71 camera-trap stations. Sources: WWF–MRAC (Yangambi Biosphere Reserve limits) and CIFOR.

from the analysis. We treated *Genetta* species as one group (Gaubert et al., 2006). We observed the black-fronted duiker *Cephalophus nigrifrons*, Peters' duiker *Cephalophus callipygus* and white-bellied duiker *Cephalophus leucogaster* in the camera-trap photographs at least once and their occurrence in the study areas was confirmed by local hunters who name them *afoli*, *mungala* and *alolu* in Turumbu, respectively. However, we could not identify them to species level in all photographs in which we detected them, and therefore we grouped them together as diurnal red duikers. Only one murid rodent species was sufficiently large and distinctive to be reliably identified in the camera-trap images: Emin's pouched rat *Cricetomys emini*. We discarded all other murid and shrew species from the analysis.

We derived standard descriptors of the mammal community based on independent detection records, defined as consecutive images of the same species taken > 30 min apart (O'Brien et al., 2003). We excluded arboreal species from the species relative abundance index and dynamic community model estimations.

Standard descriptors of the medium-sized and large terrestrial mammal community We computed the species relative abundance index at each station for each year based on the species detection frequencies; i.e. the total number of independent detections of a particular species divided by the total number of trap-days on which the particular camera-trap station was recording (O'Brien et al., 2003). We multiplied this by 100 to facilitate comparisons with previous studies. Following the protocol of Zipkin et al. (2010), we fitted a single dynamic community model with data augmentation (Royle et al., 2007; Royle & Dorazio, 2012) to estimate baseline (i.e. 2018) occupancy and the dynamic parameters that govern changes in occupancy across the subsequent 3 years of surveys and in relation to a suite of environmental and human disturbance covariates. Through the data augmentation, the model also allowed us to estimate species richness. As low detection probabilities could prevent model convergence and lead to spurious parameter estimations (MacKenzie & Kendall 2002, Dillon & Kelly 2007), we increased the species detection probability by considering a single sampling occasion as 15 consecutive trap-days and collapsed the species detection frequencies accordingly, to ensure a minimum of three sampling occasions per season. We assessed species richness by augmenting the observed number of species by 250%. We

conducted the analysis in *JAGS* using the *jagsUI* package (Kellner, 2018) implemented in *R 4.2.1* (R Core Team, 2017).

We formulated the dynamic community model following Kéry & Royle (2020), as a construction of the following conditional probability statements:

Superpopulation process: $w_k \sim Bernoulli(\Omega)$
Initial state ($t = 1$): $z_{i,1,k}|w_k \sim Bernoulli(w_k\psi_{1,i,k})$
State dynamic ($t > 1$): $z_{i,t+1,k}|w_k,z_{i,t,k} \sim$
$\quad Bernoulli(w_k (z_{i,t,k}\Phi_{i,t,k} + (1 - z_{i,t,k})\gamma_{i,t,k}))$
Observation process: $y_{i,j,t,k}|z_{i,t,k} \sim Bernoulli(z_{i,t,k}p_{i,j,t,k})$

where w is a random variable that indicates that species are part of the meta-community (M is augmented species richness = observed + potential species), Ω is a community occupancy parameter (where $M\Omega$ corresponds to the meta-community size, regional community size or gamma diversity; Iknayan et al., 2014), z is the true species occurrence state; y is observation data, as represented by the species detection history, ψ_1 is the initial occupancy probability ($t = 1$), Φ is the persistence probability ($t > 1$), γ is the colonization probability ($t > 1$), p is the detection probability and subscripts correspond to species (k), sampling occasion (j), sampling site (i) and sampling season (i.e. year, t).

Hierarchical occupancy-based models such as dynamic community models assume that the latent state processes (i.e. initial occupancy, persistence and colonization probabilities) do not vary within the sampling seasons (the closure assumption; MacKenzie et al., 2002). Following MacKenzie et al. (2006), we interpreted initial occupancy probability as the probability of a randomly selected station being used by a species at any time during the 2018 survey. Persistence refers to the proportion of stations being used at any time during a sampling season if they had been used at any time during the previous season. Colonization refers to the proportion of stations being used at any time during a season if these had not been used at any time during the previous sampling season.

We fitted seven site variables that we assumed quantify both environmental and potential human disturbance processes in our dynamic community model, to examine their effects on the initial occupancy, persistence, colonization and detection probabilities, both at the community and at the species levels, as follows: (1) per cent of forest cover within a 2-km radius, (2) per cent of recent deforestation within a 4-km radius, and distance to nearest (3) hunting trail, (4) river, (5) village, (6) road and (7) hunting/fishing camp site. We calculated per cent of forest cover using global forest change layers (Hansen et al., 2013), based on the proportion of pixels classified as forest at a 90% threshold within a 2-km radius of camera-trap stations. Similarly, we calculated the per cent of recent deforestation within a 4-km radius as the proportion of pixels classified as forest at a 90% threshold in previous years (2000–2018) but not in 2019 (i.e. forest

loss). We defined this threshold subjectively as 90%, given that the study area is characterized by dense semideciduous and evergreen forests. We also fitted three variables to detection probability: (1) effort, (2) mean monthly precipitation and (3) whether the camera station was facing a hunting trail or not. We estimated mean monthly precipitation as the mean of the monthly rainfall recorded at the Kisangani meteorological station during 1927–1996 (WMO, 2020). We considered monthly precipitation to account for the potential effect of seasonality on species detection probability as we did not survey on the same dates each year. To avoid confounding effects, we tested for correlation amongst the seven habitat covariates and retained only one of the correlated variables for the dynamic community model construction. We assumed variables to be correlated when $r > 0.7$. In addition, we z-standardized all covariates ($\mu = 0$, SD = 1), facilitating posterior comparison of the effects amongst covariates and model convergence (Stanton et al., 2015).

Descriptive statistics (mean, SD, minimum and maximum values) for each of the variables considered are summarized in Supplementary Table 1. We considered as important those station and detection covariates for which 95% of the posterior distribution (i.e. 95% credible interval) of the β coefficient excluded zero.

Species activity patterns   We explored activity patterns only for those species with a standardized relative abundance index > 1 (Table 1). We assumed (1) that the likelihood of obtaining a species record was the same throughout the 24-h time period, (2) that the species activity behaviour did not change throughout the monitoring period and (3) that species behaviour did not affect the probability of detection across all camera traps. Daytime and night-time lengths in the study area are almost constant throughout the year, with sunrise at c. 6.00 and sunset at c. 18.00. Thus, we considered nocturnal activity as that which occurred during 19.00–5.00, diurnal activity as that during 7.00–17.00, and crepuscular activity as that during 5.00–6.00 and 17.00–18.00. We rounded the time of detection up or down to the nearest full hour for analysis. We used periodic regression models to infer daily activity patterns of species by implementing circular techniques (Zar, 1996) on the hourly counts of the species and as a function of continuous trigonometric variables describing single and double complete cycles ($\sin\theta$, $\sin 2\theta$, $\cos\theta$, $\cos 2\theta$; where $\theta = 2\pi t/24$ and $t = 24$ hours). For each species, we tested all possible models built upon all possible combinations of variables and selected the best model based on the Akaike information criterion corrected for small sample size (AICc). We conducted the statistical analysis using the *R* packages *MuMIn* (Bartoń, 2019) and *AICcmodavg* (Mazerolle, 2017) and we visualized activity patterns using *Plotrix* (Lemon, 2006).

TABLE 1 Number of independent camera-trap detections of all mammals in Ngazi Forest Reserve and in the Yangambi Biosphere Reserve, Democratic Republic of the Congo (Fig. 1), during 2018–2021. Species marked with * indicate arboreal mammals that were excluded from the standardized relative abundance index (RAI) and the dynamic community modelling (Fig. 2).

Order	Family	Species	IUCN Red List category[1]	Ngazi	Yangambi	Total	Mean RAI ± SE
Macroscelidea	Macroscelididae	Checkered elephant shrew *Rhynchocyon cirnei*	LC	171	119	290	2.63 ± 0.58
Rodentia	Hystricidae	African brush-tailed porcupine *Atherurus africanus*	LC	185	92	277	2.54 ± 0.47
	Nesomyidae	Emin's pouched rat *Cricetomys emini*	LC	157	134	291	2.55 ± 0.39
	Sciuridae	Forest giant squirrel *Protoxerus stangeri**	LC	237	167	404	
Eulipotyphla	Soricidae	Shrews*		7	0	7	
Hyracoidea	Procaviidae	Western tree hyrax *Dendrohyrax dorsalis**	LC	0	1	1	
Pholidota	Manidae	White-bellied pangolin *Phataginus tricuspis**	EN	4	8	12	
		Giant pangolin *Smutsia gigantea*	EN	1	0	1	0.01 ± 0.01
		Black-bellied pangolin *Phataginus tetradactyla**	VU	2	0	2	
Cetartiodactyla	Bovidae	Bay duiker *Cephalophus dorsalis*	NT	88	47	135	1.29 ± 0.18
		Diurnal red duikers[2]		24	8	32	0.28 ± 0.08
		Blue duiker *Philantomba monticola*	LC	178	94	272	2.53 ± 0.49
		Sitatunga *Tragelaphus spekii*	LC	9	26	35	0.27 ± 0.08
	Suidae	Red river hog *Potamochoerus porcus*	LC	12	15	27	0.24 ± 0.05
	Tragulidae	Water chevrotain *Hyemoschus aquaticus*	LC	8	0	8	0.07 ± 0.06
Primates	Cercopithecidae	Red-tailed monkey *Cercopithecus ascanius**	LC	3	0	3	
		De Brazza's monkey *Cercopithecus neglectus**	LC	0	1	1	
		Olive baboon *Papio anubis*	LC	5	0	5	0.04 ± 0.02
	Hominidae	Chimpanzee *Pan troglodytes*	EN	3	2	5	0.04 ± 0.02
Carnivora	Herpestidae	Marsh mongoose *Atilax paludinosus*	LC	7	1	8	0.08 ± 0.04
		Alexander's kusimanse *Crossarchus alexandri*	LC	18	2	20	0.17 ± 0.08
	Nandiniidae	African palm civet *Nandinia binotata**	LC	1	0	1	
	Viverridae	African civet *Civettictis civetta*	LC	26	20	46	0.41 ± 0.08
		Cape genet *Genetta tigrina*[3]	LC	1	1	2	0.47 ± 0.09
		Servaline genet *Genetta servalina*[3]	LC	11	3	14	
		Giant forest genet *Genetta victoriae*[3]	LC	17	11	28	
Total	15	26		1175	752	1927	

[1]LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered.

[2]Possibly including *Cephalophus nigrifrons*, *Cephalophus leucogaster* and *Cephalophus callipygus*. These were grouped and treated as one entity in the dynamic community model analysis.

[3]An overall RAI was estimated for all species of *Genetta*, which were treated as a single entity in the dynamic community model analysis.
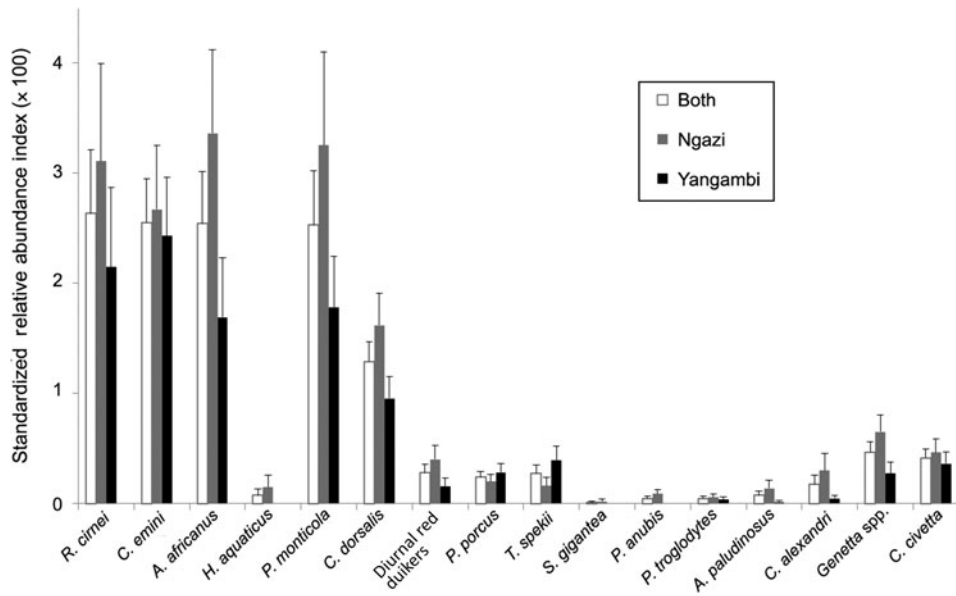
FIG. 2 Standardized relative abundance index (RAI × 100) of terrestrial mammals detected by camera traps in Ngazi Forest Reserve, the Yangambi Biosphere Reserve and both areas (Fig. 1), throughout the 4-year study period (Table 1). Species are ordered by body size and ecological guild.

Results

Because of technical failures and damage by people, the total number of camera-trap stations varied between years (Supplementary Table 2). In total, we obtained 1,927 detections during the 4-year monitoring period (10,902 camera-trap nights), corresponding to 26 mammal taxa (species or groups of species), with 19 taxa in Yangambi and 24 in Ngazi (Table 1), of which 16 are predominantly terrestrial and 10 are arboreal. We only detected four terrestrial species in Ngazi (Table 1): the water chevrotain *Hyemoschus aquaticus*, African palm civet *Nandinia binotata*, giant ground pangolin *Smutsia gigantea* and olive baboon *Papio anubis*. We recorded four species categorized as threatened on the IUCN Red List: the arboreal black-bellied pangolin *Phataginus tetradactyla* (Vulnerable), white-bellied pangolin *Phataginus tricuspis* (Endangered), the predominantly terrestrial giant ground pangolin (Endangered) and chimpanzee *Pan troglodytes* (Endangered). Arboreal species are infrequently detected by camera traps deployed on the ground and so we removed these from the subsequent analysis.

Overall, there were 0.17 independent events per camera-trap day. The most commonly detected species were the checkered elephant shrew *Rhynchocyon cirnei*, rodents (*C. emini* and African brush-tailed porcupine *Atherurus africanus*) and the small blue duiker *Philantomba monticola*. The bay duiker *Cephalophus dorsalis* exhibited intermediate abundance (1.29), whereas large ungulates (i.e. red diurnal duikers, red river hog and sitatunga *Tragelaphus spekii*) and medium-sized carnivores (Alexander's kusimanse *Crossarchus alexandri*, genets *Genetta* spp. and African civet *Civettictis civetta*) exhibited low abundances (relative abundance index < 1). Primates and giant ground pangolins

were rare (Fig. 2). Species exhibited higher abundances in Ngazi than in Yangambi. These abundance patterns were similar across years.

Distance to nearest hunting trails and to hunting/fishing camp sites were highly correlated ($r > 0.7$; Supplementary Table 3), so we discarded the latter from the dynamic community model analysis. In general, all terrestrial mammals exhibited low naïve occupancy, as we detected most species in < 10% of sites each year (Table 2). The augmented number of species (M) used for the dynamic community model was 40, including 16 observed and 24 potential or unobserved species. The estimated mean community occupancy probability (Ω) was 0.40 (95% credible interval = 0.26–0.55; Table 3), suggesting that the maximum regional community size or gamma diversity is 22 species ($M\Omega_{97.5\%}$). This indicates that a maximum of six species could potentially colonize the study area. In the Yangambi landscape, the estimated terrestrial mammal community size was the same as the total number of observed species (N_{total} in Table 3), confirming the representativeness of our survey. However, overall, only 33% of the true number of species present at each camera-trap station were detected. The estimated number of species recorded at each camera-trap station did not vary across years but in general was higher in Ngazi than in Yangambi.

Mean initial community occupancy probability (ψ_1) was correlated negatively to per cent of neighbouring deforestation at a 16-km² scale, whereas mean community persistence probability (Φ) was correlated positively with distance to the nearest road (Fig. 3, Table 3). Overall, a low mean colonization probability (γ) was estimated at the community level, and this was particularly low for 2019 (Table 3). At both the community and the species levels, mean detection probabilities (p) were low and, in all cases,

TABLE 2 Annual naïve occupancy of terrestrial mammals in Ngazi Forest Reserve and the Yangambi Biosphere Reserve (Fig. 3). Species with at least one annual naïve occupancy > 0.10 are marked with *.

	2018			2019			2020			2021		
Species	Ngazi	Yangambi	Both	Ngazi	Yangambi	Both	Ngazi	Yangambi	Both	Ngazi	Yangambi	Both
R. cirnei*	0.03	0.07	0.10	0.13	0.15	0.28	0.08	0.15	0.23	0.08	0.10	0.18
A. africanus*	0.08	0.07	0.15	0.26	0.13	0.40	0.17	0.17	0.35	0.33	0.12	0.45
C. emini*	0.17	0.15	0.32	0.28	0.23	0.51	0.12	0.21	0.33	0.18	0.20	0.39
S. gigantea	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.02	0.00	0.00	0.00
C. dorsalis*	0.15	0.15	0.30	0.13	0.17	0.30	0.25	0.13	0.38	0.31	0.04	0.35
Diurnal red duikers*	0.08	0.00	0.08	0.02	0.00	0.02	0.02	0.08	0.10	0.10	0.00	0.10
P. monticola*	0.15	0.13	0.28	0.13	0.17	0.30	0.21	0.17	0.38	0.16	0.06	0.22
T. spekii*	0.02	0.00	0.02	0.00	0.08	0.08	0.06	0.02	0.08	0.02	0.10	0.12
P. porcus*	0.05	0.10	0.15	0.00	0.02	0.02	0.04	0.04	0.08	0.10	0.06	0.16
H. aquaticus	0.02	0.00	0.02	0.00	0.00	0.00	0.04	0.00	0.04	0.00	0.00	0.00
P. anubis	0.03	0.00	0.03	0.00	0.00	0.00	0.02	0.00	0.02	0.04	0.00	0.04
P. troglodytes	0.03	0.02	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.02	0.00
A. paludinosus	0.00	0.00	0.00	0.04	0.00	0.04	0.00	0.00	0.00	0.04	0.02	0.06
C. alexandri	0.02	0.00	0.02	0.04	0.00	0.04	0.02	0.04	0.06	0.04	0.00	0.04
N. binotata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.02
C. civetta*	0.08	0.03	0.12	0.08	0.02	0.09	0.04	0.10	0.13	0.12	0.08	0.20
Genetta spp.*	0.05	0.03	0.08	0.19	0.08	0.26	0.13	0.02	0.15	0.04	0.08	0.12

correlated positively with sampling effort (Table 3 & Supplementary Table 4). Of the species with detection probabilities higher than the estimated value at the community level ($p > 0.11$), C. emini, C. dorsalis and A. africanus had high initial occupancy probabilities ($\psi_1 > 0.5$) and, along with P. monticola, high persistence probabilities ($\Phi > 0.5$; Table 4). The initial occupancy of R. cirnei was correlated negatively with both forest cover at a 4-km² scale and proportion of deforested areas at a 16-km² scale (Supplementary Table 4). A similar pattern was predicted for the initial occupancy of P. monticola in relation to degraded areas. The persistence of C. dorsalis, P. monticola and Genetta spp. was correlated positively with distance to the nearest road, whereas colonization of R. cirnei was correlated positively with distances to the nearest hunting trail and town (Supplementary Table 4).

Activity patterns are shown in Fig. 4. Cephalophus dorsalis was exclusively nocturnal (20.00–4.00), whereas P. monticola was exclusively diurnal (7.00–11.00, with a peak at 8.00). Amongst the rodents, C. emini and A. africanus were exclusively nocturnal, whereas R. cirnei was exclusively diurnal.

Discussion

Our study provides the first assessment of the terrestrial mammals of the Yangambi landscape since the designation of the Biosphere Reserve in the late 1970s, advancing our understanding of how this landscape contributes to biodiversity conservation. Of the 23 terrestrial mammal taxa (species or groups of species) observed by hunters in the Yangambi landscape over the previous 5 years (listed in van Vliet et al., 2018), we confirmed the presence of 16, including two terrestrial threatened species: P. troglodytes and S. gigantea. In addition, although arboreal species were not the focus of our study, we confirmed the presence of two additional threatened species: the black-bellied and white-bellied pangolins. The presence of the African forest buffalo Syncerus caffer nanus, yellow-backed duiker Cephalophus silvicultor, aardvark Orycteropus afer, okapi, bushbuck Tragelaphus scriptus, greater cane rat Thryonomys swinderianus and leopard Panthera pardus was not confirmed by our camera traps, despite observations by local hunters over the previous 5 years (van Vliet et al., 2018). Thryonomys swinderianus thrives in deforested areas, cultivated land and savannah. Its absence from our camera-trap photographs could be explained by the fact that no cameras were sited at the periphery of the Reserve or on farmland. The absence of the other species suggests they have been extirpated from the study area or have no established populations there.

Our assessment also confirms the depletion suggested for the Yangambi landscape based on the knowledge of hunters (van Vliet et al., 2018). The landscape has a lower mean estimated community occupancy and species richness than other conservation areas in the Congo Basin (Bruce et al., 2018; Hedwig et al., 2018; Orban et al., 2018; Bessone et al., 2020; Nakashima et al., 2020; van der Hoek et al., 2023). The species profile was characterized by the high representation of four species (C. emini, A. africanus, P. monticola and C. dorsalis) that are known to be common and highly resilient to hunting. Large ungulates and

TABLE 3 Estimated community parameters based on the dynamic community model with data augmentation (see text for details).

Parameter[1]	Year/covariate	Mean ± SD	2.50%	97.50%	Rhat[2]	n_{eff}[3]	Overlap[4]
Ω	2018–2021	0.40 ± 0.07	0.26	0.55	1.00	3,000	0
N_{total}	2018–2021	16.02 ± 0.15	16.00	16.00	1.01	3,000	0
$\mu.\alpha.l\psi1$	2018	−0.78 ± 1.22	−2.84	1.98	1.04	68	1
$\mu.\beta.l\psi1[1]$	Distance to nearest river	−0.36 ± 0.55	−1.83	0.49	1.04	93	1
$\mu.\beta.l\psi1[2]$	Distance to nearest trail	−0.43 ± 0.52	−1.72	0.35	1.02	553	1
$\mu.\beta.l\psi1[3]$	% forest cover	−0.86 ± 0.92	−2.78	0.91	1.02	2,100	1
$\mu.\beta.l\psi1[4]$	Distance to nearest village	−0.81 ± 0.66	−2.55	0.12	1.05	87	1
$\mu.\beta.l\psi1[5]$	Distance to nearest road	0.40 ± 0.47	−0.36	1.58	1.02	438	1
$\mu.\beta.l\psi1[6]$	% deforestation	−2.13 ± 1.24	−4.95	−0.29	1.03	121	0
$\mu.\alpha.l\Phi[1]$	2019	0.80 ± 0.86	−0.55	2.85	1.03	189	1
$\mu.\alpha.l\Phi[2]$	2020	0.62 ± 0.85	−0.89	2.53	1.01	373	1
$\mu.\alpha.l\Phi[3]$	2021	−0.20 ± 0.67	−1.63	1.16	1.00	579	1
$\mu.\beta.l\Phi[1]$	Distance to nearest river	−0.27 ± 0.43	−1.33	0.43	1.00	1,795	1
$\mu.\beta.l\Phi[2]$	Distance to nearest trail	0.61 ± 0.77	−0.30	2.68	1.06	1,57	1
$\mu.\beta.l\Phi[3]$	% forest cover	0.21 ± 0.87	−2.07	1.60	1.06	59	1
$\mu.\beta.l\Phi[4]$	Distance to nearest village	−0.09 ± 0.47	−1.25	0.76	1.01	3,000	1
$\mu.\beta.l\Phi[5]$	Distance to nearest road	1.31 ± 1.18	0.14	4.95	1.06	132	0
$\mu.\beta.l\Phi[6]$	% deforestation	0.27 ± 1.68	−2.99	4.34	1.00	2,553	1
$\mu.\alpha.l\gamma[1]$	2019	−2.17 ± 1.00	−4.31	−0.39	1.03	84	0
$\mu.\alpha.l\gamma[2]$	2020	−1.03 ± 0.85	−2.53	0.90	1.05	76	1
$\mu.\alpha.l\gamma[3]$	2021	−1.54 ± 0.89	−3.55	0.09	1.02	421	1
$\mu.\beta.l\gamma[1]$	Distance to nearest river	0.16 ± 0.32	−0.45	0.81	1.01	1,475	1
$\mu.\beta.l\gamma[2]$	Distance to nearest trail	−0.03 ± 0.56	−1.27	1.05	1.02	1,726	1
$\mu.\beta.l\gamma[3]$	% forest cover	0.27 ± 0.61	−0.80	1.39	1.10	1,658	1
$\mu.\beta.l\gamma[4]$	Distance to nearest village	0.42 ± 0.38	−0.30	1.24	1.01	2,310	1
$\mu.\beta.l\gamma[5]$	Distance to nearest road	−0.16 ± 0.41	−1.05	0.58	1.04	210	1
$\mu.\beta.l\gamma[6]$	% deforestation	0.78 ± 1.08	−0.67	3.62	1.15	36	1
$\mu.\alpha.lp[1]$	2018	−1.88 ± 0.54	−2.96	−0.85	1.01	208	0
$\mu.\alpha.lp[2]$	2019	−2.13 ± 0.58	−3.28	−1.04	1.02	129	0
$\mu.\alpha.lp[3]$	2020	−2.26 ± 0.49	−3.25	−1.34	1.01	235	0
$\mu.\alpha.lp[4]$	2021	−2.27 ± 0.48	−3.21	−1.33	1.00	3,000	0
$\mu.\beta.lp[1]$	Sampling effort	0.63 ± 0.09	0.47	0.81	1.00	3,000	0
$\mu.\beta.lp[2]$	Mean monthly precipitation	0.03 ± 0.07	−0.11	0.16	1.00	3,000	1
$\mu.\beta.lp[3]$	Trail	−0.01 ± 0.30	−0.69	0.51	1.00	976	1

[1]All parameter estimates (except ω and the estimated community size N_{total}) are in the logit scale. α, estimated intercept; β, effect coefficient for initial occupancy probability ($\psi1$), persistence probability (Φ), colonization probability (γ) and detection probability (p).

[2]Gelman–Rubin convergence diagnostic statistic.

[3]Effective sample size.

[4]If the 95% credible interval of the posterior distribution overlaps zero.

medium-sized carnivores exhibited particularly low abundances. The absence of *C. silvicultor* and of larger carnivores also confirms the depletion profile. Although according to the hunters the extirpation of large and threatened species (e.g. elephants) began at the time of political conflicts in the late 1990s and was linked to the presence of armed groups, more recent declines in mammal abundance are linked to hunting for food (van Vliet et al., 2018) in a context in which the local economy has collapsed and local communities could only survive through widespread occupation of the Reserve (Kipute et al., 2021). Nevertheless, besides hunting, our study highlights other pressures on wild mammals: the road network and deforestation are negatively affecting the already depleted wildlife in the Yangambi landscape.

In the context of the multiple-use landscape around the Yangambi Biosphere Reserve and to reconcile the conservation of biodiversity with its sustainable use, it is unclear whether and under what circumstances the Reserve can continue to serve as a sustainable source of food whilst preserving biodiversity. Despite the low colonization probability observed at the community level, persistence probabilities for species with high detection rates were $p > 0.5$ for *C. emini*, *P. monticola*, *C. dorsalis* and *A. africanus*, indicating stability for a few resilient species that are highly preferred by hunters and wildmeat consumers. Although abundance at the community level is amongst the lowest recorded with camera traps in the Congo Basin, the relative abundance index for these four species lies within the range recorded in Nkuba Conservation Area, in a

TABLE 4 Summarized dynamic state parameters at the community and species levels based on the global dynamic community model with data augmentation used. Species with higher detection probability (p) than that estimated at the community level are marked with *.

Community/species	ψ_1[1] Mean	SD	Φ[2] Mean	SD	γ[3] Mean	SD	p Mean	SD
Community	0.57	0.19	0.49	0.26	0.1	0	0.11	0.01
R. cirnei*	0.09	0.15	0.43	0.23	0.22	0.20	0.52	0.02
A. africanus*	0.78	0.22	0.71	0.26	0.25	0.14	0.21	0.01
C. emini*	0.98	0.12	0.64	0.19	0.29	0.21	0.23	0.01
S. gigantea	0.01	0.02	0.56	0.24	0.09	0.10	0.02	0.00
C. dorsalis*	0.84	0.21	0.69	0.28	0.32	0.16	0.16	0.01
Diurnal red duikers	0.48	0.27	0.54	0.23	0.15	0.13	0.06	0.00
P. monticola*	0.45	0.21	0.59	0.26	0.25	0.14	0.30	0.01
T. spekii*	0.01	0.02	0.59	0.26	0.12	0.13	0.20	0.01
P. porcus	0.92	0.14	0.63	0.23	0.18	0.13	0.04	0.00
H. aquaticus	0.01	0.02	0.56	0.23	0.13	0.09	0.07	0.00
P. anubis	0.11	0.16	0.57	0.23	0.15	0.08	0.03	0.00
P. troglodytes	0.25	0.26	0.55	0.25	0.12	0.11	0.03	0.00
A. paludinosus	0.00	0.00	0.56	0.24	0.11	0.13	0.06	0.00
C. alexandri	0.13	0.09	0.59	0.26	0.15	0.10	0.03	0.00
C. civetta	0.88	0.18	0.49	0.25	0.21	0.18	0.10	0.01
Genetta spp.	0.64	0.23	0.55	0.30	0.27	0.14	0.10	0.00

[1]Initial occupancy probability.
[2]Persistence probability.
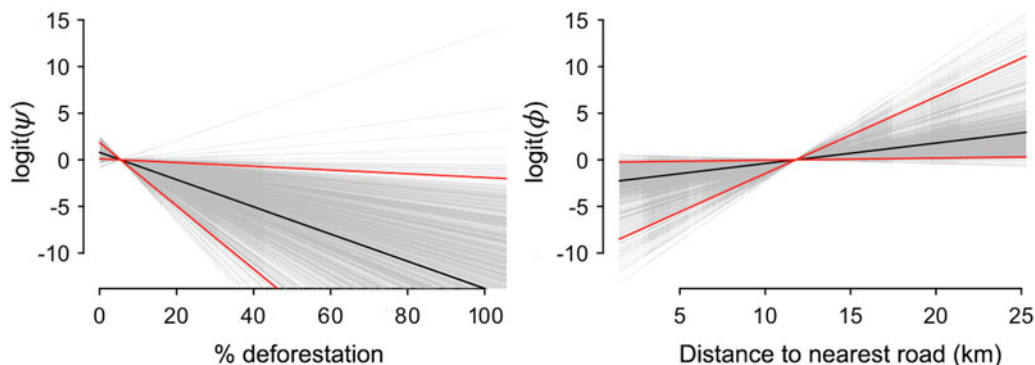[3]Colonization probability.

FIG. 3 Relationship of the initial occupancy (left) and persistence (right) probabilities at the community level of terrestrial mammals detected by camera traps in Ngazi Forest Reserve and Yangambi Biosphere Reserve combined, with per cent deforestation at a 16-km² scale and distance to nearest road, respectively. Thin grey lines are 800 random samples obtained from the Markov chain Monte Carlo posterior samples, thicker black and red lines are the mean and the lower and upper 95% credible intervals of the posterior distribution, respectively.

neighbouring province of the Democratic Republic of the Congo (van der Hoek et al., 2023). None of the most abundant species exhibited significant avoidance of hunting trails, suggesting these highly resilient species do not avoid areas frequented by hunters. We hypothesize that for these species, the following biological and ecological factors help to maintain their populations: high reproductive rates (e.g. rodents; Happold, 1987), micro-scale source–sink dynamics (e.g. *P. monticola*; Mockrin et al., 2011) and modifications of diel activity patterns. *Philantomba monticola*, which usually has bimodal daily activity (Dubost, 1980; Bowland & Perrin,

1995; Houngbégnon et al., 2020), exhibited only one activity peak in our study area. This could be interpreted as the species avoiding the hours during which hunters are active, but our data do not allow us to confirm this hypothesis.

From a conservation perspective, the management of wildlife in the Yangambi landscape should seek to limit further biodiversity loss. This could be achieved by enforcing no-harvest rules for the four threatened species and protecting them by national law. Preventing these species from being hunted would not affect local food security (van Vliet et al., 2022) because chimpanzees and pangolins are
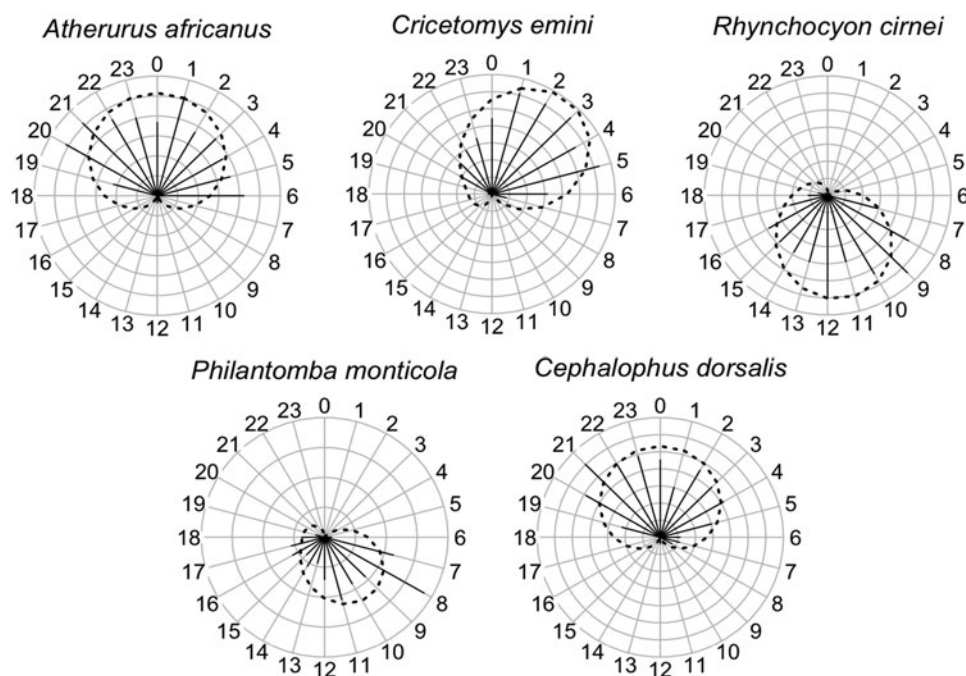
FIG. 4 Periodic regression analysis of the activity patterns of the five most commonly detected species in Ngazi Forest Reserve and Yangambi Biosphere Reserve during the 4-year monitoring period. The plot is divided into hours, with the response radial axis corresponding to the proportion of detections in each hour. Observations are shown as continuous black lines and the predicted distributions based on the best adjusted model are shown as dashed lines.

not among the most preferred species, they only represent an insignificant portion of the catch, and do not have a greater commercial value for their meat than other commonly found species. Key to the success of such enforcement measures is the development of inclusive systems that empower local governance structures to make decisions and enforce local rules over wildlife, avoiding errors of top-down regulation that have occurred in the Yangambi Biosphere Reserve in the past (Koy et al., 2019). The process also needs to foster positive behavioural change, such as through the increased involvement of hunters in wildlife research, environmental education of youth, increased livelihood opportunities that do not affect wildlife and a strategy to address human–wildlife conflict (van Vliet et al., 2022).

Our results highlight the need to consider wildlife conservation at the landscape level, maintaining connectivity between the logging concession (particularly in Ngazi) and the Yangambi Biosphere Reserve. Ngazi harbours species that were absent from the Reserve, and some that showed higher occupancy levels than in the Reserve. In addition, we highlight the need to carefully plan road development for timber-related activities and to reduce forest degradation from logging and the development of permanent cash crop agriculture.

Overall, our findings suggest that the Yangambi landscape needs to be managed with two principal purposes: ensure the persistence of the most hunted species, to guarantee local food security, and reverse the decline of the most threatened species. These can only be achieved by involving local constituencies in identifying and enforcing

sustainable hunting rules, controlling access to hunting grounds, reducing habitat destruction originating from unplanned road expansion and agriculture, and enforcing hunting bans on the most susceptible species following the national law. Such landscape-level conservation efforts will only be possible if a collaborative management model steered by local communities is developed with the participation of all constituencies.

Authors contributions Study design and fieldwork: NvV, JM, JN; data management and analysis: SQ; writing: NvV, SQ; manuscript revision; FR, PC, RN.

Conflicts of interest None.

Ethical statement This research abided by the *Oryx* guidelines on ethical standards, and those of the Center for International Forestry Research. This research was authorized under the International Institute of Tropical Agriculture's Host Agreement in the Democratic Republic of the Congo.

References

AGHA, M., BATTER, T., BOLAS, E.C., COLLINS, A.C., GOMES DA ROCHA, D., MONTEZA-MORENO, C.M. et al. (2018) A review of wildlife camera trapping trends across Africa. *African Journal of Ecology*, 56, 694–701.

ALEMPIJEVIC, D., BOLIABO, E.M., COATES, K.F., HART, T.B., HART, J.A. & DETWILER, K.M. (2021) A natural history of *Chlorocebus dryas* from camera traps in Lomami National Park and its buffer zone, Democratic Republic of the Congo, with notes on the species status of *Cercopithecus salongo*. *American Journal of Primatology*, 83, 1–11.

BARTOŇ, K. (2019) *MuMIn: multi-model inference*. R package version 1.43.6. CRAN.R-project.org/package=MuMIn [accessed 15 April 2022].

BESSONE, M., KÜHL, H.S., HOHMANN, G., HERBINGER, I., N'GORAN, K.P., ASANZI, P. et al. (2020) Drawn out of the shadows: surveying secretive forest species with camera trap distance sampling. *Journal of Applied Ecology*, 57, 963–974.

BOWLAND, A.E., & PERRIN, M.R. (1995) Temporal and spatial patterns in blue duikers *Philatomba monticola* and red duikers *Cephalophus natalensis*. *Journal of Zoology*, 237, 487–498.

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.

COAD, L., FA, J.E., ABERNETHY, K., VAN VLIET, N., SANTAMARIA, C., WILKIE, D. et al. (2019) *Toward a Sustainable, Participatory and Inclusive Wild Meat Sector*. Center for International Forestry Research (CIFOR), Bogor, Indonesia. cifor.org/publications/pdf_files/Books/BCoad1901.pdf [accessed May 2023].

DILLON, A. & KELLY, M.J. (2007) Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx*, 41, 469–477.

DUBOST, G. (1980) L'écologie et la vie sociale du Céphalophe bleu (*Cephalophus monticola* Thunberg), petit ruminant forestier Africain. *Zeitschrift für Tierpsychologie*, 54, 205–266.

FA, J.E., VAN VLIET, N. & NASI, R. (2016) Bushmeat, food security, and conservation in African rainforests. In *Tropical Conservation: Perspectives on Local and Global Priorities* (eds A.A. Aguirre & R. Sukumar), pp. 331–344. Oxford University Press, Oxford, UK.

FORRESTER, T.D., BAKER, M., COSTELLO, R., KAYS, R., PARSONS, A.W. & MCSHEA, W.J. (2017) Creating advocates for mammal conservation through citizen science. *Biological Conservation*, 208, 98–105.

GAUBERT, P., PAPEŞ, M. & PETERSON, A.T. (2006) Natural history collections and the conservation of poorly known taxa: ecological niche modeling in Central African rainforest genets (*Genetta* spp.). *Biological Conservation*, 130, 106–117.

HANSEN, M.C., POTAPOV, P.V., MOORE, R., HANCHER, M., TURUBANOVA, S.A., TYUKAVINA, A. et al. (2013) High-resolution global maps of 21st-century forest cover change. *Science*, 342, 850–853.

HAPPOLD, D.C.D. (1987) *The Mammals of Nigeria*. Oxford University Press, Oxford, UK.

HEDWIG, D., KIENAST, I., BONNET, M., CURRAN, B.K., COURAGE, A., BOESCH, C. et al. (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, 777–790.

HOUNGBÉGNON, F.G.A., CORNELIS, D., VERMEULEN, C., SONKÉ, B., NTIE, S., FAYOLLE, A. et al. (2020) Daily activity patterns and co-occurrence of duikers revealed by an intensive camera trap survey across Central African rainforests. *Animals*, 10, 2200.

IKNAYAN, K.J., TINGLEY, M.W., FURNAS, B.J. & BEISSINGER, S.R. (2014) Detecting diversity: emerging methods to estimate species diversity. *Trends in Ecology and Evolution*, 29, 97–106.

KELLNER, K. (2018) *jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses*. R package version 1.5.0. CRAN.R-project.org/package=jagsUI [accessed 15 April 2022].

KÉRY, M. & ROYLE, J.A. (2020) *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and species Richness in R and BUGS. Volume 2*. Academic Press, London, UK.

KINGDON, J. & HOFFMANN, M. (2013) *Mammals of Africa. Volume V: Carnivores, Pangolins, Equids and Rhinoceroses*. Bloomsbury Publishing, London, UK.

KIPUTE, D.D., MAMPETA, S.W., KAHINDO, J.-M.M., LELO, U.D.M., SUFO KANKEU, R., SONWA, J.D. et al. (2021) Complexity of zoning management in biosphere reserves: the case of the Yangambi Biosphere Reserve in DRC. *International Forestry Review*, 23, 55–67.

KOY, J.K., WARDELL, D.A., MIKWA, J.-F., KABUANGA, J.M., MONGA NGONGA, A.M., OSZWALD, J. & DOUMENGE, C. (2019) Dynamique de la déforestation dans la Réserve de biosphère de Yangambi (République démocratique du Congo): variabilité spatiale et temporelle au cours des 30 dernières années. *Bois & Forets des Tropiques*, 341, 15.

LEMON, J. (2006) *Plotrix*: a package in the red light district of R. *R-News*, 6, 8–12.

MACKENZIE, D.I. & KENDALL, W.L. (2002) How should detection probability be incorporated into estimates of relative abundance? *Ecology*, 83, 2387–2393.

MACKENZIE, D.I., NICHOLS, J.D., LACHMAN, G.B., DROEGE, S., ROYLE, J.A. & LANGTIMM, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255.

MACKENZIE, D.I., NICHOLS, J.D., ROYLE, J.A., POLLOCK, K.H., BAILEY, L.L. & HINES, J.E. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of species Occurrence*. Academic Press, London, UK.

MAXWELL, S., FULLER, R., BROOKS, T. & WATSON, J. (2016) The ravages of guns, nets and bulldozers. *Nature*, 536, 143–145.

MAZEROLLE, M.J. (2017) *AICcmodavg: model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.1.1. CRAN.R-project.org/package=AICcmodavg [accessed 15 April 2022].

MENCIA, A., FOURNIER, C. & DETWILER, K.M. (2021) Polyspecific associations from camera trapping data of the lesula monkey (*Cercopithecus lomamiensis*) in the Lomami National Park, Democratic Republic of the Congo. *Florida Atlantic University Undergraduate Research Journal*, 10, 8–16.

MOCKRIN, M., ROCKWELL, R.F., REDFORD, K.H. & KEULER, N.S. (2011) Effects of landscape features on the distribution and sustainability of ungulate hunting in northern Congo. *Conservation Biology*, 25, 514–525.

NAKASHIMA, Y., HONGO, S. & AKOMO-OKOUE, E.F. (2020) Landscape-scale estimation of forest ungulate density and biomass using camera traps: applying the REST model. *Biological Conservation*, 241, 108381.

NOWAK, A., ROSENSTOCK, T.S., HAMMOND, J., DEGRANDE, A. & SMITH, E. (2019) *Livelihoods of Households Living Near Yangambi Biosphere Reserve, Democratic Republic of Congo*. Center for International Forestry Research (CIFOR), Kisangani, Democratic Republic of the Congo. cifor.org/wp-content/uploads/forets/RHoMIS%20brief_DRC_final_06052019.pdf [accessed May 2023].

O'BRIEN, T.G., KINNAIRD, M. & WIBISONO, H. (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6, 131–139.

ORBAN, B., KABAFOUAKO, G., MORLEY, R., VASICEK GAUGRIS, C., MELVILLE, H. & GAUGRIS, J. (2018) Common mammal species inventory utilizing camera trapping in the forests of Kouilou Département, Republic of Congo. *African Journal of Ecology*, 56, 750–754.

R CORE TEAM (2017) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M. et al. (2016) Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, 3, 160498.

Rovero, F. & Kays, R. (2021) Camera trapping for conservation. In *Conservation Technology* (eds S.A. Wich & A.K. Piel), pp. 79–101. Oxford University Press, Oxford, UK.

Rowcliffe, J.M. (2017) Key frontiers in camera trapping research. *Remote Sensing in Ecology and Conservation*, 3, 107–108.

Royle, J.A. & Dorazio, R.M. (2012) Parameter-expanded data augmentation for Bayesian analysis of capture–recapture models. *Journal of Ornithology*, 152, 521–537.

Royle, J.A., Dorazio, R.M. & Link, W.A. (2007) Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphical Statistics*, 16, 67–85.

Stanton, R.A., Jr, Thompson, F.R. & Kesler, D.C. (2015) Site occupancy of brown-headed nuthatches varies with habitat restoration and range-limit context. *Journal of Wildlife Management*, 79, 917–926.

van der Hoek, Y., Binyinyi, E., Ngobobo, U., Stoinski, T.S. & Caillaud, D. (2023) Diversity and diel activity patterns of terrestrial mammals in the Nkuba Conservation Area, Democratic Republic of the Congo. *Oryx*, 57, 107–117.

van Vliet, N., Muhindo, J., Nyumu, J., Mushagalusa, O. & Nasi, R. (2018) Mammal depletion processes as evidenced from spatially explicit and temporal local ecological knowledge. *Tropical Conservation Science*, 11, 1–16.

van Vliet, N., Muhindo, J., Nyumu, J.K. & Nasi, R. (2019) From the forest to the dish: a comprehensive study of the wildmeat value chain in Yangambi, Democratic Republic of Congo. *Frontiers in Ecology and Evolution*, 7, 132.

van Vliet, N., Nyumu, J.K., Nziavake, S., Muhindo, J., Paemelaere, E.A.D. & Nasi, R. (2022) How do local folks value wild meat, and why it matters? A study in the Democratic Republic of Congo. *Human Ecology*, 50, 195–203.

Wearn, O.R. & Glover-Kapfer, P. (2019) Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *Royal Society Open Science*, 6, 181748.

WMO (2020) *Kisamgani Zaire, station code: 64040*. climexp.knmi.nl [accessed 26 March 2022].

Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edition. Prentice Hall, Hoboken, USA.

Zipkin, E.F., Royle, J.A., Dawson, D.K. & Bates, S. (2010) Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, 143, 479–484.