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SOME BEHAVIORAL ASPECTS OF FOREST BUFFALO (*SYNCERUS CAFFER NANUS*): FROM HERD TO INDIVIDUAL

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The forest buffalo (*Syncerus caffer nanus*) typically inhabits the dense rain forests of western and central Africa. We recorded the 1st data on the behavior and social interactions of forest buffalo in natural forest clearings that represent crucial places in the rain forest for feeding and social interactions among individuals. Data were collected from a buffalo herd during January 2002–January 2004 in the Bai-Hokou study area (Dzanga-Ndoki National Park, Central African Republic). We analyzed typical behaviors (i.e., grazing, resting or ruminating, and moving) of both the herd and individuals (from 16 to 24 buffalos), as well as the most frequent social interactions. Spatial distribution among buffalos in the herd, related to both distance from forest edge and to the season (wet versus dry seasons), showed that the adult male was commonly closer to the females than to juveniles. Individuals were generally further away from each other when in the vicinity of the forest edge. Moreover, at greater distances from the forest edge, the number of buffalos in the herd increased. During the wet season, the herd was generally smaller and individuals were more spread out within the same clearing. The most common behavior of the male, females, and juveniles was resting or ruminating. Behavioral interactions by adults were mainly addressed to juveniles.

Key words: clearing, forest buffalo, herd size, rain forest, social behavior, *Syncerus caffer nanus*

The forest buffalo (*Syncerus caffer nanus*) is 1 of the 3 recognized subspecies of African buffalo (Blancou 1935; Haltenorth and Diller 1979; Sinclair 1977), the other subspecies being the Cape buffalo (*Syncerus caffer caffer*) and the western African buffalo (*Syncerus caffer brachyceros*). These 2 latter buffalos inhabit African savannahs, whereas the forest buffalo is a forest-dwelling subspecies, inhabiting the rain forest of western and central Africa (Haltenorth and Diller 1979; Kingdon 1997; Melletti et al. 2007; Prins 1996; Sinclair 1977).

The most studied subspecies is the Cape buffalo of eastern and southern African savannahs, for which detailed descriptions of behavior and social organization are available (Grimsdell and Field 1976; Mloszewski 1983; Prins 1996; Sinclair 1977). However, very little information is available on the forest buffalo (Blake 2002; Melletti 2005; Melletti et al. 2007; Molloy 1997), probably because of its very shy behavior, limited distribution, and difficulties in observing it in dense rain forests. Studies on forest buffalo are urgently needed because it lives prevalently in the central African rain forests, a habitat particularly sensitive to human-induced alterations. Today animal conservation on the African continent is scarce (Rondinini et al. 2005) and species extinction cannot be always detected (Sinclair et al. 2002). As a result, information on the behavior and habitat of the forest buffalo is important for its conservation. This work represents the 1st study on the behavior of forest buffalo in a habitat consisting only of rain forest and natural forest clearings.

The main goal of our study was to contribute to the knowledge of some behavioral aspects of forest buffalo. In particular, we analyzed behaviors of the herd; social interactions among members of the herd; and behavior of an individual male, as well as that of females and juveniles.

Materials and Methods

Study area.—Behavioral observations were conducted in the Bai-Hokou area (2°55′N, 16°20′E) in the Dzanga sector of the

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Dzanga-Ndoki National Park, Central African Republic, from January 2002 to January 2004 (see Melletti et al. [2007] for more information on the study area).

The forest habitat of the Dzanga-Ndoki National Park is included in the Guinean–Congolian Forest and is mainly composed of mixed forests and monodominant forests of *Gilbertiodendron dewevrei* with very open understory (Blom 2001). Small forest patches (gaps) in the canopy are created by natural tree-falls or elephant activity (Carroll 1986). The only other open areas in the park are forest clearings, generally larger than gaps, which can also be maintained by elephant activity (Maisels et al. 2002; Turkalo and Fay 1995). In Bai-Hokou there are about 19 rain-forest clearings with grassy and marshy vegetation dominated by *Cyperaceae* and *Poaceae*, ranging in size between 0.4 and 5.5 ha (Klaus et al. 1998).

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 at Bai-Hokou during the 2002–2004 wet and dry seasons was 1,464 and 137.5 mm, respectively. The mean temperature in the same period was 26°C, very similar to the 26.4°C reported by Carroll (1997).

Observations of herd behavior and social interactions.— Observations were conducted on the only buffalo herd in the study area, which, at the beginning of the field study, was composed of 16 individuals moving over an area of approximately 8 km^2. During the study, the herd grew to 24 individuals (8 new calves) sharing the same area. At the beginning, the herd was composed of 1 adult male, 9 adult females, 5 juveniles, and 1 calf (i.e., a buffalo that does not reach the inguinal fold of a cow—Pineaar 1969). At the end of the study the herd was composed of 1 adult male, 9 adult females, 6 juveniles, and 8 calves.

Forest buffalos spend most of the time in natural forest clearings, and sporadic nocturnal observations showed that this species also uses clearings at night. Moreover, although forest clearings represent only 1% of the habitats in the study area (Blom 2001), results of a study on habitat preference showed a strong association between forest buffalos and clearings (Melletti et al. 2007).

Direct observations on buffalos during daylight were exclusively done when the herd was within the forest clearings, the only open areas that allowed direct observations of behaviors. For this reason, it was impossible to collect data on activity patterns continuously from morning to evening, as was done in other studies on the savannah buffalo (Prins 1996; Sinclair 1977; Winterbach and Bothma 1998) or on the forest buffalo in a more open habitat consisting of a mix of rain forest and equatorial savannah (Lopé Reserve, Gabon—Molloy 1997). We distributed the observations equally between morning (0700–1200 h) and afternoon (1200–1700 h) throughout the study period. Data were not recorded every day. On average, we recorded data on 4 days per week and days in the field were distributed equally between wet and dry seasons. Because of the many constraints and dangers of nocturnal fieldwork in the rain forest, observations at night were very few and, consequently, were excluded from our analyses.

Because of the absence of roads, observations were conducted while on foot, by using binoculars (10×), a Nikon digital camera (zoom 10×; pictures were used for individual identification of buffalos; Nikon Corporation, Tokyo, Japan), and Bushnell telemeter (4×, range 600 m and accuracy ± 1 m; Bushnell, Overland Park, Kansas) to calculate the distances in meters between individuals and from the observer to buffalos. For the identification of sex and age categories, we followed the criteria of Pineaar (1969) and Prins (1996). Although the shape and size of head and horns of adult forest buffalos, as well as body size, are much more similar between sexes than in Cape buffalo, it was possible to distinguish the male from females. Ear marks and body scars also allowed the identification of individual buffalos, as done in similar studies (e.g., small antelopes and savannah buffalo—Arcese et al. 1995; Leuthold 1970; Prins 1996).

Observations of herd were conducted by scan sampling of the group every 15 min using binoculars. During each time slot, we identified all visible individuals, recorded the entire set of individual behaviors, and registered the location of the herd within clearings (distances from forest edge and watercourse) and interindividual distances (following similar procedures in Altmann [1974] and Fragazy et al. [1992]). We recorded 3 main types of behaviors of buffalos when in the herd: grazing, resting or ruminating, and moving.

We always approached buffalos very carefully, mainly paying attention to the direction of the wind. During the 2 years of the study, we scared buffalos in the clearing only a few times; this generally happened when the wind suddenly changed direction. When scared, buffalos ran for a short distance (i.e., they always remained within the same clearing), and after a short period they calmed down, going back to their normal activities. For these reasons, and for the goal of the study, we considered the impact of the observer on the quality of the behavioral observations to be negligible.

In most cases, we were able to observe the individuals involved in the social interactions during the whole duration of their behavior, starting when an interaction began and following the sampling sequence of Altmann (1974). This sampling involved interactions between just 2 individuals, and the duration of each interaction was measured with a stopwatch. We recorded 3 main categories of social interaction: sex and age of the 1st individual running away (i.e., the buffalo that led the herd) when danger is detected (e.g., when a predator approaches, or buffalos detect the scent of the observer), sex and age of the last individual running away when danger is detected, and sex and age of an individual driving off another buffalo (i.e., an individual sends another away from a resting place). Other social interactions, such as play, copulation, and lactation, were recorded only a few times and we excluded them from the analyses.

Interindividual distances and herd size at resting places.— When possible, an observer located on the forest edge measured his distance to lone individuals and to the herd with a telemeter. Alternatively, we recorded such distances with a telemeter by calculating the differences in meters between the observer positioned at the forest edge and the focal buffalos (or the herd). We used 3 classes for distance: 0–10 m, 11–30 m, and >30 m. To calculate distances between 2 individuals, we used triangulation. The observer positioned himself relative to each buffalo to form a right angle, then distances between the observer and the 2 buffalos were measured by telemeter. The distance between the 2 individuals was calculated as the 3rd side of the right triangle.

The number of individuals forming groups and interindividual distances also were calculated at buffalo resting places. These were places used by individuals resting together, and we defined ''beds'' as the depression on the ground left by resting or sleeping buffalos (Melletti et al. 2007). Distances between individuals in the resting places were determined by measuring distances between beds when buffalos left them.

Individual behavior.—When possible, following the methodology of Altmann (1974) and Fragazy et al. (1992), we continuously observed the behaviors of a focal individual during periods of 30 min with binoculars. After each 30-min observation period, a new focal animal was randomly selected (Fragazy et al. 1992). Behaviors recorded were the same as those for the herd, (grazing, resting or ruminating, moving, and social interactions).

Statistical analyses.—For all analyses, means ± 1 *SD* are given, tests were 2-tailed, and statistical significance was set at $\alpha \leq 0.05$. We used the SAS package (release 6.11—SAS Institute Inc. 1996). Before conducting parametric tests, variables were logarithmically, square-root, or arcsin-square-root transformed when necessary to achieve a normal distribution. When transformations did not produce a normal distribution, nonparametric tests were used. A chi-square test was used to evaluate differences in the frequencies between the 3 categories of behaviors (grazing, resting or ruminating, and moving), in the herd as well as between the adult male, females, and juveniles. Finally, we used generalized linear model (GLM) procedures to obtain a mathematical description of the predictors of the different variables recorded for the behavior of buffalos. Depending on whether the probability distribution of the response variables was normal, binomial, or Poisson, they were modeled using the identity, logit, and log-link functions, respectively. Each explanatory variable and their interactions were fitted to the observed data using the GENMOD procedure of the SAS package. The statistical significance of each variable in the model was tested, and those that contributed to the largest significant change in deviance were retained. The best model for each dependent variable was selected by likelihood ratio tests for type I analysis, which results in the most-parsimonious model for explaining variation in the response variable where only significant effects are retained. Variables were incorporated into the model only when they explained more than 5% of the deviance. Response and explanatory variables were grouped in 7 main blocks: grazing, resting or ruminating, moving, maximum distances between members of the herd, frequencies of different behaviors in relation to the distance to forest edge, minimum distances between individuals (male–females and male–juveniles) in relation to forest edge distance and season (wet versus dry), and numbers of individuals in relation to distance (m) to forest edge and season (wet versus dry).

TABLE 1.—General linear model values for the main behaviors, maximum distances between individuals, and frequencies of behaviors in relation to distance from the forest edge for the forest buffalo (*Syncerus caffer nanus*) in Dzanga-Ndoki National Park, Central African Republic, 2002–2004.

Parameters	Parameter estimate ± *SE*	χ^2	*P*	% deviance explained
Grazing				83.70
No. individuals	0.35 ± 0.04	77.03	0.0001	
Distance (m) to water[a]	−3.94 ± 0.54	60.08	0.0001	
Distance (m) to forest edge[b]	3.62 ± 1.06	11.78	0.0028	
Intercept	1.20 ± 0.70			
Resting or ruminating				63.43
No. individuals	0.64 ± 0.04	216.99	0.0001	
Wet versus dry seasons	−6.24 ± 1.31	22.41	0.0001	
Distance (m) to water[a]	2.18 ± 0.56	21.61	0.0001	
Maximum interindividual distance (m)[c]	−0.09 ± 0.01	63.79	0.0001	
Intercept	7.24 ± 1.62			
Moving				98.61
Maximum interindividual distance (m)[c]	0.01 ± 0.004	10.12	0.0015	
Intercept	0.20 ± 0.16			
Maximum distance (m) between individuals				98.04
No. individuals	0.51 ± 0.13	14.74	0.0001	
Intercept	18.84 ± 2.14			
Different behavior frequencies				99.08
Frequencies × forest edge[b]	−0.22 ± 0.08	9.39	0.0091	
Intercept	1.64 ± 0.02			

[a] Distance to the nearest watercourse.

[b] Distance to the nearest forest edge.

[c] Maximum distance between 2 individuals.

RESULTS

Observations of herd behavior and social interactions.—During the behavioral observations, the number of buffalos varied from a minimum of 1 to a maximum of 24 individuals. When in the herd ($n = 1{,}470$ observations), the greatest number of individuals were observed to rest or ruminate (8.2 ± 7.7 of the herd individuals) or graze (5.2 ± 6.8 individuals), whereas they generally moved very little (1.2 ± 4.1 individuals). Higher frequencies of resting or ruminating individuals were observed in the dry (12.1 ± 7.5 individuals) than in the wet (7.7 ± 7.6 individuals) season (63.4% of the original deviance explained by the GLM; Table 1) and differences between seasons were statistically significant. When moving, the individuals in the herd were generally in greater numbers and closer together than when resting or grazing (Table 1). Frequencies of grazing, resting or ruminating, and moving increased with the distance to forest edge, as shown by a GLM explaining 99.1% of the original deviance (Table 1).

The most frequent interaction between the members of the herd was the driving off of other individuals, mainly initiated by adult females and usually directed toward a juvenile. The duration of these interactions was very short (approximately 1–5 s).

TABLE 2.—General linear model values for minimum distance between forest buffalo male and females and male and juveniles and numbers of individuals in relation to distance to forest edge and wet versus dry seasons in Dzanga-Ndoki National Park, Central African Republic, 2002–2004.

Parameters	Parameter estimate ± *SE*	χ^2	*P*	% deviance explained
Minimum distance (m) male−females				69.52
Distance (m) to forest edge[a]	11.71 ± 2.82	18.91	0.0001	
Intercept	1.67 ± 1.56			
Minimum distance (m) male−juveniles				92.01
Wet versus dry seasons[b]	−15.64 ± 7.38	4.30	0.0380	
Intercept	19.92 ± 6.39			
No. individuals				80.21
Distance (m) to forest edge[a]	2.44 ± 1.15	7.38	0.0250	
Wet versus dry seasons[b]	−2.51 ± 1.24	3.96	0.0465	
Intercept	16.26 ± 1.15			

[a] Distance to the nearest forest edge.

[b] Wet season (March–November) and dry season (December–February).

Interindividual distances and herd size at resting places.—On average, the adult male was closer to females than juveniles ($\bar{X}_{\text{male–females}} = 2.9 \pm 7.6$ m, range = 0–35 m, *n* = 59 observations; $\bar{X}_{\text{male–juveniles}} = 7.3 \pm 22.9$ m, range = 0–120 m, *n* = 59 observations). The minimum distance between the male and females was larger when buffalos were closer to forest edge and, on average, the minimum distance between the male and juveniles was closer during the wet season than during the dry season ($\bar{X}_{\text{wet}} = 3.7 \pm 9.5$ m, range = 0–39 m; $\bar{X}_{\text{dry}} = 19.9 \pm 44.4$ m, range = 1–120 m). During resting or ruminating, all distances between the male and females were closer than all distances between the male and juveniles ($\bar{X}_{\text{male–females}} = 4.2 \pm 7.1$ m, range = 0–43 m, *n* = 120 observations; $\bar{X}_{\text{male–juveniles}} = 6.1 \pm 10.6$ m, range = 0–54 m, *n* = 115 observations). A GLM explaining 69.5% of the original deviance (Table 2) showed that forest edge was the main factor determining the minimum distance between the male and females. In contrast, the minimum distance between the male and juveniles differed most between the wet and dry seasons (Table 2).

On average, group size increased with distance to forest edge (0–10 m: $\bar{X} = 13.6 \pm 45.2$ individuals, range = 2–24 individuals; 11–30 m: $\bar{X} = 16.8 \pm 9.1$ individuals, range = 3–19 individuals; >30 m: $\bar{X} = 15.4 \pm 19.9$ individuals, range = 4–20 individuals). During the wet season, herd size was smaller than in the dry season ($\bar{X}_{\text{wet}} = 14.4 \pm 22.1$ individuals, range = 2–24 individuals; $\bar{X}_{\text{dry}} = 16.9 \pm 35.9$ individuals, range = 2–24 individuals). The number of individuals grouped in the herd was related to distance to forest edge and season (wet versus dry season). This model explained 80.2% of the original deviance (Table 2).

Time budgets for the different age and sex classes.—The 134 scans of the adult male in the herd showed significant differences in the frequencies of the different types of behaviors ($\chi^2 = 15.5$, $P = 0.0001$, $n = 134$), with resting or ruminating being the most common behavior that we observed (Fig. 1). A total of 170 scans were conducted on 4 adults females. Differences in the frequencies of the behaviors were significant ($\chi^2 = 57.9$, $P = 0.0001$, $n = 170$) and showed that resting or ruminating was, again, the most common behavior of forest buffalos (Fig. 1). The 115 scans on 4 juveniles showed, as for adult male and females, a significant difference in the frequencies of the different behaviors ($\chi^2 = 64.7$, $P = 0.0001$, $n = 115$), with resting or ruminating being the most frequent daily activity (Fig. 1).

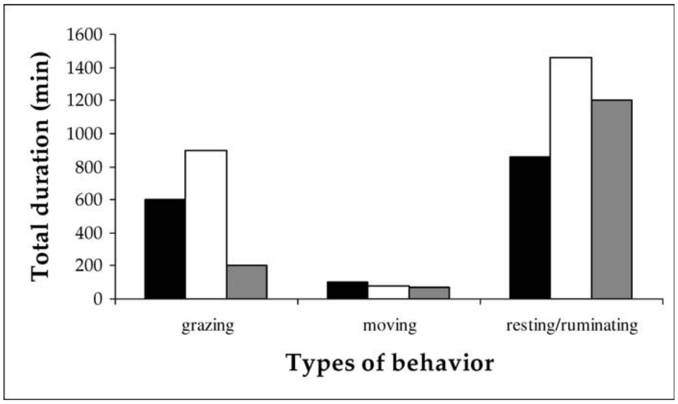

FIG. 1.—Main types of behaviors observed in forest buffalos (*Syncerus caffer nanus*) in the Bai-Hokou area, Dzanga-Ndoki National Park, Central African Republic, from January 2002 to January 2004. Black = adult male; white = adult females; gray = juveniles.

DISCUSSION

Resting and grazing, the main behavioral activities of forest buffalos, were mainly observed between water and forest edge, which might represent the best pastures within the forest clearings. The proportion of grazing individuals increased with increasing size of the group. Similar results have been observed for mountain goats (*Oreamnos americanus*—Risenhoover and Bailey 1985) and white-tailed deer (*Odocoileus virginianus*—Lagory 1985) and could be related to a decline in the time devoted to alert behavior in larger groups (generally, alertness behavior was performed by an adult female in the presence of a predator). In contrast to what was observed for savannah buffalos (Fuston 1992; Grimsdell and Field 1976; Prins 1996; Sinclair 1974; Taylor 1989), we did not record an increase in grazing during the dry season. In fact, we generally did not observe significant changes in the behavior of buffalos, except for resting, between wet and dry seasons, probably because these reflect much less seasonal variation in tropical rain forest than in savannah ecosystems.

When moving, individuals were closer to each other than when grazing, probably as an antipredator strategy. When the herd was moving and grazing, in most cases the adult male was behind the group, as also recorded for the savannah buffalo (Conybeare 1980). Moreover, when the herd escaped from danger (e.g., a predator) the last remaining individual was usually the adult male and the 1st one that led the group was always an adult female.

Although it was not possible to collect continuous information on the rhythms of activity, we generally observed a decrease in grazing rate followed by resting in the middle of the day when temperatures were highest, as shown in another study on forest buffalo in Gabon (Molloy 1997) and several studies of savannah buffalo (Grimsdell and Field 1976; Mloszewski 1983; Sinclair 1974; Stark 1986; Taylor 1989; Turner et al. 2005; Winterbach and Bothma 1998). In contrast, Beekman and Prins (1989) found a general pattern for grazing between 1000 and 1400 h in savannah buffalo. Recent studies on 34 ungulate species (Ruckstuhl and Neuhaus 2002) concluded that social affiliation was better explained by differences in activity budgets between sexes due to dimorphism in body mass than intrasexual competition for the best pastures. We did not record substantial differences in the amount of grazing behavior between the male and females we observed, as found by Turner et al. (2005) for savannah buffalo, perhaps because forest buffalo do not exhibit great differences in body mass between the sexes. Moreover, we did not observe differences in use of forest clearings between wet and dry seasons, as other studies (Macandza et al. 2004; Sinclair 1977) have found changes in use of landscapes during the dry season. Hence, competition in forest buffalos could be less pronounced than in savannah buffalos, probably because forest buffalos live in small herds with only 1 or 2 adult males (Kingdon 1997; Melletti et al. 2007; Molloy 1997), and the distribution of food resources in rain forests is patchy (Kingdon 1997; Melletti 2005).

Behavioral interactions of adults were mainly addressed to juveniles and most of the time they consisted of driving off (i.e., displacing juveniles). In a few cases, this behavior also was directed at other adults but, because of the small sample size of observations, these data were excluded from our analyses. Because these interactions were mainly concentrated in resting places, we hypothesize that individuals were competing for the best resting sites. Independently of the type of behavior, distances between individuals in forest clearings increased with the number of buffalos present. This result is partially in contrast with those of Prins (1996), who found greater distances between savannah buffalos in small herds than in large ones. However, the forest buffalo lives in smaller herds than the savannah buffalo, which could facilitate better interindividual tolerance and reduce competition for food.

The adult male was generally closer to females than to juveniles, particularly when resting. The number of individuals in the herd and minimum distance between the male and other buffalos were influenced by the distance to the forest edge and by the season. Because the forest represents crucial cover for buffalos (Melletti 2005; Melletti et al. 2007), both for resting and safety, individuals were generally further away from each other when close to forest edges. A similar trend was recorded by Lagory (1985) in white-tailed deer. In contrast, closer aggregation in clearings could be safer because of the major distances to the protection offered by the forest. Moreover, at greater distances to forest edges, the number of buffalos in the herd increased, probably due to an antipredator response; in this situation, in fact, every individual was surrounded by other buffalos. This should promote greater safety; similar behavior has been recorded in some African antelope and in white-tailed deer (Estes 1974; Jarman 1974; Lagory 1985), and follows from the hypothesis of Hamilton (1971) regarding selfish avoidance of predators by aggregation. In contrast, when visibility is low as in the forest, buffalos could reduce the probability of being detected by predators by being discreet and living in smaller herds. Similar observations also were reported by Estes (1974) and Jarman (1974) for other African ungulates and by Lagory (1985) for white-tailed deer. Leuthold (1970) and Leuthold and Leuthold (1975) reported similar results in another study on African ungulates where mean group size was higher in open than closed vegetation.

During the wet season, the herd was generally smaller and individuals were more dispersed within the same clearing; similar results were reported for the savannah buffalo (Conybeare 1980). However, Sinclair (1977) and Taylor (1989) found smaller herds of savannah buffalos in the dry compared to the wet season because of a change in food distribution. Herd size and grazing activity in forest buffalo does not seem to be much influenced by the seasonal distribution and availability of food as recorded by Sinclair (1977), Taylor (1989), and Turner et al. (2005) for savannah buffalos. However, herds remain small because food resources might be patchily distributed (Kingdon 1997; Melletti 2005).

Dynamics of the herd varied and frequently the herd split into 2 different subgroups. These merged again after 1 or 2 days to reform the original herd of 24 individuals. This pattern of fission and fusion also has been observed in savannah buffalos (Halley and Mari 2004; Monfort 1980; Prins 1996; Sinclair 1977; Stark 1986) and in white-tailed deer (Lagory 1985). The buffalo subherds always were composed of a minimum of 3 individuals with at least 1 female. Subgroups consisting of females with juveniles occurred, as found by Prins (1996) and Halley et al. (2002) in savannah buffalos. In contrast to Molloy (1997) in Lopé Reserve (Gabon), and by Kingdon (1997), lone males were never observed in our study area throughout our study; the few times that we observed lone individuals, they were always females or juveniles. The social structure of forest buffalos is constituted by 1 or 2 adult males within small herds of females and juveniles, which is different from the many bulls in the larger herds of savannah buffalos (Mloszewski 1983; Prins 1996; Sinclair 1977). This difference can result in a major vulnerability of forest buffalos. During our study we did not observe dead buffalos. However, the death of the only adult male could temporarily affect birth rates within the herd. Changes in herd size and composition during our study were all due to births. Neither immigration nor emigration was observed during this 2-year study.

Conclusions.—Forest buffalos are one of the least-known large mammals in Africa, and reside in an environment very vulnerable to human-induced alterations. Because little information is available on the behavior and habitat requirements of this species, our study provides new information and focuses on the behavior of forest buffalos both in closed rain forest and natural forest clearings. Examination of our data on habitat preferences (Melletti et al. 2007) and behavior confirms that forest clearings are crucial places for buffalos. The correct management of these habitats plays an important rule in conservation of large forest mammals.

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