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Spatiotemporal dynamics of forage and water resources shape space use of West African savanna buffaloes

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We investigated space-use patterns of the West African savanna buffalo (*Syncerus caffer brachyceros*), a little-studied subspecies occurring at the northern limit of the African buffalo's geographical range. This buffalo generally ranges in small herds (about 45 individuals) and has a low body mass (approximately 400 kg) relative to the Cape buffalo (*S. c. caffer*). We monitored the movements of 7 breeding herds in W Regional Park (Burkina Faso, Benin, Niger) using global positioning system collars and activity data loggers. Habitat selection was analyzed at both large (interseasonal) and small (intraseasonal) scales in a context where resources are segregated spatially at some times of year. Both biotic (primary production and vegetation types) and abiotic (timing of rainfall and surface water) covariates, and the extent to which neighboring herds shared space, were considered. In the dry season buffalo herds ranged close (within 5.3 ± 2.0 km, mean ± *SD*) to segments of permanent rivers. At the onset of the monsoon all herds but 1 (which had year-round access to suitable resources) performed a large (35 ± 10 km) directional movement in response to a large-scale gradient of primary production. Spatiotemporal dynamics of forage and water resources thus jointly stimulated interseasonal directional movements and shaped large (335 ± 167 km^2) annual home ranges. Furthermore, the establishment of home ranges in the wet season appears to be conditioned by a threshold (about 10%) in the availability of perennial grasses. Habitat-selection analysis at intraseasonal scale also underlines the key role played by perennial grasses for buffaloes. The spatial arrangements of home ranges of neighboring herds also suggest that interherd behavioral avoidance is a high-level constraint on foraging processes. The ability of the African buffalo to cope with contrasting environmental conditions throughout most sub-Saharan ecosystems highlights the high behavioral plasticity of this species.

Key words: behavioral plasticity, foraging, habitat selection, home range, normalized difference vegetation index (NDVI), space use, *Syncerus caffer brachyceros*, West African savanna buffalo

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Space-use dynamics and habitat selection by wild ungulates are shaped by the spatial and temporal heterogeneity of biotic and abiotic factors (Bailey et al. 1996; Fryxell et al. 2004). In addition, critical resources often are segregated spatially (e.g., the best places for feeding, drinking, resting, or lowering the predation risk might occur at great distances from each other), and such spatial segregation can vary across scales (Mueller et al. 2009). In this context animals are expected to adopt space-use and habitat-selection strategies that allow them to minimize detrimental effects of the main limiting factors so as to reach, at different scales, suitable trade-offs between several constraints and needs that must be addressed simultaneously (Godvik et al.

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2009; Massé and Côté 2009). We analyzed how space-use and habitat-selection patterns of the West African savanna buffalo (*Syncerus caffer brachyceros*) are conditioned by the spatiotemporal segregation of limiting resources and by spatial segregation between neighboring herds at both annual and seasonal scales.

The African buffalo is a large gregarious grazer common in most sub-Saharan ecosystems. This species has a variable morphology, and 4 subspecies have been recognized. So far, most studies have focused on the Cape buffalo (*S. c. caffer*), which is found in eastern and southern Africa. The Cape buffalo is characterized by a large body mass (400–800 kg) and herd sizes averaging 350 individuals. Several authors (Halley et al. 2002; Prins 1996; Ryan et al. 2006) have suggested that Cape buffalo herds might use exclusive home ranges, and Korte (2008a) suggested similar spatial arrangements for the forest-dwelling buffalo (*S. c. nanus*). By contrast, the ecology of the West African savanna buffalo remains poorly known. To date, knowledge of this subspecies comes from sporadic aerial surveys, trophy records, and a few pioneer publications (Boy 1958; East 1998; Stark 1986). The West African savanna buffalo differs from the Cape buffalo by having a smaller body mass (350–450 kg) and smaller herd sizes (40–50 individuals—Boy 1958; Cornélis 2000). The total population covers 13 West African countries and has been estimated to comprise 20,000–27,000 individuals (East 1998; Estes 1991).

Buffaloes are strongly water-dependent and need to drink daily (Sinclair 1977). In semiarid areas water availability often is restricted to a few permanent river segments during the dry season, and forage quality is low. In these conditions buffaloes face a trade-off between nutritional and water requirements (Redfern et al. 2003), and were shown on some occasions to perform relatively large interseasonal movements (Funston et al. 1994; Halley et al. 2002). In West Africa perennial grasses are a key foraging resource for grazers (Breman and De Ridder 1991; Stark 1986), because they generally present a higher feeding value (biomass, palatability, and nutrient content) than annual grasses. In addition, the energy stored in the root system of perennials allows a longer period of vegetative activity. In our study area perennials occur in high proportions mainly in remote areas where surface water is available only during the wet season. The buffalo herds living in our study area therefore were expected to face particularly severe conditions due to a spatiotemporal segregation in the availability of water and perennial grasses.

We investigated at both large (interseasonal) and small (intraseasonal) spatiotemporal scales how breeding herds use space, in relation to surface water locations and rainfall timing, and the extent to which they show marked preferences in habitat use and share space with neighboring herds. We monitored the movements of 7 herds for several months, including the dry–wet season transition, which was expected to generate the largest change in space-use patterns. We expected space-use patterns to be constrained strongly by access to surface water in the dry season and by spatial segregation between neighboring breeding herds all year. At the dry–wet season transition buffaloes were expected to shift to areas encompassing both higher quantities and qualities of forage, as measured respectively by the primary production and the proportion of perennials. At the intraseasonal scale buffaloes also were expected to display a preference for the areas characterized by high primary productivity and dominated by perennials.

Materials and Methods

Study area.—The field study was conducted from March 2007 to November 2008 in W Regional Park (WRP), a transboundary (Benin, Burkina Faso, and Niger) Biosphere Reserve located in the upper Niger Basin (11.37–12.58°N, 1.98–3.08°E). WRP covers 10,339 km^2 and supports a population of about 3,000 buffaloes. Despite occurring at a relatively low density in comparison with buffaloes in other ecosystems, the West African savanna buffalo is the most abundant ungulate of WRP (Bouché et al. 2003; Hibert et al. 2004).

The area exhibits a climatic gradient along a north–south axis from Sahelian to Sudanian climatic zones, with a mean annual rainfall ranging from 685 mm (north) to 850 mm (south). The wet season extends from April–May to September–October. Topographically, WRP is a peneplain drained by 5 main rivers (Fig. 1). After the onset of the dry season the eastern rivers generally dry out completely, and the Tapoa River shrinks to a permanent portion 4 km in length, located immediately upstream of a catchment dam. In contrast, Mekrou River dries out only partially, turning into an irregular chain of ponds. In the wet season a multitude of small depressions retain water throughout WRP, but most of them dry out rapidly, except for a few (<5) that are fed partially by natural springs or supplied with water pumps (Hibert 2007).

Vegetation in the northern section of WRP is dominated by *Combretum* shrub savanna (e.g., *Combretum* spp., *Terminalia* spp., and *Anogeissus leiocarpa*) with thorny acacias (*Acacia* spp.) and typical Sahelian trees (e.g., *Balanites aegyptiaca* and *Ziziphus mauritiana*). The southern section consists of a mosaic of shrubs and tree savannas more typical of Sudanian vegetation (e.g., *Isoberlinia doka*, *Daniellia oliveri*, and *Burkea africana*). Grasses consist mainly of annual and perennial Graminae. In the northern section annual species (e.g., *Loudetia togoensis*, *Pennisetum pedicellatum*, and *Andropogon pseudapricus*) constitute a quasi-continuous cover within which other vegetation types locally intersperse. In the northern (Sahelian) part of WRP perennial grasses (e.g., *Andropogon gayanus* and *Hyparrhenia* spp.) are confined mainly to the deeper soils of the bottomlands. Their contribution to herbaceous cover increases along a north–south gradient, and they tend to dominate the cover in the southern (Sudanian) part.

Sampling design.—An aerial survey to locate herds was performed in early March 2007 (dry season). For economic reasons this operation focused on areas where herds are known to concentrate during the dry season (Bouché et al. 2003). Five

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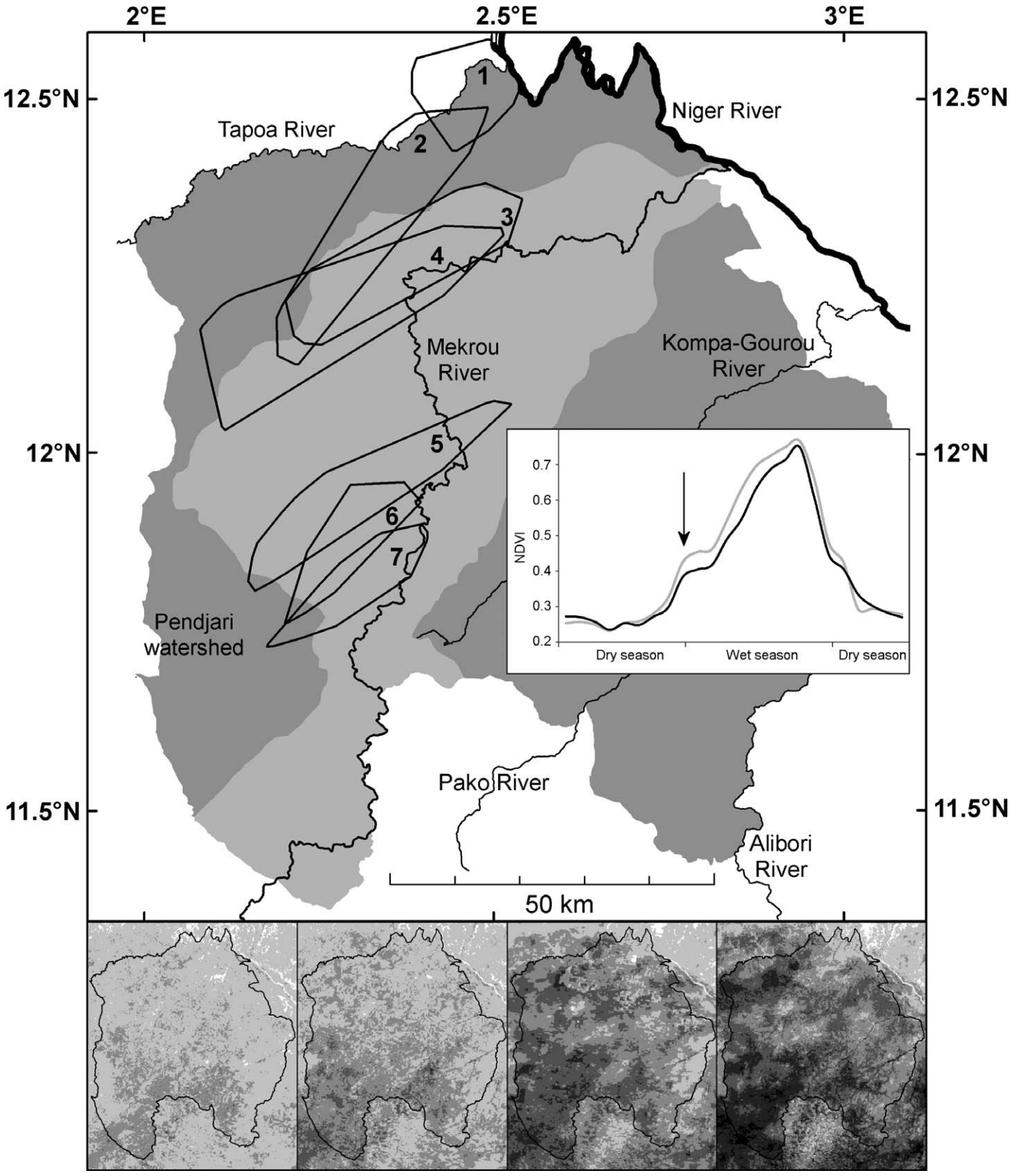


Fig. 1.—Study area, showing the annual home ranges (minimum convex polygons) of the 7 tracked herds of the West African savanna buffalo. The gray area corresponds to the W Regional Park (WRP) limits (within Benin, Burkina Faso, and Niger), with the watershed of the Mekrou River highlighted in light gray. Only the 5 major rivers are shown. The herd labels are written over the late dry season sections of the annual home ranges. At the onset of the wet season all herds except H1 shifted southwestward. The inset shows the 2007 normalized difference vegetation index (NDVI; primary production index) profile in the northeastern (black) and southwestern (gray) parts of the annual home ranges (the 2008 profile was similar). The arrow indicates the occurrence of the northeast–southwest directional movement. The 4 small bottom panels show the NDVI distribution over WRP on (from left to right) 7 April, 23 April, 9 May, and 25 May 2007; darker grays correspond to higher NDVI values. The seasonal shift started in late April–early May (see Table 2).

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ultralight aircraft simultaneously surveyed a 6-km-wide strip on each side of the 5 main rivers of WRP, along parallel transects spaced 1 km apart. All herds observed within the survey area (covering 52% of the WRP surface) were counted and located using a global positioning system. We counted all herds up to 100 buffaloes in size and estimated the size of larger herds to the nearest 10 individuals. We selected 7 breeding herds distributed in 3 groups of neighboring herds (H1 and H2, H3 and H4, and H5–H7) along a north–south axis (Fig. 1). The 1st group was located along the Tapoa River, and the 2 others were located in the north-central and south-central sections of the Mekrou River. This sample represented approximately 10% of the number of herds ranging in WRP.

Herds movements and activity monitoring.—One adult female in each herd was fitted with a global positioning system collar (4400M; Lotek Wireless Inc., Newmarket, Ontario, Canada), except for 1 herd (H6), which was tracked using a young male (about 1.5 years old, based on tooth eruption sequence—Grimsdell 1973). Animals of these age and sex categories are strongly bound to the herd (Mloszewski 1983; Prins 1996; Sinclair 1977), and their movements were assumed to be representative of those of the core herd members. The collars were equipped with an automatic release mechanism (drop-off).

Individuals were anesthetized via dart gun from a helicopter and from the ground. Anesthesia was induced by a combination of etorphine hydrochloride and xylazine, and reversed by injection of diprenorphine hydrochloride (Burroughs et al. 2006). The field operations conformed to the legal requirements of the countries in which they were carried out (authorization 284 CR/CS/07-12/DD from W Regional Park–EU Ecopas Program). Handling of the animals was carried out in accordance with guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Global positioning system collars were scheduled to acquire locations at 180-min intervals for 11 months beginning mid-March 2007. However, the collars of H4 and H6 failed after about 4 months. The tracking duration of H1 and H2 was extended to 20 months. For this purpose, a new adult female in these herds was anesthetized via dart gun and fitted in late November 2007 with a collar scheduled to acquire locations at 60-min intervals, and 1 more female was fitted in late April 2008 with a collar scheduled to acquire locations at 30-min intervals. We filtered out a few 2D (i.e., calculated using 3 satellites) and 3D (i.e., calculated using at least 4 satellites) fixes assumed to be unreliable because of a dilution of precision > 5 and > 15, respectively (Adrados et al. 2003) and finally kept about 94% (81–99%) of the fixes expected. Fixed-location tests implemented on a series of locations acquired at 180-min intervals showed that 95% of the filtered locations were within 37 ± 24 m (mean $\pm$ *SD*) of the previous one.

Activity and resting periods were monitored by a sensor included in the global positioning system collars quantifying movements of the head at 5-min intervals as 8-bit (0–255) activity values. Based on the way the activity signals varied in known situations, we considered that a buffalo was active for a given 5-min interval when the activity value was >15. In this way we computed the proportion of time that a herd was active between any 2 successive global positioning system fixes. We used these proportions to compute active utilization distributions (UDs) of seasonal home ranges (see below) and identify resting sites. Because buffaloes can move a little during resting phases but, as grazers, should continuously move when foraging, we considered that a distance (D) < 50 m between 2 successive global positioning system locations corresponded to a resting animal, even if the proportion of activity was not null (due to the possible disturbance of resting animals by flies). For technical reasons the activity data of H4 could not be downloaded. Based on activity and movement data obtained on the other herds, we set activity proportion to 0 for $D < 100$ m and to 1 otherwise.

Home-range and space-sharing computation.—We focused on the late dry season (LDS) and the early wet season (EWS) for which we have data for the 7 herds. These 2 seasons were expected to show the highest contrast, because they are separated by the onset of the monsoon. We computed the active UDs (up to the 0.95 isopleth) of the 7 herds in the LDS and EWS using a movement-based kernel density estimation method (Benhamou 2011; Benhamou and Cornélis 2010). This method improves the spatial resolution of UD estimates by considering activity times between serially correlated relocations rather than simply the spatial density of these relocations as if they were unlinked. This method also enables the elimination of estimation biases generated by topographical boundaries (Fig. 2) and makes it possible to assess space use (and thereby habitat use) more accurately than the classical (location-based) method (Worton 1989). We computed LDS and EWS UD volume overlaps to quantify the extent to which neighboring herds shared space and herds tracked for >1 year (H1 and H2) were faithful to their seasonal home ranges. For any 2 home ranges, I and J, volume overlap was computed as $O(I, J) = \Sigma_Q$ minimum$[F_Q(I), F_Q(J)]/0.95$, where F_Q is the fraction of UD in quadrat Q (Germain et al. 2008). Values range between 0 (no area shared) and 100% (identical UDs).

In addition, to get a coarse view of space use at the annual scale we estimated annual home ranges using minimum convex polygons based on all recorded locations. Because data obtained on herds tracked for long periods (11 months: H3, H5, and H7; or 20 months: H1 and H2) showed that buffaloes occupied areas located between LDS and EWS ranges at other times of the year, the minimum convex polygon method should provide annual home-range figures comparable to those obtained with this method in previous studies, even for the herds (H4 and H6) that could be tracked only during the LDS and EWS.

Although the LDS–EWS transition is temporally short (a few weeks), its recurrence each year and its consequences on spatial behavior for buffaloes involve large-scale phenomena. At this scale we focused on how the tracked herds shifted the locations of their seasonal home ranges within their annual home ranges. At a small scale, in contrast, we focused on the extent to which herds made preferential use of resources within their seasonal (LDS or EWS) home ranges.

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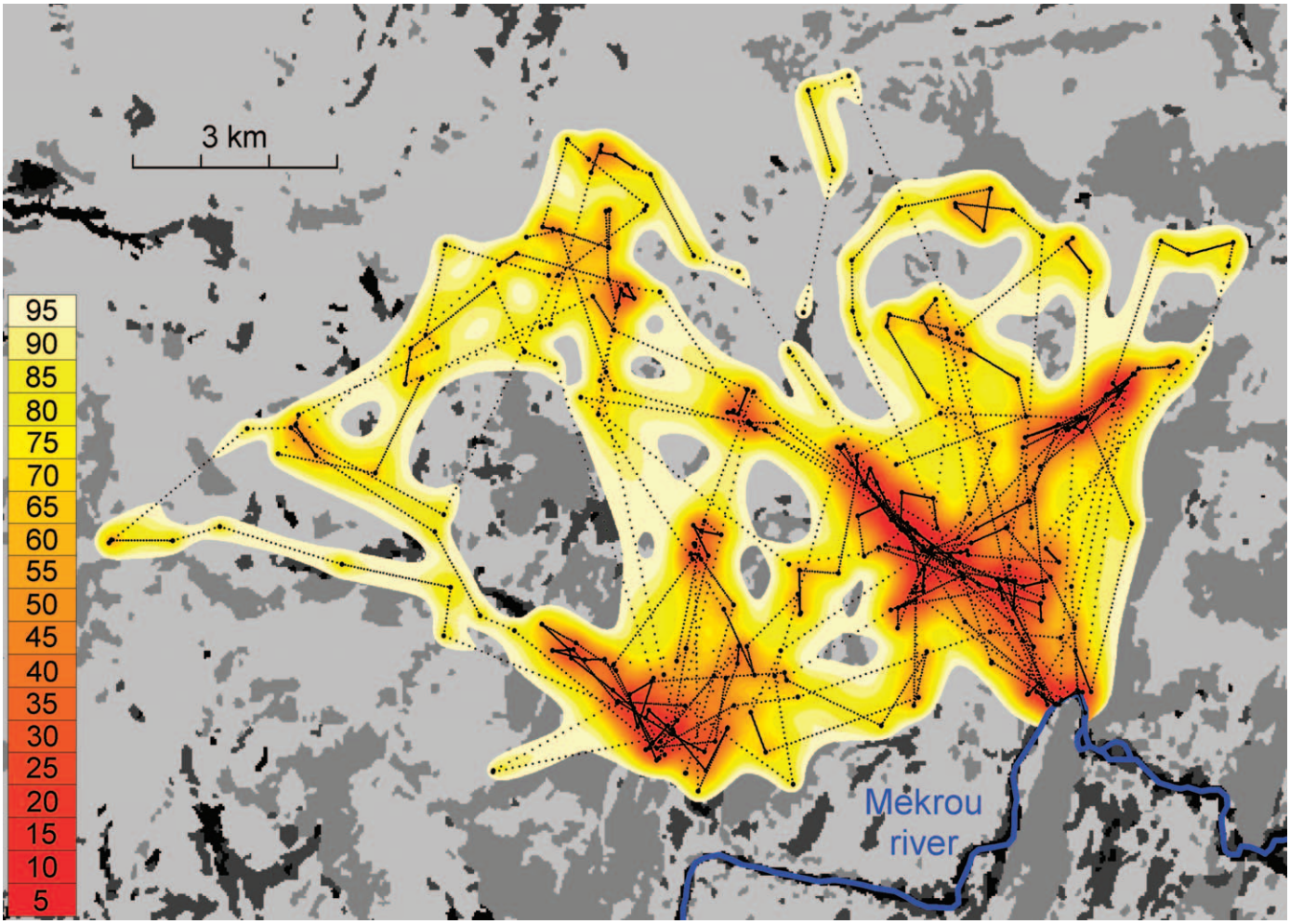


Fig. 2.—Utilization distribution (UD) of herd H3 during the late dry season 2007, computed using the movement-based kernel density estimation method (Benhamou and Cornélis 2010). Large black dots represent recorded locations, whereas small ones represent in-between interpolated locations. The Mekrou River, which never was crossed by this herd, was considered as a natural boundary in UD computation. The legend refers to the UD cumulative relative frequencies up to 95%: the value attributed to a given percentage, p, applies to the area comprised between p and p − 5% isopleths. Background (vegetation types): annuals in light gray, rocky exposures in medium gray, perennials in dark gray, riparian galleries in black.

Habitat-selection analyses.—Available environmental information consisted of 4 data sets. The first 2 were related to water distribution. The 1st one was a map specifying the locations of the permanent river segments and ponds in the LDS 2007 and 2008, as recorded in the field using a handheld global positioning system receiver. This data set was used to investigate water dependence of the West African savanna buffalo. The 2nd one listed the daily rainfall events recorded at 2 wardens' quarters located in the vicinity of buffalo LDS ranges. These records were used to investigate the relation between rainfall timing and large-scale movements of the tracked buffaloes.

The 3rd data set was a sylvo-pastoral vegetation map derived from a 30-m-resolution Landsat ETM7 satellite scene initially built up by De Wispelaere (2004) and updated in 2007. This map was used to test the preference of buffaloes for areas dominated by perennial grasses. Seven vegetation types initially have been recognized in our study area. Because some of them were quite uncommon and therefore not available to every herd, we derived a simplified, 4-type map by merging the 3 types dominated by annual grasses into ''annuals'' and the 2 types dominated by perennial grasses into ''perennials.'' The other 2 types, ''rocky exposures and iron pans with open vegetation'' and ''riparian galleries and thickets,'' were kept and will be referred to hereafter simply as ''rocky exposures'' and ''riparian galleries.'' We addressed habitat selection at the smaller scale (i.e., within seasonal home ranges) by comparing habitat use and availability. We assessed habitat availability within the 95% UD contours, active habitat use via the UDs (based only on activity time), and habitat use at rest from the resting locations. Because habitat selection for foraging and resting are not necessarily similar, computing habitat use by herds during activity and rest periods separately should provide results that are easier to interpret than those from an entire data set. Habitat preferences were investigated within the LDS and EWS home ranges through compositional

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analysis (Aebischer et al. 1993). In contrast, at the larger scale habitat use and availability could not be compared reliably because some parts of the study area might have been inaccessible to some herds due to potential constraints such as exclusive space use and water access. We therefore assessed the preference for perennials at the larger scale through the change in their relative availability from LDS to EWS home ranges when the water constraint was relaxed; that is, we looked at the extent to which buffalo herds shifted their home ranges from the LDS to the EWS in search of areas offering a better coverage of perennials when they were no longer constrained to exploit areas close to permanent river segments.

The 4th data set consisted of a 16-day composite normalized difference vegetation index (NDVI) series of maps at 250-m resolution (MODIS Mod13Q1 product, from January 2007 to December 2008; http://modis.gsfc.nasa.gov). It was used to investigate the role of primary production as a reliable space-use predictor at both the small (intraseasonal) and the large (interseasonal) scales. NDVI estimates the amount of active photosynthetic biomass (Pettorelli et al. 2005) and can be considered as a valuable proxy for net primary production in West African Sahelian grasslands (Prince 1991). Low-quality and missing data due to clouds or bad atmospheric conditions (6% of the entire data set) were rectified by temporal interpolation. We combined this data set with the vegetation map to generate a series of 16-day NDVI maps with a 30-m resolution by attributing a unique NDVI value to each vegetation type for each 16-day period. This value was computed as the mean of the NDVI values obtained on all 250 × 250-m quadrats, encompassing only the vegetation type considered. At the large scale NDVI temporal profiles were analyzed for the entire study area and related to the locations of the herds within their annual home ranges in the LDS and EWS. At the small scale we investigated whether NDVI can predict space-use intensity within LDS and EWS home ranges by determining the extent to which NDVI and UD values were correlated. For this purpose NDVI maps based on home ranges during the LDS and EWS were computed (at 30-m and 250-m resolutions) as the average of the initial 16-day NDVI maps weighted by the number of days of each NVDI map included in each seasonal home range.

Statistical analyses.—Computations of UDs (using the movement-based kernel density estimation method) and ratios used : available for the various habitat types were performed using the BRB/MKDE program (Benhamou 2011; Benhamou and Cornélis 2010; available upon request from SB). Compositional analysis of habitat selection rests on the computation of Wilks' distance Λ as the ratio of the determinant of the mean-corrected (i.e., centered) matrix of sums of squares and cross-products of the log-ratio (used : available) differences over the determinant of the raw matrix (Aebischer et al. 1993). With 7 herds and 4 habitat types, the variable $-7\ \mathrm{Ln}(\Lambda)$ followed a χ^2_3 law, which therefore was used to test whether a global effect of the vegetation heterogeneity on space use existed. Probabilities of rejecting the null hypothesis of no relative preference when comparing any pair of habitat types were based on exact permutation tests (2007 and 2008 values, for herds H1 and H2, were averaged to avoid pseudoreplication). These tests were performed using self-made Pascal programs. The fractions of UDs occurring within the nearest drinking location were computed using ArcGis (version 9.3.1; ESRI, Inc., Redlands, California). Minimum convex polygons were estimated using the ArcGis Geospatial Modelling Environment extension (www.spatialecology.com).

Table 1.—Annual home ranges of 7 West African savanna buffalo herds in W Regional Park (Niger, Burkina Faso, Benin) during 2007–2008 (H1 and H2) or during 2007 (H3–H7). The herd sizes correspond to the numbers of animals in the herds at the time of capture.

		Minimum convex polygon	
Herd identity	Herd size	Area (km^2)	Length (km)
H1	45	193	15
H2	70	440	50
H3	30	407	40
H4	44	620	53
H5	57	330	49
H6	19	186	28
H7	20	172	31

Results

Buffalo concentrations and herd size.—A total of 2,317 buffaloes was counted. Mean (± *SD*) herd size computed from the aerial survey data set was 46 ± 30 individuals (n = 50 herds) when excluding small (≤5) groups of bachelor males, and the biggest herd was estimated to contain about 150 individuals. In WRP the highest buffalo densities were found along the Mekrou River. In contrast, densities along the 3 main eastern rivers were quite low because of the unavailability of surface water in the dry season.

Large-scale space-use dynamics.—All herds except H1 performed a southwestern shift at the onset of the EWS. As a consequence, most annual home ranges showed a northeast–southwest elongated shape (Fig. 1), with a main axis length of 41.8 ± 10.5 km (mean ± *SD*, without H1). Their resultant size, as estimated approximately using the minimum convex polygons, was large (335 ± 167 km^2; Table 1). The shift in location between the LDS and the EWS clearly coincided with the coming of the 1st heavy rains (Table 2). It was performed by all herds, although it was nondirectional for H1. For the other 6 herds shifts (means ± *SD*s) corresponded to large (35.3 ± 10.1 km), fast (15.2 ± 5.6 km/day), and straight (beeline distance/path length travelled: 0.80 ± 0.09) southwestward ($-137^\circ \pm 10^\circ$) movements lasting a few (2.6 ± 0.7) days.

The analysis of the NDVI temporal profiles showed that both the launching and the orientation of the directional movement closely matched those of a large-scale NDVI gradient occurring within the study area during the 1st month of the EWS (Fig. 1). Primary production thus flushed earlier in the southwestern parts of annual home ranges than in their northeastern parts. Before and after this period NDVI values

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Table 2.—Annual shifts in movement observed in 7 West African savanna buffalo herds in W Regional Park (Niger, Burkina Faso, Benin) at the dry–wet season transition in 2007–2008 (H1 and H2) or during 2007 (H3–H7). In the ''Starting date'' column values in parentheses give the number of days between the beginning of the shift and the arrival of the 1st heavy rain (a negative value indicates anticipation). Orientation is measured trigonometrically (counterclockwise) from east. The last column gives the availability of perennial grasses before the seasonal shift (late dry season [LDS]) and after the shift (early wet season [EWS]). Parenthetical values in the last column correspond to the percentages of vegetation dominated by perennial grasses (perennials) in the areas temporarily prospected (but not settled) by herds H2 and H3.

			Distance (km)			Perennials (%)	
Herd	Starting date	Duration (days)	Traveled	Beeline	Orientation (°)	LDS	EWS
H1	27 April 2007 (0)	6.6	57	3	—	10	9
H1	21 May 2008 (0)	3.9	38	7	—	11	11
H2	28 April 2007 (1)	2.1	44	36	−123	16	19 (3)
H2	20 May 2008 (−1)	4.1	35	22	−126	17	23 (6)
H3	1 May 2007 (4)	2.9	38	33	−143	8	11 (6)
H4	27 April 2007 (0)	2.1	50	41	−146	10	11
H5	19 April 2007 (−2)	2.9	35	32	−145	18	53
H6	19 April 2007 (−2)	2.3	27	21	−125	22	31
H7	23 April 2007 (1)	2.0	19	15	−146	18	48

were almost uniformly low and high, respectively, over the entire study area.

The herds displayed contrasting ranging patterns at the endpoint of the directional shift, depending on the proportions of perennials encompassed in the areas they reached. During the LDS, when herds were confined to the neighborhood of permanent river segments, available habitats corresponded mainly to annuals (58–70% for H2–H7) or rocky exposures (57% for H1). The proportion of perennials available within the LDS home range was therefore limited at this time of year (8–22%). Just after the shift, 4 herds (H4–H7) established EWS home ranges close to the endpoint of the shift in areas where the proportion of perennials was higher (Table 2). In contrast, the 2 other herds that undertook a directional movement (H2, both in 2007 and 2008, and H3) reached areas containing lower proportions of perennials and gradually retreated through a transitory phase lasting 2–3 weeks. During this phase these 2 herds did not establish a home range but progressively moved northeastward. These 2 herds eventually established their EWS home ranges in areas close to the riverine areas they exploited during the LDS. The single herd that did not make any directional shift, H1, performed a rotational movement within its annual home range (both in 2007 and in 2008). It foraged during the LDS along the Niger River, whose banks are covered by *Echinochloa stagnina* (burgu or hippo grass), a perennial grass providing excellent pasture when the waters recede. This herd then moved in the EWS to a series of nearby areas providing at this time a green flush of another perennial grass, *Andropogon gayanus*, and finally came back along the Niger River during the early dry season. Whatever the patterns of space use, herds settled EWS ranges in areas encompassing at least 9% of perennial grasses.

Small-scale habitat preferences.—During the LDS, when surface water availability became limited, space-use patterns clearly confirmed the expected dependence of West African buffaloes on water: 95% of each UD occurred within 5.3 ± 2.0 km (mean ± *SD*) of surface water, and 50% occurred within 1.4 ± 0.6 km (Fig. 3). Unexpectedly, buffaloes did not range evenly on both sides of the permanent river segments. The major fractions (mean ± *SD*) of the UD (87% ± 11%) were located on one side (H1 was excluded from calculations, because the Niger River cannot be crossed).

At the small scale variations in NDVI could explain only 2% on average of variations in space use within the LDS and EWS home ranges, both at the initial (250 m) and improved (30 m) resolutions, whatever the season considered. Contrary to what we had hypothesized, buffalo space use at the small scale therefore could not be predicted by a global index of primary production.

Use of the 4 habitat types within both LDS and EWS home ranges was significantly different from random, whether considering active use or use for resting (Table 3). The percentage (mean ± *SD*) of active-use time was slightly different between the 2 seasons: 57% ± 8% during the LDS and 65% ± 10% during the EWS. During the LDS habitat selection appeared to be similar for activity and resting:

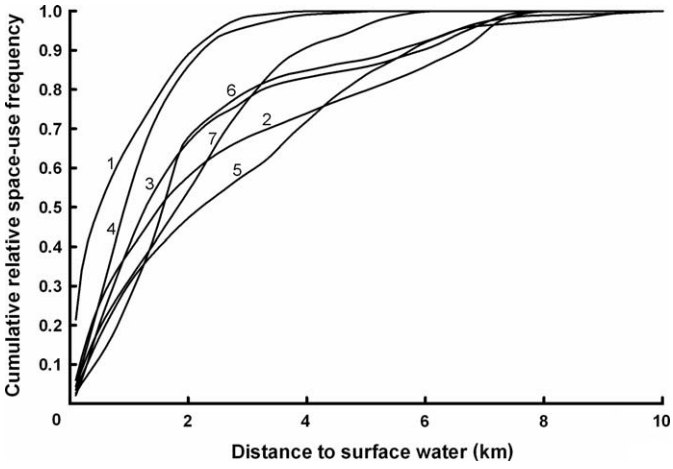


Fig. 3.—Cumulative relative space-use frequency of 7 buffalo herds global positioning system–tracked in W Regional Park (Niger, Burkina Faso, Benin) as a function of distance to surface water (river pools and ponds) during the late dry season 2007.

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Table 3.—Vegetation selection of 7 West African savanna buffalo herds in W Regional Park (Niger, Burkina Faso, Benin) during 2007–2008, showing normalized values of the relative preferences (mean ± *SE*), during activity and resting periods in the late dry season and early wet season, for the 4 vegetation types. Habitat types with a value larger or smaller than 0.25 are relatively preferred or avoided, respectively. Statistical tests showed that the relative preferences or avoidances were globally significant ($P < 0.05$, $n = 7$, *d.f.* = 3) in all cases. Gal = riparian galleries and thickets; Per = vegetation dominated by perennial grasses; Ann = vegetation dominated by annual grasses; Roc = rocky exposures and iron pans with open vegetation.

	Late dry season		Early wet season	
	Active	Resting	Active	Resting
Gal	0.33 ± 0.03	0.37 ± 0.04	0.26 ± 0.02	0.14 ± 0.07
Per	0.29 ± 0.03	0.38 ± 0.03	0.32 ± 0.03	0.36 ± 0.01
Ann	0.20 ± 0.02	0.18 ± 0.03	0.23 ± 0.01	0.33 ± 0.07
Roc	0.18 ± 0.02	0.07 ± 0.02	0.19 ± 0.02	0.17 ± 0.06
χ^2	9.75	17.15	14.24	12.59
P	0.02	<0.01	<0.01	<0.01

buffalo herds tended to prefer riparian galleries and perennials and avoid rocky exposures (especially for resting; Table 4). The preference of active herds for perennials over annuals was marginally nonsignificant, however. During the EWS buffalo herds clearly preferred perennials while active and both perennials and annuals for resting. In contrast, riparian galleries and rocky exposures tended to be avoided. The relative preference for perennials, however, was not significantly higher in the EWS than in the LDS (exact permutation test: $P > 0.10$).

It is also worth noting that the overuse of riparian galleries during the LDS resulted from a recurrent need to drink rather than from a deliberate search for riparian vegetation. Riparian galleries were significantly overused during the LDS: they represented 4% ± 1% (mean ± *SD*) of the home-range areas at this time of the year but were used 6% ± 1% of activity time (exact permutation test comparing riparian galleries and the rest of the home range: $P = 0.015$). However, this did not hold true when considering only riparian galleries without available surface water (corresponding to 64% ± 14% of the riparian galleries at this time of the year: $P > 0.10$). The direct comparison between riparian galleries with and without surface water showed that the former were significantly more exploited than the latter ($P = 0.04$).

Space sharing and spatial fidelity.—The drawing of annual home ranges as minimum convex polygons (Fig. 1) suggested a substantial overlap among areas used by the different herds. However, volume overlap computations of LDS and EWS UDs showed that herds tended to move within exclusive areas. Although H1 and H2 exploited contiguous areas along the Tapoa River all year, they never came into contact, and the maximum UD overlap was almost null (<2%). Similarly, H5–H7 exploited contiguous areas along the west side of the Mekrou River during the LDS and more southwestern areas in the EWS, but the maximum UD overlap reached only 7% (between H6 and H7 in the EWS; all other overlap values were fully or almost null). However, a quite large UD overlap (21%) existed between H3 and H4 during the LDS, and the 2 herds might have come in very brief contact (within 500 m for <1 h) 4 times at time intervals of at least 1 week. The herds we tracked during 20 months (H1 and H2) also were relatively faithful to the sites they exploited in successive years, both in the LDS and in the EWS, with UDs between years overlapping from 24% to 70%.

Table 4.—Probabilities based on exact permutation tests of rejecting the null hypothesis of no relative preference when comparing any pair of habitat types used by West African savanna buffalo herds ($n = 7$), during activity and resting periods in the late dry season (LDS) and early wet season (EWS), in W Regional Park (Niger, Burkina Faso, Benin). Gal = riparian galleries and thickets; Per = vegetation dominated by perennial grasses; Ann = vegetation dominated by annual grasses; Roc = rocky exposures and iron pans with open vegetation.

		Gal		Per		Ann	
		Active	Resting	Active	Resting	Active	Resting
Per	LDS	>0.10	>0.10				
	EWS	>0.10	0.03				
Ann	LDS	0.02	0.05	0.08	0.02		
	EWS	>0.10	>0.10	0.02	>0.10		
Roc	LDS	0.02	0.02	0.03	0.02	>0.10	0.02
	EWS	0.05	>0.10	0.03	0.08	>0.10	>0.10

Discussion

We showed how space-use dynamics of West African buffalo breeding herds were related to dynamics of forage and water resources. During the LDS the herds we tracked were forced to range close to permanent river segments. The onset of the monsoon induced a marked gradient in global primary production (NDVI) occurring at a large spatial scale and relaxed the constraint of water access. All herds then performed a shift in location in the gradient direction at the transition from dry to wet season, except one herd, which had access to suitable conditions (both forage and water) all year. Habitat-selection analysis emphasized the importance of perennial grasses at both intra- and interseasonal scales.

The shifts in location between the LDS and the EWS performed by the herds we tracked resulted in larger (172–620 km^2) and more elongated annual home ranges than usually observed for this species (Ryan et al. 2006). To our knowledge, directional movements as large as those performed by 6 of the 7 herds we studied at the transition between the dry and the wet seasons have not been documented elsewhere for African buffaloes, except in Botswana (Halley et al. 2002). In West Africa the onset of the EWS is triggered every year by an intertropical rain front that progresses northeastward (Lamb and Lele 2006). Consequently, primary production starts to increase a few weeks earlier in the southwestern part than in the northeastern part of our study area, resulting in a southwest–northeast gradient in primary production at a large spatial scale, but limited to a narrow temporal window. Within this window

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primary production appeared to have a high predictive value for large-scale buffalo movements. Also, one-third of the herds shifted southwestward a few days before the rainfall reached their LDS home ranges and so appear to have detected rainfall events occurring 30–35 km away. Such an ability to track large-scale environmental changes is a key parameter in the understanding of movement and distribution patterns of free-ranging savanna ungulates (Holdo et al. 2009).

Although the gradient in primary production appeared to be the main determinant of large-scale shifts at the onset of the EWS, its action clearly was modulated by the proportion of perennials available. Buffalo herds chose to establish EWS home ranges only at locations where this proportion reached a 9% threshold. The herds accessing areas encompassing lower proportions of perennials did not settle there but wandered for a few weeks without establishing new home ranges. For these latter herds it seems that the removal of water constraints opened transitory foraging opportunities on plateaus that provided more food resources than the depleted bottomlands.

Contrary to what occurred at a large spatial scale, we found within seasonal home ranges that NDVI had no predictive value for buffalo space-use patterns. Because NDVI measures the photosynthetic activity of woody and herbaceous vegetation without distinction, this covariate might be inappropriate to predict space-use patterns of grazers at a small spatial scale (Holdo et al. 2009; Ito et al. 2006). In contrast, the herds we tracked displayed at the small spatial scale a clear preference for areas dominated by perennials, both in the LDS and the EWS. In the LDS active buffalo herds appeared to show higher preferences for riparian galleries, but this was due largely to the presence of water. Furthermore, at this time of year the low quality of habitats, including areas dominated by perennials, forces buffaloes to feed less selectively and switch part of their diet to browse on trees potentially associated with both types of grasses (Sinclair 1977; Stark 1986). In the EWS perennials clearly were selected, stressing the key role of this type of grass to bridge the gap of the dry–wet season transition.

Abiotic factors, such as distribution of surface water and rainfall patterns, determine distribution and movement patterns of wild ungulates at large scales (Boone et al. 2006; Boyce et al. 2003; Fortin et al. 2003), and most authors (Bailey et al. 1996; Senft et al. 1987) agree that they act as a higher-level constraint within which foraging mechanisms operate. Our results suggest that social relationships between herds also might act as a high-level constraint on habitat selection all year by preventing herds from accessing forage and water resources occurring within home ranges of other herds. Neighboring herds tended to display contiguous (i.e., adjacent) home ranges year-round. In the absence of such constraints, the dependence on overdispersed resources, such as drinking locations in the LDS, would result both in disjunct home ranges for herds exploiting distant resources and in high space-sharing for herds exploiting a common one. In our study neighboring herds exploiting common segments of permanent rivers clearly tended to segregate their space use. Moreover, based on elementary optimal foraging principles, we expected buffalo herds to center their LDS home ranges on permanent river segments, but results showed that they never ranged evenly on both sides. Another possibility would be that herds simply tend to avoid areas depleted by neighboring herds, but we did not find any evidence of forays made by a given herd within the home range of a neighboring one that would suggest prospective assessments of forage quality. Spatial segregation between neighboring herds therefore was most likely to rely on behavioral avoidance (i.e., territoriality). The quasi-absence of direct contacts suggests that home ranges were not defended actively, although spatial segregation of the herds might have been helped by scent marks. This suggests that buffaloes found a way to exploit exclusive home ranges without spending substantial energy in their defense.

Considerable variation of herd size occurs in African buffalo, probably in relation to the quality and availability of grass cover. The smallest herds (10–20 individuals) were reported in forest–savanna mosaic landscapes of central Africa (Korte 2008b) and the largest (up to 2,000 individuals) in the floodplains of eastern and southern Africa (Prins 1996; Sinclair 1977). Within populations differences in herd sizes also were observed, and Korte (2008b) and Winnie et al. (2008) suggested that herd sizes tend to be smaller where food resources are poor. Similar trends were observed in the African elephant (*Loxodonta africana*—Barnes 1983; Leuthold 1976). The mean herd size we found in WRP buffaloes was small, about 45 individuals, similar to herd sizes previously estimated in this subspecies (Boy 1958; Rouamba and Hien 2004; Stark 1986). Body mass in the West African savanna buffalo also is about one-half that of the Cape buffalo, leading to a biomass per herd approximately 15 times less for the former. In contrast, annual home-range sizes in our study area were larger than those reported for Cape buffalo, although in part due to a large seasonal shift. Small body and herd sizes of West African savanna buffaloes might reflect adaptations to a poor-quality environment, allowing them to better meet energetic requirements. The large sizes of annual home ranges we observed are not necessarily inherent to this subspecies, however, because they result from the particular spatiotemporal segregation of forage and water occurring in our study area. The ability of the African buffalo to cope with contrasting environmental conditions throughout most sub-Saharan ecosystems, by modulating a large array of biological traits, highlights a high degree of behavioral plasticity.

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