Habitat preferences of the secretive forest buffalo (Syncerus caffer nanus) in Central Africa

M. Melletti¹, V. Penteriani² & L. Boitani¹

1 Department of Animal and Human Biology, University of Rome 'La Sapienza', Rome, Italy 2 Department of Conservation Biology, Estación Biológica de Doñana, CSIC, Seville, Spain

Keywords

Abstract

Syncerus caffer nanus; habitat preference; rainforest; recce; resting places; wet and dry season.

Correspondence

Mario Melletti, Department of Animal and Human Biology, University of Rome 'La Sapienza', VIe. dell'Università 32, 00185 Rome, Italy.

Email: mario.melletti@tiscali.it

The forest buffalo Syncerus caffer nanus is one of the three subspecies of African buffalo inhabiting the rainforests of Western and Central Africa. Because of its secretive behaviour and main habitat (dense rainforests), there is little quantitative information on the habitat preferences of this buffalo. We present here the first data on the frequencies of this species along a habitat gradient ranging from clearings and rivers to forests, as well as the characteristics of the buffalo's resting places. We recorded information from a buffalo herd during the period January 2002–January 2004 in the Bai-Hokou area (Dzanga-Ndoki National Park, Central African Republic). Resting places were firstly compared with available habitat (i.e. resting vs. random sites) and, successively, comparisons were made between diurnal versus nocturnal and wet versus dry season resting places. Forest buffalos were found to be highly dependent on clearings, as well as on the more open forest stands, characterized by large trees and open canopy. Such preferences could be due to the tendency of the buffalos to rest all together; open patches are likely to facilitate social interactions between the members of the herd.

Introduction

The forest buffalo Syncerus caffer nanus is one of the three recognized subspecies of African buffalo (Blancou, 1935; Sinclair, 1977; Haltenorth & Diller, 1979), the other subspecies being the Cape buffalo Syncerus caffer caffer and the Western African buffalo Syncerus caffer brachyceros. Whereas these two latter buffalos inhabit African savannahs, the forest buffalo is a forest-dwelling species, inhabiting the rainforests of Western and Central Africa (Sinclair, 1977; Haltenorth & Diller, 1979; Prins, 1996; Kingdon, 1997). Sinclair (1977) proposed a fourth subspecies, Syncerus caffer aequinoctialis, inhabiting the savannahs of Central Africa.

The most studied subspecies is the Cape buffalo of eastern and southern African savannahs (Sinclair, 1977; Mloszewski, 1983; Prins, 1996). At present, little information is available on the ecology and behaviour of the forest buffalo. This includes (1) estimates of local distribution and abundance (e.g. Blake, 2002), (2) the presence of this buffalo in habitats other than primary forest, such as burning equatorial savannahs (Molloy, 1997), savannahs and clearings (Chamberlan, Maurois & Maerechal, 1995; Maisels, 1996), savannahs and secondary forests (Prins & Reitsma, 1989) and open swampy meadows (Blake, 2002), and (3) the preference for grasses along forest roads as feeding habitats (Hoppe-Dominik, 1992). In comparison with the detailed descriptions of habitat preferences for the savannah buffalo

(e.g. Melton, 1987; Funston, Skinner & Dott, 1994; Mugangu, Hunter & Gilbert, 1995), there is little quantitative information available on the habitat preferences of the forest buffalo. This is probably due to both its very secretive behaviour (M. Melletti, pers. obs.) and its limited distribution. Information on the forest buffalo is urgently needed because it lives prevalently in the Central Africa rainforests, which represent a habitat particularly sensitive to humaninduced alterations. For example, selective logging of African rainforests has resulted in the migration of people into remote areas, contributing to increased poaching of large mammals (e.g. elephants) and degradation of c. 2.3×10^6 ha of forest each year during the 1990s (Achard et al., 2002). Consequently, human practices represent a threat for the high biodiversity of tropical forest, which supports about 50% of described species and an even larger number of unknown species (Dirzo & Raven, 2003). Moreover, and despite the fact that recent studies on habitat suitability have shown that the Congo basin (the stronghold of the forest buffalo range of distribution) is the richest region of the African continent, studies of habitats and animal conservation remain inadequate in the area (Rodrigues et al., 2004; Rondinini, Stuart & Boitani, 2005). As a result, information on the habitat requirements of the forest buffalo is crucial for its conservation and the correct management of tropical forested habitats, as well as the conservation of the many other forest-dwelling species that depend on them.

The main aim of this study was to contribute to the knowledge of the forest buffalo by studying its habitat preferences. In accord with Hall, Krausman & Morrison (1997), we define 'habitat preference' as the consequence of the habitat selection process (i.e. the process an organism uses to choose a habitat), resulting in the disproportional use of some resources over others. In particular, we analysed (1) the frequencies of this species along a habitat gradient ranging from clearings and rivers to dense forests and (2) the characteristics of the buffalo's resting places, depending on (a) the available habitat (i.e. resting vs. random sites), (b) the period of the day in which they were used (i.e. diurnal vs. nocturnal resting places) and (c) the season (i.e. wet vs. dry, the two main seasons of Central Africa rainforests; Carroll, 1997).

Study area

The observations of movements of a buffalo herd and forest measurements were recorded, from January 2002 to January 2004 included, in the Bai-Hokou area (2155[®]N, 16120[®]E; Fig. 1), in the Dzanga sector of the Dzanga-Ndoki National Park, Central African Republic. Bai-Hokou forests were selectively logged for a period of c. 10 years, from 1972 to

1980, with the extraction of c. 1-2 trees ha⁻¹. Since the establishment of Dzanga-Ndoki National Park in 1990, logging was stopped, and few human activities are now allowed within the park boundaries (e.g. tourism and scientific research). In an external buffer area, the Dense Forest Special Reserve, natural resources are exploited in a manner not always sustainable (e.g. there are no data yet in this area for traditional hunting by BaAka pigmies and hunting for commerce is unsustainable). Human population density is quite low (Sawmill) and the majority of people are concentrated in the town of Bayanga and along the main road connecting the town of Nola to Cameroon (Blom, 2001). The fauna and flora of the park are rich and diverse (Fay et al., 1990), with some species of endemic bats (Lunde & Beresford, 1997). Poaching with guns and wire snares is common in the whole Dzanga area. Among the largest mammals in the park are the western lowland gorillas Gorilla gorilla, chimpanzees Pan troglodytes, forest elephants Loxodonta cyclotis, bongos Tragelaphus euryceros and leopards Panthera pardus (Carroll, 1986a; Fay, 1989).

The forested habitat of the Dzanga-Ndoki National Park is part of the Guinean-Congolian forest and is dominated by mixed forests and monodominant forests of Gilbertiodendron dewevrei with very open understorey

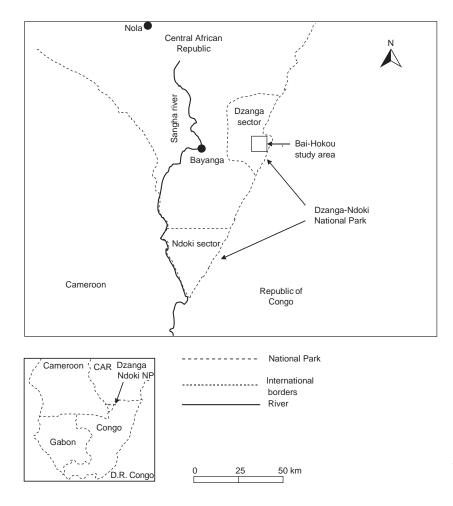


Figure 1 Map of the Bai-Hokou study area (2155¹N, 16120¹E), in the Dzanga sector of the Dzanga-Ndoki National Park, Central African Republic, where from 2002 to 2004 a herd of forest buffalos Syncerus caffer nanus was studied.

(Blom, 2001). With the exception of forest gaps created by natural tree falling or elephant activity (Carroll, 1986b), the only other open areas in the park are the forest clearings maintained by elephant activity (Turkalo & Fay, 1995). In the Bai-Hokou study area, there are about 19 forest clearings ranging in size between 1 and 5 ha.

The tropical climate is characterized by a wet season from March to November and a dry season from December to February. The mean annual rainfall is 1365 mm at Bayanga and the mean temperature is 26.4 IC (Carroll, 1997). In particular, the mean rainfall at Bai-Hokou during the 2002–2004 wet and dry seasons was 1464 and 137.5 mm, respectively (C. Cipolletta, pers. comm.).

Methods

Buffalo herd structure

We studied the only buffalo herd of the Bai-Hokou area composed of 16 individuals over a surface of c. 8 km² at the beginning of the study. During the study the herd grew to 24 individuals sharing the same area. At the beginning, the herd was constituted by nine adult cows, one adult bull, five juveniles and one calf (i.e. a buffalo that does not reach the inguinal fold of the cow; Pineaar, 1969). At the end of the study the herd was composed of 10 adult cows, one adult bull, one subadult bull, one subadult cow, five juveniles and six calves. Two individuals, one subadult bull and one unidentified, died in 2005 (C. Cipolletta, pers. comm.). Unlike the report by Molloy (1997), lone males were never observed in our study area throughout the study.

Classification of forest habitat types

Following the categories proposed by Boulvert (1986), Carroll (1997) and Blom (2001), we distinguished five types of forested habitat for the Dzanga-Sangha forest: (1) mixed forest, characterized by a mixture of open and very dense understorey; (2) monodominant forest of Gi. dewevrei, with open understorey dominated by Palisota sp.; (3) seasonally inundated forest (i.e. riparian forest along the watercourses and swamps); (4) clearing, which are open areas with grassy and marshy vegetation dominated by Cyperaceae spp. and Poaceae spp., similar to the forest clearings of northern Congo described by Blake (2002); and (5) forest with dense understorey, that is mixed forest with thick understorey dominated by Haumania sp. and other Marantaceae and Zingerberaceae with liana tangles.

Buffalo frequencies across habitats in wet and dry seasons: recce method

The recce method is a sampling method that allowed us to determine the distribution and relative degree of use along a habitat gradient from clearings to forest. The name derives from the French word 'reconnaissance'. It was described for the first time by Richard Barnes in 1989 in an unpublished report, The Poor Man Guide to Counting Elephant (see

Hall et al., 1998; McNeilage et al., 1998 for more details). The recce (1) does not require a straight line and permits deviations up to 401 from a straight line (e.g. to avoid obstacles) and (2) requires much less effort per unit distance than linear transects, covering four times more ground (see Walsh & White, 1999 for more details). Our recce followed a path of least vegetation resistance along the elephant's trails, watercourses and trails.

Recce sampling was conducted during 2002 and 2003 in both the wet and dry season. Each recce was always walked by one of us (M. M.) and one tracker (BaAka pygmy). Each recce started from the border of the clearings and rivers frequented by the herd and spanned 2 km into the forest. Recce were separated from each other by a distance of 250 m. Every year during the study period, the same 12 recce were walked once in the wet and dry season, that is each recce was walked four times (Fig. 2a). This represented a total sampling effort of 96 h. We walked each recce with the same compass direction and, for each buffalo's dung that we recorded, we measured the distance from the nearest

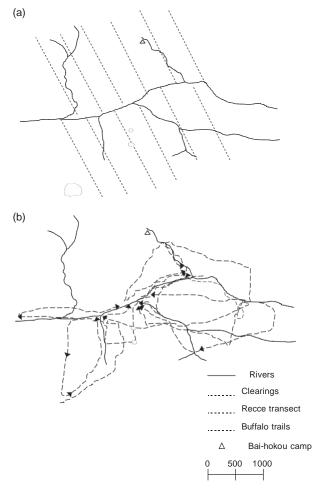


Figure 2 Distribution of the 12 recce transect (a) and buffalo trails (b) in the study area. Both recce and trails were walked during the 2002 and 2003 wet and dry seasons.

clearing and forest edge. The change in the type of vegetation crossed by each recce was recorded and measured by a hipchain. To avoid underestimates of dung numbers, we never walked a recce just after a big rain.

Habitat used by buffalos between wet and dry seasons: buffalo trails

This method allowed us to record supplemental information on the different forest habitat types crossed by buffalo during both the wet and dry season, and to find the buffalo's resting places.

We followed 55 different buffalo trails from 2002 to 2003 in both seasons (n_{wet} season $_{2002} = 15$, n_{wet} season $_{2003} = 15$ and n_{dry} season $_{2002} = 12$, n_{dry} season $_{2003} = 13$; Fig. 2b), when we measured (1) the length of all the different habitat types used by buffalos with a hipchain and (2) the distance of traces to the nearest clearing, river and forest edge by a hipchain. The whole distances travelled by the group of buffalos, which were recorded by the buffalo trails, were also recorded in a map to obtain an estimate of the herd's home range.

Characteristics of resting places

From 2002 to 2004, we analysed the characteristics of 62 resting places to describe the habitat preferences of forest buffalos when resting. We found the resting places by following the buffalo's trails and we considered each of them as (1) nocturnal, when we observed the herd moving inside the forest just before sunset and the day after we found a resting place by following the traces left by the herd during such a crepuscular movement, and (2) diurnal, when we directly observed resting buffalos during diurnal observations.

The characteristics of resting places were recorded within a 10-m-radius plot centred on them. The plot contained four transects at each of the four cardinal points. Tree parameters were measured on those trees intercepted by the transects, based on the line intercept method (Bonham, 1989). Moreover, to compare the vegetation of resting places with available vegetation in the study area, we repeated the same measurements within an equivalent number of randomly selected control plots. Following Penteriani, Faivre & Frochot (2001), the control plots were centred on one randomly selected cardinal point, located 150 m from the resting places. For each resting place, we recorded nine variables: (1) number of trees; (2) tree circumference (cm); (3) tree height (m); (4) height (m) of tree trunk; (5) height (m) of tree crowns; (6) canopy cover (%); and the distances (m) to the nearest (7) clearing, (8) river and (9) forest edge. The heights of trees, trunks and crowns were measured using a photographic lens with a fine metric scale (Penteriani et al., 2001). Whereas tree circumferences were measured by tape, other distances were measured by a hipchain. The canopy cover was calculated as the percentage of sky obstructed by vegetation on black-and-white photos (28 mm lens) of canopy cover, on a grid with 1 mm² (see Penteriani & Faivre, 1997 for more details).

Statistical analyses

Before parametric tests, variables were logarithmically, square-root or arcsin-square-root transformed, where necessary, to achieve a normal distribution. When transformations did not produce a normal variable, nonparametric tests were used. For all analyses, means are given T 1 sp, tests were two-tailed and statistical significance was set at a ζ 0.05.

Buffalo frequencies from clearings (as obtained by the recce method) were analysed by Spearman's bivariate correlations. The t-test compared both (1) the distances of traces to main habitat types and (2) the amount of forest habitat crossed by buffalo trails between the wet and dry seasons. The Mann–Whitney test was used for differences in the amount of clearings crossed by buffalo traces between wet and dry seasons.

Finally, we tested the significance of each variable in the resting places using a generalized linear model (GLM) procedure. This allowed us to obtain a mathematical description of the predictors of the different response variables. Depending on the probability distribution of the response variables being normal, binomial or Poisson, they were modelled using the identity, logit and log link function, respectively. Each explanatory variable and their interactions were fitted to the observed data using the GENMOD procedure of the SAS package (SAS Institute, 1996). The statistical significance of each variable was in turn tested by the model, retaining those that contributed to the largest significant change in deviance. The best model for each dependent variable was selected by likelihood ratio tests for type I analysis, which results in the most adequate model for explaining variation in the response variable where only significant effects are retained. The variables were incorporated into the model only when they explained more than 5% of the deviance. To reduce collinearity and the number of variables presented to GLM models, we used the method of variable reduction proposed by Green (1979). In this method, pairs of intercorrelated variables (r40.6) are considered as estimates of a single underlying factor. Only the variable judged of greatest importance to the studied species is retained for analysis. Of the remaining variables, only those for which high univariate differences (PO0.1) were detected have been included in the analyses. After reduction, response and explanatory variables were grouped into three main blocks: (1) used versus random resting sites; (2) diurnal versus nocturnal resting sites; (3) wet versus dry resting sites.

Results

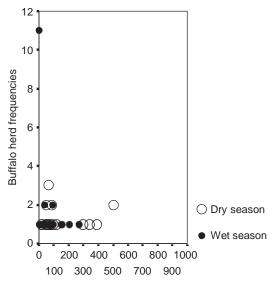
Buffalo frequencies across habitats in wet and dry seasons

The presence of buffalo herd was strictly related to clearings, the possibility to find it being negatively related with the distance to clearings ($r_s = -0.14$, P = 0.0001, n = 48).

The herd moved over larger distances from clearings into the forest in the dry (152.2 T 175.1 m, range = 0-500 m) rather than in the wet season (66.0 T 72.5 m, range = 0–272 m; t= -2.51, P = 0.015, n_{dry season} = 26 and n _{wet season} = 29; Fig. 3). The importance of clearings was also supported by the boundaries of the approximate home range of the buffalo herd of Bai-Hokou, showing an area of c. 8 km² centred around the main clearings of the study area. Direct observations of the herd and buffalo traces both support the hypothesis that the buffalos moved among all the available clearings (all within a few hundred metres) on a rotational basis. Six large clearings out of 19 were regularly used for feeding and resting by the studied herd, the others being visited only irregularly, probably because of scarce grass compared with the larger ones.

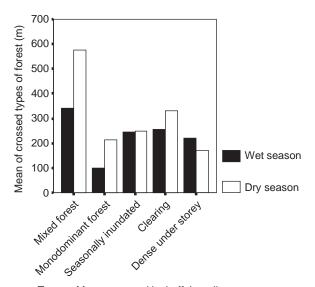
Habitat used by buffalos between wet and dry seasons

Only the amount of (log transformed) mixed forest used by buffalos varied significantly between the wet (341.1 T 318.6 m) and dry seasons (575.7 T 506.2 m; t = 2.32, P = 0.02, d.f. = 86, $n_{wet season} = 60$, $n_{dry season} = 28$; Fig. 4). In fact, the amounts of monodominant forest (100.0 T 88.9 m for wet and 174.8 T 117.4 m for dry;z = -0.92, P = 0.40, d.f. = 5, $n_{wet season} = 3$, $n_{dry season} = 4$), seasonally inundated forest (243.9T 172.0m for wet and 247.1 T 210.0 m for dry; z=-0.92, P=0.40, d.f.=31, n_{wet} season=22, n_{dry season}=11), clearings (256.1 T 280.9 m for wet and 330.6 T 259.1 m for dry; z = -1.38, P = 0.167, d.f. = 31, n_{wet} season = 18, n_{dry} season = 15) and dense understorey forests (219.2 T 188.2 m for wet and 170.0 T 198.0 m for dry; z=0.32, P=0.76, d.f. = 8,



Distance to clearing as revealed by recce method

Figure 3 Variation of forest buffalo Syncerus caffer nanus frequencies from clearing to forest during both the dry (from December to February) and wet (from March to November) seasons. The frequencies of most traces were concentrated in the first 300 m around clearings.



Types of forest crossed by buffalo trails

Figure 4 Distribution of buffalo Syncerus caffer nanus trails within the five main types of habitat of the rainforest of the Dzanga-Ndoki National Park. Whereas the use of the different habitats seemed to be quite homogeneous during the wet season (March–November), the buffalo herd was more frequently located in the patches of mixed forest during the dry season (December–February).

 n_{wet} season=8, n_{dry} season=2) did not show significant differences between seasons.

Characteristics of resting places

Used versus random resting places

The 62 resting places that we found mainly differed from the random sites for tree height, number of trees, types of bed and distance to the forest edge. This model explained 43.62% of the original deviance (Table 1). The data revealed that the buffalo's resting places were (see also Table 2): (1) farther to forest edges than random places (because most of them were located in the clearings), (2) surrounded by fewer and larger trees than random places and (3) preferentially on a substrate of earth and sand.

Diurnal versus nocturnal resting places

Diurnal resting places mainly differed from nocturnal ones for canopy cover, and the interaction term was represented by canopy \times distance to the forest edge. This model explained 60.6% of the original deviance (Table 1). The mean distance of a resting place to the forest was shorter for nocturnal than diurnal resting places. In fact, most nocturnal resting places were into the forest, unlike the diurnals that were mainly in the clearings (Table 3). The interaction between the canopy features and the distance to the forest edge showed again the preference for quite open stands of forest, characterized by older trees and larger distances between trunks.

Table 1 Characteristics of the fore	est huffalo Syncerus caffer	nanus resting places $(n - 62)$
	est bullato Syncerus canel	ranus resulty places (r = 02)

	Parameter			% deviance explained	
Resting places parameters	estimate T SE	w ²	Р		
Used versus random				43.62	
Types of bed ^a		17.44	0.0016		
Earth ^b	-24.23 T 0.91				
Leaves	-22.76 T 0.85				
Sand	-23.73 T 0.55				
Tree height (m) ^c	0.13 T 0.05	18.33	0.0001		
No. of trees ^c	0.40 T 0.18	4.96	0.026		
Distance (m) to forest edge ^d	-1.85 T 4539.1	8.98	0.0027		
Intercept	25.91 T 1.46				
Diurnal versus nocturnal				60.6	
Canopy cover (%) ^c	0.05 T 0.01	29.87	0.0001		
Canopy × d.f. ^d	0.22 T 1563	5.51	0.019		
Intercept					
Wet versus dry seasons				84.13	
Types of bed ^a		12.97	0.024		
Earth ^b	0.40 T 0.84				
Leaves	0.29 T 0.89				
Sand	-1.30 T 0.80				
Intercept	0.69 T 0.61				

Generalized linear model values are reported for comparisons between (1) resting and random places, (2) diurnals and nocturnal resting places and (3) resting places during the wet and dry seasons. Dzanga-Ndoki National Park (Central African Republic, 2002–2004).

^aFor this categorical variable, we only reported the parameter T se of the significant types of bed (earth, leaves and sand, respectively). ^bEarth (a mix of humus and organic material).

^cIn a plot of 10 m.

^dDistance to the nearest forest edge.

Table 2 Values (mean, sp, min. and max.) of the nine variables used to compare resting and random places (n=62) of a forest buffalo Syncerus
caffer nanus herd in the Dzanga-Ndoki National Park (Central African Republic, 2002–2004)

Variable	Resting sites			Random sites		
	х́Т sd	Min.	Max.	хТ sd	Min.	Max.
No. of trees ^a	0.73 T 1.50	0	6	2.13 T 1.44	0	5
Tree circumference (cm) ^a	42.87 T 79.93	3	300	15.04 T 19.22	3	120
Tree height (m) ^a	19.92 T 10.06	0	30	16.19 T 9.31	0	30
Height (m) of tree trunk ^a	4.5 T 4.4	1.6	11	1.8 T 1.1	0.3	5.5
Height (m) of tree crown ^a	4.0 T 4.0	1.5	10	1.7 T 1.4	0.1	10
Canopy cover (%) ^a	39.03 T 42.28	0	95	61.17 T 32.64	0	95
Distance (m) to clearing ^b	82.8 T 129	0	600	273 T 300	0	1600
Distance (m) to river ^b	82 T 125	0	600	202 T 206	0	1380
Distance (m) to forest edge ^b	17.30 T 18.6	0	60	0.66 T 5	0	40

^aIn a plot of 10 m.

^bAll the distances are nearest distances.

Wet versus dry seasons resting places

Wet resting places differed from dry ones for one variable only, the type of bed. This model explained 84.13% of the original deviance (Table 1) and showed that earth and leaves were the main substrate used for resting during the wet season, whereas sand resting places were mainly preferred during the dry season. We compared nine variables (Table 4).

Discussion

The results from our study showed a strong association between forest buffalos and clearings, as well as the most open stands of the forest, characterized by the largest trees and most open canopy. Such a preference for quite open patches of forests could be explained by the tendency of buffalos to rest all together, with individuals very close to

Variable	Diurnal sites			Nocturnal sites		
	х́Т sd	Min.	Max.	х́Т sd	Min.	Max.
No. of trees ^a	0.23 T 0.84	0	4	1.44 T 1.9	0	6
Tree circumference (cm) ^a	23 T 18	13	44	67 T 110	3	300
Tree height (m) ^a	9.44 T 11	0	25	23 T 7	2	30
Height (m) of tree trunk ^a	2.7 T 2.30	0.7	6	4.50 T 4.40	1.6	11
Height (m) of tree crown ^a	2.40 T 2.20	0.8	4.5	4.1 T 4.0	1.5	10
Canopy cover (%) ^a	9.6 T 27.2	0	90	72.8 T 29.1	0	95
Distance (m) to clearing ^b	20.3 T 70.9	0	350	141 T 115.4	0	300
Distance (m) to river ^b	19.8 T 55.5	0	320	139.6 T 110.5	25	330
Distance (m) to forest edge ^b	29.2 T 15.6	0	60	4.0T 10.7	0	35

Table 3 Values (mean, sp, min. and max.) of the nine variables used to compare the diurnals and nocturnal resting places (n=46) of a forest buffalo Syncerus caffer nanus herd in the Dzanga-Ndoki National Park (Central African Republic, 2002–2004)

^aIn a plot of 10 m.

^bAll the distances are nearest distances.

Table 4 Values (mean, sp, min. and max.) of the nine variables used to compare the resting places (n=62) between wet and dry seasons of a forest buffalo Syncerus caffer nanus herd in the Dzanga-Ndoki National Park (Central African Republic, 2002–2004)

Variable	Wet season			Dry season		
	X T SD	Min.	Max.	X T SD	Min.	Max.
No. of trees ^a	0.54 T 1.33	0	6	1.04 T 1.7	0	6
Tree circumference (cm) ^a	19.7 T 13	5	44	60.9 T 105	3	300
Tree height (m) ^a	22.38 T 8.6	0	30	16.47 T 11.2	0	30
Height (m) of tree trunk ^a	4.5 T 4.4	1.6	11	4.0 T 3.5	1	8
Height (m) of tree crown ^a	4.1 T 4	1.5	10	3.9 T 3.2	1.2	7
Canopy cover (%) ^a	41.54 T 43.5	0	95	34.78 T 40.7	0	95
Distance (m) to clearing ^b	86.3 T 118.9	0	400	76.1 T 149.7	0	600
Distance (m) to river ^b	84.8 T 115.1	0	450	77.5 T 144.6	0	600
Distance (m) to forest edge ^b	15.8 T 18.7	0	60	20.7 T 18.6	0	40

^aIn a plot of 10 m.

^bAll the distances are nearest distances.

each other and often in body contact (Melletti, 2005). Therefore, they probably use this type of resting site because it facilitates physical and visual contact between herd members.

Forest sites seemed to be used more frequently during the night. This is probably due to the nocturnal activity of elephants in clearings and because the forest cover could represent good antipredator strategy. Moreover, nocturnal resting sites were used more in the dry season, when the herd moved over larger distances within the forested patches and used more often mixed forest. Direct observations of buffalo herds also support such a preference for clearings and open forested patches (Melletti, 2005). In fact, during 7 years of gorilla tracking in the Bai-Hokou study area, only once was a buffalo sighted more than 2 km from clearings (C. Cipolletta, pers. comm.). This is particularly interesting when considering that clearings only represent 1% of habitats in the Bai-Hokou area (Blom, 2001). Moreover, in the transects of the M.I.K.E. (Monitoring the Illegal Killing of Elephants) in the Dzanga-Ndoki National Park, a few buffalo traces were mainly recorded in clearings and swampy areas (J. Bruno, pers. comm.). Similar habitat preferences

were also evidenced by Prins & Reitsma (1989), Maisels (1996), Tutin, White & Mackanga-Missandzou (1997) and Blake (2002). Clearings probably represent a habitat of crucial importance for the presence and survival of forest buffalo, as well as other large mammals such as elephants and bongos. In fact, they seem to be attracted by the elevated concentration of minerals in both the water and soil of clearings, these also representing areas of high visibility (contrary to habitats of dense forest) that facilitate social interactions among individuals (Klaus, Klaus-Hugi & Schmid, 1998; Turkalo & Fay, 2001).

Conservation implications

In the two groups of clearings adjacent to Bai-Hokou (i.e. Dzanga and Mongambe, 20 km from the Bai-Hokou study area), another small group of buffalos was located in the same study period (10 individuals in Dzanga - A. Turkalo, pers. comm. - and possibly four individuals in Mongambe - park's guards, pers. comm.). Therefore, the actual estimate of the forest buffalo population in the

Dzanga sector of Dzanga-Ndoki National Park is 32 individuals at least (Melletti, 2005).

If the presence of the forest buffalo depends on grassy patches (i.e. clearings) in the forest, the clearing dynamics in tropical areas need to be taken into account for effective management plans of buffalos and other large African herbivores. Rainforest clearings show a tendency to be rapidly recolonized by shrubs and small trees, mainly in areas without elephants (Maisels et al., 2002). In fact, high densities of elephants can create and maintain clearings in the rainforest (Turkalo & Fay, 1995). As a consequence, in those areas in which forest buffalos and elephants share the same area, an antipoaching patrol represents a priority because it directly protects elephants and also allows clearings to be maintained (Turkalo & Fay, 1995; Maisels et al., 2002).

Moreover, and independently from the benefits for buffalos, several human activities can be supported by a policy of clearing management. In the rainforest region, clearings, equatorial savannah and swamps are the only natural open areas. The correct management of these habitats can favour the observation of some charismatic, forest-dwelling species (e.g. elephants and gorillas) in the dense rainforests, where visibility is very low (see Tutin et al., 1997 for more details). For example, ecotourism is already implemented in the Dzanga-Shanga National Park (Blom et al., 2004) and clearings represent important places for watching elusive species. Thus, the protection of clearings has the dual role of benefiting species such as the forest buffalo and allowing a controlled rise of ecotourism that, consequently, enhances the incomes of local people.

Acknowledgements

We thank the Director of the Dzanga-Sangha Project, M. Abel Alafei and his entire staff. Particular thanks for their precious help to A. Turkalo, C. Oertle, D. Renner, L. Steel, N. Orbell, L. Sarno, G. Schwarzer, U. Brown, A. Bruckman, J. Bruno of the M.I.K.E. (Monitoring the Illegal Killing of Elephants) project, as well as to the Dzanga-Shanga National Park guards and WWF staff in Bangui. Special thanks to J.-C. Thibaud for his help during the troubles of the coup d'etat in Bangui. Many thanks to the Bai-Hokou staff for their support during the different phases of the present work, in particular to F. Pani, Guy, Pulvanny, J.-B. Bopanzognako and Patrice. We would like to mention the indispensable work of the BaAka trackers that made this research possible; Any, Beakoko, Benzino, Bokaya, David, Doku, Elemo, Nyele, Mbanda, Messan, Mobambu, Mobongele, Mokedi, Mokoko, Molongo, Mongo, Mossimba, Ndiki, Ngombo, Poupe, Zendı, Zou extended precious help in fieldwork. A special thanks to A. Todd and F. Maisels for the advice during fieldwork. Additional thanks are also due to E. Tortellim, C. Maggio, L. Toma, G. Nganare, J. Dobanti, R. Isotti, E. Randi, S. Masi, A. Manciocco, V. Vericello, A. Ghiurghi, Carla, G. Graziani, N. Spagnoletti, F. Calo and G. Cragnotti. The

first draft was improved by the comments of two anonymous referees, and M. Mirabile was extremely patient all during the writing of the paper. We thank L. Molloy for her kindness and for the master's thesis on forest buffalo.

M. M. thanks his family for immense support during the stay in Africa. Finally, a special thanks to C. Cipolletta and D. Greer for helping M. M. throughout his stay in Bai-Hokou and making this work possible.

References

- Achard, F., Hugh, D.E., Hans-Jurgen, S., Mayaux, P., Gallego, J., Timothy, R. & Malingreau, J.P. (2002). Determination of deforestation rates of the world's humid tropical forests. Science 297, 999–1002.
- Blake, S. (2002). Forest buffalo prefer clearings to closedcanopy forest in the primary forest of northern Congo. Oryx 36, 81–86.
- Blancou, L. (1935). Buffles de L'Oubangui-Chari-Tschad. Terre Vie 5, 202–221.
- Blom, A. (2001). Ecological and economic impacts of gorilla based tourism in Dzanga-Sangha, Central African Republic.PhD thesis, Wageningen University, the Netherlands.
- Blom, A., Cipolletta, C., Brunsting, A.M.H. & Prins, H.H.T. (2004). Behavioral responses of gorillas to habituation in the Dzanga-Ndoki National Park, Central African Republic. Int. J. Primatol. 25, 179–196.
- Bonham, C.D. (1989). Measurements for terrestrial vegetation. New York: John Wiley & Sons.
- Boulvert, Y. (1986). Carte phytogéographique de la République Centrafricaine à 1:1 000 000. Editions de l'ORSTOM, Notice Explicative No. 104, Paris.
- Carroll, R.W. (1986a). Status of the lowland gorilla and other wildlife in the Dzanga-Sangha region of south western Central African Republic. Primate Conserv. 7, 38–41.
- Carroll, R.W. (1986b). The status, distribution and density of the lowland gorilla (Gorilla gorilla gorilla), forest elephant (Loxodonta africana cyclotis), and associated dense forest fauna in south western Central African Republic: research towards the establishment of a reserve for their protection. Unpublished report, Yale University, New Haven.
- Carroll, R.W. (1997). Feeding ecology of lowland gorillas (Gorilla gorilla gorilla) in Dzanga-Sangha Reserve of Central African Republic. PhD thesis, University of Yale.
- Chamberlan, C., Maurois, C. & Maerechal, C. (1995). Etude mammologique dans le Parc National d'Odzala. Programme ECOFAC, Composante, Congo.
- Dirzo, R. & Raven, P.H. (2003). Global state of biodiversity and loss. Annu. Rev. Environ. Res. 28, 137–167.
- Fay, J.M. (1989). Partial completion of a census of the lowland gorilla (Gorilla gorilla gorilla) in the Central African Republic. Mammalia 53, 203–215.
- Fay, J.M., Spinage, C.A., Chardonnet, B. & Green, A.A. (1990). Central African Republic. In Antelopes global

survey and action plans: 99–109. East, R. (Ed.). Gland: IUCN.

- Funston, P.J., Skinner, J.D. & Dott, H.M. (1994). Seasonal variation in movement patterns, home range and habitat selection of buffaloes in a semi-arid habitat. Afr. J. Ecol. 32, 100–114.
- Green, R.H. (1979). Sampling design and statistical methods for environmental biologists. New York: John Wiley & Sons.
- Hall, J., White, L.J.T., Inogwabini, B.I., Omari, I., Simons Morland, H., Williamson, E.A., Saltonstall, K., Walsh, P., Sikubwabo, C., Bonny, D., Kiswele, K.P., Vedder, A. & Freeman, K. (1998). Survey of Grauer's gorillas Gorilla gorilla graueri and chimpanzees Pan troglodytes schweinfurthi in the Kahuzi-Biega National Park lowland sector and adjacent forest in eastern Congo. Int. J. Primatol. 19, 207–235.
- Hall, L.S., Krausman, P.R. & Morrison, M.L. (1997). The habitat concept and a plea for standard terminology. Wildl. Soc. Bull. 25, 173–182.
- Haltenorth, T. & Diller, H. (1979). Elseviers Gids van de Afrikaanse Zoogdieren. Amsterdam: Elsevier.
- Hoppe-Dominik, B. (1992). Habitatnutzung von Waldbuffel, Syncerus caffer nanus, Bongo, Tragelaphus eurycerus, und Waldelefant, Loxodonta africana cyclotis, auf Forst-Fahrwegen im Regenwaldgebiet der Elfenbeinkuste. Saugetierkundliche Mitteinlungen 34, 31–41.

Kingdon, J. (1997). The Kingdon field guide of African mammals. London: Academic Press.

Klaus, G., Klaus-Hugi, C. & Schmid, B. (1998). Geophagy by large mammals at natural salt licks in the rainforest of Dzanga National Park, Central African Republic. J. Trop. Ecol. 14, 829–839.

Lunde, D. & Beresford, P. (1997). Noteworthy records of bats from Central African Republic. Bat Res. News 38, 19–20.

- Maisels, F. (1996). Synthesis of information concerning the Parc National d'Odzala, Republic of Congo. Projet ECOFAC Composante, Congo.
- Maisels, F., Inkamba-Nkulu, C., Boudjan, P. & Blake, S. (2002). Research and monitoring report. Nouabale-Ndoki project, Nouabale-Ndoki National Park, WCS, Congo.
- McNeilage, A., Plumptre, A., Brock-Doyle, A. & Vedder, A. (1998). Bwindi Impenetrable National Park, Uganda. Gorilla and large mammals census 1997. Working paper 14, WCS, New York.
- Melletti, M. (2005). Habitat preferences and characteristics of resting places of forest buffalo in Central Africa: conservation implications. Master's thesis, University of Rome "La Sapienza", Italy.
- Melton, D.A. (1987). Habitat selection and resource scarcity. S. Afr. J. Sci. 83, 646–651.
- Mloszewski, M.J. (1983). The behavior and ecology of the African buffalo. Cambridge: Cambridge University Press.

- Molloy, L.M. (1997). Forest buffalo, Syncerus caffer nanus, and burning of savannas at Lope Reserve, Gabon. Master's thesis, University of Florida, USA.
- Mugangu, T.E., Hunter, M.L. & Gilbert, J.R. (1995). Food, water and predation: a study of habitat selection by buffalo in Virunga National Park, Zaire. Mammalia 59, 349–362.
- Penteriani, V. & Faivre, B. (1997). Breeding density and nest site selection in a goshawk Accipiter gentilis population of Central Apennines (Abruzzo, Italy). Bird Study 44, 136–145.
- Penteriani, V., Faivre, B. & Frochot, B. (2001). An approach to identify factors and levels of nesting habitats selection: a cross scale analysis of goshawk preferences. Orn. Fenn. 78, 159–167.
- Pineaar, U. deV. (1969). Observations on developmental biology, growth and some aspects of the population ecology of African buffalo (Syncerus caffer Caffer Sparrman) in the Kruger National Park. Koedoe 12, 29–53.
- Prins, H.H.T. (1996). Ecology and behaviour of the African buffalo. Social inequality and decision making. London: Chapman & Hall.
- Prins, H.H.T. & Reitsma, J.M. (1989). Mammalian biomass in an African equatorial rain forest. J. Anim. Ecol. 58, 851–861.
- Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling R, M., Fishpool, L.D.C., Da Fonseca, G.A.B., Gaston, K.J., Hoffamann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, L.W., Watts, M.E.J. & Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. Nature 428, 640–643.
- Rondinini, C., Stuart, S. & Boitani, L. (2005). Habitat suitability models and the shortfall in conservation planning for African vertebrates. Conserv. Biol. 19, 1488–1497.
- SAS Institute (1996). SAS/STAT software: changes and enhancements through release 6.11. Cary, NC: SAS Institute.
- Sinclair, A.R.E. (1977). The African buffalo. Chicago: University of Chicago Press.
- Turkalo, A. & Fay, J.M. (1995). Studying elephants by direct observation: preliminary results from Dzanga clearing, Central African Republic. Pachyderm 20, 45–54.
- Turkalo, A. & Fay, J.M. (2001). Forest elephant behaviour and ecology. Observations from the Dzanga saline. In Conservation and ecology of African rain forest: 207–213.
 Weber, W., White, L., Vedder, A. & Naughton, L. (Eds). Ithaca: Yale University Press.
- Tutin, C.E.G., White, L.J.T. & Mackanga-Missandzou, A. (1997). The use by rain forest mammals of natural forest fragments in an equatorial African savanna. Conserv. Biol. 11, 1190–1203.
- Walsh, P.D. & White, L.J.T. (1999). What it will take to monitor forest elephant populations. Conserv. Biol. 13, 1194–1202.