

Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna

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Competitive relationships among mobile animals may be expressed through dynamically changing spatial relationships over different time frames. Less common species that are apparently inferior competitors may be able to coexist with more abundant species by concentrating in regions of the landscape little utilized by the former at spatio-temporal scales from annual or seasonal ranges to the specific foraging localities exploited at different stages of the annual cycle. Spatial relationships may be influenced further by dependencies on other resources, predation risks and facilitatory interactions under certain conditions. Our study aimed to determine whether competition with more abundant zebra and buffalo restricted the abundance of sable antelope in a region where these three tall-grass grazers overlapped in their herd distributions. We tracked the simultaneous movements of animals representing herds of these species over two dry seasons and one wet season using GPS-GSM collars, and estimated seasonal or monthly range extents and their overlap. We also compared daily separation distances between these animals against the null pattern expected if their movements had been independent, and assessed how prior grazing by buffalo influenced the subsequent use of these localities by sable. The range of the sable herd was mostly separated from the seasonal range of the buffalo herd during the late dry season of 2006 and throughout the dry season of 2007. Seasonal home ranges of zebra herds overlapped partially with the range of the sable herd during most of the year. Even during times when their ranges overlapped, sable were rarely recorded within < 1 km of the buffalo herd. Prior grazing by buffalo beyond a threshold level inhibited later use of these localities by sable, but the sable were nevertheless able to exploit places that were little utilized by buffalo at that time. Sable were less able to evade overlap with the small, mobile zebra herds, and hence more vulnerable to competitive exclusion by zebra than by buffalo. Our findings demonstrate how less abundant species can restrict competition from more abundant competitors through dynamic spatial partitioning in regions where their home ranges overlap.

According to fundamental ecological principles, species cannot coexist if they depend on the same resources in the same places at the same time. Hence resource partitioning occurs via distinctions in resource selection or in the places or times when shared resources are exploited (Chase and Liebold 2003). Species that are superior competitors may concentrate their resource use in the most favourable localities, potentially leaving lightly exploited gaps that can be exploited by inferior competitors as refuges from competition (Inouye 1999). In other circumstances, dominant species may expand their resource use to the places occupied by inferior competitors following the depression of resources in their favoured habitats (Rosenzweig 1991). Especially for large herbivores, resource selection may be expressed at a hierarchy of spatial scales, from landscape regions occupied to the plant species and parts consumed (Senft et al. 1987). Mobile consumers respond also to temporal variation in resource features associated with seasonal cycles of

growth and senescence by plants, affecting food availability and its nutritional quality, with availability affected further by the feeding impacts of other species with overlapping resource dependencies (Ritchie 2002). Access to food may be restricted further by requirements for other resources, such as surface water for drinking (Western 1975). A further influence comes from spatial variation in exposure to predation, potentially affected by the presence of other species that share a common predator (Holt 1977).

This complex spatio-temporal milieu has made it difficult to establish the mechanisms preventing or enabling the coexistence of species with similar resource requirements, including notably the diverse assemblage of grazing and browsing ungulates occupying African savanna ecosystems. Past studies have elucidated how grazers favouring distinct grass heights can show shifting spatial segregation over gradients in soils and associated grass types (Bell 1970, Murray and Illius 1996). Grazing by larger species can also

facilitate food access by smaller herbivores through promoting regrowth of more nutritious foliage (McNaughton 1976). Furthermore, smaller species may concentrate in smaller patches offering higher quality food than those exploited by larger species (Ritchie and Olff 1999, Crooms and Olff 2006, Laca et al. 2010).

However, little attention has been directed towards establishing how ungulate species that are similar in their grass height preference can coexist (but see Arsenault and Owen-Smith 2011, Kleynhans et al. 2011). Certain species typically associated with relatively tall grassland have become a source of conservation concern because of their declining populations, including roan antelope *Hippotragus equinus*, sable antelope *Hippotragus niger* and tsessebe *Damaliscus lunatus* in the Kruger National Park (Harrington et al. 1999, Owen-Smith and Ogutu 2003), and hartebeest *Alcelaphus buselaphus* in northern Kenya (Georgiadis et al. 2007). These low-density species are vulnerable to being out-competed by more abundant species depressing grass height through their grazing pressure. They are also susceptible to predator-mediated declines when increases in the abundance of high-density species attract more predators into the habitats that these rarer antelope occupy (Owen-Smith and Mills 2006).

New opportunities to untangle the interplay of competitive interactions among large herbivores have been opened through developments in Global positioning system (GPS) telemetry (Cagnacci et al. 2010). This technology enables simultaneous spatial relationships among samples of animals fitted with GPS collars to be documented in fine temporal detail over complete annual cycles or even longer periods. Hierarchical resource selection operating over various spatiotemporal scales has been described from GPS tracking of the movements of single ungulate species (Fryxell et al. 2008), but not previously documented for several potentially competing herbivore species with overlapping ranges.

Our study was aimed broadly at establishing the factors restricting the abundance of sable antelope in the Kruger National Park (KNP). Sable antelope showed a patchy distribution concentrated in the northern and western regions of the park (Chirima et al. unpubl.). Across this broad landscape, the occurrence of sable herds was negatively related to high densities of impala and wildebeest *Connochaetes taurinus*, but showed substantial overlap with the distribution of zebra *Equus quagga* and buffalo *Syncerus caffer* (Chirima et al. unpubl.). Moreover, sable, zebra and buffalo share a similar dependency on relatively tall grass and utilised many of the same grass species (Macandza et al. unpubl.).

The specific investigation we report here was aimed at establishing the extent to which temporal and spatial partitioning in the use of resources by these three grazers restricts the extent of competitive overlap and enables the coexistence of sable antelope. Our analysis addresses seasonal or shorter term range use and its implications for dynamic resource partitioning. Our starting hypotheses were as follows:

1. Sable would concentrate their use of space in local sections of the regional landscape infrequently used by buffalo and zebra.
2. Range overlap between sable and the two more abundant grazers would decline from the wet season into the

dry season in response to intensifying interspecific competition for diminishing food resources.

3. Sable would avoid foraging in those localities that had been grazed by buffalo or zebra earlier in the seasonal cycle, to restrict resource competition.
4. Alternatively, if grazing facilitation was influential, sable would tend to favour areas previously grazed by the larger buffalo, particularly during the wet season when grass regrowth occurs.

Material and methods

Study area

Our study area extended from Punda Maria Camp (22°68'S, 31°018'E) in northern Kruger National Park southwards towards the Mphongolo River, encompassing an area of about 500 km². A total of around 200 sable counted there in 1988 had decreased to two separate herds totalling 30 animals by late 2001 (Henley 2005), and to a single breeding herd of about 20 animals by the commencement of our study in mid-2006. A large herd of about 400 buffalo was present, an increase from 140 individuals recorded in 1993. We estimated a local population of 200–300 zebra, down from a peak of around 600 zebras counted in 1989. Earlier aerial counts indicated local totals of about 700 impala and 50 waterbuck, but no wildebeest, tsessebe or roan antelope (Viljoen 1993).

The vegetation was predominantly mixed *Combretum* savanna woodland on sandstone, mixed sandstone–basalt and granite substrates, and *Colophospermum mopane* woodland or shrubland on basalt- or shale-derived soils (Gertenbach 1983, Venter 1990). During the 2005/2006 rainfall year (July–June), Punda Maria camp received higher rainfall (743 mm) than the long term (1960–2007) mean rainfall of 560 mm, while 2006/2007 was a dry year (419 mm). Over 80% of the annual total rainfall generally falls during the wet season spanning October to March. The first substantial rains of the wet season occurred in early November in 2006, and at the end of September in 2007. Surface water became restricted mostly to pools in the Mphongolo River by August in 2006 in both years.

Study design and data collection

In late May 2006, GPS-GSM collars (Africa Wildlife Tracking; <www.awt.co.za>) were placed on three adult females in the sole sable herd of about 20 animals, four female zebra in separate herds numbering 5–7 animals each, and two female buffalo together in the sole buffalo herd occupying the study area, numbering around 400 animals. The buffalo herd was usually split between sub-units of approximately 200 individuals, each fortuitously represented by one of the collars. To extend coverage through a second dry season, in June 2007 new collars were fitted to an adult female in each of the same sable and buffalo herds, while additional collars were placed on female zebra in two new herds within the range of the sable herd. Because herds of these species are typically cohesive (Estes 1991, Skinner and Chimimba 2005), we assumed that the movements of these collared

females represented the movements of their herds. The schedule set was for GPS coordinates to be recorded routinely every six hours at 2:00, 8:00, 14:00 and 20:00 between June 2006 and September 2007. Consequently, the study period spanned two dry seasons (2006 and 2007) and one wet season (2006/2007). Two of the collars represented the movements of the sable herd and the buffalo herd through both dry seasons. Four zebra collars operated through the dry season of 2006, and five throughout the 2007 dry season. Accuracy of the GPS locations was generally < 10 m, and fewer than 5% of scheduled locations were missed. Because the collared zebra herds represented only a sample of the total number of zebra herds using the study area, we also recorded the locations of all zebra herds seen while conducting field observations, to ensure that the overall presence of zebra did not deviate detectably from that represented by the collared animals.

Data analysis

To document broad overlap in species presence, we mapped total annual ranges of each species as 100% minimum convex polygons (MCP), including all GPS herd locations provided by all of the collars representing each species. To reveal seasonal distinctions in range utilization patterns, we mapped two dimensional range utilization distributions using the adaptive kernel method (Worton 1989) and h-reference to select the smoothing parameter in Home Range Tools extension for ArcGIS ver. 9.3 (Rodgers et al. 2007). The locations used to assess overlap in resource utilization were restricted to the times of the day when foraging activity was likely to predominate, i.e. 8:00 and 20:00. Following Borger et al. (2008), we estimated the total range and the core range at species level using the 90% and 50% kernel probability contours, respectively. Areas enclosed by these contours were estimated using Hawth's Tools for ArcGIS 9.3. GPS coordinates were projected into WGS 1984 datum, UTM zone 36S, before the analysis.

Seasonal divisions were based on shifts between distinct home ranges by the sable antelope herd, omitting transitional periods. Accordingly, we distinguished the following seasonal blocks: early dry season of 2006, June–September; late dry season of 2006, 5 October–8 November; wet season, 15 November 2006–April 2007; early dry season of 2007, May–July; and late dry season of 2007, 19 August–October 2007.

We used the proportional overlap between the monthly or seasonal species distribution ranges as a measure of spatial separation between species (Doncaster 1990, White and Garrott 1990, Kernohan et al. 2001), for both the total and core ranges using ET Geowizards in ArcGIS 9.3. Following White and Garrott (1990) and Kernohan et al. (2001), spatial overlap was calculated by dividing the extent of the range shared between sable and zebra or buffalo by the extent of either the total or the core sable range, using the following formula:

$$HR_{A,B} = \frac{AB}{A} \times 100$$

where $HR_{A,B}$ is the percentage of the sable range shared with zebra or buffalo, AB is the extent of the range shared

between sable and zebra or buffalo, and A is the extent of the sable range.

To establish daily spacing between the sable herd and buffalo or zebra herds during foraging periods, we calculated the distance between the locations of the sable herd at 8:00 and 20:00 and the locations of each buffalo and zebra herd recorded at these same times, respectively. Distances between concurrent herd locations were estimated using Hawth's Tools in ArcGIS 9.3. Exploratory analysis showed that range overlap between sable and zebra or buffalo was very low during the late dry season. Therefore, we restricted the analysis of daily separation between species to the wet and early dry seasons. For statistical analysis, we grouped separation distances between simultaneous herd locations into 1 km bins and calculated the frequency distribution of separation distances during periods when the core ranges of the species overlapped. Sable and buffalo overlapped in their core ranges in July 2006, December 2006 and March 2007, while overlap between sable and zebra herds occurred in June 2006 and July 2007. To establish whether the locations of the sable herd during these months were independent of where buffalo or zebra herds were present at that time, we randomized the order of sable locations during these months (minimum 30 trials), then re-calculated the separation distances and compared the frequency distribution of separation distances between the observed and the random ordering of sable locations using the Kolmogorov–Smirnov (K-S) two sample test in SYSTAT 11.0 for Windows.

To establish short-term movement responses by sable to the proximity of buffalo or zebra, we restricted the analysis to months when ranges of buffalo and zebra herds overlapped with the range of the sable herd. For these months, we estimated separation distances between sable and buffalo or zebra locations concurrently at 8:00. To establish whether

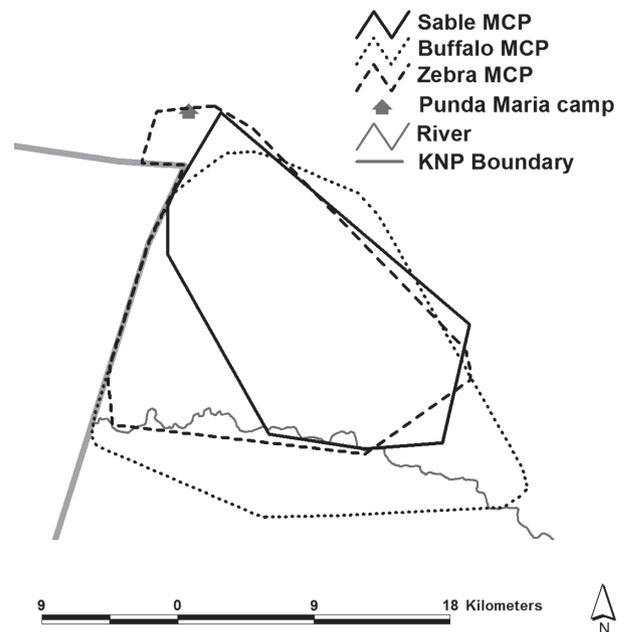


Figure 1. Annual minimum convex polygons of species ranges showing the broad overlap in space occupation among the collared herds of sable, zebra and buffalo.

sable moved away following close contact with buffalo or zebra herds, we compared the subsequent diel displacement distance of the sable herd when it had been less than 1 km from buffalo or zebra with the median diel displacement of the sable herd for that month. The diel displacement was the distance between sable herd locations at the same time (specifically 8:00) on successive days.

To establish how prior foraging by a buffalo herd influenced the subsequent use of local grid cells by sable, we plotted the monthly sable records within each grid cell amalgamated into three-month seasons against the accumulated number of buffalo records within these cells since

the start of the wet season prior to the sable presence. We assigned GPS locations to grid squares approximately 1×1 km using latitude and longitude coordinates. The records used were for the morning (8:00) and evening (20:00) times of day when the animals were most likely to be foraging. Hence each point represents a half-day, and points considered were restricted to the seasonal home range of the sable herd. Each buffalo location record was assumed to represent a herd of approximately 200 animals. In the few cases where a buffalo herd moved into a cell that had earlier been occupied by the sable herd during that month, records of sable presence were scored separately for the

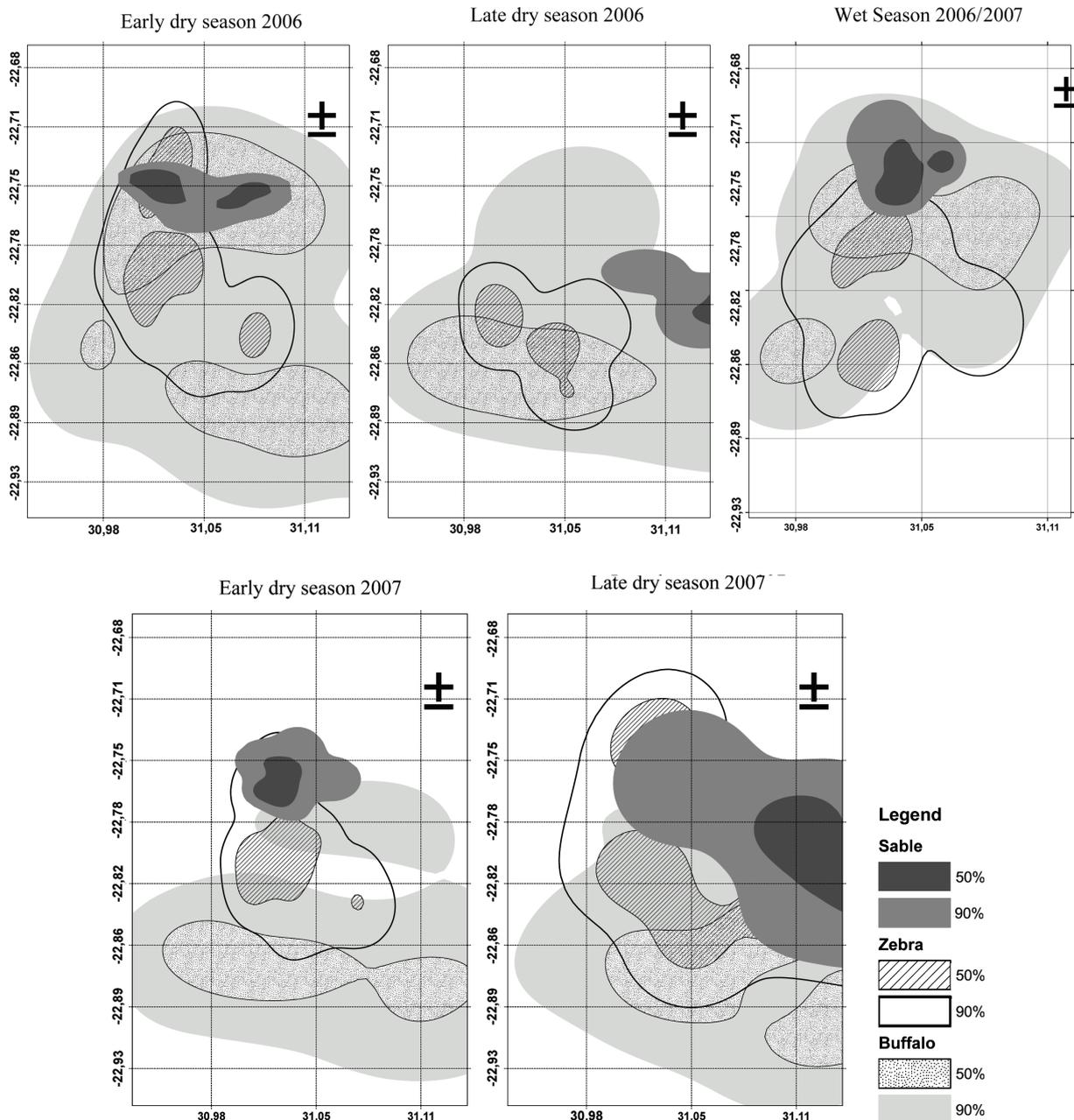


Figure 2. Seasonal total (90%) and core (50%) utilization distributions of the sable herd, and all collared buffalo and zebra herds in the study area during different seasons: Early dry season 2006 (June–September), Late dry season 2006 (5 October–8 November), Wet season (15 November 2006–April 2007), Early dry season 2007 (May–July) and Late dry season 2007 (19 August–October). Dark stippling and dark grey shading represent sable core and total ranges, respectively. Stripes and line fill represent zebra core and total ranges, respectively. Light stippling and light grey shading represent buffalo core and total ranges, respectively.

period before and after the arrival of the buffalo. This analysis was restricted to the 2006/2007 seasonal cycle, because the period spanned by our GPS tracking did not cover the wet season of 2005/2006. The start of the wet season, representing commencement of grass growth, was taken to be the beginning of November. To assess the statistical robustness of patterns, we compared the proportion of cells with more than one record of sable presence above and below a pivotal region of 2.5–3 buffalo herd grazing days, using a simple χ^2 -test. We recognise that that this approach does not strictly meet the requirements for null hypothesis testing because it was ad hoc, and because successive GPS locations were not independent. We did not undertake a similar analysis for zebra because our collared zebra herds represented a small sample of the total number of zebra herds in the study area.

Results

Broad range overlap

The two collared buffalo shared a common annual range that encompassed almost the entire extent of the study area, and extended beyond it to the south. The range spanned by the various collared zebra herds also covered virtually the entire study area. The home range occupied by the sable herd was nested mostly within that of the buffalo and collared zebra herds (Fig. 1).

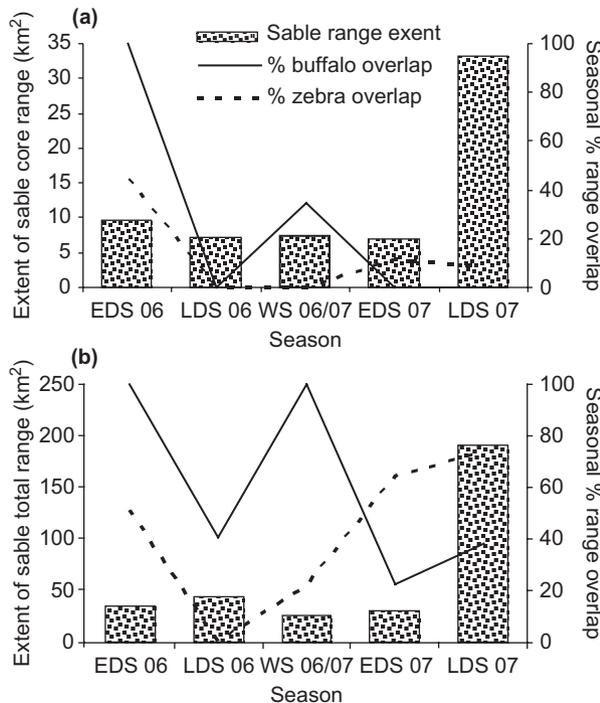


Figure 3. Seasonal changes in the home range extent of the sable herd and its proportional overlap with the ranges of buffalo and collared zebra herds through 2006–2007: (a) core ranges; (b) total ranges. EDS = early dry season, WS = wet season, LDS = late dry season.

Seasonal range shifts and overlap

The sable herd showed a concentration of use in the north-west of the study area during the wet season of 2006/2007 and early dry season periods of both years (Fig. 2). During the late dry season, the sable shifted their range to occupy a distinct southeastern region from October into early November in 2006, and from mid-August through October in 2007. During the latter periods, they travelled 6–8 km every few days to drink from pools in the Mphongolo River in the south, crossing through the buffalo dry-season range during these journeys.

Although the buffalo moved widely over most of the study area during the wet season of 2006/2007 and early dry seasons of both years, they showed a region of low utilization in the centre of the study area. Part way through the dry seasons of both years, they shifted to the vicinity of the Mphongolo River, and remained near the river through the remainder of the dry season, thereby occupying a range distinct from that of the sable herd.

During most of the wet season and the early dry season periods, the collared zebra herds occupied the west-central region of the study area, lightly utilized by the buffalo and mostly avoided by sable. Later in the dry season when

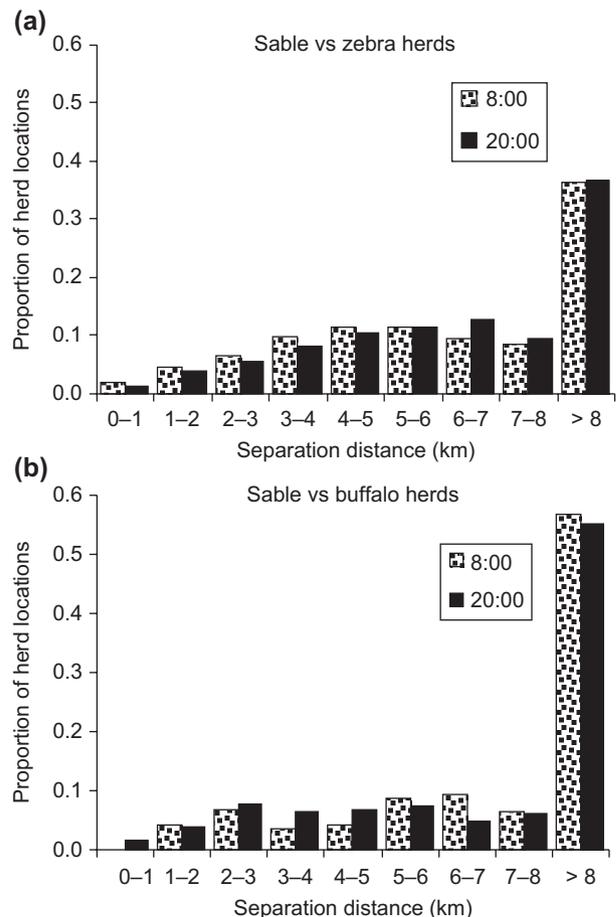


Figure 4. Frequency distribution of separation distances between sable and (a) collared zebra at 8:00 ($n = 1156$) and 20:00 ($n = 1166$) and (b) collared buffalo at 8:00 ($n = 529$) and 20:00 ($n = 535$), aggregated over the wet season and early dry season.

surface water became limiting, some of these zebra herds moved southward and concentrated their space use either near the river, or near the pool in the gravel pit. Overlap between the core ranges covered by the zebra herds and the sable core range occurred only during parts of the early dry seasons of both years, although there was some overlap in total ranges during the wet season. Somewhat greater overlap between the sable range and the total range covered by collared zebra was evident during the late dry season of 2007, because one of the newly collared zebra herds had a range extending further eastwards than the ranges recorded for other zebra herds.

As a result of these patterns, core foraging areas within the seasonal home ranges utilized by the three long-grass grazers were generally distinct. There was zero overlap between the core areas utilized by sable and buffalo in the late dry seasons of both years and during early dry season of 2007 (Fig. 3a). The core areas used by sable and the collared zebra did not overlap during the wet season of 2006/2007 and late dry season of 2006, while only about 10% of the sable core range fell within the core range of the collared zebra herds during the early and late dry seasons of 2007. During the early dry season of 2006, the sable core and total ranges were enclosed within buffalo core and total ranges, respectively. Overlap between the total ranges of the sable and buffalo herds declined from the wet to late dry season (Fig. 3b).

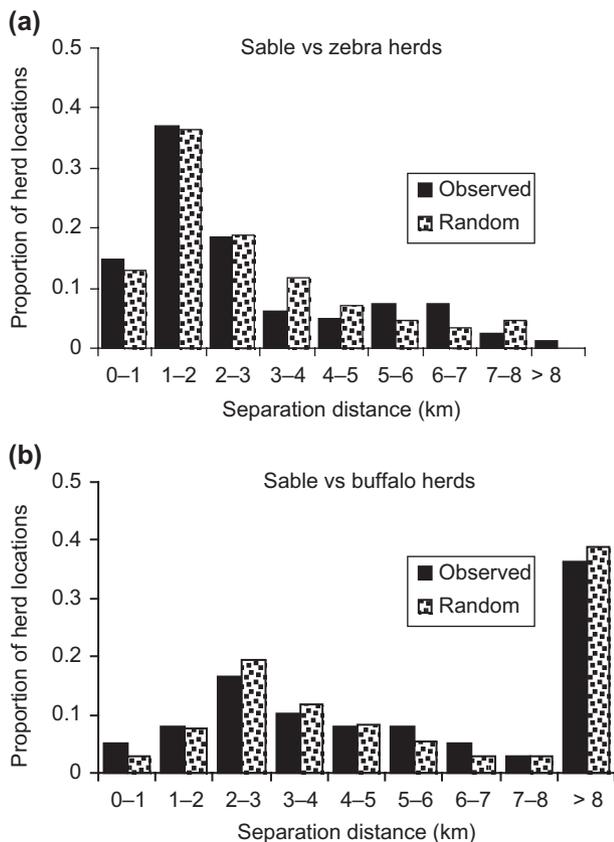


Figure 5. Frequency distribution of separation distances between observed sable locations and random ordering of sable locations to (a) zebra ($n = 81$ and $n = 85$, respectively) and to (b) buffalo ($n = 147$ and $n = 144$, respectively) during months of overlap in core areas.

Short term spacing

Sable were generally > 3 km away from either buffalo herd and > 1.5 km away from the collared zebra herds, even during months of high overlap in core ranges. Over the whole course of the wet season and early dry season, the sable

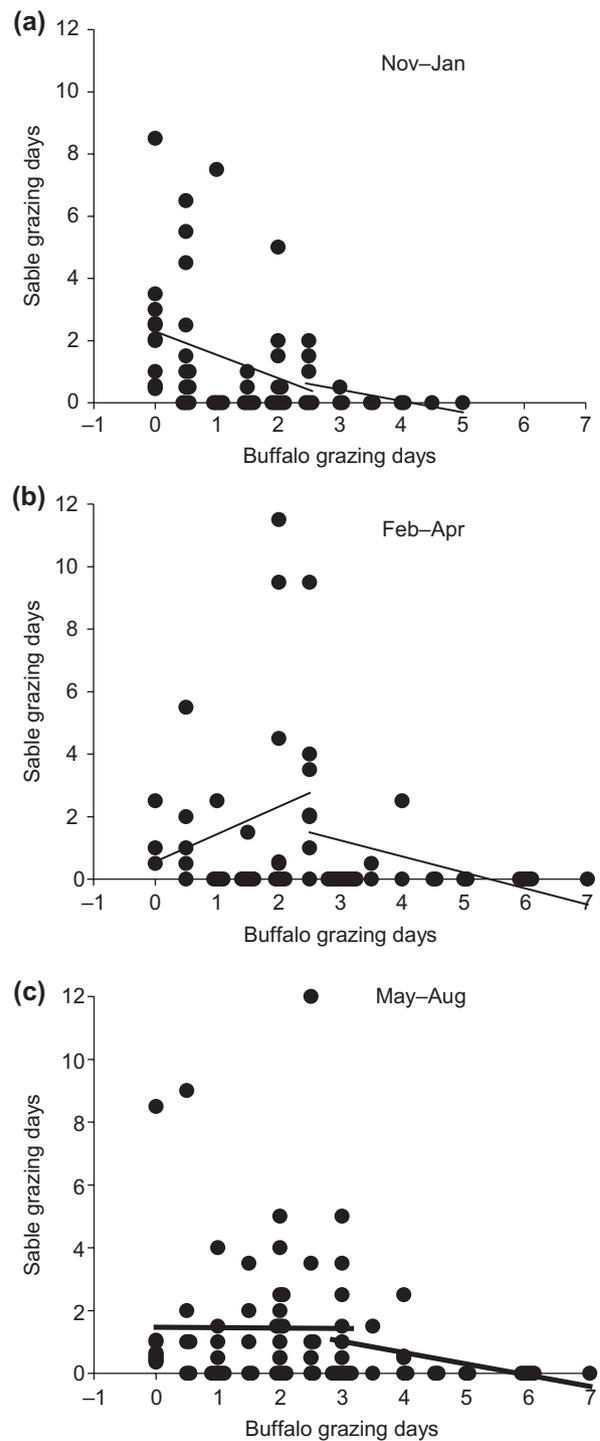


Figure 6. Relationship between records of sable presence during foraging times of day within approximately 1 km^2 grid cells and the prior presence of buffalo herds during these times of day during (a) early wet season (Nov-Jan), late wet season (Feb-Apr) and early dry season (May-Aug). Trend lines through scatter of points on either side of pivotal value of 2.5–3 herd grazing days are indicated.

Table 1. Supporting statistics for Fig. 6, comparing relative use by the sable herd (categorized as ≤ 0.5 herd days vs ≥ 1 herd days) of 1 km² blocks that had previously been grazed by the buffalo herd above or below the specified threshold level. Each independent record represents the presence of a sable or buffalo herd for half a day during a grazing time.

Period	Buffalo grazing threshold (herd days)	Use by sable (herd days)				Statistics	
		Below threshold		Above threshold		χ^2	p
Period		≤ 0.5 days	≥ 1 days	≤ 0.5 days	≥ 1 days		
Nov–Jan	< 2.5	24	20	13	3	16.9	0.001
Feb–Apr	≤ 2.5	20	16	22	1	18.4	< 0.001
May–Aug	≤ 3	18	23	13	2	17.3	0.001

herd was within < 1 km of either collared buffalo during foraging times of the day in < 1% of records, and within this distance from collared zebra herds in < 3% of records (Fig. 4). Out of 718 joint locations between sable and buffalo recorded during the entire study period, separation distances shorter than 1 km were recorded on only 10 occasions during the morning or evening foraging periods. Of the 1379 joint locations between the sable herd and one of the zebra herds, a separation distance of < 1 km was recorded on 24 occasions. The frequency distribution of separation distances comparing observed and the randomized ordering of sable locations indicated that the locations of the sable herd were independent of those of the collared zebra herds, but perhaps influenced to some degree by the nearby presence of a buffalo herd (Fig. 5; K-S between sable and buffalo = 0.47, $p = 0.065$; K-S between sable and zebra = 0.1, $p = 0.83$).

Accumulated prior grazing by buffalo had a significant negative influence on the subsequent presence of sable in that block, which persisted from the wet season months through the dry season of 2007 (Fig. 6, Table 1). There appeared to be a threshold relationship, with the sable herd tending to avoid localities where a buffalo herd had grazed for more than 2–3 days. Below the pivotal value of 2.5 grazing days by a buffalo herd, the presence of sable appeared to be positively related to prior grazing by buffalo during the late wet season months of February–April, but not later into the dry season. However, the p-values shown in Table 1 must be interpreted with reservation for the reasons mentioned in the methods section.

Discussion

The sable herd moved over an annual range that was almost completely enclosed within the annual range exploited by the large buffalo herd. Nevertheless, the seasonal ranges used by sable, buffalo, and zebra were partially distinct and, in the case of sable and buffalo, almost completely separate through most of the dry season of the drier year. Hence, in the context of our first hypothesis, the sable herd was able to utilise regions of the local landscape that were being little used by the two abundant grazers at that time. Furthermore, range use overlap between the sable and the buffalo herd was effectively zero during the critical late dry season because of the shift in range by the buffalo herd to the vicinity of the river. The distinct dry season range used by the sable during this time of the year had received little use from the buffalo herd, and the avoidance for grazing of the riparian zone by the sable could have been related to the depletion of forage there by the buffalo (but could also have been influenced by

a high predation risk where the buffalo were concentrated). The sable herd was seldom recorded in the region where the collared zebra herds tended to concentrate, associated with open shrubby savanna on basaltic soils (Macandza et al. unpubl.). This region had supported a substantial number of sable herds prior to the sable population decline, indicating that it was not intrinsically unsuitable habitat for sable (Chirima et al. unpubl.). Hence despite some temporary overlap in range use during the wet season, there was relatively little range overlap between the sable and both other grazers during the time of the year when resources were most limiting. Even when there was range overlap, the sable herd was seldom located close to the buffalo, but somewhat more frequently recorded near one of the collared zebra herds. Water use patterns contributed additionally to spatial separation during the dry season: the buffalo herds remained in close proximity to pools in the river through much of the dry season; zebra herds used other water sources as well as the river; while sable foraged in a plateau region 6–8 km from the river in between journeys to drink (Cain et al. 2012).

While foraging, sable generally exploited localities that had received little prior grazing by buffalo, but seemed to be drawn towards localities that had been lightly grazed by buffalo in the late wet season. Avoidance of areas grazed much by buffalo was readily done during the early wet season, before there had been much time for the buffalo to expand their grazing coverage after the initiation of grass growth. However, the sable herd was still able to find patches lightly grazed by buffalo later in the seasonal cycle. It appears that grazing by buffalo competitively inhibited subsequent grazing by sable through the resultant resource depression, except perhaps during the late wet season when grass regrowth occurred. This restriction of grazing overlap with buffalo was facilitated by the aggregation of the buffalo (apart from bachelor males) in one or two large herds. The grazing impacts of the numerous small zebra herds were more diffusely spread and thus less easily evaded in time.

Our findings do not preclude the possibility that sable antelope herds were displaced from parts of their former range following the increased abundance of zebra, via either resource depression or mediation through a shared predator (Owen-Smith et al. 2012, Macandza et al. unpubl.). Nevertheless, they reveal how the sable herd that had survived was able to restrict competitive overlap with buffalo through dynamic spatial separation in time as well as space.

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References

- Arsenault, R. and Owen-Smith, N. 2011. Competition and coexistence among short grass grazers in the Hluhluwe-iMfolozi Park, South Africa. – *Can. J. Zool.* 89: 900–907.
- Bell, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. – In: Watson, A. (ed.), *Animal populations in relation to their food resources*. Blackwell, pp. 112–124.
- Borger, L. et al. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. – *Ecol. Lett.* 11: 637–650.
- Cagnacci, F. et al. 2010. Animal ecology meets GPS-based radio-telemetry: a perfect storm of opportunities and challenges. – *Phil. Trans. R. Soc. B* 365: 2157–2162.
- Cain, J. W. III, et al. 2012. The costs of drinking: comparative water dependency of sable antelope and zebra. – *J. Zool.* 286: 58–67.
- Chase, J. M. and Liebold, M. A. 2003. Ecological niches: linking classical and contemporary approaches. – Univ. of Chicago Press.
- Cromsigt, J. P. G. M. and Olff, H. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. – *Ecology* 87: 1532–1541.
- Doncaster, C. P. 1990. Non-parametric estimates of interactions from radio-tracking data. – *J. Theor. Biol.* 143: 413–443.
- Estes, R. D. 1991. *Behavior guide to African mammals: including hoofed mammals, carnivores, primates*. – Univ. of California Press.
- Fryxell, J. M. et al. 2008. Multiple movement models by large herbivores at multiple spatio-temporal scales. – *Proc. Natl Acad. Sci. USA* 105: 19114–19119.
- Georgiadis, N. J. et al. 2007. Savanna herbivore dynamics in a livestock-dominated landscape. II. Ecological, conservation and management implications of predator restoration. – *Biol. Conserv.* 137: 473–483.
- Gertenbach, W. P. D. 1983. *Landscapes of the Kruger National Park*. – Koedoe 26: 9–121.
- Harrington, R. et al. 1999. Establishing the causes of the roan population decline in the Kruger National Park, South Africa. – *Biol. Conserv.* 90: 69–78.
- Henley, S. 2005. *Habitat dependency and nutritional ecology of sable antelope in two regions of the Kruger National Park*. – Report to South African National Parks, Skukuza.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. – *Theor. Popul. Biol.* 12: 197–229.
- Inouye, B. 1999. Integrating nested spatial scales: implications for the coexistence of competitors on a patchy resource. – *J. Anim. Ecol.* 68: 150–162.
- Kernohan, B. J. et al. 2001. Analysis of animal space use and movements. – In: Millsbaugh, J. J. and Marzluff, J. M. (eds), *Radio tracking and animal populations*. Academic Press, pp. 125–166.
- Kleynhans, E. J. et al. 2011. Resource partitioning along multiple niche dimensions in differently sized African grazers. – *Oikos* 120: 591–600.
- Laca, E. A. et al. 2010. Allometry and spatial scales of foraging in mammalian herbivores. – *Ecol. Lett.* 13: 311–320.
- McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. – *Science* 191: 92–94.
- Murray, M. G. and Illius, A.W. 1996. Multispecies grazing in the Serengeti. – In: Hodgson, J. and Illius, A. W. (eds), *The ecology and management of grazing systems*. CAB Int., pp. 247–272.
- Owen-Smith, N. and Ogutu, J. O. 2003. Rainfall influences on ungulate population dynamics in the Kruger National Park. – In: du Toit, J. T. et al. (eds), *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, pp. 310–331.
- Owen-Smith, N. and Mills, M. G. M. 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. – *Ecol. Monogr.* 76: 73–92.
- Owen-Smith, N. et al. 2012. Shrinking sable antelope numbers in Kruger National Park: What is suppressing population recovery? – *Anim. Conserv.* 15: 195–204.
- Ritchie, M. 2002. Competition and coexistence of mobile animals. – In: Sommer, V. and Worm, B. (eds), *Competition and coexistence*. Springer, pp. 109–131.
- Ritchie, M. and Olff, H. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. – *Nature* 400: 557–562.
- Rodgers, A. R. et al. 2007. HRT: home range tools for ArcGIS 1.1. – Ontario Ministry of Natural Resources, Ontario, Canada.
- Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanisms. – *Am. Nat.* 137 (suppl.): 5–28.
- Senft, R. L. et al. 1987. Large herbivore foraging and ecological hierarchies. – *BioScience* 37: 189–799.
- Skinner, J. D. and Chimimba, C. T. 2005. *The mammals of the Southern African subregion*. – Cambridge Univ. Press.
- Venter, F. J. 1990. *A classification of the land for management planning in the Kruger National Park*. – PhD thesis, Univ. of South Africa.
- Viljoen, P. C. 1993. *Ecological aerial surveys in the Kruger National Park: 1992*. – Scientific report 2/93, National Parks Board, Skukuza, South Africa.
- Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. – *E. Afr. Wildlife J.* 13: 265–286.
- White, G. C. and Garrott, R. A. 1990. *Analysis of wildlife radio-tracking data*. – Academic Press.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. – *Ecology* 70: 164–168.