Effects of habitat and season on the grouping of forest buffalo resting places

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Introduction

Forest buffalo (Syncerus caffer nanus Boddaert, 1785) is the only forest-dwelling subspecies of the African buffalo, of which the other two subspecies inhabit savannah lands (Blancou, 1935; Sinclair, 1977; Haltenorth & Diller, 1979; Mloszewski, 1983; Prins, 1996). Present knowledge on the ecology and behaviour of the forest buffalo is very limited, probably because of its shy nature and limited distribution. However, available information on this subspecies indicates that it is regularly associated with open habitats (e.g. clearings and equatorial savannah within the rainforest) where it obtains its main food resources (Prins & Reitsma, 1989; Chamberlan, Maurois & Maerechal, 1995; Maisels, 1996; Molloy, 1997; Blake, 2002; Melletti, 2005; Melletti, Penteriani & Boitani, 2007a,b).

In contrast to the savannah buffalo (Syncerus caffer caffer Sparrman, 1779), which can form herds of hundreds to thousands of individuals (e.g. Sinclair, 1977; Mloszewski, 1983; Prins, 1996), the forest buffalo lives in smaller groups (5–25 individuals), probably because of the patchy distribution of food resources in the rainforest (Haltenorth & Diller, 1979; Mitani & Rodman, 1979; Kingdon, 1997; Molloy, 1997; Melletti, 2005; Melletti et al., 2007a).

In other social ungulates, larger and more tightly packed groups are more common in open habitats than in closed habitats. One hypothesis to explain this that has received support from numerous studies suggests that larger and tighter groups confer greater protection against predators (e.g. Malbrant & Maclatchy, 1949; Sinclair, 1977; Lagory, 1985; Taylor, 1989; Gerard et al., 2002; Lingle, 2003). In this study, we examined whether a similar pattern is observed in a group of forest buffalo living in the Bai-Hokou study area of Dzanga-Ndoki National Park, Central African Republic, where open habitats are limited (1% of total area; Blom, 2001).

We investigated whether buffaloes at rest were packed more tightly in open habitat (forest clearings) than in closed habitat (forest) and if there were differences between seasons (dry versus wet). In particular, we analysed buffalo resting places because this allowed us to study the grouping behaviour in rainforest areas where the dense vegetation did not allow direct observation of the herd.

Study area

The study was conducted from January 2002 to January 2004 in the Bai-Hokou area (2°55′N, 16°20′E) of Dzanga-Ndoki National Park (Dzanga sector), Central African Republic (Fig. 1). A description of the study area has been explained in detail by Carroll (1986) and Blom (2001). Our study unit comprised one herd of buffaloes, which ranged in group size across the study period from sixteen to 24 individuals (Melletti et al., 2007b).

Classification of habitat types

We followed the vegetation categories proposed by Boulvert (1986), Carroll (1997) and Blom (2001). Four main habitat types were identified: (i) mixed forest (mixture of open and dense under storey); (ii) marantaceae forest (mixed forest with thick under storey dominated by species of the family Marantaceae); (iii) monodominant forest (mainly Gilbertiodendron dewevrei De Wild, 1952 with open under storey); and (iv) clearings (open areas with grassy vegetation of the families Cyperaceae and Poaceae).

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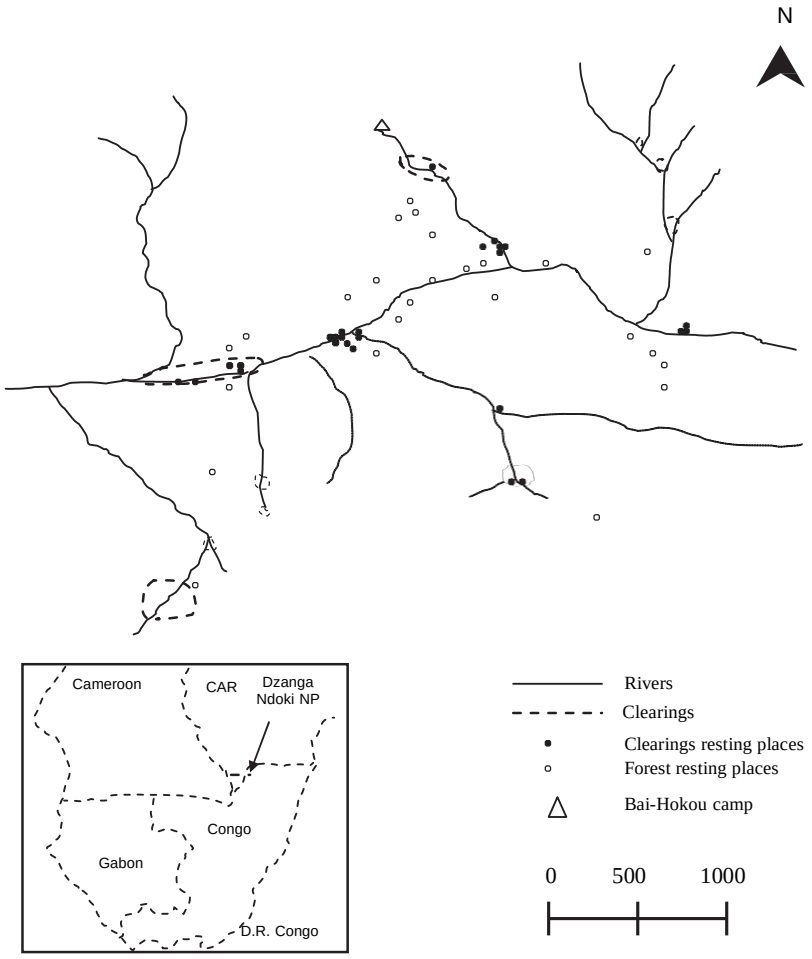

Fig 1 Location of the Bai-Hokou study area (Dzanga-Ndoki National Park, Central African Republic) and position of forest buffalo resting places in both clearings and forest patches

Methods

To investigate the effects of habitat (forest versus clearing) on grouping behaviour, we recorded for each resting place the group size (number of buffaloes at a specific resting site) and the nearest neighbour distance (measured as the distance between each bed centre and the nearest bed). We defined a bed as a clearly visible depression on the ground created by a resting buffalo. The resting places in the forest were located by following buffalo tracks with the help of a native guide. When we observed buffaloes at their resting places, we usually waited until the herd moved away before measuring the distances between beds.

Parametric or nonparametric tests were used, depending on the distribution of data. The Mann–Whitney test was used to test for differences in the distances between neighbouring beds in two separate analyses: (i) in the forest versus the clearings and (ii) in the wet versus the dry season (clearing data only).

The Kruskal–Wallis test was used to test for differences in the nearest neighbour distances among the three forest habitat types (i.e. mixed forest, marantaceae forest and monodominant forest). Student's t-test was used to compare: (i) the nearest neighbour distances (in both mixed and monodominant forest patches) between wet and dry seasons and (ii) the size of the buffalo group when in the clearing or within the forest as a whole (i.e. by combining three types of forest habitats). For all analyses, mean values are given ± 1 SD, tests were two-tailed and statistical significance was set at a £ 0.05.

Table 1 Values (mean, SD, min and max) for distances between forest buffalo beds in four habitat types in wet and in dry seasons

	Wet			Dry		
Habitat types	$\bar{x}$ ± SD	min	max	$\bar{x}$ ± SD	min	max
Mixed forest	3.43 ± 4.49	0	30	2.32 ± 2.81	0	20
Marantaceae forest	2.57 ± 2.33	0.5	8	–	–	–
Monodominant forest	2.82 ± 2.26	0	10	4.29 ± 3.99	0.5	15
Clearing	1.97 ± 4.76	0	54	2.84 ± 4.17	0	120

Dzanga-Ndoki National Park, Central African Republic. All distances are in metres.

Results and discussion

In the 51 resting places (N_{forest} = 25; $N_{clearing}$ = 26; Fig. 1) that we located in the study area, the nearest neighbour distances were shorter in the clearings than in the forest as a whole ($z = -7.17$, $P = 0.0001$, $n = 676$). Nearest neighbour distances also varied across the three forest habitat types ($v^2 = 15.44$, $df = 2$, $P = 0.0001$, $n = 343$; Table 1).

The nearest neighbour distances differed between seasons (wet versus dry) in the clearings ($z = -4.04$, $P = 0.0001$, $n = 332$), in the mixed forest ($t = 2.37$, $df = 237$, $P = 0.02$, $n = 239$) and in the monodominant forest patches ($t = -1.97$, $df = 81$, $P = 0.05$, $n = 83$). In general, buffaloes at rest grouped more tightly during the wet season in clearings and in the marantaceae forest (Table 1). Buffalo groups were more dispersed in the mixed forest in the wet season than in the dry season (Table 1).

Our results are difficult to interpret. Seasonal variation in food availability, particularly where limited in the rainforest, may play a role in producing seasonal variation in grouping behaviour.

Many studies have investigated the effects of habitat on animal grouping behaviour, particularly with respect to the variation in herd size because of conspecific attraction or anti-predatory strategy (e.g. Leuthold, 1970, 1975; Walther, 1972; Leuthold & Leuthold, 1975; Lagory, 1985; Turkalo & Fay, 2001; Gerard et al., 2002; Lingle, 2003). During our study, we did not observe predation on the forest buffalo. Leopard (Panthera pardus Linnaeus 1758) predation on buffalo is rarely observed in the rainforest; however, has demonstrated that it occurs often enough to make up over 10% of the biomass consumed (Henschel, Abernethy & White, 2005).

In this study, the relatively small differences recorded within the whole set of distances and the few buffalo predators (leopards and rarely hyenas) do not allow to interpret the recorded differences in such a way. We found no evidence to support the hypothesis that grouping behaviour in forest buffalo is the result of an anti-predator strategy. The nearest neighbour distances were similar across habitat types and seasons and few predators were observed. Another explanation for our results involves the prevalence of objects that may obstruct buffalo movement and selection of resting places. Whereas in the clearings there are no obstructing elements (e.g. trees, dense vegetation) limiting the availability of resting places, forested patches have numerous obstacles. This may also explain the differences in nearest neighbour distances recorded among the different forest types, each one corresponding to a different internal structure and consequently, a different degree of space limitation.

The different availability of unobstructed and free space in clearings versus forest as a whole could also explain why the number of resting buffaloes was higher in the clearings than in the forest (clearing: $\bar{x} = 13$; $SD = 4.2$; $n = 26$, forest: $\bar{x} = 10.8$; $SD = 6.6$; $n = 25$), although there was no significant difference in herd size among clearing and forest ($t = -1.42$; $df = 49$; $P = 0.16$; $n = 51$).

The higher buffalo abundance in the clearings than inside the forest may represent an additional support to the importance of habitat openness for this species in the dense rainforest, as reported in Melletti et al. (2007a,b).

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