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THE SPATIAL AND SOCIAL ORGANIZATION OF
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AT LOPE NATIONAL PARK, GABON

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THE SPATIAL AND SOCIAL ORGANIZATION OF FOREST BUFFALO (SYNCERUS CAFFER NANUS) AT LOPE NATIONAL PARK, GABON

By

LISA MARIE KORTE

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ABSTRACT

THE SPATIAL AND SOCIAL ORGANIZATION OF FOREST BUFFALO (SYNCERUS CAFFER NANUS) AT LOPE NATIONAL PARK, GABON

By

LISA MARIE KORTE

The Congo Basin forests of central Africa are home to one of the least-studied large mammals, the forest buffalo (*Syncerus caffer nanus*). Though several comprehensive studies have been completed on the familiar Cape buffalo (*Syncerus caffer caffer*), few data exist for forest buffalo. Data are needed for this forest-dwelling subspecies to aid conservation planning in the Congo Basin. This region became a global conservation priority in 1999, when six heads of state from the Central African nations signed the Yaoundé Declaration, promising to conserve 10% of their nations' forests as protected areas. In 2002, the president of Gabon fulfilled this promise when he created Gabon's first national parks. One of these new national parks is Lopé National Park, where I spent two years studying forest buffalo. The goal of my research was to provide basic information on habitat preference and social structure of forest buffalo.

I tracked nine radiocollared adult female forest buffalo between December 2002 and December 2004. Home ranges of these buffalo averaged 4.55 km^2 in area; the percent of home range overlap between individual radiocollared buffalo was small. Distance analysis of habitat use from radiotracking data was used to assess forest buffalo habitat selection at two spatial scales. At the landscape scale, buffalo selected savanna and marsh habitat over forest habitat within a 72-km^2 study area. Thus, forest buffalo home ranges were savanna-dominated despite the greater amount of forest habitat available at the park. At the scale of home range (2.30 km^2 to 7.64 km^2), habitat selection within home ranges varied with season. Adult female forest buffalo preferred forest habitat between March and August but preferred marsh to forest between September and February. Forest buffalo dwell in forest habitat, feed on savanna grasses, and wallow in marshes, utilizing all habitat types within the landscape. Although the subspecies is forest-dwelling, forest buffalo depend on open habitat adjacent to continuous forest.

Eighteen forest buffalo herds used the study area with an estimated population of 342 individuals (~ 5 buffalo/km^2). Mean group size for these 18 herds was 12 ± 2 (range of means = 3-24), considerably smaller than Cape buffalo herds. For eight radiocollared forest buffalo, mean group size was stable, varying little throughout the day, seasonally, or between savanna and marsh habitat. However, herd size varied widely across herds, from fewer than ten individuals in the smallest herds to more than 20 buffalo in the largest. Large herd size is associated with home ranges that contain substantial areas of open habitat, and thus more food resources than forested habitats.

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The Lopé research station, Station d'Etudes des Gorilles et Chimpanzés (SEGC), provided me with a place to live, field assistants, and vehicles, and

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INTRODUCTION

My dissertation examines the spatial and social organization of forest buffalo (*Syncerus caffer nanus*), a subspecies of African buffalo. This forest-dwelling subspecies of African buffalo differs markedly in geographic range, morphology, and behavior from the familiar Cape buffalo (*Syncerus caffer caffer*). The species range is throughout Sub-Saharan Africa. Forest buffalo occur in the Congo Basin forests of central Africa whereas Cape buffalo are on the savannas of eastern and southern Africa. Body size of forest buffalo (250-320 kg) is approximately half that of the 400-800 kg Cape buffalo (Haltenorth & Diller 1980). Horn shape and horn orientation of the two subspecies also differ. Forest buffalo have small, swept-back horns without the lateral extensions of Cape buffalo horns. Behaviorally, forest buffalo herds are smaller than Cape buffalo herds. Average herd size in Cape buffalo is 350 individuals, with the largest herds reaching into the thousands (Mloszewski 1983; Prins 1996; Sinclair 1977). Group size of forest buffalo has been estimated at 20 based on survey data in the colonial literature (Jarman 1974). Kingdon (1982) suggests that the suite of differences observed between these two subspecies of African buffalo reflects adaptations for living in savanna versus forest habitat. However, this has not been tested since our knowledge of forest buffalo is limited in part due to the logistical challenges of studying forest animals (Blake 2002).

The goal of my research was to provide basic information on habitat preferences and social structure of forest buffalo. Though several comprehensive studies on Cape buffalo have been completed throughout its range (Conybeare

1980; Funston et al. 1994; Halley & Mari 2004; Halley & Minagawa 2005; Halley et al. 2002; Hunter 1996; Mloszewski 1983; Prins 1996; Ryan et al. 2006; Sinclair 1977; Taolo 2003), comparable data for forest buffalo are lacking. Information on forest buffalo comes mostly from surveys of African forest mammals (Blake 2002; Prins & Reitsma 1989; Sidney 1965; Tutin et al. 1997; White 1994). However, one recent study successfully tracked a single herd of forest buffalo at Dzanga-Ndoki National Park in the Central African Republic (Melletti et al. 2007a). Like Cape buffalo, forest buffalo are grazers (i.e., they feed almost exclusively on grass) yet the geographic range of the forest buffalo is primarily forest, where grasses are limited to open areas along rivers or streams, and in forest clearings or small savanna patches within the forest landscape (Blake 2002; Melletti et al. 2007a). This presents interesting ecological questions about forest buffalo that can only be addressed by observational research that reveals their habitat use and social structure.

Another impetus for understanding forest buffalo ecology is to inform conservation initiatives in the Congo Basin. Despite the lack of information on forest buffalo behavior and ecology, this subspecies is highlighted as important for conservation planning in the Congo Basin forests (Blake 2002; Coppolillo et al. 2004; Melletti et al. 2007a; Melletti et al. 2007b). The creation of new national parks in the region was inspired by the recognition of the Congo Basin forests as a global conservation priority (Kamdem-Toham et al. 2003). In Gabon, Lopé National Park is one of the largest of thirteen national parks created in 2002 to protect the forest and unique wildlife of the region. At Lopé NP, buffalo are one of the most abundant large mammals of the forest-savanna mosaic in the northeast corner of the park (Tutin et al. 1997). Forest buffalo are clearly visible in the savanna habitat during the September through November wet season (Molloy 1997). This visibility could tie in with tourism to generate revenue for the Lopé NP if the population is managed effectively. However, few studies have focused on forest buffalo (Alers & Blom 1988; Molloy 1997) and park managers lack the basic information needed for managing forest buffalo. The success of the newly created national parks will depend on park staff acquiring the data needed to sustain wildlife populations and make sound management decisions.

Overview of chapters

In Chapter I, I investigate how forest buffalo use habitat. It seems unlikely that forest buffalo, a large grazing species, would have a geographical range that is heavily forested. Grass, the primary food source of buffalo, is widely scattered in small flushes in the forest landscape. Kingdon (1982) suggests that small clearings found within forests could support forest buffalo because the humid climate provides sufficient food resources for this large grazer throughout the year. Indeed, forest buffalo concentrate in forest clearings and along rivers and streams within the forest, and are rarely seen where clearings or water are absent (Blake 2002; Melletti et al. 2007a). In Chapter I, I examine habitat selection at two spatial scales for eight radio-collared forest buffalo at Lopé NP. First, I compare home range area composition to the overall landscape. Then, I compare locations of buffalo within their home range area to the habitat composition of the home range. I demonstrate that buffalo feed in open areas, wallow in marsh habitat, and increase use of forest habitat when food resources in open areas are low. Although the geographic range of forest buffalo is the forest habitat of central Africa, forest buffalo depend on open habitat adjacent to forest habitat for feeding and resting sites. The work presented in Chapter I has been accepted for publication in the Journal of Mammalogy.

The objectives of Chapter II were to document group size in forest buffalo at Lopé NP and examine the influence of season, habitat, and time of day on group size, factors that are known to influence group size in other ungulates (Borkowski & Furubayashi 1998; Brashares & Arcese 2002; Hirth 1977; Jarman 1974; Marchal et al. 1998). Mean herd size of Cape buffalo is 350 individuals with a range of 12 to more than 1,500 individuals (Prins 1996; Sinclair 1977). In Chapter II, I report group size of forest buffalo at Lopé NP. Eighteen forest buffalo herds used the study area with an estimated population of 342 individuals (~ 5 buffalo/km^2). Mean group size for the 18 herds was 12 ± 2 (range of means = 3-24), considerably smaller than Cape buffalo herds. For eight radiocollared forest buffalo, mean group size was stable, varying little with time of day, across seasons, or between savanna and marsh habitat. However, herd size varied widely across herds, from fewer than ten individuals in the smallest herds to more than 20 buffalo in the largest. Large herd size is associated with home ranges that contain substantial areas of open habitat, and thus more food resources than forested habitats. At Lopé NP, food resources probably have more influence on group size of forest buffalo than predation due to the low predation pressure on adult animals and enforced hunting restrictions.

In Chapter III, I report on inter-birth intervals and gestation period of forest buffalo. Since little is known about calving and inter-birth intervals in forest buffalo, these data are valuable despite the small sample size. Recent work by Ryan et al. (2007) on reproductive ecology in African buffalo describes a longer gestation period for Cape buffalo than would be expected given their body size. They suggest the protracted gestation period is an adaptation to the seasonal environment. Of the nine radiocollared adult female buffalo, gestation period could be determined for only one. The ten-month gestation period observed was slightly shorter than that reported for Cape buffalo (11.5 months; Sinclair 1977). I found an inter-birth calving interval of two years with 67% calf mortality. The high mortality rate combined with long inter-birth intervals may contribute to low reproductive rates, and should be noted by park managers. Calf survival seems to be influenced most strongly by the availability of food resources at Lopé NP, but further studies are needed. Chapter III is in press at the African Journal of Ecology.

In Chapter IV, I examine herd switching among nine radiocollared adult female forest buffalo. In Cape buffalo, adult females, subadults and juveniles live in mixed herds throughout the year, whereas adult male Cape buffalo move among mixed herds or form bachelor herds when not attached to a mixed herd (Mloszewski 1983; Prins 1996; Sinclair 1977; Turner et al. 2005). Adult female Cape buffalo were not known to switch herds. However, recent studies of Cape buffalo in Botswana and South Africa report evidence of herd-switching in adult female Cape buffalo (Cross et al. 2005; Halley et al. 2002). In Chapter IV, I report that only one of the nine radiocollared adult female buffalo at Lopé NP switched herds during the two-year study period. Also, forest buffalo had well-defined home ranges with small areas of overlap. Unlike Cape buffalo, there was little evidence of herd-switching among adult female forest buffalo, suggesting a more stable social structure in forest buffalo.

In Chapter V, I present a plan for integration of park management and capacity building for wildlife managers with long-term ecological research of forest buffalo. Conservation planning for species will be most successful when an understanding of an animal's ecology can be integrated into the management objectives of the parks and reserves in which it lives. In this final chapter, I examine the relationship between forest buffalo (*Syncerus caffer nanus*) and the objectives presented in the Lopé National Park Management Plan 2006-2011. Forest buffalo, one of the most abundant large mammals on the savannas of Lopé NP, have the potential to be a focus of research, management, and training activities. Because the results of these activities could increase revenue for the park and increase funding for conservation activities, I consider how a long-term conservation study of forest buffalo could benefit each park objectives. An institutional collaboration between the Lopé research station and the training center to promote this study could make a significant contribution to both park management and the training of scientists in Gabon. Study results from Lopé NP could be applied to protected areas throughout the Congo Basin Forest Region of central Africa.

Chapter I

Korte, L. 2008. Habitat selection at two spatial scales and diurnal activity patterns of adult female forest buffalo. Journal of Mammalogy 89.

Chapter I

HABITAT SELECTION AT TWO SPATIAL SCALES AND DIURNAL ACTIVITY PATTERNS OF ADULT FEMALE FOREST BUFFALO

Introduction

Ungulates are the focus of many studies of mammalian ecology and space use. Antelope are of particular interest due to their considerable variation in morphology, geographic range, and behavior among the species and the number of species (i.e., 143 species within Family Bovidae). Because wild populations are observable and captive populations are easily managed, the group is well-studied. Early studies highlighted important relationships between feeding style and habitat use by African antelopes (Gwynne & Bell 1968; Jarman 1974). Subsequently, advanced statistical techniques and a phylogeny of extant species have been used to verify the significant correlation between habitat use and feeding styles in ungulates (Pérez-Barbería et al. 2001). However, few studies have examined habitat use for single species that range across a variety of habitats (Brashares & Arcese 2002; Brashares et al. 2000; Jarman 1974). Data are lacking for analysis of habitat selection for those species that may provide the most insight on the relationship between feeding style and habitat use. Here, I investigate space use of the African buffalo (*Syncerus caffer*). This large-bodied grazer (Halley & Minagawa 2005; Hofman & Stewart 1972; Janis 1988; Jarman 1974) has both savanna and forest-dwelling populations (Haltenorth & Diller 1980; Kingdon 1997; Sinclair 1977).

Differences in morphology, geographic range, and behavior are evident among subspecies of *Syncerus*. The 2 most widely recognized subspecies are the savanna or Cape buffalo (*Syncerus caffer caffer*), and the forest buffalo (Syncerus caffer nanus; Grubb 1972; Wilson & Reeder 2005). The more familiar Cape buffalo are massive animals, weighing 250-800 kg, with downward curved horns (Haltenorth & Diller 1980; Sinclair 1977). At weights of 250-320 kg, forest buffalo are approximately one-half the size of Cape buffalo (Haltenorth & Diller 1980). Forest buffalo have small, swept back horns without the lateral extension characteristic of Cape buffalo.

Cape buffalo have been studied in most detail in the savannas of eastern and southern Africa where vast, open grasslands support herds averaging 350 animals, with large groups reaching into the thousands (Conybeare 1980; Funston et al. 1994; Halley & Mari 2004; Halley & Minagawa 2005; Halley et al. 2002; Hunter 1996; Mloszewski 1983; Prins 1996; Ryan et al. 2006; Sinclair 1977; Taolo 2003). In contrast, the geographic range of *S. c. nanus* is the Congo Forest Basin region of central Africa (Haltenorth & Diller 1980; Kingdon 1997; Sinclair 1977). Due to the forest habitat and their elusive lifestyle, few data exist for *S. c. nanus* (Blake 2002; Melletti et al. 2007a). Relative to Cape buffalo, much less is known about space use of forest buffalo.

Although some studies of forest buffalo have addressed space use, conclusions are limited due to short study periods and small sample sizes. At Lopé National Park, Gabon, Molloy (1997) found that forest buffalo fed on the flush of new grass on savannas, but data collection was limited to 1 6-month period and home range estimates relied solely on visual observations of only 3 groups. Though Abernethy (K. A. Abernethy, Station des Etudes des Gorilles et Chimpanzés, Gabon, in litt.) later tracked radiocollared forest buffalo over a 2-year period at Lopé NP, the sample size (i.e., 1 adult female and 1 adult male) was too small for analysis of habitat selection (Aebischer et al. 1993). At Dzanga-Ndoki National Park, Central African Republic (CAR), forest buffalo were highly dependent on forest clearings, but observations were of a single group (Melletti et al. 2007a). For analysis of habitat selection, home range data with larger sample sizes are needed.

Kingdon (1982) suggested that small open areas found within forests could support forest buffalo because the humid climate provides sufficient food resources for this large grazer throughout the year. For mammals, habitat productivity and body mass influence areas of home ranges (Harestad & Bunnel 1979; McNab 1963). Home range size increases with body mass (McNab 1963); however, smaller home ranges are found in more productive habitats (Fisher & Owens 2000; Harestad & Bunnel 1979). Although field surveys indicate that forest buffalo use open habitat within the forest landscape (Blake 2002; Prins & Reitsma 1989; Tutin et al. 1997; White 1994), data on space use within home ranges are needed to test if forest buffalo select open areas.

In this study, I used radiotelemetry to examine diurnal space use of adult female forest buffalo at Lopé National Park, Gabon. My objectives were to 1) estimate home range areas, 2) examine ranging patterns, 3) assess habitat use at 2 spatial scales, and 4) record diurnal activity of forest buffalo. I compare my findings for forest buffalo with observations of Cape buffalo and analyze how forest buffalo use habitat within the forest landscape.

Materials and Methods

Study area.—I observed buffalo in Lopé National Park, Gabon. This 5000-km^2 park is located in the center of Gabon just south of the equator (S 00° 12' 04; E 11°36' 05; Fig. 1.1). White (1983) classifies the park as lowland tropical rainforest. Average total annual rainfall is 1500 mm, unevenly distributed over 2 dry seasons (December-February and June-August) and 2 wet seasons (March-May and September-November). Temperatures fluctuate little throughout the year with maxima ranging from 27-31°C and minima from 20-22° C (White & Abernethy 1997).

The ungulate community at Lopé NP includes forest buffalo, forest elephant (*Loxodonta cyclotis*), sitatunga (*Tragelaphus spekii*), bushbuck (*Tragelaphus scriptus*), red river hog (*Potamochoerus porcus*), water chevrotain (*Hyemoschus aquaticus*), and 7 species of duikers (*Cephalophus*; Tutin et al. 1997). Leopards (*Panthera pardus*), the only large carnivore at Lopé NP, are a natural predator of the ungulate community. Forest buffalo were 1 of the main prey items found in leopard scat; however, based on analysis of bones in the scat, leopards apparently prey only on juvenile buffalo (Henschel et al. 2005). Hunting pressure by humans on the population of forest buffalo is low because the park headquarters is adjacent to the study area and because tourists and researchers use the area on a daily basis.

The research site included 3 habitat types: marsh, savanna, and forest. Digital maps of the northeast area of the park are available to researchers at the Lopé field station, Station d'Etudes des Gorilles et Chimpanzés (SEGC), in the form of ArcView 3.x (Environmental Systems Research Institute 1999) shape files, and include the locations of roads, rivers, marsh, savanna, and forest habitat types. For marsh habitat that had not been previously mapped, I measured the perimeter of marsh habitat, created shape files, and added the marsh shape files to the digital map collection at SEGC. Thus, maps including marsh, savanna, and forest habitat were available for analyses.

Observations of buffalo were restricted to the mosaic of savanna, marsh, and forest habitat in the northeast corner of the park. The majority of the park is forest habitat and large mammal surveys by White (1994) suggested there were few buffalo in the forest adjacent to the mosaic habitat. When present, large mammals are clearly visible in the savanna habitat. Sixty kilometers of road traverse this mosaic and are used by tourists and researchers. Park management staff annually burn the savannas, maintaining the open areas that would otherwise be colonized by forest (Peyrot et al. 2003). These open areas facilitate the viewing of large mammals on safari drives, and provide scenic vistas for tourists. Savanna areas are burned in small sections based on natural fire breaks and roads in the landscape. Small patches are burned as soon as the rains have stopped each year, when grasses are sufficiently dry to burn well. A few small areas are burned each week during the 2nd dry season through the end of September or beginning of October, depending on rain and burning conditions.

This patchy burning creates flushes of new grass, and the number of buffalo observed in the savanna areas is low in July but increases in August and remains high through December (based on observations between July and December 1996; Molloy 1997).

Observations of animals and data sampling.— The first 3 months of observation (September–December 2002) were used to identify groups of forest buffalo. Three fixed road circuits were established to monitor buffalo, so that individuals from different groups could be selected for radiocollaring. These circuits covered all open savanna areas visible from roads and each circuit was surveyed at least 4 times each month (twice during the morning, 0630-0930 h, and twice during the late afternoon, 1530-1830 h). Date, time, location, group size, and activity of individuals were recorded. Age class and sex were determined for the majority of individuals in each group. If there was a clear view and buffalo were within 50 m of the observer, a Sony digital video camera (model DCR-TRV140 NTSC) was used to record buffalo. Videos were reviewed to note additional unique characteristics that could be used to recognize individuals. Distinct pelage characteristics and horn morphology were used to differentiate individuals. Using easily recognizable buffalo as indicator animals, it was possible to distinguish groups.

Radiocollars were placed on 8 adult female buffalo (AF1-AF8) during the 1st week of December 2002. Four collars were manufactured by HABIT, Inc. (Victoria, British Columbia) and 4 by Telonics, Inc. (Mesa, AZ); receivers from both companies were used to track buffalo. Females were from 8 different groups, which represented about one-half of the groups using the study area. Ideally, Börger et al. (2006) recommend that telemetry studies strive to maximize the number of animals with radiocollars; however, I was limited by the number of collars. Therefore, I chose to sample animals within the same sex and age class (i.e., adult females) because core group members in Cape buffalo are adult females (Mloszewski 1983; Prins 1996; Sinclair 1977). Sampling additional sex and age classes during this study would have severely reduced sample size (Aebischer et al. 1993).

Two collars malfunctioned with 1 failure in July 2003 and a 2nd in October 2003. In early December 2003, the collar on AF3 that failed in October 2003 was replaced. A 2nd collar was placed on a new adult female (AF9) in the same group as the remaining buffalo (AF5) with the malfunctioning collar. The 2nd collar failed immediately resulting in 1 group with 2 collared buffalo (AF5 and AF9), but neither collar emitting a signal. Without the signal, it was not possible to locate animals when they were in forest habitat. Observations were therefore limited to visual observations of these 2 animals for the 2nd year of the study. Hence, data for adult females AF5 and AF9 were used only for the analysis of home range overlap and were excluded from the analyses of habitat selection and activity patterns. I therefore report results for 7 adult females over a 2-year period for the analyses of habitat selection and diurnal activity patterns.

During 3 study periods (December 2002 through April 2003, July through December 2003, and July through December 2004), radiocollared animals were located twice per week on different days. To ensure that animals were tracked throughout the day, daily observations were blocked into four 3-hour observations periods (i.e., 0630-0930, 0930-1230, 1230-1530, and 1530-1830). Each animal was tracked at least twice during each of 4 daily observation periods over the course of a month. However, observations were reduced to 1 location per week between 0900-1500 during May through June 2003 and January through June 2004. Opportunistic observations of radiocollared animals outside the search periods were also recorded. For each observation, date, time, location, group size, and activity state of individuals were recorded.

Activity data were collected during observations when radiocollared animals were visible. Focal animal surveys on radiocollared individuals lasted 20 min with an activity recorded every minute. A group scan was conducted if the collared animal was not alone; the activity of each animal in the group was recorded every 5 min for 20 min. Observations were only recorded during daylight hours. Visual observations were also limited to open savanna or marsh areas because observing animals in the forest resulted in animals either running from or toward the observer. In both cases, behavior was changed due to the observer.

All research was conducted under a permit from the Gabon Ministry of Water and Forests and under the direction of SEGC, the field station of the Centre Internationale de Recherche Médicales de Franceville (CIRMF). Work with live animals was carried out in a humane manner and in accordance with the guidelines of the American Society of Mammalogists (Gannon et al. 2007) and

Michigan State University. Veterinarians from the Wildlife Conservation Society's Field Veterinary Program handled the buffalo sedation for radiocollar placement.

Determination of home ranges.—I plotted the locations of radiocollared animals as points in an ArcView 3.x (Environmental Systems Research Institute 1999) shape file. Each collared animal had a point shape file, with date, time seen, time of first and last telemetry fix, activity, number of buffalo in group, notes, departure time, and type of observation (i.e., visual or fix) recorded into the attribute table.

I used the local nearest-neighbor convex-hull construction (LoCoH; Getz and Wilmers 2004) to estimate the area of the home range for each radiocollared buffalo, as well as Minimum Convex Polygons (MCP) for comparison with previous studies. Locations used for the estimations included visual observations of the animals and telemetry fixes and were statistically independent because observations were recorded during different time periods if recorded on the same day (an infrequent occurrence) or different days for the majority of observations. I used the animal movement analysis ArcView extension (Hooge & Eichenlaub 1997) to determine the MCP and to calculate its area. While the MCP method is an accepted standard for calculating ranges and is widely used because of its simplicity (Burgman & Fox 2003; White & Garrott 1990), it has been criticized because presence of outliers can dramatically overestimate the home range area (Burgman & Fox 2003). Thus, LoCoH has been advanced by Getz and Wilmers (2004) and was 1st used to estimate ranges for African buffalo in South Africa (Ryan et al. 2006).

I used the LoCoH (Local Convex Hull) Homerange Generate ArcView extension to estimate area of the home range for each radiocollared buffalo (see Getz and Wilmers 2004 and Ryan et al. 2006 for details). This extension uses the locations to create the convex hull with each location and its *k* nearest neighbors. Because the *k* parameter is user-selected, I ran this method for *k* values from 2 to 40 to identify the plateau that gives stable-area values across a range of *k* values that represent the estimated area of the home range. When several plateaus occurred, I chose *k* values that eliminated the unused areas within the range because the topology of the study area did not include lakes, mountains, or inhospitable habitats that may be avoided by buffalo. This selection process followed the "minimum spurious hole covering" rule (Getz & Wilmers 2004) and I report *k* values for estimated LoCoH home range areas. I used a Mann-Whitney-U test to compare the estimated areas of the 2 methods (LoCoH and MCP).

I also examined home range overlap between individuals and between years for each individual. To determine whether radiocollared buffalo maintained discrete home ranges, I calculated the percentage of home range overlap between radiocollared buffalo based on areas calculated using the LoCoH method. Home range overlap between years for individual radiocollared buffalo was examined with the Mann-Whitney-U test. This test also was used to test for differences in the area of home ranges between years.

Habitat measurements and landscape variables.—To measure available habitat in the overall landscape, a 72-km^2 study area was delineated based on the merged LoCoH home range areas of the radiocollared buffalo with a 1-km buffer. The habitat composition of the study area was 2.45% marsh, 43.20 % forest, and 54.35% savanna. Forest habitat within the study area included forest fragments, which have been described by Tutin et al. (1997): 1) gallery forest (narrow strips of forest along watercourses continuing at one end to join the main forest), 2) "corridor" (a narrow gallery linked at both ends to forest), and 3) bosquets (small forest blocks completely surrounded by savanna; Fig.1.2). Forest habitat in the study area also included continuous forest.

Habitat selection and distance analysis.—Several methods exist to compare resource use and availability (Thomas & Taylor 2006); I used Euclidean distances to assess nonrandom habitat use and to rank the habitat types (Conner & Plowman 2001). The distance analysis is robust to telemetry error and unlike compositional analysis can include zero-use areas without influencing Type I error (Bingham & Brennan 2004). Each radiocollared buffalo was treated as 1 sample.

I used the Nearest Features ArcView extension (v. 3.8a; Jenness 2004) to calculate distances between animal locations and the nearest representative of each habitat type; distances for each animal were averaged for the analysis. I examined both 2nd order selection of habitat within the landscape and 3rd order selection of habitat within the home range (Johnson 1980). For comparison at the landscape level, 2,500 random points were generated in the study area and distances between each habitat type and each random location were calculated and averaged to create an average distance for each habitat type. I calculated ratios for each animal by dividing the distance associated with buffalo locations by distances derived from random locations within the study area. I used a MANOVA to determine if the mean ratio vectors differed from a vector of 1, which indicates non-random use. To test for significant differences between individual ratios for each habitat type and the available habitat in the study area, univariate *t*-tests were used. Habitats were ranked using pair-wise habitat comparisons to construct a ranking matrix of *t*-statistics.

For analysis within the home range, locations of buffalo were paired with a random location within each home range and distances to each habitat for the random locations were calculated. For each season, the ratios for each animal were calculated by dividing the buffalo locations by distances derived from random locations within the home range. Then I used the distance analysis as described above to determine if use was significantly different from random locations and to rank habitats. All statistics for the distance analysis were performed in SAS (version 9.1; SAS Institute Inc. 2002) using code provided by Conner and Plowman (2001) with $\alpha=0.05$.

Diurnal activity pattern.—I used MANOVA in SAS (version 9.1; SAS Institute Inc. 2002) to examine diurnal activity patterns for the 7 adult female forest buffalo with functioning radiocollars, testing for overall effects of habitat, year, season, and time of day on activity (feeding, active, and inactive). I tested for significant differences attributable to habitat and time of day among the means for each of the 3 behavioral categories. I used analysis of variance (proc GLM in SAS) followed by LSD (least square difference) to test for significant differences in activity categories of buffalo between savanna and marsh habitat type and among time periods.

Results

Ranging patterns.—The MCP and LoCoH methods for calculating home range areas yielded similar results with no significant difference between the estimated home range areas for the 2 methods (MCP N=7, LoCoH N=7, U=29, P=0.31). However, because the MCP method is more likely to overestimate home range areas (e.g., for buffalo AF4 and AF6, Fig. 1.2), LoCoH area estimates are reported and used for analyses. Please note that Figure 1.2 in this dissertation is presented in color.

Radiocollared adult female forest buffalo maintained home ranges that were less than 8 km^2 and of the same size and in the same location from year to year. Mean home range area was 4.55±0.72 km^2, with individual areas ranging from 2.30 km^2 to 7.64 km^2 for the 7 collared buffalo included in the analysis (Table 1.1; Fig. 1.2). The total number of locations was not correlated with estimated home range area (r^2=0.23, P>0.05, N=7), indicating that increased sample size would not have resulted in larger home ranges. Individual home range areas were not significantly different between year 1 (December 2002–November 2003) and year 2 (December 2003–November 2004; Mann-Whitney U- test; year 1 N=7, year 2 N=7, U=26, P=0.45) with the percent of home range overlap between years ranging from 50% to 91% for the 7 individuals.

Overlap in home ranges between radiocollared buffalo.—The percent of home range overlap between individual radiocollared buffalo was small (Table 1.2). The 1 exception was 99% overlap between AF5 and AF9, which were members of the same group. Four buffalo (AF1, AF2, AF4, and AF7) had ranges that overlapped with AF6. She used a long and narrow range, running north and south in the center of the study area (Fig. 1.2). Thus, the perimeter of her range had the greatest opportunity to overlap with others, and the highest percentages of overlap (28%, 18%, and 17%) involved her home range. Excluding AF5, AF6, and AF9, the percent of home range overlap between any 2 individuals was ≤ 7%, including adjacent ranges where overlap was most often zero or < 1%. The number of locations in areas of overlap was small and there were few occasions when 2 radiocollared buffalo were present in the overlapping area at the same time. Overlap occurred primarily in savanna areas with almost no home range overlap in forest habitat, especially forest galleries.

Habitat selection based on distance analysis.—The average distance between the location of a buffalo and the nearest marsh, savanna, and forest habitat was 141.45 m, 24.49 m, and 66.32 m, respectively. In the study area, the average distance between randomly selected locations and the nearest marsh, savanna, and forest habitat was 390.98 m, 115.73 m, and 56.15 m, respectively. At the landscape level, the analysis of distance ratios indicated that locations of forest buffalo differed from random locations ($F=268.82$, *d.f.* = 3, 4, $P<0.0001$). Buffalo were found closer to marsh ($t=-13.31$, *d.f.* = 6, $P<0.0001$) and to savanna ($t=-27.09$, *d.f.* = 6, $P<0.0001$) than expected based on the relative availability of these habitats in the study area. There was no difference between locations of buffalo and random points with regard to distance to forest (*t*=0.87, *d.f.* = 6, *P*=0.4179). A ranking of habitats indicated that buffalo were found significantly closer to savanna than marsh habitat and significantly closer to marsh habitat than to forest habitat within the study area (Table 1.3).

The proportion of locations within each habitat type varied with season (Fig. 1.3); therefore, habitat selection within home ranges was examined by season. The analysis of distance ratios indicated that locations of buffalo differed from random locations for all seasons: Mar-May (*F*=68.49, *d.f.* = 3, 10, *P*<0.0001), Jun-Aug (*F*=5.89, *d.f.* = 3, 11, *P*=0.0120), Sep-Nov (*F*=7.96, *d.f.* = 3, 11, *P*=0.0042), and Dec-Feb (*F*=5.89, *d.f.* = 3, 11, *P*=0.0120). During Mar-May, buffalo were found closer to forest (*t*=-7.66, *d.f.* = 12, *P*<0.0001) than expected and associated less with savanna (*t*=4.13, *d.f.* = 12, *P*=0.0014) than expected; there was no difference between locations of buffalo and random points with regard to marsh (*t*=1.85, *d.f.* = 12, *P*=0.0890). Buffalo were found closer to marsh than expected during Sep-Nov (*t*=-4.53, *d.f.* = 13, *P*=0.0006) and Dec-Feb (*t*=-4.12, *d.f.* = 13, *P*=0.0012), but associated less with marsh habitat than expected during Jun-Aug (*t*=-4.12, *d.f.* = 13, *P*=0.0012). During June-February, there were no differences between locations of buffalo and random points with regard to distance to savanna (Jun-Aug *t*=0.92, *d.f.* = 13, *P*=0.3755; Sep-Nov *t*=-0.67, *d.f.* = 13, *P*=0.5168; Dec-Feb *t*=0.92, *d.f.* = 13, *P*=0.3755) or to forest (Jun-Aug *t*=1.93, *d.f.* = 13, *P*=0.0761; Sep-Nov *t*=1.90, *d.f.* = 13, *P*=0.0805; Dec-Feb *t*=1.93, *d.f.* = 13, *P*=0.0761).

Within home ranges, a ranking of habitats indicated that forest was proportionally used most during March through August when buffalo were found significantly closer to forest than marsh or savanna (Table 1.3). During September through February, buffalo were located significantly closer to marsh than forest whereas there was no significant difference between marsh and savanna or between forest and savanna.

Diurnal activity patterns and behavior.—Buffalo tended to use savannas for feeding and marsh areas for resting during daylight hours (Fig. 1.4). The mean proportion of time spent feeding varied with habitat (F=29.55, *d.f.* = 1, 441, P<0.0001) and time of day (F=5.57, *d.f.* = 3, 441, P=0.0009); buffalo most often fed on savannas in the early morning. During daylight hours, buffalo spent more than 30% of their time feeding. Active behavior also varied with habitat (F=9.03, *d.f.* = 1, 441, P=0.0028) and time of day (F=4.48, *d.f.* = 3, 441, P=0.0041). Buffalo were most active in savanna habitat and in the late morning (0930-1230). Buffalo spent less than 15% of daylight hours in active behaviors. As would be expected, periods of inactivity also varied with habitat (F=46.30, *d.f.* = 1, 441, P<0.0001) and time of day (F=9.99, *d.f.* = 3, 441, P<0.0001). Inactive behaviors were most often observed in marshes in the late afternoon. During daylight hours, buffalo spent more than 38% of their time inactive.

Proportions of time spent in different behaviors did not differ between years (F=0.85, *d.f.* = 6, 874, Λ=0.99, P=0.5309) or among seasons (F=0.34, *d.f.* = 9, 1061.3, Λ=0.99, P=0.9604). However, behavior varied significantly among individuals (F=2.02, *d.f.* = 18, 1225.2, Λ=0.92, P=0.0070). This variation could be attributed to 1 individual (AF8) that spent a larger proportion of daylight hours feeding (56%) than inactive (38%). The other 6 buffalo spent a larger proportion of daylight hours inactive (54%) than feeding (37%). When AF8 was removed from the model, there was no overall effect of individuals.

While it was not possible to visually monitor animals when they were tracked to forest areas, it was possible to monitor the signal emitted from the collar. Over the first 18 months of the study, animals were monitored for 20 minutes after pinpointing their location in a forest area. During this time, it was possible to determine if animals remained stationary or moved away. Based on 303 observations, buffalo remained in place during the 20-min observation period and were most likely resting in 1 location. Buffalo were relatively inactive during daylight hours between March and August, when more than 60% of their locations were in forest habitat (Fig. 1.3).

Discussion

Home range size.—Home range size for adult female forest buffalo at Lopé NP (2.30-7.64 km^2) was considerably smaller than home range sizes for Cape buffalo, which have been reported at 10.50 to 296.3 km^2 in eastern Africa (Prins 1996; Sinclair 1977), and over 1000 km^2 in southern Africa (Hunter 1996). Small home range size relative to that of Cape buffalo was expected based on the much smaller body size of forest buffalo and the higher productivity of their habitat, 2 factors that can influence home range size (Harestad & Bunnel 1979; McNab 1963).

Larger home ranges typically occur in less productive habitats (Harestad & Bunnel 1979). While habitat productivity is usually expressed in terms of mean annual net primary productivity or NPP (Murphy 1975), a more available measure, annual rainfall, was used here, following Harestad and Bunnell (1979) and Fisher and Owens (2000). Based on available NPP data, regions with high annual rainfall typically have higher NPP (Murphy 1975 1977). In eastern Africa, mean home range size of Cape buffalo is < 200 km^2 (mean annual rainfall > 600 mm; Prins 1996; Sinclair 1977); however, home range size notably increases to > 1000 km^2 (a 5-fold increase) in the arid region along the border of Botswana and Zimbabwe (mean annual rainfall ~ 500 mm; Hunter 1996). Where NPP data are available, tropical forest has a higher NPP than savanna (Murphy 1977; 1975) indicating the potential for patches of grass in a forest opening to provide buffalo a constant food source.

The forest buffalo at Lopé NP, an area with high annual mean rainfall (1500 mm), inhabit a much more productive area than do most Cape buffalo (Conybeare 1980; Hunter 1996; Prins 1996; Sinclair 1977). In addition, the annual burning of savanna at Lopé NP creates open grass areas that provide food for buffalo. Home range size of forest buffalo in my study was similar to that of 2 radiocollared forest buffalo examined in a pilot study at Lopé between December 1998 and June 2000; in that case, home range size for a solitary adult male was 4.94 km^2 (N=82 locations) and 3.70 km^2 for an adult female (N=88 locations; K.A. Abernethy, in litt.). Despite the small size of these areas, the humid climate provides sufficient food resources for this large grazer throughout the year. Thus, home range sizes observed in Lopé NP support Kingdon's (1982) hypothesis that small open areas found within rain forest could support forest buffalo, and follow the predicted relationship of home range size to body size and habitat productivity.

Ranging patterns.—My data demonstrate that groups of forest buffalo at Lopé NP occupy separate home ranges. Adjacent home ranges showed very little overlap (typically < 1%) and radiocollared buffalo from different groups were rarely present in the overlapping area at the same time. Large areas of overlap were in savanna areas, but buffalo tended to use forest galleries within their home ranges separately. One individual (AF6) that overlapped considerably in space with 4 other radiocollared buffalo spent little time in the areas of home range overlap and moved to the southern portion of her home range via forest galleries. In contrast, the percent of overlap between the other 4 pairs with adjacent home ranges was small. Despite distinct home ranges and occasional encounters, territorial defense was not observed among forest buffalo at Lopé NP. Similar discrete home ranges with little evidence of territorial defense have been described for Cape buffalo (Prins 1996; Sinclair 1977). The finding of exclusive forest buffalo home ranges at Lopé is consistent with the hypothesis that a single group of forest buffalo occupies a forest clearing (Blake 2002).

Patterns of home range use by radiocollared buffalo suggest that forest buffalo are more sedentary than Cape buffalo, for which seasonal movement has been observed (Funston et al. 1994; Halley & Mari 2004; Halley et al. 2002; Ryan et al. 2006; Taolo 2003). Adult female forest buffalo were consistently and reliably located in the same areas throughout the 2-year study period whereas Cape buffalo can migrate 10-40 km between seasons in Botswana (Halley et al. 2002). Cape buffalo return to the same dry-season home ranges (Halley and Mari 2004) indicating site fidelity, which I also observed for forest buffalo. The home range of 1 forest buffalo (AF1) in my study included 96% of the home range of a single radiocollared adult female buffalo tracked at Lopé between 1998 and 2000 (K.A. Abernethy, in litt.). This same area also was used by a group that I studied in 1996 (Molloy 1997), suggesting that occupation of an area by groups of buffalo probably extends over longer periods than the 2-year timespan of my study. Home ranges of forest buffalo in Lopé NP appeared remarkably stable in both time and space.

Habitat selection at the landscape level.—My data suggest that forest buffalo select proportionally more open habitat (marsh and savanna) and use continuous forest less than would be expected based on available habitat at the landscape level (Fig. 1.2, Table 1.3). Surveys of large mammals in forests (Blake 2002; Prins & Reitsma 1989; White 1994) have found that forest buffalo are absent or present at low densities in continuous forest, which similarly suggests that buffalo avoid continuous forest. For example, in the continuous forest area adjacent to my study area, mammal surveys over 2 14-month periods covering 2 annual cycles reported few observations of forest buffalo and low estimates of biomass (White 1994). During March and April, 2 graduate students repeated 1 of the White (1994) transects and found that dung of forest buffalo was absent from the continuous forest (Bankert & Schenk 2003). Low estimates of biomass or few signs of forest buffalo in continuous forest have been reported from other forest sites in Gabon and the Republic of Congo (Blake 2002; Prins & Reitsma 1989). My landscape-level results and work on forest buffalo in C.A.R. (Melletti et al. 2007a) suggest that forest buffalo select open habitat for their home ranges, where their main food source, grass, is plentiful, rather than continuous forest.

Habitat selection within home ranges.—Forest buffalo had stable, savanna-dominated home ranges, but habitat use within home ranges varied with season (Fig. 1.3), and for at least a portion of the year buffalo preferred forest habitat during daylight hours (Table 1.3). Between March and August >60% of locations of forest buffalo were in forest habitats; however, forest habitat represented <50% of the area of home ranges of forest buffalo (Table 1.1). Continual 12-hour monitoring during daylight hours of 3 of the radiocollared forest buffalo confirmed high use of forest between February and May (Bankert & Schenk 2003). In addition, buffalo dung was commonly found in forest fragments in April and May 2003; significantly less dung was present in savanna, marsh, and continuous forest during these months (Bankert & Schenk 2003). Tourists visiting the park between March and August sometimes leave with an impression that the park has no buffalo because buffalo primarily use forest habitat during the daylight hours.

Forest fragments, galleries, and corridors are used by forest buffalo more often than continuous forest and most individuals based their home ranges in a single forest fragment or gallery (i.e., 10-33% of the locations for AF1, AF2, AF3, AF4 and AF6). Adjacent home ranges of radiocollared buffalo had minimal overlap in savanna areas and no, or smaller areas of overlap, in forest fragments or galleries. In addition, buffalo remained close to the savanna areas and did not penetrate deep into the forest. Even animals with home ranges on the edge of the continuous forest remained near the forest edge. This is consistent with the low biomass of buffalo reported for continuous forest (White 1994) and the high biomass of buffalo found in forest fragments at Lopé (Tutin et al. 1997).

The March-through-August period of high forest use includes wet and dry periods with similar temperature ranges, which suggests that forest buffalo use forest habitat for reasons unrelated to rainfall or temperature alone. Small streams run throughout the landscape at Lopé NP, which eliminates the need for migration of forest buffalo during the dry season based on limited water resources. Similarly, Cape buffalo in the Serengeti show little movement within home ranges, remain near watercourses, and maintain smaller home ranges than those of sympatric migrating ungulates during the dry season (Sinclair 1977). In areas dominated by forest or bush, Cape buffalo feed exclusively on grasses and forbs and stable isotope analysis has confirmed that they are not consuming the leaves of trees or bushes (Halley & Minagawa 2005). Buffalo at Lopé NP moved into the savannas to feed on the flush of new grass when the savannas were burned at the end of the June-through-August dry season and were highly visible on the savanna areas between September and February. Although they dwell in forest habitat, forest buffalo depend on open habitat for food.

Marshes also were an important open habitat between September and February. Home ranges of forest buffalo were 4% marsh and 19% of locations of buffalo were in marsh habitat, despite the small percentage of marsh habitat in the study area (only 2.45% marsh). The mud wallows within marsh habitat contributed to the preference for marsh habitat, especially between September and February. After early morning feeding bouts in the savanna areas, buffalo at Lopé NP often retire to a wallow and rest in the marsh until sunset. Groups tended to frequent 1 or 2 wallows within their range and it appeared that repeated use of the same wallow enhanced water and mud conditions. On the Ishasha Plateau of Virunga National Park, Democratic Republic of Congo, African buffalo use wallows for thermoregulation and drinking (Mugangu et al. 1995) and, among temperate bovids, bison (*Bison bison*) wallow to gain relief from biting insects (McMillan et al. 2000).

Because my analyses were limited to data from diurnal observations of adult female buffalo, some differences may be observed for male buffalo and/or nocturnal observations. Males may differ in home range size based on observations of Cape buffalo, where adult males wander more widely (Halley & Mari 2004; Prins 1996). However, the 4.94-km^2 home range area estimated for the solitary adult male monitored in a pilot study (K.A. Abernethy, in litt.) fell within the range of areas for radiocollared adult females reported in my study. In addition, adult females with radiocollars were in groups that included an adult male, which was regularly with the group (Chapter II). For the majority of visual observations, the adult male was with the group, and I had no observations of the identified males from these groups in locations outside the home range areas of the groups. For a definitive result, it would be necessary to track adult males.

Nocturnal locations of radiocollared forest buffalo would most likely not significantly change the location of the home ranges or estimated home range area. Given the stability of the ranges over the 2 years of the study, it seems unlikely that animals would leave their ranges only at night, resulting in a location or size change. But, nocturnal observations may influence activity patterns and habitat selection within home ranges. For the majority of Cape buffalo, grazing is done during the nighttime hours (Prins 1996; Sinclair 1977; Taolo 2003), which suggests that the early morning peak of feeding observed at Lopé NP may be a continuation of nocturnal feeding. If forest buffalo at Lopé NP spend more time feeding at night, then use of savanna habitat would increase whereas use of forest and marsh would decrease. Therefore, nocturnal observations may change conclusions about habitat preferences within home ranges, especially if forest buffalo are using the savanna areas at night during the peak of diurnal use of forest, i.e., March through August. Regardless of how the overall patterns of habitat use may change with nocturnal data for activity patterns, the diurnal observations of adult female buffalo demonstrate that habitat preference changes with season based on food availability.

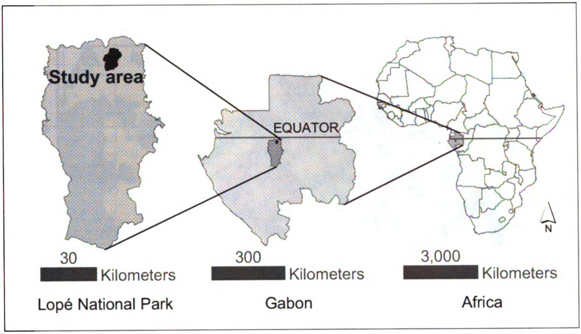
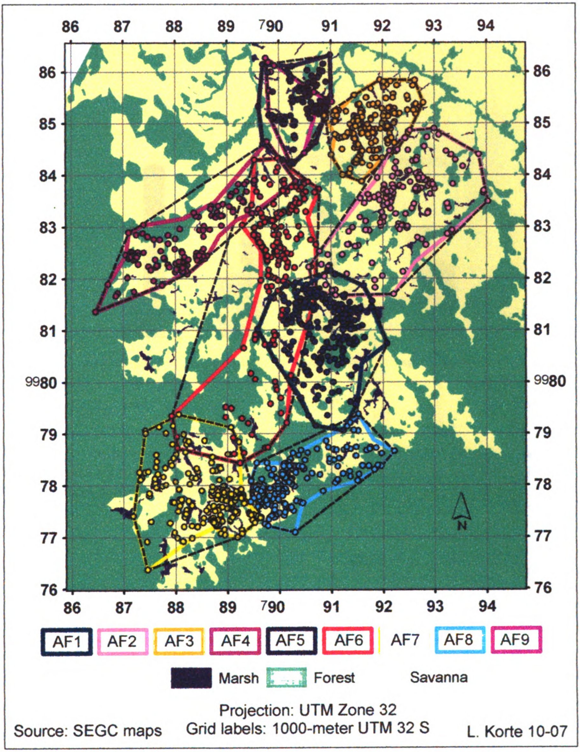


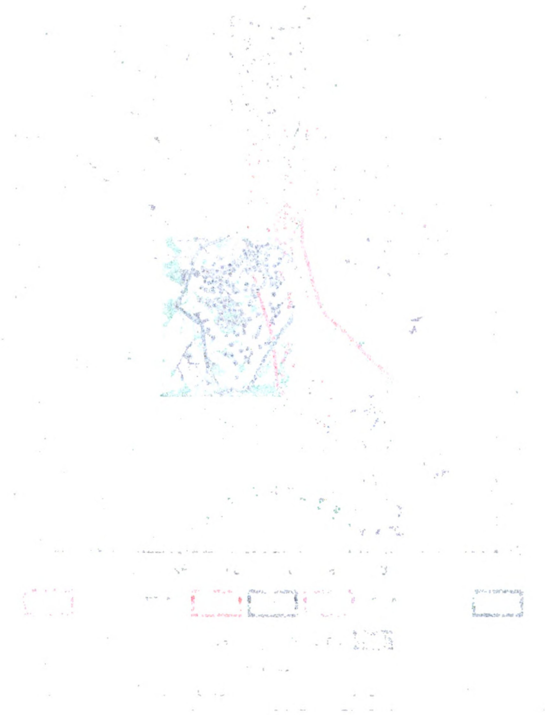
Figure 1.1. Geographic location of study area in Lopé National Park, Gabon



Projection: UTM Zone 32

Source: SEGC maps Grid labels: 1000-meter UTM 32 S L. Korte 10-07

Figure 1.2. Locations (points), 100% MCP (black polygons), and LoCoH (color polygons) home range estimates for 9 adult female forest buffalo (AF1-AF9; *Syncerus caffer nanus*) with radiocollars at Lopé National Park, Gabon, December 2002 - December 2004.



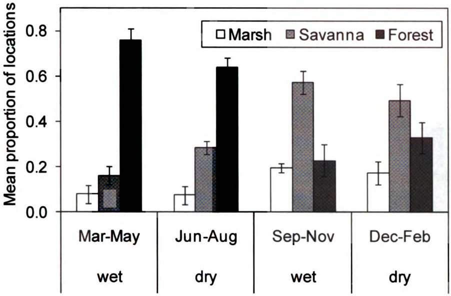
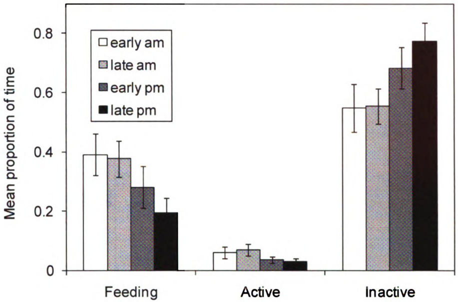


Figure 1.3. Mean proportion of locations (± SE) during daylight hours in each habitat by season for 7 radiocollared adult female forest buffalo at Lopé National Park, Gabon, December 2002-December 2004.

A) Marsh



B) Savanna

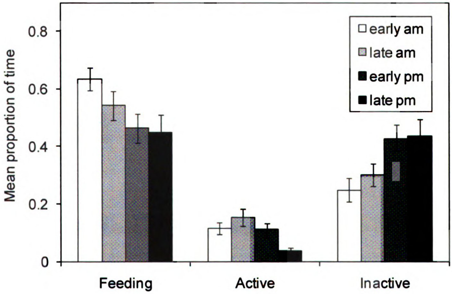


Figure 1.4. Mean proportion of time (± SE) spent in each activity category by habitat type (A) Marsh and (B) Savanna, and time of day for 7 radiocollared adult female forest buffalo at Lopé National Park, Gabon, December 2002-December 2004.

Table 1.1. Home range estimates based on 100% MCP (minimum convex polygon) and LoCoH (local area nearest-neighbor convex-hull) methods for nine radio-collared adult female (AF) forest buffalo (*Syncerus caffer nanus*) at Lopé National Park, Gabon, during December 2002-December 2004, including number of locations, *k*, and habitat composition of home ranges (ranked by home range size in ascending order).

Age class, sex class, ID	Number of locations	Area (km^2) 100 % MCP	Area (km^2) LoCoH	*k*	% area for each habitat types based on LoCoH area estimates		
					Marsh	*Savanna*	*Forest*
AF9[a]	72	1.38	1.25	15	8	88	4
AF5[a]	145	2.26	2.19	20	5	82	13
AF3	215	2.41	2.30	19	3	81	16
AF8	219	3.46	2.77	21	3	49	48
AF4	192	4.49	3.49	34	3	67	30
AF1	252	4.99	4.71	28	8	72	20
AF7	215	5.23	4.72	25	8	50	42
AF2	161	6.50	6.19	21	3	72	25
AF6	185	10.56	7.64	31	3	61	36
Mean (SE)	205 (11)	5.38 (0.99)	4.55 (0.72)		4 (1)	65 (5)	31 (4)
Range	161-252	2.41-10.56	2.30-7.64		3-8	49-81	16-48

[a] AF5 & AF9 analysis limited to overlap of home ranges.

Table 1.2. Range overlap between individual adult female (AF) forest buffalo based on LoCoH home range area estimates. Values are the percentage of the range of a buffalo (row) shared with another buffalo (column).

	AF1	*AF2*	*AF3*	*AF4*	*AF5*	*AF6*	*AF7*	*AF8*	*AF9*
AF1	---	7	0	0	0	26	0	<1	0
AF2	5	---	<1	0	0	<1	0	0	0
AF3	0	1	---	0	0	0	0	0	0
AF4	0	0	0	---	<1	16	0	0	0
AF5	0	0	0	<1	---	0	0	0	56
AF6	16	<1	0	7	0	---	10	0	0
AF7	0	0	0	0	0	17	---	0	0
AF8	<1	0	0	0	0	0	0	---	0
AF9	0	0	0	0	99	0	0	0	---

Table 1.3. The ranks and pair-wise habitat comparisons based on (a) mean distance of a forest buffalo from habitat A/mean random distance to habitat A within the study area, (b) mean distance of a forest buffalo from habitat A/mean random distance to habitat A within the animal's LoCoH home range area by season.

Level of analysis	*Rank*[a]	*Pair-wise comparisons*[b]		
			marsh	savanna
a) Habitat selection within study area	savanna>>>marsh>>>forest	savanna	t=2.72 (P=0.0347)	—
		forest	t=-4.10 (P=0.0063)	t=-4.84 (P=0.0029)
b) Seasonal habitat selection within estimated home ranges (LoCoH)				
Mar – May	forest>>>marsh>>>savanna	savanna	t=-3.85 (P=0.0023)	—
wet season		forest	t=4.67 (P=0.0005)	t=5.33 (P=0.0002)
Jun – Aug	forest>>>marsh>>>savanna	savanna	t=-3.74 (P=0.0025)	—
dry season		forest	t=3.95 (P=0.0017)	t=4.09 (P=0.0013)
Sep – Nov	marsh=savanna	savanna	t=-0.96 (P=0.3542)	—
wet season	marsh>>>forest savanna=forest	forest	t=-3.09 (P=0.0085)	t=-1.58 (P=0.1389)
Dec – Feb	marsh=savanna	savanna	t=-2.10 (P=0.0554)	—
dry season	marsh>>>forest savanna=forest	forest	t=-3.38 (P=0.0049)	t=-0.33 (P=0.7437)

[a] Note:>>> denotes a significant difference between variables.

[b] The *t*-statistic testing the null hypothesis that (mean distance of a forest buffalo from habitat A/mean random distance to habitat A)–(mean distance of a forest buffalo from habitat B/mean random distance to habitat B)=0

Chapter II

VARIATION OF GROUP SIZE AMONG AFRICAN BUFFALO HERDS IN A FOREST-SAVANNA MOSAIC LANDSCAPE

Introduction

Comparative studies of group size in African antelope have contributed much to our understanding of social organization (Jarman, 1974; Brashares, Garland & Arcese, 2000; Shultz & Dunbar, 2006). However, considerable variation in group size occurs in some species, potentially confounding the interpretation of interspecies comparisons (Brashares et al. 2000; Jarman 1974). Fortunately, this intraspecific variation is, in itself, valuable for elucidating the factors that influence group size and structure. Indeed, because populations of a species have a shared evolutionary history, the influence of various ecological factors (e.g. resource distribution, predation pressure, and habitat structure) on group size can be examined without the confounding influence of phylogenetic effects (Brashares & Arcese 2002).

African buffalo (*Syncerus caffer*) are an example of a species that occurs in habitats ranging from closed forest to open savanna habitat. Cape buffalo (*Syncerus caffer caffer*) and forest buffalo (*Syncerus caffer nanus)* are the two most widely recognized of the five *Syncerus* subspecies (Wilson & Reeder 2005). Cape buffalo, weighing 400 to 800 kg, are larger than forest buffalo, occur throughout the savanna areas of eastern and southern Africa (Haltenorth & Diller 1980; Sinclair 1977), and have a mean group size of 350 (range 12 to more than 1,500; Prins 1996; Sinclair 1977). Cape buffalo have been the focus of several comprehensive studies (Mloszewski 1983; Prins 1996; Sinclair 1977); only a few studies have been done on forest buffalo and the results of those studies are limited by small sample sizes (Abernethy 1998, 1999, 2000; Melletti et al. 2007a; Melletti et al. 2007b) and short study periods (≤ 6 months; Molloy, 1997; Alers and Blom, 1988). The smaller, forest-dwelling *S. caffer nanus* (250-320 kg) is found in the forests of central Africa (Haltenorth & Diller 1980; Sinclair 1977).

Few data are available for group size of forest buffalo. Comparative studies of African antelope use an estimated group size of 20 for forest buffalo (Brashares et al. 2000; Jarman 1974; Shultz & Dunbar 2006), though forest buffalo also are reported to occur in groups of eight to ten buffalo (Mloszewski 1983; Sidney 1965). These estimates are based on single observations from the colonial literature, but one recent study has tracked group size of a forest buffalo herd during a two-year period. This herd at Dzanga-Ndoki National Park in the Central African Republic increased from 16 to 24 due to eight births with neither immigration nor emigration (Melletti et al. 2007b). In the Dzanga-Ndoki herd, smaller group size was observed during the wet season and the herd frequently split into two subgroups.

Season, habitat, and time of day are factors known to influence group size in ungulates (Borkowski & Furubayashi 1998; Brashares & Arcese 2002; Hirth 1977; Jarman 1974; Marchal et al. 1998). Seasonal variation in group size has been observed in Japanese sika deer (*Cervus nippon*) with largest group size during seasons when food resources were optimal (Borkowski & Furubayashi 1998). Group size in sika deer increased during the morning and evening periods, but the authors suggest that these are large feeding aggregations rather than groups with close links (Borkowski & Furubayashi 1998). Similar aggregations are formed in the European roe deer (*Capreolus capreolus*) when deer feed in large open fields during the morning and evening periods (Marchal et al. 1998). In fallow deer (*Dama dama*), the largest groups are formed in open habitat (Apollonio et al. 1998). Hirth (1977) reported an inverse relationship between group size and vegetation cover for white-tailed deer (*Odocoileus virginianus*).

African buffalo are large grazers, feeding primarily on grass (Halley & Minagawa 2005; Hofman & Stewart 1972; Janis 1988). On a continental scale, group size of African buffalo is small in forests relative to savannas (Jarman 1974; Sinclair 1977). This probably reflects the distinct differences in quantity and dispersion of food between these habitats (Jarman 1974). If the quantity and dispersion of food influence group size, then group size should vary with habitat type and across seasons at a local level as well.

Here, I inquired whether season, habitat, or time of day influence group size of forest buffalo at Lopé National Park, Gabon. My study area was a forest-savanna mosaic where the amount and condition of grass varies with habitat and season (White & Abernethy 1997). Habitat types are distinct in regard to food resources for buffalo at Lopé NP, where forest habitat lacks grass for these large grazers and grass is abundant in open habitat. The quantity of food increases during wet seasons, when the savannas have a flush of new grass. I tested three hypotheses, specifically asking whether group size is larger (1) during wet seasons, (2) in savanna habitat, or (3) during early mornings. Group size was expected to increase during wet seasons because of the flush of new grass. If large groups were feeding aggregations, large group size was expected during early morning periods when buffalo are feeding in savanna habitats (Chapter I). I also investigated the relationship between group size and three home range variables (1) total area, (2) area of open habitat, and (3) percent of the total area that was open habitat. Herds with the largest home range areas and greatest amount of open habitat within their home range were expected to have large group size.

Materials and Methods

Study area.—Lopé National Park is primarily forest habitat, but the northeast corner of the park (0° 10′ S, 11° 35′ E) is a mosaic of savanna, marsh, and forest fragments, including gallery forest along streams (Tutin et al. 1997; Fig. 1.1). The 72 km^2 study area included open (2.45% marsh and 54.35% savanna) and closed (43.20% forest) habitat. Mean annual rainfall in the study area is 1500 mm, and rainfall varies seasonally. March-May and September-November are the two seasons with the highest rainfall; December-February is relatively dry, but the driest period is June-August. Temperatures fluctuate little throughout the year, with monthly maxima ranging from 26-32° C and minima from 20-22° C (White & Abernethy 1997).

Sources of group size data: radiocollared buffalo.—In December 2002, radio collars were placed on eight buffalo (AF1-AF8), representing eight different herds. Collars were placed on adult females to maximize sample size within one age and sex class. I selected adult females because adult females form the core of Cape buffalo herds (Mloszewski 1983; Prins 1996; Sinclair 1977) and preliminary study suggested that social structure of forest buffalo was similar to that of Cape buffalo (Molloy 1997). Each buffalo was in a group of >3 at the time of immobilization and collaring. Due to the failure of the collar on AF5, a ninth collar was placed in December 2003. This ninth female (AF9) was in the same group as AF5. HABIT, Inc. (Victoria, British Columbia) manufactured five of the collars and Telonics, Inc. (Mesa, AZ) manufactured the other four collars; I used receivers from both companies to track buffalo.

During three periods of the study (December 2002 through April 2003, July through December 2003, and July through December 2004), radiocollared buffalo were located twice weekly. To ensure that radiocollared buffalo were tracked throughout the day, daily observations were blocked into four 3-hour observation periods (i.e., 0630-0930, 0930-1230, 1230-1530, and 1530-1830). Over the course of a month, each radiocollared buffalo was tracked at least twice during each of these four daily observation periods (i.e., a minimum of 8 observations per month). Observations were reduced to one location per week between 900-1500 during May and June 2003, and January through June 2004 (i.e., a minimum of 4 observations per month).

Group size (i.e., number of individuals including the radiocollared buffalo), date, time, and location, were recorded for each sighting (i.e., observation) of a radiocollared buffalo. Buffalo that were within meters of each other and were coordinated in their activity at the time of observation were considered a single group (Leuthold 1976). A count of all buffalo per sighting was feasible in savanna and marsh habitat, where buffalo were clearly visible. It was not always possible to see each buffalo well enough for identification to sex and age class, but when possible age class and sex were determined. For example, when buffalo where lying in a wallow, it was possible to count buffalo, but not necessarily sex and age all individuals, especially juveniles and calves. Age classes reported for Cape buffalo were used to estimate age class of forest buffalo (i.e., calves:<12 months, juveniles: between 12 and 24 months, subadults: 2-5 years, and adults: >5 years; Pienaar 1969; Sinclair 1977). Visual observations were limited to savanna and marsh habitat because observing buffalo in the forest resulted in animals either running away from or toward the observer, which made it impossible to obtain an accurate count.

Research was conducted under permit from the Gabon Ministry of Water and Forests, and under the direction of Station d'Etudes des Gorilles et Chimpanzés (SEGC), the field station of the Centre International de Recherches Médicales de Franceville (CIRMF). Veterinarians from the Wildlife Conservation Society's Field Veterinary Program handled the buffalo sedation for radio collar placement. Radio collars were left on buffalo for future research.

Statistical analysis: radiocollared buffalo.—Analyses were performed using SAS statistical software (SAS Institute Inc. 2002), and where appropriate, mean values ± S.E. are reported. Group size data based on sightings of radiocollared forest buffalo were analyzed for the effect of individual, season, habitat, and time of day using a mixed linear model (PROC MIXED). Because individual had a significant effect on group size, the mixed linear model was also used for group size data of each radiocollared buffalo to analyze the effect of season, habitat, and time of day on group size. For seasons, the least-squared means (using LSMEANS within PROC MIXED) were computed and compared to test for significant differences in mean group size between seasons and among years (e.g. Jun-Aug 2003 compared with Sep-Nov 2003, Jun-Aug 2003 compared with Jun-Aug 2004). For pairs of seasons with a significant difference, I used a paired Student's t-test ($\propto$= 0.05) to compare the mean number of radiocollared buffalo for which I observed significant differences in group size between seasons to the mean for those with no change in group size between seasons.

Sources of group size data: circuit surveys.—Three fixed road circuits of 23 km, 22 km, and 18 km in length were established to record group size of buffalo herds without a radiocollared buffalo. Circuits covered savanna and marsh habitat visible from roads, and each circuit was surveyed at least four times every month (twice during the morning, 0630-0930, and twice during the late afternoon, 1530-1830) from September 2002 to May 2003, July to December 2003, and July to December 2004.

Group size was defined as the number of individual buffalo counted per sighting. Buffalo within approximately 200 meters of one another were treated as one sighting or observation (i.e., as members of the same group). Sightings of buffalo were usually separated by more than 1 km; thus buffalo in different groups were rarely in visual contact with each other. The number of sightings per circuit ranged from 0-14 (mean=3). For each sighting, group size, date, and location were recorded. When feasible, sex and age class were recorded for each buffalo as well. Distinct characteristics of individual buffalo (e.g. pelage and horn morphology) made it possible to distinguish among different social groups or herds. Buffalo that were repeatedly observed in a single sighting were identified as members of the same herd.

Results (mean, maximum, and minimum size of group) from the two observation methods, (1) telemetry, and (2) circuit surveys for sightings of radiocollared buffalo were compared using Mann-Whitney-U tests.

Home range characteristics based on radiocollared buffalo.—Digital maps of the northeast area of the park are available to researchers at SEGC in the form of ArcView 3.x shape files (Environmental Systems Research Institute 1999), and include the location of roads, rivers, marsh, savanna, and forest habitat types. I plotted locations of radiocollared buffalo as points in an ArcView shape file and used these points with the Local Convex Hull (LoCoH) Homerange Generate ArcView extension to estimate home range area for each radiocollared buffalo (Getz & Wilmers 2004; Ryan et al. 2006). I also measured the amount of each habitat type within each home range area.

Group size variation among radiocollared buffalo was examined in relation to three home range variables: (1) total home range area, (2) area of open habitat in the home range, and (3) percent of the total area that was open habitat in the home range. I used a Pearson's correlation coefficient ($\propto = 0.05$) to test whether mean group size for radiocollared buffalo was significantly correlated with each of the three home range variables. Data from two radiocollared buffalo

(AF5 and AF9) were excluded from the home range analysis because their collars failed within six months, and without signals from collars, it was not possible to track these buffalo to forest locations. The relationships between maximum group size and each of the three home range variables were also examined.

Results

Does group size vary?—For radiocollared buffalo, mean group size for all observations was 14±3 (1-46). Mean group size was stable with little variation in group size between marsh and savanna habitats or throughout the day, but there was evidence of some variation across seasons. When data from circuit survey, telemetry, and opportunistic observations of radiocollared buffalo were combined, significant effects on group size of radiocollared buffalo ($F_{[8,874]}$=99.75; P<0.0001), time of day ($F_{[3,874]}$=2.62; P=0.0515), and season ($F_{[7,874]}$=16.25; P<0.0001) were observed in the mixed linear model. Only the effect of habitat (marsh or savanna) was not significant ($F_{[1,874]}$=0.04; P=0.8445). In addition to the overall model, analysis was completed for each radiocollared buffalo because of the significant differences in group size among the radiocollared buffalo (Table 2.1). No significant effect of habitat type on group size was observed for the radiocollared buffalo; mean group size was 15 for both marsh (15±0.48) and savanna habitat (15±0.33). Also, no significant effect of time of day on group size was observed for eight of the nine radiocollared buffalo.

Season had a significant effect on group size for five of the nine radiocollared buffalo (Table 2.1). Differences between pairs of seasons were consistent among radiocollared buffalo with a tendency for larger group size during wet seasons than during dry seasons. But, group size was larger during dry than wet seasons in a few cases. For pairs of seasons showing a significant difference in group size, the mean number of radiocollared buffalo exhibiting no change in group size (i.e. stable; mean=5.44) was significantly greater than the mean number of buffalo exhibiting a seasonal change in group size (mean=2.56; t_{17}=-5.88, P=<0.0001).

Variation of group size among herds.—Eighteen herds used the study area with an estimated population of 342 individuals, ~ 5 buffalo/km^2 (Fig. 2.1). The estimated total population is based on the sum of maximum group size for the 18 herds. All herd members were not together at all times, and observations of subgroups were common. For herds of fewer than 10 individuals, all buffalo were known; for larger herds (i.e., >10 animals), the adult males and the majority of adult females were known. Individuals were repeatedly observed with the same herds based on these known individuals. For example, all members of Herd G were identified and individuals in this herd were only observed with other buffalo from Herd G. Though buffalo were often observed in subgroups, herd size was stable. For example, group size for AF8 (Herd G) was consistently small, and never exceeded 12 during 144 observations (Fig. 2.2). In contrast, AF2 was consistently observed in a large group (mean=27±1; range 6-46; Herd Q). She was observed with fewer than 10 buffalo during only eight of 78 observations, and the majority of sightings (65%) included >20 buffalo.

Home range characteristics.—Because group size did not differ between marsh and savanna habitat, these two habitat types were combined (i.e. open habitat) for analysis of home range areas. Both mean and maximum group size were significantly positively related to home range area and to the amount of open habitat in the home range of radiocollared buffalo (Table 2.2; Figure 2.3). Percent of open habitat in the home range was not significantly related to mean or maximum group size (Table 2.2).

Method of data collection.—Since radiocollared buffalo were observed during circuit surveys, it was possible to use results from the radiocollared buffalo to compare telemetry observations with circuit survey observations. Minimum group size was significantly lower for observations made using telemetry than for groups assessed solely on the basis of circuit surveys, whereas mean group size and maximum group size for telemetry and circuit surveys did not differ significantly (Table 2.3).

Group composition.—The majority of forest buffalo sightings were of >2 individuals (Figure 2.4). Observations of > 2 buffalo usually consisted of several adult females with their young and one or two adult males that regularly associated with their respective herds. In 96 circuit survey observations of >2 buffalo, all individuals were identified to sex and age class. For the 85 sightings with juveniles and calves, the overall ratio of adults and subadults to juveniles and calves was 1:2, suggesting that offspring of more than one generation remain with the females. The ratio of adult males to adult females was 1:6. Solitary buffalo were more often males (80%) than females (20%; N=102). Of the nine radiocollared females, five were never observed alone and the other four collared animals collectively were viewed alone on only nine occasions (AF4 n=4; AF5 n=2; AF6 n=2; AF8 n=1).

Discussion

Among forest buffalo observations the variation of group size was large (range 1-46). However, within herds, group size was stable with little variation across seasons, between savanna and marsh habitat, and time of day. The number of observations of buffalo increased when the savannas were flush with new grass, but herd size remained stable. It was also expected that group size would be larger during morning feeding activity when buffalo use savanna areas (Chapter I). However, large group size was observed during the morning for only one of the eight radiocollared buffalo. Also, group size did not differ between marsh and savanna habitat. Feeding aggregations occurred within herds, but not among herds.

Herds varied in number of buffalo, with small herds consistently small in size (i.e. fewer than 10 buffalo) and other herds consistently large with more than 20 buffalo. Forest buffalo group size could be predicted based on previous observations of the herd, unlike several ungulate species where groupings are often unstable (Barrette 1991; Clutton-Brock et al. 1982; Estes 1991; Hillman 1987; Leuthold 1970). Herd mates from a single forest buffalo herd were occasionally separated in different subgroups, but individuals returned to the herd. Melletti et al. (2007b) observed a similar pattern at Dzanga-Ndkoi NP where a herd of 24 forest buffalo was often split into two subgroups.

Telemetry observations had less bias than circuit survey sightings because circuit surveys relied on visual observations of buffalo and tended to miss the smallest groups. Although method of data collection influences group size in forest buffalo, radio collars allowed groups of <3 individuals to be detected, while circuit surveys were useful for monitoring groups that did not contain a radiocollared buffalo.

Herd size and food resources.—Analysis of home range areas indicated a positive relationship between both maximum group size and mean group size of forest buffalo with home range area and the amount of open habitat in the home range area. Further study to determine group size and area of forest clearings used by buffalo is needed to test this relationship at other forested sites. At other forested sites in the region, food conditions are similar and buffalo rely on forest clearings (Blake 2002; Melletti et al. 2007a). Based on results from radiocollared buffalo at Lopé NP, large group size would be expected for herds that used the largest clearings.

Forest buffalo social organization.—Forest buffalo herds were smaller than Cape buffalo herds, but were similar in composition. Forest buffalo groups observed at Lopé contained fewer than 50 buffalo, whereas Cape buffalo herds can exceed 1000 individuals (Sinclair 1977). The core members were adult females and their young. Unlike Cape buffalo, adult male forest buffalo were consistently observed with the same herds throughout the year. Taolo (2003) observed adult male Cape buffalo joining breeding herds in the late dry season at Chobe National Park, Botswana, and male buffalo alternated between mixed female-young herds and small, male herds at Hluhluwe-iMfolozi Park, South Africa, during the six-month mating season (Turner et al. 2005). At Lopé, adult males were not observed leaving herds to form bachelor groups. However, male forest buffalo were more often observed alone or in pairs than females, and not all males were associated with a herd.

Solitary aging adult female buffalo were observed at Lopé in addition to the more common solitary males. For example, three old females (without radio collars) were often solitary and eventually disappeared. Although no carcasses were found, these females most likely died before the end of the study. Similarly, the adult female radiocollared buffalo in the Lopé pilot study (Abernethy 1998, 1999, 2000) and AF4 in this study spent increasingly more time away from their groups until they died. Instead of becoming solitary, AF6 spent the last four months of the study associated with a smaller herd. Notably, she was the only radiocollared buffalo to switch herds. The unusually high number of observations of aging buffalo was probably due to low predation on adult buffalo and hunting restrictions. Forest buffalo were one of the main prey items found in leopard scat at Lopé; however, based on analyses of bones in the leopard scat, leopards were found to prey only on juveniles (Henschel et al. 2005). Due to the low predation pressure on adult buffalo and enforced hunting restrictions in the study area, food resources probably have more influence than predation on group size in forest buffalo at Lopé NP.

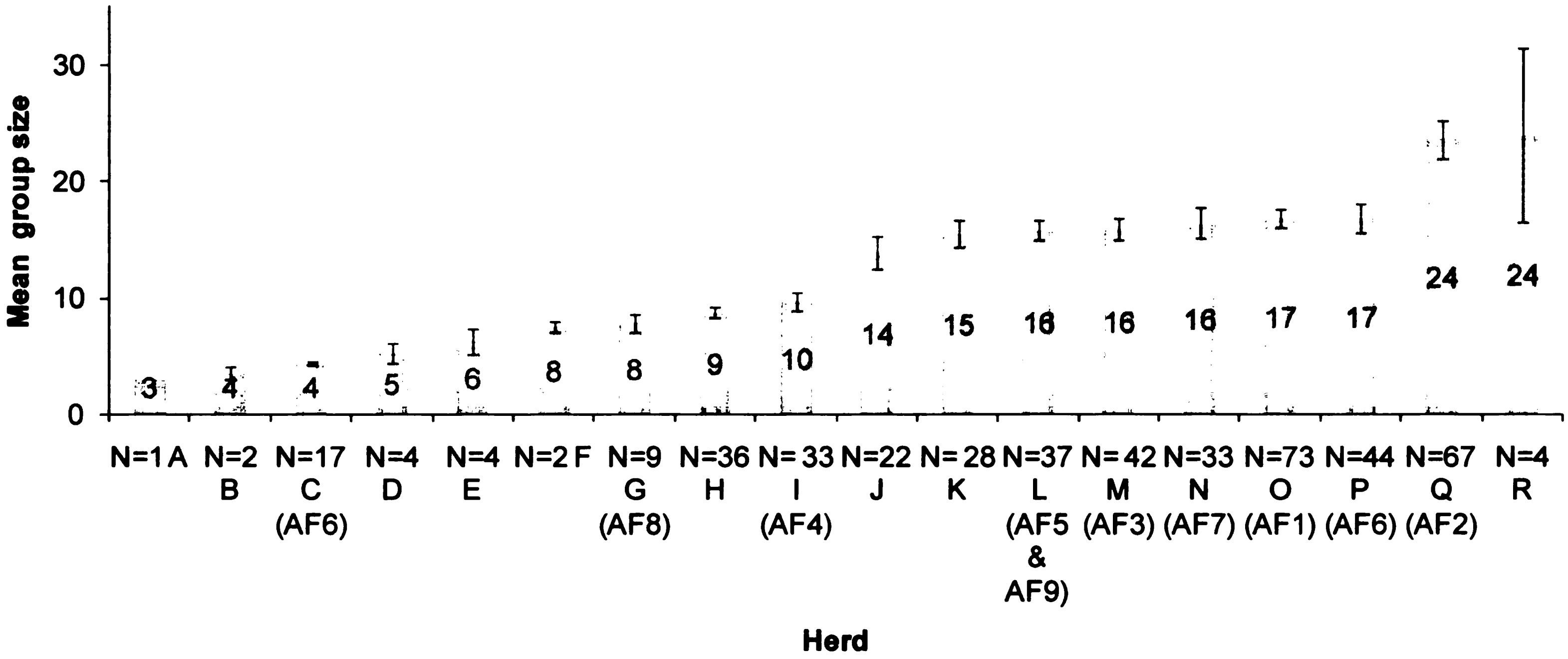


Figure 2.1. Mean group size of forest buffalo herds at Lopé National Park, Gabon, (September 2002-December 2004) based on circuit survey data. Means are based on observations of >2 buffalo for 249 circuits. N=the number of observations, including observations with and without radiocollared buffalo. Observations include all age classes. Mean herd size =11.91±1.55. Range of group size for each herd was: A (3); B (3-4); C (3-5); D (3-7) E (3-8); F (7-8); G (5-12); H (3-14); I (3-17); J (4-24); K (3-24); L (5-24); M (4-23); N (3-26); O (4-26); P (4-30); Q (3-43); and R (10-44). AF6 was consistently observed with Herd P until August 2004, when she was first observed with Herd C, in which she remained through the end of the study period.

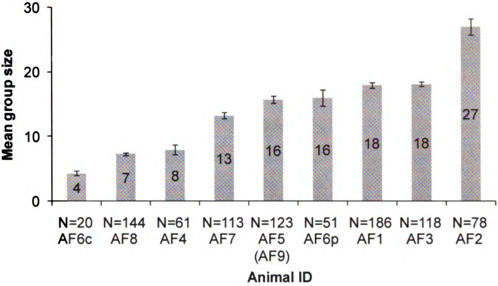


Figure 2.2. Mean group size of forest buffalo sightings that contained a radiocollared adult female (AF) at Lopé National Park, Gabon, December 2002-December 2004. N=the number of observations, representing all observations of radiocollared buffalo including sightings on circuit surveys and telemetry and opportunistic observations. Observations include all age classes. Group size range for each buffalo: AF6c (1-8); AF8 (2-12); AF4 (1-18); AF5 (1-25); AF6p (1-30); AF1 (2-29); AF3 (5-24); and AF2 (6-46).

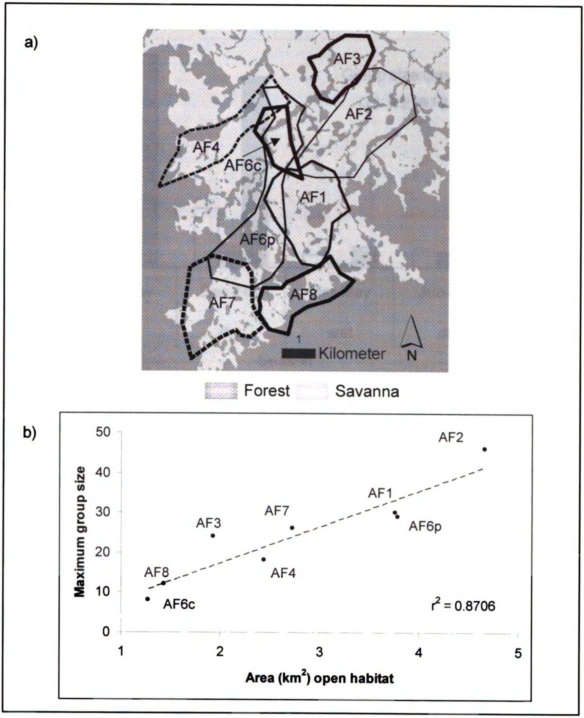


Figure 2.3. a) Home range of each radiocollared buffalo in the study area at Lopé National Park, Gabon (December 2002 – December 2004); b) Maximum size of group based on observations that included a radiocollared adult female (AF) forest buffalo in relation to the area of open habitat in the home range of those females. Each data point represents maximum group size (N=8) defined by the presence of a radiocollared buffalo. Positive correlation between maximum group size and areas of open habitat is significant (t=6.35, $P<0.05$).

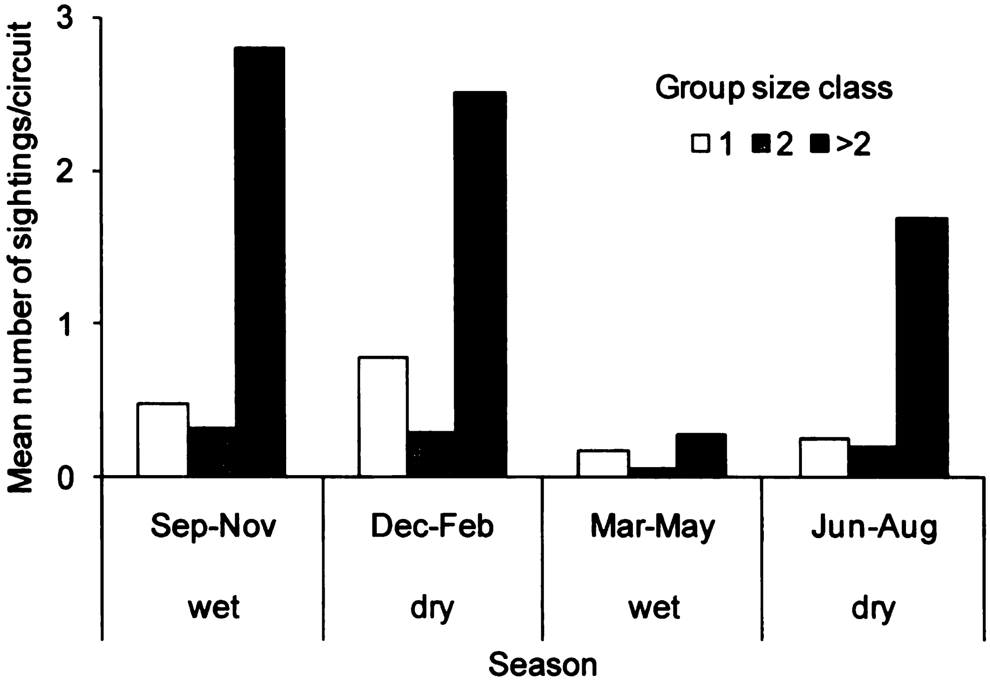


Figure 2.4. Seasonal distribution of forest buffalo group size at Lopé National Park, Gabon, based on circuit survey data. The y-axis represents the number of observations in each group size class divided by the total number of circuits per season. Mean group size for all sightings of buffalo, including solitary buffalo, was 11±0.34 based on 775 observations during 249 circuits.

Table 2.1. Effect of time of day, season, and habitat type (marsh or savanna), on size of forest buffalo groups that contained radiocollared adult females (AF) at Lopé National Park, Gabon, December 2002 – December 2004.

Animal ID			Habitat type		Time of day		Season	
	Numerator d.f.	Denominator d.f.	F Value	P	F Value	P	F Value	P
AF1	7	174	2.50	0.1155	3.38	0.0195*	6.42	<0.0001*
AF2	7	66	0.75	0.3894	0.47	0.7011	0.84	0.5578
AF3	7	106	1.58	0.2119	0.16	0.9202	0.49	0.8402
AF4	7	49	0.53	0.4715	0.66	0.5833	4.75	0.0004*
AF5	7	111	0.62	0.4328	1.13	0.3386	11.93	<0.0001*
AF6p	5	45	0.05	0.8267	1.20	0.3191	4.19	0.0033*
AF6c	1	11	-	-	1.35	0.3081	2.28	0.1519
AF7	7	101	1.35	0.2473	0.97	0.4088	2.01	0.0613
AF8	7	132	0.24	0.6270	0.77	0.5150	7.27	<0.0001*

*P<0.05

Table 2.2. Correlation coefficients (r) between mean and maximum size of group and home range characteristics based on adult female buffalo with a radio collar (N=8).

Variable	Mean group size	Maximum group size
Home range area (km^2)	0.69*	0.84*
Area of open habitat in home range (km^2)	0.83*	0.93*
Percent of total home range area that was open habitat	0.25	0.09

*P<0.05

Table 2.3. Comparison of mean group size estimates for telemetry data versus data collected on circuit surveys for nine radiocollared adult female buffalo at Lopé National Park Gabon, December 2002-December 2004.

Group size	Mean ± SE (range)		Mann-Whitney-U test
	telemetry	*circuit surveys*	
Minimum	2 ± 0.29 (1-3)	4 ± 1 (2-8)	U=69.5, P=0.0134
Mean	13 ± 2 (4-27)	15 ± 2 (4-25)	U=50, P=0.4015
Maximum	24 ± 4 (8-46)	22 ± 4 (5-43)	U=47, P=0.5660

Chapter III

Korte, L. 2008. Calving and inter-birth intervals of forest buffalo at Lopé National Park, Gabon. African Journal of Ecology.

Chapter III

CALVING AND INTER-BIRTH INTERVALS OF FOREST BUFFALO AT LOPE NATIONAL PARK, GABON

Introduction

The five subspecies of African buffalo *Syncerus caffer* (Sparrman 1779) can be assigned to the nominate *caffer* division and the *nanus* division (Wilson & Reeder 2005). The larger Cape buffalo, *Syncerus caffer caffer*, (400 to 800 kg) occurs throughout the savanna areas of eastern and southern Africa, and has a mean group size of 350 (Haltenorth & Diller 1980; Prins 1996; Sinclair 1977). The smaller forest-dwelling *Syncerus caffer nanus* (250-320 kg) is found in the forests of western and central Africa. Cape buffalo have been the focus of several comprehensive studies (Mloszewski 1983; Prins 1996; Sinclair 1977); however, few data exist for forest buffalo (Blake 2002; Melletti et al. 2007a). Based on a two-year telemetry study, I present calving and inter-birth interval data for forest buffalo in Gabon and compare results to calving intervals of Cape buffalo.

Materials and Methods

Eight adult female forest buffalo were fitted with radiocollars (Telonics, Inc., Mesa, AZ and HABIT, Inc., Victoria, British Columbia) at Lopé National Park, in December 2002 (AF1-AF8). Due to collar failure, a ninth collar was placed in December 2003 (AF9). Animals were tracked on a weekly basis (mean number of locations = 205/buffalo) from December 2002 through December 2004. When radiocollared animals were observed, notes on young in close proximity to adult females were recorded (i.e. age, sex, distinct characteristics). A Sony digital video camera (model DCR-TRV140) was used to record mother-young pairs when the view was clear. Collared females were from eight different herds having defined home ranges with small areas of overlap (Chapter I).

Buffalo home ranges were predominately savanna habitat despite greater availability of forest habitat at the study site (Chapter I). A controlled burning program maintains these savannas, creating open areas for tourists to observe large mammals (White & Abernethy 1997). Savannas, burned during the June through August dry season, provide a flush of new grasses grazed by buffalo during the September through November wet season. Green grass, available during the December through February dry season, becomes tall, dry, and less palatable for buffalo by the March through April wet season.

Results

Four collared females (AF1, AF2, AF3, AF8) had a single young with them when collared, and their young remained in close proximity to them throughout the two years of study (Table 3.1). Of those, three did not calve after collaring. The fourth (AF8) had a second calf when her first calf was two years old. The first calf remained with her after the birth of the second calf.

Four collared females (AF4, AF6, AF7, AF9) provided little information on calving intervals. AF4 was never observed with young. Each of the remaining three had no young at the time of collaring, but had a single calf during the study. AF6 had a calf four months after collaring in April 2003, but lost the calf by July 2003. She was not observed with another calf through the end of the study. AF7 had a calf 19 months after collaring in July 2004, but lost the calf within four months. AF9 was collared in December 2003, had a calf in August 2004, and lost the calf within a month. AF7 and AF9 lost their calves during the last four months of study, leaving insufficient time for gestation of another calf.

The remaining radiocollared animal (AF5) gave birth twice during the two-year study. She calved in March 2003, but lost her calf within four months. She was observed mating with an adult male on 19 August 2003 and her second calf was born in June 2004, suggesting a calving interval of 16 months. The estimated 10 month gestation period is similar to the 11.5 gestation period reported for Cape buffalo (Sinclair 1977). Her second calf survived through the remaining six months of study.

In summary, ten young were observed with the nine radio-collared females. Four of those were with radiocollared animals at the time of collaring and remained with the females throughout the two-year study. Six were born after collaring. Two of those calves survived the remaining six months of study. Four of the six calves disappeared before reaching four months of age (i.e., 67% mortality).

Discussion

The calving interval at Lopé is at least two years between surviving young. Similar intervals are reported for Cape buffalo with a range from 15 to 25 months at sites in South Africa, Tanzania, and Uganda (Grimsdell 1969; Prins 1996; Sinclair 1977). Because food quality improved with grazing pressure, early work suggested a positive relationship between population density and reproductive rate in African buffalo (Grimsdell 1969); however, a long calving interval (two years) has been recorded for Cape buffalo in Tanzania (Prins 1996) despite a high population density (18-20 buffalo/km^2). In this case, social factors and herd structure also influenced reproductive rate, indicating that population density alone does not explain calving intervals of Cape buffalo (Prins 1996). At Lopé, forest buffalo exhibit a relatively long calving interval with a low population density (~5 buffalo/km^2; Chapter II). Clearly, there is a need to further investigate factors that influence calving intervals.

This study found a high mortality rate for calves (67%). At Lopé, cause of death for the calves was not determined because carcasses were not found. However, buffalo calves are a primary prey of leopard *Panthera pardus* in the study area (Henschel et al. 2005). Another important factor may be food availability. The two surviving calves born in June and July, and their lactating mothers soon had access to the seasonal flush of new grass during the September through November wet season. The two calves born in March and April when food resources were low did not survive past four months. In Cape buffalo, breeding ecology is closely related to seasonal availability of resources (Pienaar 1969; Prins 1996; Ryan et al. 2007). The long calving interval and high calf mortality at Lopé may contribute to a low reproductive rate. Further research of the reproductive biology of forest buffalo, especially in regard to the seasonality and availability of resources, is recommended.

Table 3.1. Time between births for nine radio-collared adult female (AF) forest buffalo (*Syncerus caffer nanus*) at Lopé National Park, Gabon, December 2002-December 2004.

Animal ID	*Young with female at time of collaring (December 2002)*	*Births*	*Calf mortality*	*Young with female December 2004*	*Time between births*
AF1	female calf	none	none	two year old	at least two years
AF2	female calf	none	none	two year old	at least two years
AF3	one year old male	none	none	three year old	at least two years
AF4	None	none	—	none	------
AF5	None	March 2003: sex unknown	March 2003 calf lost before July 2003		16 months
		June 2004: male		calf*	
AF6	None	April 2003: sex unknown	lost before July 2003	none	-------
AF7	None	July 2004: female	lost by November 2004	none	-------
AF8	female calf	July 2004: male		two year old and calf*	two years
AF9	none (collared: December 2003)	August 2004: sex unknown	lost by September 2004	none	------

*Only two calves that were born to radiocollared females during study and survived until at least 6 months of age.

Chapter IV

HERD-SWITCHING IN ADULT FEMALE AFRICAN FOREST BUFFALO *SYNCERUS CAFFER NANUS*

Introduction

Recent evidence suggests that herd-switching in African buffalo *Syncerus caffer* (Sparrman 1779) is more common than previously reported (Cross et al. 2005; Halley et al. 2002). Traditionally, buffalo herds were considered stable with little movement of buffalo among herds (Estes 1991; Kingdon 1982; Prins 1996; Sinclair 1977). Although male buffalo were known to form small bachelor groups when not with the large herds, female buffalo and their young were viewed as core herd members. Recent studies in Botswana and South Africa have documented adult females switching herds and dispersing distances of > 100 km (Cross et al. 2005; Halley et al. 2002). These studies focus on Cape buffalo, *Syncerus caffer caffer*, a savanna-dwelling subspecies; however, less is known about the smaller, forest-dwelling subspecies, *Syncerus caffer nanus*. I report a single case of herd-switching over a distance of < 1 km from a telemetry study of nine adult female forest buffalo at Lopé National Park, Gabon.

Material and Methods

In December 2002, eight adult female forest buffalo, representing eight different groups, were fitted with radio collars (Telonics, Inc., Mesa, AZ and HABIT, Inc., Victoria, British Columbia) at Lopé National Park. Due to collar failure, a ninth collar was placed in December 2003. This ninth female (AF9) was in the same group as AF5. Buffalo were tracked on a weekly basis from December 2002 through December 2004 with a mean total number of locations of 205 per buffalo. When radiocollared buffalo were observed, notes on all buffalo in the group were recorded in order to distinguish individual buffalo as well as herds. In addition, a Sony digital video camera (model DCR-TRV140) was used to record buffalo when the view was unobstructed.

Results

One radiocollared buffalo switched herds. Between December 2002 and July 2004, she was observed in a herd with a mean group size of 17 (range 4-30). In August 2004, she joined a smaller herd of four buffalo where she remained the last five months of the study. The switch from a larger to a smaller herd, resulted in a reduction of home range from 4.17 km^2 to less than half that (i.e., 1.54 km^2). The other eight radiocollared buffalo remained with their respective herds.

Discussion

The single case of herd-switching among nine radiocollared buffalo at Lopé NP suggests that forest buffalo herds are more stable than Cape buffalo herds. Among Cape buffalo, herd-switching can be frequent among adult females (Cross et al., 2005; Halley et al., 2002), but only one radiocollared adult female switched herds in this study of forest buffalo. To better understand social networks, Cross et al. (2005) proposed a new association index based on data from Cape buffalo at Kruger National Park, South Africa. In the Kruger study, fission events were defined as two radiocollared animals observed in the same group and subsequently observed in different groups. For the Lopé buffalo, there were no cases of two radiocollared buffalo observed in the same group and subsequently observed in different groups.

If Lopé buffalo had a similar fission pattern to that of the Kruger buffalo, then about 19 fission events would be expected. At Kruger, where approximately 90 Cape buffalo were radio-collared among 4-12 herds with a combined population of 3,000 buffalo, 185 fission events were recorded among adult females and juveniles over a two-year period. Nine collared forest buffalo were tracked among 18 herds in the Lopé population of 342 buffalo. However, no fission events occurred among radiocollared buffalo at Lopé and only one radiocollared buffalo switched herds during the two-year study. In addition to radiocollared buffalo, the same recognizable individuals (i.e., about 6-10 adult females and 1-2 adult males per herd) were consistently observed with herds. Thus, my data suggest that fission events are less common in forest buffalo than in Cape buffalo.

Distribution of resources may influence fission events in African buffalo. In Botswana, herd-switching occurred during wet seasons when Cape buffalo herds migrate and fragment into smaller subgroups (Halley et al. 2002). Water resources are not limited during the dry season and forest buffalo do not migrate at Lopé NP (Chapter I). Small streams flow throughout the forest habitat and each herd has several water resources within their home range areas. Forest buffalo home range areas are well defined with small areas of overlap (Chapter I). Despite having adjacent home range areas, radiocollared buffalo from different herds were never observed together.

Small herd size may explain the rarity of fission events observed among forest buffalo. Cape buffalo group size is considerably larger than that of forest buffalo at Lopé (i.e., 12 ± 2 with a range of 3-24; Chapter II). Although groups as small as 12 have been observed in Cape buffalo, mean size is 350 with the largest herds reaching into the thousands (Prins 1996; Sinclair 1977). Halley et al. (2002) suggest that subgroups rather than individuals are switching among Cape buffalo herds. Cape buffalo herds appear to be aggregations of subgroups, whereas forest buffalo herds are small and stable with relatively little switching between herds. Notably, the only buffalo to switch herds was an older buffalo and she was the single member of her original herd to switch. Her switch may have been a reflection of her condition and inability to move with her original larger herd. Further investigation of association patterns in forest buffalo with an increased sample size of collared buffalo would be useful to understand why buffalo switch herds.

Chapter V

PERSPECTIVES ON THE ROLE OF BUFFALO IN CONSERVATION AT LOPE NATIONAL PARK, GABON

Introduction

Conservation planning for wildlife depends on knowledge of the animal's biology as well as the management objectives within protected areas. The newly created parks in the Congo Basin Forest region of Central Africa present an opportunity to consider fresh approaches to park management. The Congo Basin is a priority for global conservation and is one of only three regions of the world (along with the Amazon Basin and the island of New Guinea) designated as a tropical wilderness area (Mittermeier et al. 1998). These regions are recognized for their high biodiversity combined with large expanses of intact tropical forest and low human populations. Though the tropical forest of the Amazon Basin covers a larger area than the Congo Basin, many locations in the Amazon are devoid of large animals (Redford 1992). Only the Congo Basin forests retain relatively abundant populations of large mammals.

The Amazon rainforest and the savannas of Africa have been the focus of conservation activities for many years, but Africa's Congo Basin only recently received international recognition as a conservation priority (Kamdem-Toham et al. 2003). In the 1999 Yaoundé Declaration, six heads of state from Central African nations committed 10% of forest areas in their countries to become protected areas to safeguard their tropical timber and wildlife. The region's wildlife includes many charismatic, large mammals such as gorillas (*Gorilla g.*

gorilla), chimpanzees (*Pan t. troglodytes*), mandrills (*Mandrillus sphinx*), elephants (*Loxodonta cyclotis*), and buffalo (*Syncerus caffer nanus*). In 2002, President Omar Bongo of Gabon fulfilled his promise by creating thirteen new national parks covering 30,000 km^2 or 10% of Gabon's land mass. At 5,000 km^2, Lopé National Park is one of the largest of the parks and the conservation community views it as the emerging Yellowstone of Gabon.

Though the creation of national parks provides the legal documentation to protect habitats, laws alone will not lead to conservation of natural resources (Brashares et al. 2001; Newmark & Hough 2000). Efficient and well-planned activities are essential for conservation, and fundamental ecological data are crucial for planning (Milner-Gulland & Bennett 2003). However, planning in the Congo Basin is difficult because data on animals, plants, and social conditions are often lacking, and protected areas are often ineffectively managed (Blom 2004; Kamdem-Toham et al. 2003). Further research can provide information for planning and zoologists must be proactive in making recommendations that will contribute to the success of park management plans (Pullin & Knight 2001). However, to build the capacity of African wildlife biologists, greater efforts are needed to integrate research, training, and park management (Durant et al. 2007; McNeilage & Robbins 2007). The case study of the Serengeti Cheetah Project by Durant et al. demonstrates successful integration of long-term research and management in conservation. In this final chapter, I consider how long-term research of forest buffalo could be integrated with park management and training at Lopé NP.

Throughout my two-year study on the spatial and social organization of forest buffalo at Lopé National Park (Chapters I-IV), I had the opportunity to conduct research, collaborate with park managers, and mentor national and international students. Park management activities (i.e., savanna burning) influence buffalo behavior (Molloy 1997), buffalo provide relatively easy viewing for park visitors, and buffalo have been a focal species for training of national wildlife professionals. Given the important role buffalo play in this region, an increased effort should be made to expand conservation activities at Lopé NP to include this species. Such a program must fit with other conservation priorities given limited personnel, funding, and expertise. However, a focus on forest buffalo that integrates research, park management, and training could make a positive contribution to conservation planning. After an introduction to African buffalo and the institutions at Lopé NP, I consider each of the objectives of the Lopé National Park Management Plan for 2006-2011 and discuss how further research of forest buffalo could contribute to achieving each objective. Regionally, establishment of a long-term conservation study of buffalo could play a leading role in making Lopé NP a model for conservation in the Congo Basin.

Forest buffalo

Forest buffalo are one of five recognized subspecies of African buffalo (Wilson & Reeder 2005). These subspecies differ in geographic range, morphology, and behavior. The largest of the subspecies is *Syncerus caffer caffer*, the 400-800 kg Cape buffalo of the savannas of east and southern Africa (Grubb 1972; Kingdon 1997; Sinclair 1977). At 250-320 kg, forest buffalo of the Congo Basin are the smallest of the subspecies (Haltenorth & Diller 1980; Kingdon 1997). Cape buffalo also have largest groups, with a mean group size of 350 and large herds that reach into the thousands (Prins 1996; Sinclair 1977). Among forest buffalo, group size is small with a mean group size of less than 20 individuals (Chapter 2; Jarman 1974; Melletti et al. 2007b; Mloszewski 1983; Sidney 1965). Cape buffalo are known for the distinct lateral curve of their horns, whereas forest buffalo lack the lateral extension and have small, swept back horns. Kingdon (1982) suggests that this suite of differences observed among the African buffalo subspecies reflect adaptations for living in savanna versus forest habitat.

Forest buffalo are recognized as an important species for conservation planning based on their spatial requirements, ecological function, vulnerability, and socioeconomic significance (Blake 2002; Coppolillo et al. 2004; Melletti et al. 2007a). At Lopé NP, buffalo home range areas are predominately savanna habitat, but buffalo also use forest and marsh habitat within these ranges (Chapter I). Thus, their home ranges and use of these areas include all habitat types at Lopé NP. Buffalo are the only large grazing ungulate and juvenile buffalo are an important prey species for leopards (*Panthera pardus*, Henschel et al. 2005). Though protected near park headquarters, buffalo are vulnerable to hunting in Gabon (Laurance et al. 2006b). People value buffalo for their meat as well as their potential as one species in a suite of African forest mammals that will draw international tourists. Working with local communities and developing tourism are both objectives of the Lopé NP Management Plan.

Lopé National Park Management Plan

With the enthusiasm generated by the creation of the new national parks in Gabon, researchers and park staff created the Lopé National Park Management Plan for 2006-2011. The long-term vision of the plan is to have Lopé NP become a model and leader for conservation efforts in the Congo Basin. The management plan includes a desire to incorporate local, national, and international interests and values in its management objectives. Clearly, this will be a major challenge since expectations for how the park resources are used differ among these stakeholders. For example, when international tourists visit Lopé NP, they hope to see as many large mammals as possible. In contrast, local communities prefer low densities of wildlife to reduce the risk of large mammal confrontations, including crop-raiding and threats to people. A focus on buffalo has the potential to manage the diverse expectations for Lopé NP and surrounding communities.

Park management, research, and training institutions at Lopé National Park

The park headquarters, the Lopé research center, and the Lopé Training Center, are based within 11 km of each other. The park headquarters is supported by the Gabonese government and there is a history of significant funding from the European Union. The history of legal protection of the region began in 1946 when the area was designated the Lopé-Okanda Wildlife Reserve. In 2002, the Lopé-Okanda Wildlife Reserve became Lopé National Park with the creation of the 13 national parks in Gabon.

Researchers based at the Lopé research station are advisors to park management and work closely with park staff to plan activities, such as savanna burning and monitoring of wildlife populations within the park. The Gabonese International Center for Medical Research (CIRMF) founded the Lopé research station (Station d'Etudes des Gorilles et Chimpanzés, SEGC) for the study of gorillas and chimpanzees in 1983. Since the 1990s, the research station has expanded its program to include the general ecology of the park. The Lopé research station has the longest running continuous ecological monitoring research program in the region, representing a valuable source of data for comparative and longitudinal studies. In addition, the Wildlife Conservation Society (WCS) provides the Lopé research station with funding for conservation activities. In 2003, the director of the Lopé research station established the Lopé Training Center to improve scientific capacity of Gabonese conservation professionals.

History of buffalo research at Lopé

Research on Lopé forest buffalo began in the late 1980s and continues today. The first buffalo study focused on the vegetation of the savanna areas (Alers & Blom 1988). Field surveys of mammals conducted in the 1990s documented the abundance of forest buffalo in the savanna areas (Tutin et al. 1997), but found few signs of buffalo in forest habitat (White 1994). Following those surveys, Molloy (1997) examined the influence of savanna burning on forest buffalo. In 1998, radio-collars were placed on one adult female and one adult male to test the feasibility of a telemetry study of buffalo at Lopé NP (Abernethy 1998, 1999, 2000). Subsequently, a two-year telemetry study during 2002-2004 based on nine radio-collared buffalo representing eight different herds examined the spatial and social organization of Lopé buffalo (Chapters I-IV). Van Hooft et al. (2000) used tissue samples from Lopé buffalo for a study of African buffalo population genetics. Most recently (2006), Van Hooft collected additional genetic samples, and during the summer of 2007, one of his graduate students collected forest buffalo dung samples for a preliminary study of buffalo diet and parasites.

Although many species at Lopé NP might serve as a focus for conservation efforts, buffalo have characteristics that make them especially suitable. First, conditions for buffalo research at Lopé NP are favorable with low predation, little hunting pressure, and seasonally abundant food resources (Chapters I & II). Second, forest buffalo research is straightforward compared with other sites in the Congo Basin. At other sites, buffalo tend to use forest clearings that are scattered throughout difficult terrain with typically only one herd using each clearing or set of clearings (Blake 2002; Melletti et al. 2007b). In contrast, several herds of buffalo can be studied simultaneously in the savanna areas at Lopé NP. These savanna areas also facilitate telemetry studies because the buffalo can be collared at minimal risk to the buffalo and buffalo can be tracked easily. In addition, buffalo are clearly visible in the forest-savanna habitat mosaic after savanna burning (Molloy 1997).

Lopé NP Management Plan Objectives

Protect and conserve species.—The first objective of the Lopé NP Management Plan is to protect species. All populations of African buffalo (*Syncerus caffer*) are categorized as lower risk/conservation dependent on the IUCN Red List of Threatened Species (IUCN 2007). Being a conservation dependent species means that if existing conservation activities for buffalo were to end, the African buffalo would be listed in a threatened category, a more severe listing. However, this assessment is out-of date and the population trend was downward at the last assessment. Given that African forests are threatened by logging, hunting of wildlife, and insufficient funds to manage protected areas (Kamdem-Toham et al. 2003), there is a need to protect and conserve forest buffalo. A long-term conservation study which collects biological, behavioral, ecological, and health data of importance to the conservation of African buffalo in the Congo Basin would provide managers of protected areas with data to inform their decision making.

Conserve habitat and ecological processes.—The Lopé NP Management Plan calls for the conservation of unique habitats and ecological processes within the park. The majority of Lopé NP is forest and most importantly the park protects tropical forest habitat. However, the northeast corner of the park is a mosaic of forest-savanna habitat, which has also been noted as an important habitat to protect and sustain. This mosaic supports abundant wildlife populations and a unique array of plant species (Tutin et al. 1997; Ukizintambara et al. 2007). The savanna areas were traditionally maintained by early inhabitants of Lopé and today park managers preserve open habitat through savanna burning to create scenic vistas for tourists (Tutin et al. 1997; White & Abernethy 1997). Without the annual savanna burning, the savannas areas would be colonized by forest species and return to forest habitat (Oslisly 2001).

Forest buffalo include savanna area within their home ranges and use the forest-savanna mosaic with no migration into the continuous forest (Chapter I). After the savanna burning during the June through August dry season, buffalo feed on the flush of new grass from September through February and use the forest habitat adjacent to the savannas during March through August when the savanna grasses are dry, tall, and less palatable. Home ranges of forest buffalo are stable in size and location over at least a few years and might remain stable over several years (Chapter I). Given the close link between savanna condition and forest buffalo use of savanna habitat, buffalo are a key species for guiding savanna management.

Traditionally, savannas are burned by igniting savanna edges and allowing large swaths of savanna to burn. These areas are burned over a few days in late August and early September, creating one or two large flushes of new grass. To create additional flushes of grass over longer time periods, I suggest that small burns are staggered in time and space within buffalo home range areas (Figure 1.2). Within home ranges, firebreaks could be used to limit fires to discrete patches. Burning savannas over a longer time period could provide buffalo herds with new grass over several weeks and increase the period of buffalo visibility, a benefit for tourism as well as research and training. The greater number of flushes may also lead to an increase in the number of buffalo given the additional food resources. These benefits will be discussed further in the following sections, which address tourism, research, and training.

A potential problem with multiple burning is the amount of time and labor it takes to implement this plan. Based on my field assistant's preliminary trials of this method, burning in small patches over several months is a more laborious and time-consuming process than the currently used method of burning large savanna areas over a short time period without firebreaks. Therefore, professional training in prescribed burns is recommended for park managers as well as logistical support and incentives to implement plans. After the savanna burning, the time period buffalo use savannas and number of buffalo using the savannas should be monitored to determine how the burning patterns influence buffalo. Further study should not be limited to buffalo. The impact of savanna burning on other species including plants and animals has yet to be assessed. Thus, further study of the impact of savanna burning will be needed to evaluate how well habitats are conserved and ecological processes are maintained at Lopé NP.

Protecting archeological sites.—To my knowledge, forest buffalo and archeologists have yet to clash at the archeological sites scattered throughout the Lopé savannas. However, buffalo often rest on hilltops that include archeological sites. From the hilltops, there are clear views across the savanna to the forest edge and often a breeze to ward off heat and insects. And, the Lopé savannas support high densities of elephants and buffalo (Tutin et al. 1997). Lopé NP contains archeological sites dating from the Upper Pleistocene to the

Post-colonial period and the excavated sites at Lopé cover the longest and most complete archeological sequence in Central Africa (Ndong 2002). The 40,000 years of human presence in the region contributed to maintaining the forest-savanna mosaic at Lopé (Ndong 2002; Oslisly 2001). Thus, the Lopé sites represent a long history and need adequate protection. The Lopé NP Management Plan recommends that more delicate and older archeological sites may need to be sheltered from high concentrations of wildlife. Buffalo use archeological sites, but their impact on these sites has yet to be investigated. Therefore, buffalo use of archeological sites should be quantified to reduce the risk of any potential damage to important sites by buffalo.

Developing profitable tourism activities.—A long-term study of forest buffalo could benefit tourism activities. In particular, a well-implemented savanna burning plan could result in several buffalo herds clearly visible in the savanna areas over extended periods of time. Seeing buffalo is exciting for tourists, especially when other wildlife in the area less visible. Buffalo on the savannas also assure visitors that the wildlife in the park is well-protected. When tourists drive through empty savanna areas without buffalo, it can be difficult for them to appreciate why Lopé is a national park. The creation of the national parks was expected to generate alternate sources of revenue, and Gabon needs to diversify its economy (Laurance et al. 2006a). Though gorillas are what attract tourists to Gabon, savannas must be populated with wildlife for tourism to succeed. Tourists visiting Africa expect to see abundant wildlife, especially if they have previously visited sites in eastern and southern Africa. Therefore, Gabon will need to maximize the potential of each wildlife encounter. Tourists will gain an appreciation for the abundance of wildlife at Lopé NP, when they take a sunset drive on a savanna among several herds of buffalo.

If park revenue can be generated from forest buffalo, it would reduce dependency on international funding and base economic gain in local resources and institutions. When appropriately managed, safari hunting generates revenue and contributes to community development (Lewis 1995; Loveridge et al. 2007; Mayaka et al. 2005). Although hunting is illegal at Lopé NP, it may be worth considering the participation of international sport hunters in the darting of buffalo for radio collar placement. Another consideration would be to involve sport hunters in the handling of problem buffalo. On occasion, park management will kill a buffalo if a particular buffalo has injured a person. However, a clear and consistent protocol for addressing problem buffalo does not appear to exist. Having sport hunters involved could potentially increase revenue for the park via trophy fees as well as reduce the negative impact of wildlife on the local community.

Promoting local participation in all conservation activities.—Positive interactions between members of the Lopé community and wildlife could increase the community's interest in protecting species and supporting the park. The increased visibility of buffalo on the savanna can also be used to provide the local communities with opportunities to view wildlife. Forest buffalo are an ideal species to engage the local community because buffalo are relatively easy to observe compared with other African forest mammals. Tracking of radiocollared buffalo provides a thrilling wildlife demonstration and often leads to visual observations of the collared buffalo. Positive interactions with animals give people a better understanding and appreciation for wildlife (Moorman 2006). When I took school children to radio-track buffalo, they could follow a signal from the radio collar and eventually identify the collared buffalo in a herd. Forest buffalo were rather undisturbed by this interaction and several children could participate. Buffalo will continue to feed, rest in a wallow, or meander across the savanna despite children's observations. Positive interactions between members of the local community and wildlife will increase the community's interest in protecting species and supporting the park (Steinmetz et al. 2006).

The success of any park will depend on the park having a positive impact on the local community (Wilkie et al. 2006). Benefits to the local community must come through employment, development, or activities managed by park staff because people are prohibited from harvesting natural resources in the park. Though some employment opportunities exist for tour guides and work with the Lopé research station and training center, these positions benefit only a few individuals. Funding from the European Union has helped to support infrastructure for the park, but is neither consistent nor unlimited. The park has not generated sufficient revenue to provide funding for development projects such as building schools or clinics. It seems the local community would have greater incentive to reduce poaching if they received direct benefits from the protected wildlife.

Managing forest buffalo for a sustainable harvest to benefit the local community could be considered since buffalo populations appear to be increasing. The number of herds and individual buffalo at Lopé increased between 1996 and 2004. I estimated that 212 buffalo in 13 herds used the study area between July and December 1996 (Molloy 1997). During the 2002-2004 study, the estimated population was 342 buffalo in 18 herds (Chapter II). This increase is probably due to low predation on adult buffalo and the enforcement of hunting laws. Although Henschel at al. (2005) found evidence of leopard predation on juvenile buffalo in the study area, they found no evidence of predation on adult buffalo. The frequent observation of older solitary females at Lopé NP suggests that predation pressure on adult buffalo is low (Chapter II). In addition, the Lopé buffalo population is protected from hunting due to the proximity to park headquarters. In southwest Gabon, areas where hunting pressure is high have fewer forest buffalo than sites with no hunting (Laurance et al. 2006b).

The consideration of sustainable harvest of buffalo should not be done at the expense of the good viewing conditions for buffalo at Lopé NP. To maintain high numbers of buffalo and calm herds, a transparent system for determining the number of buffalo in the population is required. And, the appropriate number as well as age and sex class to harvest over what time period would need to be determined.

Develop training and multidisciplinary research.—The final objective of the Lopé NP Management Plan is to have the park become a resource for training and research in the Congo Basin. An institutional collaboration between the research station and the training center to establish a long-term conservation study of forest buffalo would advance scientific research and contribute to park management and capacity building of national scientists. Few studies have focused on African forest mammals and there is still much to be learned about the behavior and ecology of forest buffalo. As previously discussed, conditions for studying buffalo at Lopé NP are favorable with the ability to access and study several different herds. Collaboration among park management, the research station, and the training center can be facilitated by their geographic proximity and current cooperative relationships. Since the establishment of the training center, trainees have participated in buffalo research and learned telemetry techniques by tracking forest buffalo. Buffalo proved to be an ideal species for learning about animal behavior and survey techniques because buffalo can be readily observed from a distance and radio-tracked with little disturbance of the herds. From a multidisciplinary perceptive, study of the savanna burning at Lopé NP is an excellent opportunity to link studies of vegetation with buffalo biology and park management activities.

Summary of recommendations

This paper took a first look at how each management objective of the Lopé National Park Management Plan relates to forest buffalo. Ultimately, managers must determine whether they would like wildlife populations to increase, decrease, or remain stable, and to implement appropriate management plans. Table 5.1 is a summary of the objectives of the Lopé NP Management Plan with the management recommendations and potential benefits that could result with implementation of these suggestions. Clearly, further work will be needed to determine how any one of these recommendations could be implemented. And, forest buffalo would need to be monitored to provide the data for appropriate planning. For example, home range area estimates should be updated on an annual basis for planning savanna burns. Though harvest of buffalo could be considered to benefit the local communities, it would require detailed population data to determine appropriate harvest levels as well as the time periods between harvests. Given buffalo data required to make informed management decisions, a long-term conservation study on forest buffalo could make a significant contribution to park management. In addition, a long-term conservation study will provide opportunities for national scientists to develop their field research skills. Buffalo have the potential to be a model species for integration of research, management, and capacity building at Lopé National Park.

Table 5.1. Summary of objectives in the Lopé National Park Management Plan (2006-2011) with management recommendations specific to forest buffalo and the potential benefits that could result from implementation of these activities.

Park objectives	**Management recommendations**	**Potential benefits**
Protect and conserve species	Collect biological, behavioral, ecological, and health data of importance to the conservation of African buffalo in the Congo Basin	Data available for protected area managers to make informed decisions
Conserve habitats and ecological processes	1) Provide training in controlled burning techniques for park managers 2) Use buffalo home range data to plan savanna burning	1) Longer time periods to view buffalo 2) Increased number of flushes of new grass, which could perhaps lead to an increase in the number of buffalo as a result of more food
Protect archeological sites	Quantify buffalo use of archeological sites to assess if buffalo have an impact on the sites	Reduced risk of wildlife damage to archeological sites
Develop profitable tourism activities	1) Plan savanna burning to maximize visibility of buffalo 2) Consider the participation of sport hunters in the darting of buffalo	Increased revenue for the park
Promote local participation in all conservation activities	1) Offer safari drives for viewing buffalo to the local community 2) Consider sustainable harvest of buffalo for the local community	Engagement of the local community and Improved protection at the park
Develop training and multidisciplinary research	Research station, training center, and park management collaborate to establish a long-term conservation study of buffalo	Increased capacity of scientists and resources in the region

REFERENCES

Abernethy, K. 1998. Rapport d'activities. SEGC (Station d'Etudes des Gorilles et Chimpanzés), CIRFM (Centre International de Recherchers Médicales de Franceville), Lopé, Gabon.

Abernethy, K. 1999. Rapport d'activities. SEGC (Station d'Etudes des Gorilles et Chimpanzés), CIRFM (Centre International de Recherchers Médicales de Franceville), Lopé, Gabon.

Abernethy, K. 2000. Rapport d'activities. SEGC (Station d'Etudes des Gorilles et Chimpanzés), CIRFM (Centre International de Recherchers Médicales de Franceville), Lopé Reserve.

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology **74**:1313-1325.

Alers, M. P. T., and A. Blom. 1988. La végétation, les buffles et l'aménagement des savanes de la Lopé. Ministère des Eaux et Forêts., Libreville.

Apollonio, M., S. Focardi, S. Toso, and L. Nacci. 1998. Habitat selection and group formation pattern of fallow deer *Dama dama* in a submediterranean environment. Ecography **21**:225- 234.

Bankert, D., and M. F. Schenk. 2003. Habitat use of the forest buffalo (*Syncerus caffer nanus*) at the Lopé National Park, Gabon. Master's thesis, Wageningen University, Wageningen, The Netherlands.

Barrette, C. 1991. The size of axis deer fluid groups in Wilpattu-National-Park, Sri-Lanka. Mammalia **55**:207-220.

Bingham, R. L., and L. A. Brennan. 2004. Comparison of Type I error rates for statistical analyses of resource selection. Journal of Wildlife Management **68**:206-212.

Blake, S. 2002. Forest buffalo prefer clearings to closed-canopy forest in the primary forest of northern Congo. Oryx **36**:81-86.

Blom, A. 2004. An estimate of the costs of an effective system of protected areas in the Niger Delta - Congo Basin Forest Region. Biodiversity and Conservation **13**:2661-2678.

Börger, L., N. Franconi, G. d. Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology **75**:1393–1405.

Borkowski, J., and K. Furubayashi. 1998. Seasonal and diel variation in group size among Japanese sika deer in different habitats. Journal of Zoology **245**:29-34.

Brashares, J. S., and P. Arcese. 2002. Role of forage, habitat and predation in the behavioural plasticity of a small African antelope. Journal of Animal Ecology **71**:626-638.

Brashares, J. S., P. Arcese, and M. K. Sam. 2001. Human demography and reserve size predict wildlife extinction in West Africa. Proceedings of the Royal Society of London Series B-Biological Sciences **268**:2473-2478.

Brashares, J. S., T. Garland, Jr., and P. Arcese. 2000. Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. Behavioral Ecology **11**:452-463.

Burgman, M. A., and J. C. Fox. 2003. Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. Animal Conservation **6**:19-28.

Clutton-Brock, T. H., F. D. Guinness, and S. D. Albon 1982. Red Deer. Behavior and Ecology of Two Sexes. University of Chicago Press, Chicago.

Conner, L. M., and B. W. Plowman. 2001. Using Euclidean distances to assess nonrandom habitat use. Pages 275–290 in J. J. Millspaugh, and J. M. Marzluff, editors. Radio Tracking and Animal Populations. Academic Press, San Diego, California.

Conybeare, A. 1980. Buffalo numbers, home ranges, and movement in the Sengwa Wildlife Research Area, Zimbabwe. South African Journal of Wildlife Research **10**:89-93.

Coppolillo, P., H. Gomez, F. Maisels, and R. Wallace. 2004. Selection criteria for suites of landscape species as a basis for site-based conservation. Biological Conservation **115**:419-430.

Cross, P. C., J. I. Lloyd-Smith, and W. M. Getz. 2005. Disentangling association patterns in fission-fusion societies using African buffalo as an example. Animal Behaviour **69**:499-506.

Durant, S. M., S. Bashir, T. Maddox, and M. K. Laurenson. 2007. Relating long-term studies to conservation practice: The case of the Serengeti Cheetah Project. Conservation Biology **21**:602-611.

Environmental Systems Research Institute. 1999. ArcView version 3.2. ESRI, Redlands, California, USA.

Estes, R. D. 1991. The Behavior Guide to African Mammals. The University of California Press, Berkeley.

Fisher, D. O., and I. P. F. Owens. 2000. Female home range size and evolution of social organization in macropod marsupials. The Journal of Animal Ecology **69**:1083-1098.

Funston, P., J. Skinner, and H. Dott. 1994. Season variation in movement patterns, home range and habitat selection of buffaloes in a semi-arid habitat. African Journal of Ecology **32**:100-114.

Gannon, W. L., R. S. Sikes, and the Animal and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy **88**:809-823.

Getz, W. M., and C. C. Wilmers. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography **27**:489-505.

Grimsdell, J. J. R. 1969. Ecology of the Buffalo in western Uganda. Ph.D., Cambridge University, Cambridge.

Grubb, P. 1972. Variation and incipient speciation in the African buffalo. Z. Säugetierkunde **37**:121-144.

Gwynne, M. D., and R. H. V. Bell. 1968. Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature **220**:390–393.

Halley, D. J., and M. Mari. 2004. Dry season social affiliation of African buffalo bulls at the Chobe riverfront, Botswana. South African Journal of Wildlife Research **34**:105-111.

Halley, D. J., and M. Minagawa. 2005. African buffalo diet in a woodland and bush-dominated biome as determined by stable isotope analysis. African Zoology **40**:160-163.

Halley, D. J., M. E. J. Vandewalle, M. Mari, and C. Taolo. 2002. Herd-switching and long-distance dispersal in female African buffalo, *Syncerus caffer*. African Journal of Ecology **40**:97-99.

Haltenorth, T., and H. Diller 1980. A Field Guide to the Mammals of Africa including Madagascar. Collins, London.

Harestad, A. S., and F. L. Bunnel. 1979. Home range and body weight -- a reevaluation. Ecology **60**:389-402.

Henschel, P., K. A. Abernethy, and L. J. T. White. 2005. Leopard food habits in the Lopé National Park, Gabon, Central Africa. African Journal of Ecology **43**:21-28.

Hillman, J. C. 1987. Group size and association patterns of the common eland (*Tragelaphus oryx*). J. Zool. Lond. **213**:641-663.

Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildlife Monographs **53**:3-55.

Hofman, R. R., and D. R. M. Stewart. 1972. Grazer or browser: a classification based on stomach-structure and feeding habits of East African ruminants. Mammalia **36**:226-240.

Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to Arcview. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK.

Hunter, C. G. 1996. Land uses on the Botswana/Zimbabwe border and their effects on buffalo. South African Journal of Wildlife Research **26**:136-150.

IUCN. 2007. IUCN Red List of Threatened Species. 2007 IUCN Red List of Threatened Species.

Janis, C. M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. Pages 367–387 in D. E. Russell, J. P. Santoro, and D. Sigogneau-Russel, editors. Proceedings of the VIIth International Symposium on Dental Morphology 1986 Mém. Mus. Natn. Hist. Nat, Paris.

Jarman, P. J. 1974. The social organisation of antelope in relation to their ecology. Behaviour **48**:215-267.

Jenness, J. 2004. Nearest Features. Jenness Enterprises, Flagstaff, AZ.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preferences. Ecology **61**:65-71.

Kamdem-Toham, A., A. W. Adeleke, N. D. Burgess, R. Carroll, J. D'Amico, E. Dinerstein, D. M. Olson, and L. Some. 2003. Forest conservation in the Congo Basin. Science **299**:346-346.

Kingdon, J. 1982. East African Mammals: An Atlas of Evolution in Africa, Volume III, Part C (Bovids). The University of Chicago Press, Chicago.

Kingdon, J. 1997. The Kingdon Field Guide to African Mammals. Academic Press, San Diego.

Laurance, W. F., A. Alonso, M. Lee, and P. Campbell. 2006a. Challenges for forest conservation in Gabon, central Africa. Futures **38**:454-470.

Laurance, W. F., B. M. Croes, L. Tchignoumba, S. A. Lahm, A. Alonso, M. E. Lee, P. Campbell, and C. Ondzeano. 2006b. Impacts of roads and hunting on central African rainforest mammals. Conservation Biology **20**:1251-1261.

Leuthold, W. 1970. Observations on the social organization of impala, *Aepyceros melampus*. Z Tierpsychol **27**:693-721.

Leuthold, W. 1976. Group size in elephants of Tsavo National Park and possible factors influencing it. The Journal of Animal Ecology **45**:425-439.

Lewis, D. M. 1995. Importance of GIS to community-based managment of wildlife - lessons from Zambia. Ecological Applications **5**:861-871.

Loveridge, A. J., J. C. Reynolds, and E. J. Milner-Gulland. 2007. Does sport hunting benefit conservation? Pages 222-238 in D. W. Macdonald, and K. Service, editors. Key Topics in Conservation Biology. Blackwell Publishing Ltd, Malden, MA.

Marchal, C., J. F. Gerard, B. Boisaubert, and E. Bideau. 1998. Instability and diurnal variation in size of winter groupings of field roe deer. Revue D Ecologie-La Terre Et La Vie **53**:59-68.

Mayaka, T. B., T. Hendricks, J. Wesseler, and H. H. T. Prins. 2005. Improving the benefits of wildlife harvesting in Northern Cameroon: a co-management perspective. Ecological Economics **54**:67-80.

McMillan, B. R., M. R. Cottmam, and D. W. Kaufman. 2000. Wallowing behavior of American Bison (*Bos bison*) in the Tallgrass Prairie: an examination of alternate explanations. American Midland Naturalist **144**:159-167.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. The American Naturalist **97**:133-140.

McNeilage, A., and M. M. Robbins. 2007. Primatology comes to Africa. African Journal of Ecology **45**:1-3.

Melletti, M., V. Penteriani, and L. Boitani. 2007a. Habitat preferences of the secretive forest buffalo (*Syncerus caffer nanus*) in Central Africa. Journal of Zoology **271**:178-186.

Melletti, M., V. Penteriani, M. Mirabile, and L. Boitani. 2007b. Some behavioral aspects of forest buffalo (*Syncerus caffer nanus*): from herd to individual. Journal of Mammalogy **88**:1312-1318.

Milner-Gulland, E. J., and E. L. Bennett. 2003. Wild meat: the bigger picture. Trends in Ecology & Evolution **18**:351-357.

Mittermeier, R. A., N. Myers, J. B. Thomsen, G. A. B. da Fonseca, and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conservation Biology **12**:516-520.

Mloszewski, M. J. 1983. The Behaviour and Ecology of the African Buffalo. Cambridge University Press, Cambridge.

Molloy, L. M. 1997. Forest buffalo, *Syncerus caffer nanus*, and burning of savannas at Lopé Reserve, Gabon. Master's thesis, University of Florida, Gainesville, FL.

Moorman, R. S. 2006. Benefits of local residents visiting La Selva Biological Station, Costa Rica. Environmental Conservation **33**:89-99.

Mugangu, T. E., J. M.L. Hunter, and J. R. Gilbert. 1995. Food, water, and predation: a study of habitat selection by buffalo in Virunga National Park, Zaire. Mammalia **59**:349-362.

Murphy, P. G. 1975. Net primary productivity in tropical terrestrial ecosystems. Pages 217-231 in H. Lieth, and R. H. Whittaker, editors. Primary Productivity of the Biosphere. Springer-Verlag, New York.

Murphy, P. G. 1977. Rates of primary productivity in tropical grassland, savanna, and forest. Geo-Eco-Trop **1**:95-102.

Ndong, A. A. 2002. Synthesis of recent archaeological data about the settlement of the fauna reserve of Lope during the Holocene. Anthropologie **106**:135-158.

Newmark, W. D., and J. L. Hough. 2000. Conserving wildlife in Africa: Integrated conservation and development projects and beyond. Bioscience **50**:585-592.

Oslisly, R. 2001. The History of Human Settlement in the Middle Ogooué Valley (Gabon): Implications for the Environment. Pages 101-118 in W. Weber, L. J. T. White, A. Vedder, and L. Naughton-Treves, editors. African Rain Forest Ecology and Conservation. Yale University Press, New Haven.

Pérez-Barbería, F. J., I. J. Gordon, and C. Nores. 2001. Evolutionary transitions among feeding styles and habitats in ungulates. Evolutionary Ecology Research **3**:221-230.

Peyrot, B., R. Oslisly, S. Abdessadok, M. Fontugne, C. Hatte, and L. White. 2003. Paleoenvironments of the late Pleistocene and Holocene in the Lopé reserve (Gabon); Approach by geomorphologic, sedimentologic, phytologic, geochimic, and anthropogenic indicators of the environments recording the Lopé depression. Anthropologie **107**:291-307.

Pienaar, U. d. V. 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. Chapman & Hall, London.

Prins, H. H. T., and J. M. Reitsma. 1989. Mammalian biomass in an African Equatorial rain forest. Journal of Animal Ecology **58**:851-861.

Pullin, A. S., and T. M. Knight. 2001. Effectiveness in conservation practice: Pointers from medicine and public health. Conservation Biology **15**:50-54.

Redford, K. H. 1992. The empty forest. Bioscience **42**:412-422.

Ryan, S. J., C. U. Knechtel, and W. M. Getz. 2006. Range and habitat selection of African buffalo in South Africa. Journal of Wildlife Management **70**:764-776.

Ryan, S. J., C. U. Knechtel, and W. M. Getz. 2007. Ecological cues, gestation length, and birth timing in African buffalo (*Syncerus caffer*). Behavioral Ecology **18**:635-644.

SAS Institute Inc. 2002. SAS/STAT Software: Statistical analysis software version 9.1. SAS Institute Inc., Cary, North Carolina.

Shultz, S., and R. I. M. Dunbar. 2006. Both social and ecological factors predict ungulate brain size. Proceedings of the Royal Society B-Biological Sciences **273**:207-215.

Sidney, J. 1965. The past and present distribution of some African ungulates. Trans. Zoo. Soc. Lond. **30**:1-396.

Sinclair, A. R. E. 1977. The African Buffalo. A Study in Resource Limitations of Populations. University of Chicago Press, Chicago.

Steinmetz, R., W. Chutipong, and N. Seuaturien. 2006. Collaborating to conserve large mammals in Southeast Asia. Conservation Biology **20**:1391-1401.

Taolo, C. L. 2003. Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana. Dissertation, Norwegian University of Science and Technology, Trondheim, Norway.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. The Journal of Wildlife Management **70**:324-336.

Turner, W. C., A. E. Jolles, and N. Owen-Smith. 2005. Alternating sexual segregation during the mating season by male African buffalo (*Syncerus caffer*). Journal of Zoology **267**:291-299.

Tutin, C. E. G., L. J. T. White, and A. Mackanga-Missandzouu. 1997. The use by rain forest mammals of natural forest fragments in an Equatorial African savanna. Conservation Biology **11**:1190-1203.

Ukizintambara, T., L. White, K. Abernethy, and C. Thébaud. 2007. Gallery forests versus bosquets: conservation of natural fragments at Lopé National Park in central Gabon. African Journal of Ecology **45**:476-482.

van Hooft, W. F., A. F. Groen, and H. H. T. Prins. 2000. Microsatellite analysis of genetic diversity in African buffalo (*Syncerus caffer*) populations throughout Africa. Molecular Ecology **9**:2017-2025.

White, F. 1983. Vegetation of Africa: a descriptive memior to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. Unesco, Paris.

White, G. C., and R. A. Garrott 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA.

White, L., and K. Abernethy 1997. A Guide to the Vegetation of the Lopé Reserve Gabon. Multipress-Gabon, Libreville, Gabon.

White, L. J. T. 1994. Biomass of Rain-Forest Mammals in the Lopé Reserve, Gabon. Journal of Animal Ecology **63**:499-512.

Wilkie, D. S., G. A. Morelli, J. Demmer, M. Starkey, P. Telfer, and M. Steil. 2006. Parks and people: Assessing the human welfare effects of establishing protected areas for biodiversity conservation. Conservation Biology **20**:247-249.

Wilson, D. E., and D. M. Reeder, editors. 2005. Mammal Species of the World. The John Hopkins University Press, Baltimore.