African Journal of Ecology 🦽

Assessing species occurrence and species-specific use patterns of bais (forest clearings) in Central Africa with camera traps

Julia Gessner¹*, Rainer Buchwald¹ and George Wittemyer²

¹Vegetation Science and Nature Conservation Group, Carl von Ossietzky University, 26111 Oldenburg, Germany and ²Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523,U.S.A.

Abstract

The impacts of increasing resource extraction on biodiversity in the Central African rainforest are largely unknown, in part due to the lack of baseline data on species occurrence across the basin. Natural forest clearings (bais) in this region are key habitats for a variety of vertebrates and offer opportunities for monitoring species distribution. Information on species composition, however, is lacking from the majority of areas (except for long-term study sites). Approaches and protocols for short-term bai assessments can greatly advance such baseline knowledge. This study demonstrates that camera traps provide an effective method for species inventories (species occurrence and temporal activity patterns) and monitoring at bais across the broader region. In comparison with direct observational studies, they performed especially well regarding rare and nocturnal species. Camera traps during sampling sessions of 4 weeks or less recorded previously undocumented, and 65-94% of the mammals known to use each of seven Central African bais. Results indicate that many mammal species, in particular African forest elephants (Loxodonta africana cyclotis), visit bais preferentially at night. This underlines the urgent need for monitoring tools providing both diurnal and nocturnal data to provide baseline data that address conservation and management objectives.

Key words: activity patterns, bais, camera traps, Central Africa, mammals, monitoring

Résumé

Les impacts de l'extraction croissante des ressources sur la biodiversité de la forêt pluviale d'Afrique centrale sont

encore fort méconnus, notamment en raison du manque de données de référence sur la présence des espèces dans tout le bassin. Les clairières naturelles (bais) de cette région sont des habitats cruciaux pour toute une variété de vertébrés et elles offrent de bonnes possibilités de suivre la distribution de certaines espèces. Pourtant, les informations manquent pour la majorité des endroits (à l'exception des sites d'études à long terme). Approches et protocoles pour des évaluations des bais à court terme peuvent faire progresser fortement ces connaissances de base. Cette étude montre que les pièges photographiques constituent une méthode efficace pour des inventaires d'espèces (présence d'espèces et schémas temporels des activités) et pour le suivi dans les bais au-delà de la région frontalière. En comparant avec des études par observations directes, ils ont donné des résultats particulièrement bons pour des espèces rares et nocturnes. Des pièges photographiques utilisés pendant les sessions d'échantillonnage ont enregistré des espèces jusque-là non documentées et de 65 à 94 % des mammifères connus pour fréquenter chacun des sept bais d'Afrique centrale. Les résultats indiquent que de nombreuses espèces animales, et particulièrement les éléphants de forêt (Loxodonta africana cyclotis), visitent de préférence les bais pendant la nuit. Ceci souligne le besoin urgent d'instruments de suivi qui fournissent à la fois des données diurnes et nocturnes, afin d'obtenir des données de référence pour répondre aux objectifs de la conservation et de la gestion.

Introduction

In the Central African rain forest basin, biodiversity is facing increasing threats from habitat alteration caused by resource exploitation and accompanying increased

^{*}Correspondence: E-mail: julia_gessner@gmx.net

poaching. Meanwhile, there is a lack of baseline data on animal species occurrence and density across the basin. As such, there is an urgent need for species distribution monitoring programmes, but the best approach to monitor biodiversity across this vast remote system remains unresolved. Natural forest clearings, locally known as bais, in the Central African rain forest have been identified as key sites for research on the regions fauna (Turkalo & Fay, 1995). These geophysical features attract large numbers of otherwise forest dwelling species (birds, mammals and reptiles), allowing a unique opportunity for behavioural observation, census and sampling of cryptic species. Direct observations at bais provide important monitoring data on mammal populations and insight in the ecology of numerous species, including large mammals such as the African forest elephant (Loxodonta africana cyclotis) and the western lowland gorilla (Gorilla gorilla gorilla) (Turkalo & Fav. 1995: Breuer et al., 2008). But logistic and financial constraints restrict such observational studies to a relatively small number of bais. Little is known regarding the species composition and distribution across the broader region, despite the importance of such information for conservation and management objectives. Consequently, development of monitoring protocols best suited for shortterm bai studies is needed.

Elephants are known to visit bais more frequently during the night than day (Turkalo & Fay, 2001; Momont, 2007), and it is speculated that such nocturnal behaviour is common to many forest species. Due to difficulties in data collection during the night, few studies of night-time bai use or species activity have been conducted. Wrege *et al.* (2012) used acoustic monitoring tools to assess the numbers of elephants for long time periods at several bais in Gabon. Inference on the age and sex classes of this vocal species can be drawn from acoustic data (Wrege *et al.*, 2012), but this approach is less suitable for nonvocal species or where external factors such as human activities impact vocalization rates.

This study is the first to use camera traps to investigate the diurnal and nocturnal use of bais in Central Africa by medium to large-sized mammals. Here, we present results from a camera trap study at seven bais in Cameroon and the Republic of Congo, conducted during both the wet and dry seasons. Species composition and activity patterns of large mammals visiting the different bais were summarized. We compare camera-trap-based data with that from observations and discuss the efficacy of our study protocols and the potential of camera traps as a bai monitoring tool.

Material and methods

Clearings within the Lobeke (Cameroon) and the Nouabale-Ndoki (Republic of Congo) National Parks (NP) as well as the latter's surrounding area were the focus of this study (Fig. 1). Both parks are part of the Sangha Trinational protected areas complex in Central Africa. The Nouabale-Ndoki NP has never been exploited, while part of Lobeke has been selectively logged before its declaration as National Park in 2001 (Stromayer & Ekobo, 1992; MINEF, 2004); logging concessions are located adjacent to both protected areas. The climate is equatorial with mean annual rainfall around 1600 mm and an average annual temperature of about 25°C. The major dry season (<100 mm rainfall per month) lasts from December to February, and the major rainy season from September to November (MINEF, 2004). The area hosts important populations of large mammals such as the African forest elephant, the bongo antelope (Tragelaphus euryceros) and the western lowland gorilla (Stokes et al., 2010).

Infrared camera traps (Reconvx hyperfire HC500, Holmen, WI, USA) were set-up around seven bais during the rainy and dry season for approximately 2 weeks for each season. The bais (two in Lobeke, five in Nouabale-Ndoki and its periphery) were selected based on accessibility, representativeness in terms of size and distribution in terms of spatial separation between bais. Due to an ongoing long-term bai study at Mbeli, camera traps were employed only once in the rainy season for 3 weeks to minimize disturbance of animals. As direct sunlight may influence the cameras' performance, cameras were installed in the adjacent forest facing animal trails leading into the respective bai. At each bai, two to six camera traps, depending on the size of a bai, were deployed on distinct trails. The main criterion for the selection of trails was separation from other trails by approximately 300 m, or 150 m at small bais. Care was taken to use equal numbers of large (>30 cm) and small (\leq 30 cm) trails at each bai, unless only large animal trails could be reliably identified. To record both small and large animals, cameras were positioned at 30-50 cm height and a distance of at least 2 m from the trail. Camera traps worked 24 h a day and were set to no delay, that is, to be triggered by all motion events without a quiet period. Information on the date and time was automatically imprinted on each photo. Entirely swampy bais were avoided in this study as animal trails are difficult to distinguish in such habitats.

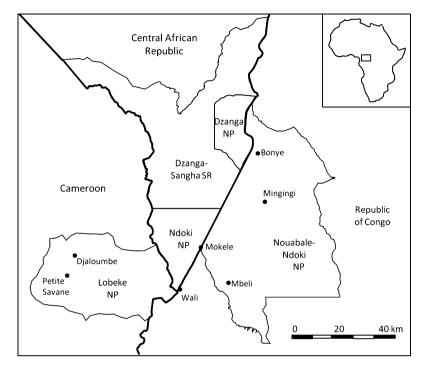


Fig 1 Map showing the study area in Central Africa. The seven bais surveyed are located in the Lobeke (Cameroon) and Nouabale-Ndoki (Republic of Congo) National parks as well as the latter's surrounding area. Both National parks together with the Dzanga and Ndoki National Parks as well as the Dzanga-Sangha Special Reserve (Central African Republic) constitute the Trinational de la Sangha protected area

In total, 47 camera trap sessions of approximately 2 weeks were conducted across seasons and bais, with five cameras being taken down by elephants and a leopard within a few days of set-up. Two of these cameras worked for 3 days and were included; the other three failed cameras were excluded from analysis. We further excluded failed images, where the camera was either triggered by sunlight or the flash was blocked by a leaf or branch resulting in a dark picture.

Data collation and analysis

For all pictures, the animal species captured was identified. Any fleeing behaviour was noted as well as the direction of each animal (walking to or coming from the bai) and whether an animal was walking alone or in a group; a group was defined as animals of the same species walking in the same direction with a maximum interval of 10 min between individuals. When an individual or group of the same species passed a camera trap twice within 30 min (see also O'Brien, Kinnaird & Wibisono, 2003), distinct features of the animals (e.g. notches and holes in the ears of elephants) were studied on the pictures to assess whether it was the same individual or group. Double counts identified in this manner were excluded from analysis.

To investigate diurnal and nocturnal activity patterns, the time interval from 6:00 to 17:59 was considered as daylight hours and the night from 18:00 to 05:59 according to dawn and dusk in the equatorial forest. Elephant diurnal visiting rates were compared with nocturnal rates at different bais (excluding Petite Savane due to its small sample size). Regarding activity patterns of the remaining species, data from all bais were combined due to low sample sizes. Seasonal differences in species presence and activity were compared where camera trap stations functioned during both seasons (excluding Mbeli bai). As the number of recording days in both seasons varied slightly, station-specific data collected were compared for the period of fewest collection days. We further examined the use of small versus large trails by different mammal species. To account for differences in sampling effort across trail size classes, trapping rates (i.e. the numbers of records divided by the respective number of recording hours) were compared.

Statistical analyses of daily activity patterns of different mammal species were conducted using circular statistics in the program Oriana version 4.01 (Kovach, 2011). Data were plotted on a circular scale with 24 hourly sections, and the total length of the circular axis representing 1 day. The Rayleigh's uniformity test was used to evaluate the probability that the data (e.g. records of different mammal species) were distributed uniformly on the circular axis. To compare more than two samples, for example, differences in the distributions of elephants at different bais, the Watson–Williams F-test was used (Kovach, 2011).

Differences between the numbers of elephants visiting each bai during the day versus the night were investigated using Wilcoxon tests. Nonparametric tests were used for all analysis because normality was not reached after data transformation. The Spearman correlation coefficient was calculated to test for correlations between the numbers of elephants during the night versus the day at each bai. The Mann–Whitney *U*-test was applied to examine differences regarding the number of elephants between the rainy and the dry season as well as large versus small trails. All noncircular statistics were performed in SPSS version 20 (IBM, Armonk, NY, USA). Statistical significance was set at $\alpha \leq 0.05$.

Results

Camera trap data summary

In 697 camera trap days (15282 h), 5772 photo events were recorded, 280 of which could not be identified and were excluded from further analysis. In total, 25 mammal species were identified (listed in Table 1) besides mice, squirrels, a giant pouched rat (*Cricetomys* sp.), birds and humans.

For each bai, species captured by camera traps were compared with species lists provided by long-term studies conducting direct observations (of at least 1 year) at the respective bai (Nzooh Dongmo, 2003; Mowawa, 2006; Dieudonne, 2010; K. Greenway, pers. comm.), with the exception of Mokele bai where no such observational data were available (Table 1). At Bonye, Mingingi and Wali,

 Table 1
 Mammal species recorded at different bais. The total number of species recorded at each bai by camera traps, direct observations

 (Nzooh Dongmo, 2003; Mowawa, 2006; Dieudonne, 2010; K. Greenway, pers. comm.) and in combination

Species	Bonye	Mbeli	Mingingi	Mokele	Wali	Djaloumbe	Petite Savane
Brush-tailed porcupine Atherurus africanus	+		+			+	+
Marsh mongoose Atilax paludinosus	+	1	+			1	1
Peter's duiker Cephalophus callipygus	1	1	1	+	*	1	1
Bay duiker Cephalophus dorsalis	+	*			+	+	*
Blue duiker Cephalophus monticola	1	1	+	+	+	1	1
Black-fronted duiker Cephalophus nigrifrons	1		1	+			
Yellow-backed duiker Cephalophus silvicultor	+	+		+	1	1	1
Agile mangabey Cercocebus agilis	+	*		+		+	+
Moustached monkey Cercopithecus cephus		*				*	1
De Brazza's monkey Cercopithecus neglectus	+	*				*	*
African civet Civettictis civetta		1			+	1	
Spotted hyaena Crocuta crocuta	+						
Genet Genetta sp.	+		+	+		1	1
Western lowland gorilla Gorilla g. gorilla	*	1	1	+		1	1
Guereza colobus Guereza colobus	*	*	*			1	1
Water chevrotain Hyemoschus aquaticus	*	+	+	+	1	1	1
Giant hog Hylochoerus meinertzhageni	+	1				1	1
African forest elephant Loxodonta a. cyclotis	1	1	1	+	1	1	1
Chimpanzee Pan troglodytes		*	1			1	*
Leopard Panthera pardus	1	1	+		+	1	*
Red river hog Potamochoerus porcus	1	1	1			1	1
Pangolin Smutsia sp.						1	1
African forest buffalo Syncerus caffer nanus	1	1	1	+	1	1	1
Bongo Tragelaphus euryceros	1	1	1	+	+	1	1
Sitatunga Tragelaphus spekei	1	*	1		+	*	1
Camera traps	18	13	15	11	10	20	18
Direct observations	12	18	9	-	5	20	20
Total	21	20	16	11	11	23	22

Species only recorded by camera traps (+) or direct observations (*) as well as by both (1) are indicated.

camera traps yielded higher numbers of species than direct observations recording 86%, 94% and 91%, respectively, of the total number of species detected by both methods (Table 1). In contrast, at Mbeli and Petite Savane, camera traps recorded fewer species than those recorded during long-term direct observations, detecting 65% and 82%, respectively, of the total number of species provided by both methods. At Djaloumbe, each method detected 87% of the total known species.

Semi-aquatic bai living species of the subfamily *Lutrinae* only recorded by direct observations were excluded as it is assumed that they would not be detected by camera traps on forest trails. At Bonye bai, first evidence was provided for the occurrence of the spotted hyaena in the north of Nouabale-Ndoki NP.

Temporal patterns of use

Mammal species recorded by camera traps solely during the day include the agile mangabey, the guereza colobus and the marsh mongoose. Records of the civet, the spotted hyaena, the genet, the pangolin and the brush-tailed porcupine were only made during the night. Leopard captures were predominantly at night (nine of eleven). Information on capture time of different species visiting the bais is presented (Table 2).

Activity patterns of forest elephants revealed by camera traps showed evidence of preference for nocturnal bai visits (Fig. 2 and Table 2). Distributions differed significantly across bais (Watson–Williams F-test: F = 4.917, df = 6, df₂ = 3898, P < 0.05). Significantly more elephants were

recorded during the night in all bais, with the exception of Petite Savane where few (34) elephants were captured (Table 3). Altogether, 86% of elephants visited the bais during the night (95% at Mokele, 93% at Djaloumbe, 91% at Mbeli, 88% at Petite Savane, 87% at Mingingi, 84% at Wali and 74% at Bonye). Bonye demonstrated the greatest diurnal elephant use among the studied bais. High numbers of elephants (more than 50) were recorded between 14:00 and 18:00, while at other bais, more than 50 elephants were only recorded after 18:00. Only for Mokele bai, a significant correlation was found between the numbers of elephants recorded during the day and the night (Table 3).

Data collected for approximately 9800 recording hours at six bais were used for the investigation of differences between months of the rainy and the dry season. No significant differences regarding the number of elephants between both seasons were detected except at Dialoumbe bai (Table 3). At Wali, more (although not significant) buffaloes were recorded in the rainy season (33 individuals) than in the dry season (eight) (Mann-Whitney U-test: U = 87.5, n = 16, P > 0.05); at Mokele (39) individuals) and Petite Savane (nine), buffaloes were recorded solely in the rainy season. More bongos (although not significant) were recorded during the dry season in comparison with the rainy season (111 and 56 animals, respectively: Mann–Whitney U-test: U = 110, n = 16, P > 0.05) at Djaloumbe. At Mokele, bai bongos were filmed only in the rainy season (41 records). At the remaining bais and for other species, not enough records were available for the investigation of seasonal patterns.

Table 2 Time of mean activity for different mammal species recorded by camera traps combining data from all bais

Species	Time of mean activity	Rayleigh test
Tragelaphus spekei	$06:22 \pm 03:32$ circstdev	r = 0.649, z = 5.1, n = 12, P < 0.05
Cephalophus nigrifrons	$10:15 \pm 03:25$ circstdev	r = 0.669, z = 9.9, n = 22, P < 0.05
Cephalophus callipygus	$11:23 \pm 03:35$ circstdev	<i>r</i> = 0.642, <i>z</i> = 41.6, n = 101, <i>P</i> < 0.05
Cephalophus monticola	$11:31 \pm 05:14$ circstdev	<i>r</i> = 0.39, <i>z</i> = 39.7, n = 261, <i>P</i> < 0.05
Gorilla gorilla gorilla	$14:14 \pm 03:02$ circstdev	<i>r</i> = 0.729, <i>z</i> = 26.1, n = 49, <i>P</i> < 0.05
Hylochoerus meinertzhageni	$16:44 \pm 03:32$ circstdev	r = 0.729, z = 26.1, n = 49, P < 0.05
Potamochoerus porcus	$19:23 \pm 05:28$ circstdev	<i>r</i> = 0.359, <i>z</i> = 14.9, n = 116, <i>P</i> < 0.05
Cephalophus silvicultor	$21:04 \pm 02:29$ circstdev	r = 0.808, z = 14.4, n = 22, P < 0.05
Loxodonta africana cyclotis	$22:44 \pm 04:07$ circstdev	<i>r</i> = 0.557, <i>z</i> = 1212.4, n = 3905, <i>P</i> < 0.05
Hyemoschus aquaticus	$23:14 \pm 03:04$ circstdev	<i>r</i> = 0.724, <i>z</i> = 27.2, n = 52, <i>P</i> < 0.05
Cephalophus dorsalis	$23:59 \pm 02:46$ circstdev	<i>r</i> = 0.769, <i>z</i> = 17.1, n = 29, <i>P</i> < 0.05
Syncerus caffer nanus	$01:05 \pm 03:53$ circstdev	<i>r</i> = 0.595, <i>z</i> = 51.1, n = 144, <i>P</i> < 0.05
Tragelaphus euryceros	$01:58 \pm 05:12$ circstdev	r = 0.395, z = 55.4, n = 355, P < 0.05

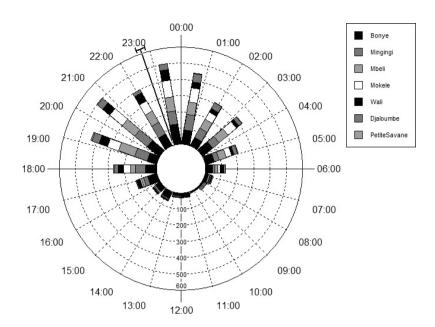


Fig 2 Circular histogram illustrating the distribution and mean of elephant numbers recorded by camera traps throughout the day across all bais. The numbers of elephants differs significantly from a random distribution (r = 0.556, z = 1212.4, n = 3905, P < 0.05) with 22:44 being the mean time of elephant activity

Table 3 Mean time of elephant activity at different bais revealed by circular statistics

	Elephant activity pattern		Day versus night	Dry versus wet season	
	Time of mean activity \pm circstdev	Wilcoxon test	Spearman's correlation	Mann–Whitney U-test	
Bonye	$22:27 \pm 05:07$	z = 4.706, n = 31, P < 0.05	r = 0.223, n = 31, P > 0.05	U = 88, n = 15, <i>P</i> > 0.05	
Mokele	$23:07 \pm 03:27$	z = 4.541, n = 29, $P < 0.05$	r = 0.388, $n = 29$, $P < 0.05$	U = 57, n = 14, P > 0.05	
Djaloumbe	$23:10 \pm 03:51$	z = 5.175, $n = 40$, $P < 0.05$	r = 0.013, $n = 40$, $P > 0.05$	U = 68.5, n = 14, P > 0.05	
Mingingi	$22:29 \pm 03:56$	<i>z</i> = 4.920, n = 32, <i>P</i> < 0.05	r = 0.134, $n = 32$, $P > 0.05$	U = 91, n = 15, <i>P</i> > 0.05	
Petite Savane	$21:43 \pm 04:53$	z = 1.872, $n = 34$, $P > 0.05$	r = 0.071, $n = 34$, $P > 0.05$	U = 86.5, n = 15, P > 0.05	
Wali	$22:08 \pm 03:58$	z = 4.865, n = 32, P < 0.05	r = 0.024, $n = 32$, $P > 0.05$	U = 115, n = 16, P > 0.05	
Mbeli	$23:00 \pm 03:46$	z = 3.921, n = 20, $P < 0.05$	r = 0.195, n = 20, P > 0.05	-	

Significant differences between numbers of elephants recorded during the day versus the night (Wilcoxon test) as well as correlations between numbers recorded during the day and the night (Spearman's correlation) are indicated. Significant differences between the number of elephants recorded in the rainy versus the dry season (Mann–Whitney *U*-test) are provided for each bai (excluding Mbeli where camera traps were set-up only during the rainy season).

Impact of trail size

Camera traps at large trails yielded significantly more photos than those set-up at small trails and higher numbers of records per observation hour for elephants (Mann–Whitney *U*-test: $n_L = 18$, $n_S = 10$; $U_{Total} = 30$, P < 0.05; $U_{Elephants} = 36$, P < 0.05). In total, more bongos were recorded on large trails than on small trails (3.45 and 0.24 records per 10 h of observation, respectively), although this was not significant (Mann–Whitney *U*-test: U = 73.5, $n_L = 18$, $n_S = 10$, P > 0.05). Certain species

were more often recorded on small trails, such as the water chevrotain, the marsh mongoose and some duiker species (Fig. 3).

Discussion

In the present study, camera traps were employed at each bai for a relatively short period of three to four weeks. Yet, they recorded most (65-94%) of the mammal species known to visit the respective bai (as derived from both

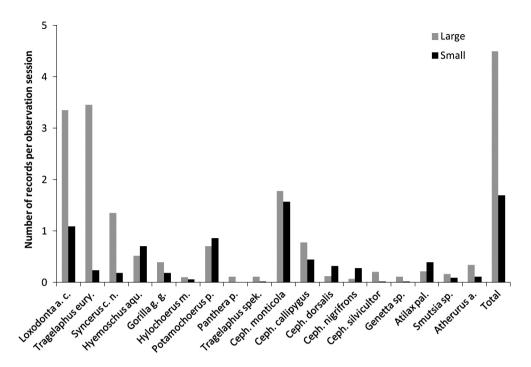


Fig 3 Usage of small (black bars; n = 10) versus large (grey bars; n = 18) trails by different mammal species. Observation rates are presented as numbers of observations per 100 h for all species except elephants, which are presented as number per 10 h. Observation rates of total species are also presented as number per 10 h. Species with <10 records have been excluded from the graph although they are represented in the 'total' category

camera traps and long-term studies using direct observations). These results confirm that camera trapping is an effective method for species inventories as it has been shown in other studies on medium to large-sized mammals (Rovero, Tobler & Sanderson, 2010). While a two-week time frame per season appeared to capture most species (see also Gompper et al., 2006), capture effectiveness was greater at some bais than others. This might be due to the sampling design, species density or differences in baispecific characteristics (mineral resources, feeding plants, human activity, etc.). Probably because of the 24-h sampling, a number of (primarily nocturnal) species were observed with the camera survey approach that were not seen during direct observations. Consequently, camera traps provide high-quality species occupancy data in the forest setting (see also Matsubayashi et al., 2007) with much lower man-hour requirements than direct observations.

Species not detected by camera traps were mainly arboreal monkeys that, as part of their antipredator behaviour, do not typically enter bais on trails (Janson, 1998; Blake *et al.*, 2010; Link *et al.*, 2011). Only the durations searching for food. Camera traps appear highly applicable for the detection of species using permanent trails to enter clearings such as forest elephants, bongos and forest buffaloes (Klaus-Hügi, Klaus & Schmid, 2000; Blake, 2002). Results show that large trails were more frequently used and captured significantly higher numbers of elephants than small trails, although small trails were of importance to capture smaller species such as the water chevrotain, the marsh mongoose and duiker species. In general, results indicate that camera traps have a very low impact on forest mammals because among the 467 captures that showed animal reaction, only twelve depicted fleeing. The feasibility of identifying age and sex classes and even individual forest elephants found in the present study confirms findings from Varma, Pittet & Jamadagni (2006) that camera traps have potential for the study of the population structure of elephants.

guereza colobus is known to regularly visit bais for longer

As expected, diurnal species such as the western lowland gorilla, the chimpanzee, the agile mangabey, the guereza colobus and the marsh mongoose were recorded by camera traps solely during the day (Estes, 1992; Djagoun *et al.*, 2003; Kingdon, 2003), while the bongo visited the bais preferentially in the night (Klaus-Hügi, Klaus & Schmid, 2000; Elkan, 2003). Large numbers of buffalo have been recorded at clearings during the day by several studies (Magliocca, 2000; Melletti *et al.*, 2007; Gessner, 2008), yet camera traps recorded significantly higher numbers of buffaloes during the night at all bais except Djaloumbe. Camera traps showed a clear distinction between diurnal (blue duiker, Peter's duiker and black-fronted duiker) and nocturnal (bay duiker) duiker species (Estes, 1992; Kingdon, 2003). Although the yellow-backed duiker is thought to be active both during day and night (Kranz & Lumpkin, 1982; Newig, 2001), this species was recorded by camera traps only during the night.

Applying acoustic monitoring tools at six forest clearings in Gabon, Wrege et al. (2012) found that 79% of all elephant visitation occurred at night. Similar results were found in the present study with 74-95% of the elephants visiting the seven bais during the night. At Bonye, higher percentages of elephants (23.3%) were recorded during the day than at the remaining bais (6.3-15.7%) with increasing numbers from 14:00 on (Fig. 2). Bonve is located very close to Dzanga bai, C.A.R. (23 km), and many individually identified elephants are known to frequent both clearings (Inkamba-Nkulu, 2007). A long-term, individually based monitoring project at Dzanga has recorded high densities of elephants throughout the day with increasing numbers in the afternoon (Turkalo & Fay, 1995). Consequently, it is possible that elephants show a similar activity pattern at these clearings as they share the same elephant population and are both rarely frequented by poachers. As forest clearings represent easy hunting grounds, it is generally assumed that higher visitation rates of elephants during the night reflect the elephants' reaction to poaching pressure (see Ruggiero, 1999). Our sample of human captures was too small to investigate any such relationship, but indicates camera traps may be a useful metric to identify levels of human pressure.

At each bai, a significant difference between the number of elephants recorded during the day and the night was detected (except Petite Savane). No significant correlation between day and night numbers of elephants was found for any of the bais except Mokele. This confirms findings from Wrege *et al.* (2012) who recorded large changes in nocturnal elephant numbers without proportional changes in daytime numbers. Although our data are limited by the short-study period and the fact that camera traps only faced selected trails (not providing total numbers of animals visiting a bai), our results indicate that care has to be taken by inferring demographic trends when monitoring changes in elephant numbers only during the day.

Seasonal differences in the number of elephants recorded were not significant, with the exception of Djaloumbe bai. In contrast, camera trap data suggest that overall more buffalo visited the bais during the rainy season. While insights drawn are from a relatively short period and may not allow understanding of seasonal use, results show that camera traps are presumably able to provide necessary data for greater insight to seasonal use patterns given more thorough sampling.

In conclusion, the present study demonstrates that camera traps are valuable tools for species inventories and monitoring of certain mammal species, especially African forest elephants, at bais. Camera traps allow simultaneous monitoring of multiple bais, allowing direct comparison, and are especially time and cost-effective in remote areas. As such, camera trap data are likely to be the best means to conduct species distribution modelling and implement a large-scale monitoring programme. Camera traps cannot replace direct observations that provide more precise individual-based demographic and behavioural data. Yet, camera traps provide important data on mammal species activity patterns day and night, with the latter being a time of high mammal activity which is missed by direct observations. Further, longterm studies are needed combining direct observations and camera traps at bais to investigate the relation of data provided by camera traps and numbers of individual animals visiting a bai.

Acknowledgements

We thank the Ministere de l'Economie Forestiere et de l'Environnement, Republic of Congo, and the Ministere de la Recherché Scientifique et de l'Innovation, Cameroon, for permission to conduct research. We are grateful to staff of WCS Congo and WWF Cameroon for logistical and administrative support. Many thanks to Marius Sienne Metsio and numerous field assistants for their support and field expertise, to Marie Manguette for valuable advice on data analysis and to WWF Germany for providing camera traps. This research was funded by Rufford Small Grants Foundation, Twycross Zoo Conservation Welfare Fund and Idea Wild. J.G. received a scholarship from the German Academic Exchange Service.

References

BLAKE, S. (2002) Forest buffalo prefer clearings to closed-canopy forest in the primary forest of northern Congo. Oryx 36, 81–86.

BLAKE, J.G., GUERRA, J., MOSQUERA, D., TORRES, R., LOISELLE, B.A. & ROMO, D. (2010) Use of mineral licks by white-bellied spider monkeys (Ateles belzebuth) and red howler monkeys (Alouatta seniculus) in eastern Ecuador. Int. J. Primatol. 31, 471-483.

BREUER, T., BREUER-NDOUNDOU HOCKEMBA, M., OLEJNICZAK, C., PARNELL, R. & STOKES, E. (2008) Physical maturation, life-history classes and age estimates of free-ranging western gorillas insights from Mbeli Bai, Republic of Congo. Am. J. Primatol. 70, 1 - 14

DIEUDONNE, E.B. (2010) Rapport annuel 2010 du suivi d'observations de bai Wali. Unpublished report, WCS Republic of Congo.

DJAGOUN, C.A.M.S., AKPONA, H.A., SINSIN, B., MENSAH, G.A. & DOSSA, N.F. (2003) Mongoose species in southern Benin: preliminary ecological survey and local community perceptions. Mammalia 73. 27-32.

ELKAN, P.W. (2003) Ecology and conservation of bongo antelope (Tragelaphus eurycerus) in lowland forest, Northern Republic of Congo. Dissertation. University of Minnesota.

ESTES, R.D. (1992) Behavior Guide to African Mammals. Including Hoofed Mammals, Carnivores, Primates. The University of California Press, Berkeley and Los Angeles, CA, USA.

GESSNER, J. (2008) Survey of mammals at Ikwa bai – Nki National Park, south-east Cameroon in terms of conservation and ethology with a focus on the African forest buffalo (Syncerus caffer nanus). MSc thesis, Carl von Ossietzky University Oldenburg, Germany.

GOMPPER, M.E., KAYS, R.W., RAY, J.C., LAPOINT, S.D., BOGAN, D.A. & CRYAN, J.R. (2006) A comparison of noninvasive techniques to survey carnivore communities in Northeastern North America. Wildl. Soc. Bull. 34, 1142-1151.

INKAMBA-NKULU, C. (2007) Structure and movements of a geophagous population of forest elephants in the Congo basin. MSc thesis, University of East Anglia.

JANSON, C.H. (1998) Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. Behaviour 135, 389-410.

KINGDON, J. (2003) The Kingdon Field Guide to African Mammals. A&C Black Publishers Ltd., London.

KLAUS-HÜGI, C., KLAUS, G. & SCHMID, B. (2000) Movement patterns and home range of the bongo (Tragelaphus eurycerus) in the rain forest of the Dzanga National Park, Central African Republic. Afr. J. Ecol. 38, 53-61.

KOVACH, W.L. (2011) Oriana for Windows, Version 4.01. Kovach Computing Services, Anglesey, Wales.

KRANZ, K.R. & LUMPKIN, S. (1982) Notes on the Yellow-backed duiker (Cephalophus sylvicultor) in captivity with comments on its natural history. Int. Zoo. Yearb. 22, 232-240.

LINK, A., GALVIS, N., FLEMING, E. & DI FIORE, A. (2011) Patterns of mineral lick visitation by spider monkeys and howler monkeys in Amazonia: are licks perceived as risky areas? Am. J. Primatol. 73, 386–396.

MAGLIOCCA, F. (2000) Etude d'un peuplement de grands mammiferes forestiers tropicaux frequentant une clairiere: Structure des populations: utilisation des ressources: coexcistence intra- et interpopulationnelle. Dissertation, Universite de Rennes, France.

MATSUBAYASHI, H., LAGAN, P., MAJALAP, N., TANGAH, J., SUKOR, J. & KITAYAMA, K. (2007) Importance of natural licks for the mammals in Bornean inland tropical rain forests. Ecol. Res. 22, 742-748.

MELLETTI, M., PENTERIANI, V., MIRABILE, M. & BOITANI, L. (2007) Some behavioral aspects of forest buffalo (Syncerus caffer nanus): from herd to individual. J. Mammal. 88, 1312-1318.

MINEF. (2004) Plan d'amenagement du parc national de Lobeke et de sa zone peripherique: Periode d'execution: 2005-2009. Ministere de l'environnement et des forets. Yaounde. Cameroon

MOMONT, L. (2007) Selection de l'habitat et organisation sociale de l'éléphant de forêt, Loxodonta africana cyclotis (Matschie 1900), au Gabon. Dissertation, Museum National d'Histoire Naturelle, Paris.

MOWAWA, B.S. (2006) Suivi de l'elephant de foret (Loxodonta africana cyclotis) aux bais de Mabale, Mingingi et Bonye dans le Parc National Nouabale-Ndoki. Unpublished report, WCS Republic of Congo.

NEWIG, H. (2001) Bushmeat hunting and management: implications of duiker ecology and interspecific competition. Biodivers. Conserv. 10, 99-118.

NZOOH DONGMO, Z.L. (2003) Suivi ecologique dans le parc national de Lobeke et sa zone peripherique: donnees de base sur la dynamique des populations de grands et moyens mammiferes et des activites anthropiques. Unpublished report, WWF Cameroon.

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. Anim. Conserv. 6, 131-139.

ROVERO, F., TOBLER, M. & SANDERSON, J. (2010) Camera-trapping for inventorying terrestrial vertebrates. In: Manual on Field Recording Techniques and Protocols for all Taxa Biodiversity Inventories (Eds J. EYMANN, J. DEGREEF, C. HÄUSER, J. C. MONYE, Y. SAMYN and D. VANDENSPIEGEL). Abc Taxa, 8.

RUGGIERO, R. (1999) The effects of poaching disturbance on elephant behaviour. Pachyderm 13, 42–44.

STOKES, E.J., STRINDBERG, S., BAKABANA, P.C., ELKAN, P.W., IYENGUET, F.C., MADZOKE, B., MALANDA, G.A.F., MOWAWA, B.S., MOUKOUMBOU, C., OUAKABADIO, F.K. & RAINEY, H.J. (2010) Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. PlosOne 5, e10294.

STROMAYER, K.A.K. & EKOBO, A. (1992) The distribution and number of forest dwelling elephants in extreme southeastern Cameroon. Pachyderm 15, 9-14.

TURKALO, A. & FAY, J.M. (1995) Studying forest elephants by direct observation: preliminary results from the Dzanga clearing, Central African Republic. Pachyderm 20, 45-54.

TURKALO, A. & FAY, J.M. (2001) Forest Elephant behavior and ecology: observations from the Dzanga saline. In: African Rain

Forest Ecology & Conservation: An Interdisciplinary Perspective (Eds W. Weber, L. White, A. Vedder and L. Naughton-Treves). Yale university press, New Haven and London.

VARMA, S., PITTET, A. & JAMADAGNI, H.S. (2006) Experimenting usage of camera-traps for population dynamics study of the Asian elephant Elephas maximus in southern India. *Curr. Sci.* 91, 324–331. WREGE, P.H., ROWLAND, E.D., BOUT, N. & DOUKAGA, M. (2012) Opening a larger window onto forest elephant ecology. *Afr. J. Ecol.* 50, 176–183.

(Manuscript accepted 27 March 2013)

doi: 10.1111/aje.12084