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Home range occupation and habitat use of sable antelope in the Okavango Delta region of northern Botswana

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Abstract

Animals selectively utilize their environments within a hierarchical framework. Our study addressed how the home ranges of sable antelope selectively incorporated the landscape and habitat types available to them. It was conducted in a region of northern Botswana where the sable population was expected to be thriving, in contrast to their threatened status in the wild in South Africa. The movements and habitat use of three neighbouring sable herds were recorded by global positioning system (GPS) telemetry during parts of the seasonal cycle in a region adjoining the seasonally flooded Okavango Delta. Total home range extents covered by these herds were larger than those found for sable in other areas, and local population densities, taking into account the herd sizes, were accordingly lower than in these other areas. Access to surface water appeared to be the main limitation on seasonal home range occupation. Almost all of the local vegetation types were utilized, but sable herds generally favoured dryland grassland during the dry season and floodplain grassland during the wet season, contrary to what we had expected. Hence, it appeared that local home range occupation and habitat use by the three sable antelope herds could be influenced more by interactions with potential competitors and predators than by intrinsic habitat suitability.

Key words: competition, Global Positioning System telemetry, movements patterns, sable antelope

Résumé

Les animaux utilisent leur environnement sélectivement, selon un cadre hiérarchique. Notre étude cherchait à savoir la façon dont les domaines vitaux de l'antilope sable intégraient sélectivement les types de paysages et d'habitats qui leur sont disponibles. Elle fut menée dans une région du nord du Botswana où la population d'antilopes sable était connue comme florissante, contrairement à l'Afrique du Sud où leur statut est menacé à l'état sauvage. Les déplacements et l'utilisation de l'habitat de trois hardes voisines d'antilopes sable furent enregistrés par télémétrie GPS pendant certaines parties du cycle saisonnier, dans une région voisine du delta de l'Okavango, régulièrement inondé. Le total des domaines vitaux couverts par ces hardes était supérieur à celui relevé pour des sable d'autres régions, et la densité des populations locales, compte tenu de la taille des hardes, était par conséquent plus faible que dans des autres régions. L'accès à l'eau libre s'est avéré être le principal facteur limitant l'occupation de l'espace vital saisonnier. Presque tous les types locaux de végétation étaient fréquentés mais, contrairement à nos attentes, les hardes de sable préféraient généralement les prairies sèches pendant la saison sèche et les prairies inondées pendant la saison des pluies. Il s'est donc avéré que l'occupation locale du domaine vital et l'utilisation locale de l'habitat par les trois hardes d'antilopes sable pouvaient être plus influencées par des interactions avec d'éventuels compétiteurs et prédateurs que par des qualités intrinsèques de l'habitat.

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Introduction

Utilization of the environment by large herbivores may be expressed within a hierarchical framework of levels of selection (Johnson, 1980; Senft *et al.*, 1987). Our study was focused on the home range occupation within the regional landscapes and habitat use within home ranges of sable antelope (*Hippotragus niger*), a species that has undergone a substantial decline in abundance in South Africa's Kruger National Park (Owen-Smith *et al.*, 2012), raising concerns about its wider conservation status. However, aerial counts of wildlife in northern Botswana (Department of Wildlife and National Parks, unpublished records) showed no consistent downward trend by sable antelope there since 1990. Hence, the aim of our study was to document the habitat dependence of sable antelope in a region where we expected the species to be thriving, for comparison with regions where its long-term persistence seemed to be in jeopardy.

Abiotic factors including temperature, precipitation, topography and the availability of surface water impose physiological constraints on species and therefore determine geographic range limits (Soberón & Peterson, 2005). Biotic relationships with predators and competitors further restrict the places that can support viable local subpopulations and therefore where home ranges can be established (Gaston, 1991; Chirima *et al.*, 2013). These home ranges may be occupied individually, or shared by members of a herd. Seasonal variation in habitat conditions and resource availability may restrict the period within the year when particular localities can be occupied, leading to seasonal shifts between distinct home ranges (Borger *et al.*, 2006). Within these ranges, core regions may be utilized most intensively (Kernohan, Gitzen & Millspaugh, 2001). Home ranges of neighbouring individuals or groups of the same species can overlap to some extent (e.g. African buffalo *Syncerus caffer*, Cornelis *et al.* 2011). The extent of the regional landscapes occupied by home ranges and intensity of use of the habitats within them ultimately determines the local population density attained (Harestad & Bunnell, 1979).

Our specific objectives were

1 To determine the annual and seasonal home range extents of sable herds in the study area

2 To establish which sections of the study area were excluded from the home ranges of these sable herds, indicating unsuitable habitat

3 To compare the relative proportions of the habitat types included within the home ranges during different periods of the year.

Methods

Study area

The Okavango Delta is an approximately 22000 km^2 alluvial fan situated in the Kalahari basin within northern Botswana (Gumbricht, McCarthy & McCarthy, 2004). The study area was located in the north-east of the Delta comprising three concessions, hereafter labelled the Kwedi area (Fig. 1). The 'buffalo fence' completed in 2002 formed the north-western boundary and blocked the movements of sable herds in this direction. Permanent open water to the south defined the southern limit. Other borders extended arbitrarily about 1 km beyond the furthest recorded locations of sable herds during the study, encompassing an area of 252 km^2. Soils adjoining the Delta are mainly composed of Aeolian sands with alluvial clay soils locally around the edge of permanent water. The region is relatively flat with elevations about 980 m above

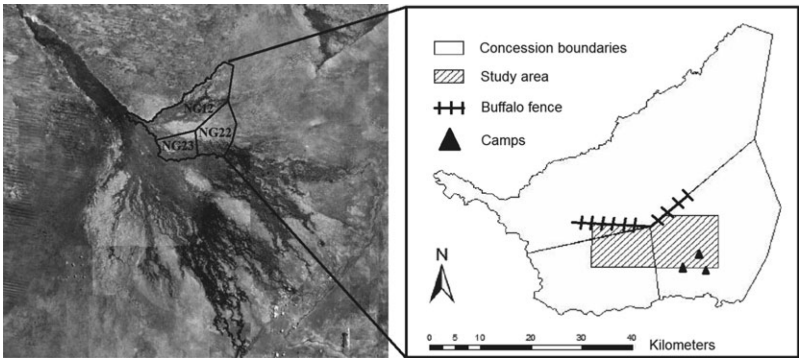

Fig 1 Location of the Kwedi (NG22), Duba Plains (NG23) and Mapula (NG12) concessions, the buffalo fence, camps and study area limits north-east of the Okavango Delta

sea level. The vegetation types interspersed in this region were classified as floodplain grassland, dryland grassland, open savannah, mixed woodland, Mopane woodland and Kalahari apple-leaf woodland, teak woodland, and silver cluster-leaf woodland. Potentially competing grazers present included African buffalo, blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), impala (*Aepyceros melampus*), red lechwe (*Kobus leche*), tsessebe (*Damaliscus lunatus*), common waterbuck (*Kobus ellipsiprymnus*), African elephant (*Loxodonta africana*) and hippopotamus (*Hippopotamus amphibius*). Predators included lion (*Panthera leo)*, leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), wild dog (*Lycaon pictus*), black-backed jackal (*Canis mesomelas)* and side-striped jackal (*Canis adustus*).

The climate is semiarid with summer rainfall mainly between November and April. Mean annual precipitation in the region averaged 513 mm (annual range 288–1145 mm) from records at Shakawe and Maun between 1964 and 1994 (McCarthy, Bloem & Larkin, 1998). Flood water originating in Angola reaches the Delta between February and May to peak during August, and subside by October (Gumbricht, Wolski & McCarthy, 2004). During the study, rainfall was recorded at a weather station in the study area. Nil monthly rainfall defining the onset of the dry season was recorded in April in both 2009 and 2010. Rainfall ending the dry season was recorded at the end of October in 2009 and beginning of November in 2010. For analysis, the dry season was divided between early (April–July) and late (August–October) segments. Grass growth commenced during November, defining the transition period between seasons. December–March was defined as the wet season. Rainfall over the calendar year amounted to 500 mm in 2009 and 436 mm in 2010. Exceptionally high floods dependent on rainfall in the Angola catchment occurred in both 2009 and 2010, but with majority of the flood water receding by early September in both years. July was the coldest month with a mean monthly temperature of 16°C, while October was the hottest month with a mean monthly temperature of 26°C. Pans retaining surface water into the dry season known to tourist guides were augmented by those in remote areas identified using Google Earth (CNES/SPOT image dated 31/05/2008). Whether water was still available in these pans was monitored towards the end of each month. The presence of predators and competing grazers, comprising zebra, tsessebe, wildebeest, impala and buffalo, was noted casually while driving between the camp and the sable herds to be observed, but could not be recorded objectively given this travel bias.

Data collection

The locations of sable antelope herds were supplied by collars containing a global positioning system (GPS) unit, ultra high frequency (UHF) and very high frequency (VHF) transmitters, and batteries designed to last a year, procured from Africa Wildlife Tracking (http://www.awt.co.za). GPS devices recorded the date, time of day, latitude and longitude coordinates every hour, which were stored on board. Collars were fitted to individual females representing each of the three sable herds present in the study area, apart from a small herd of four animals that later joined one of the collared herds. Collars were fitted to the Eastern and Western herds in August 2009 and to the Central herd in October 2009. The Western herd was the largest, including 19 animals at the end of 2009, while the Eastern and Central herds were smaller with 14 and 12 animals, respectively. Capture operations using immobilizing drugs were conducted by qualified veterinarians under conditions approved as meeting the ethical criteria applied by the University of the Witwatersrand (Ethical Clearance Ref no: 2012/06/04). Data stored in the collars were downloaded periodically using a UHF modem, with VHF R-1000 Telemetry Receiver that was used to get within 500 m of the herd. GPS devices on the Eastern and Western herds stopped operating in December 2009 and these collars were replaced in early March 2010 and were removed at the end of November 2010. The female from the Central herd bearing the collar was killed by lions in August 2010, but the GPS device that was recovered had stored data only up to the end of March 2010.

Data analysis

Hourly GPS locations of three collared females were projected with Universal Transverse Mercator (UTM) zone 34S and the WGS 1984 spheroid and loaded into the Adaptive Local Convex Hull (*a*-LoCoH) toolbox (http://locoh.cnr.berkeley.edu/arctutorial; Getz & Wilmers, 2004) in ArcGIS 9.3.1. This method was used to estimate annual and seasonal home range areas, adopting the 'minimum spurious hole covering' (MSHC) rule to determine appropriate a and k values for joining location points. The estimated area covered by the distribution should level off once all spurious holes are covered, but should increase again when real gaps in the distribution become totally or partially covered. We initially fixed the value of k at three and plotted increasing values of a against the range area until it began to level off. With a fixed at that value, we then varied k and plotted the k value against range area until the MSHC was again determined. We then used the joint values of a and k to determine the final home ranges. Annual and seasonal home range extents were defined using 95% isopleths, while core ranges were assessed from 50% probability isopleths. For comparison with other studies, minimum convex polygons (MCP) enclosing the total home range, including unoccupied gaps and occasional excursions, were also derived. The effective local density of each herd was calculated by dividing the number of animals forming the herd by the extent of the 95% annual home range.

A map of the vegetation types within the study area was created using Google Earth (CNES/SPOT image dated 31/05/2008). Polygons were digitized around eight distinct vegetation types recognizable from the image based on prior ground knowledge of the area. Seventy ground control points, randomly selected across the whole study area, were visited to verify the vegetation type assignments. The digitized vegetation polygons were then converted to shapefiles. Digitizing errors were fixed using standard topology generation procedures implemented within ArcMap 10.0. Areas of each vegetation type within the study area were determined using Hawths Analysis Tools (http://www.spatialecology.com) in ArcGIS 9.3.1, and used to calculate their proportional availability within the overall study area, excluding sections with permanent water. To establish which vegetation types that were present at landscape level were under-represented at home range level, we compared the proportion constituted by each vegetation type within the demarcated home ranges with their overall availability within the study area. We also compared proportional availability of these vegetation types within the core ranges to their availability within the annual home ranges of the herds.

Results

Annual, seasonal and core ranges

The three sable herds occupied adjacent home ranges along the edge of the permanent water (Figs. 2a–d). No other sable herd was recorded to the north and east of these ranges. A sable herd lacking a collar was reportedly seen to the west of the strip of permanent water forming the western limit of the range of the Western herd. The total MCP ranges of neighbouring herds overlapped marginally, but there was almost no overlap between the annual or seasonal ranges defined using 95% isopleths in *a*-LocoH. The late dry season ranges occupied by the three herds tended to be located in the north, away from the permanent water, while the wet season ranges were moved southwards, with the early dry season range spanning both regions. The southward shifts occurred during November in the transition between the late dry and wet seasons. The wet season ranges of the Central and Western herds partially overlapped their dry season ranges while the Eastern herd exhibited a distinct gap between its wet and dry season ranges. Total MCP ranges (Eastern herd: 38.5 km²; Western herd: 40.5 km²; Central herd: 61.6 km²) encompassed almost twice the areas estimated for the annual home ranges defined by *a*-LoCoH (Eastern herd: 20.7 km²; Western herd: 21.5 km²; Central herd: 31.0 km²). Seasonal ranges covered around half or more of the annual ranges of the three herds, allowing for undersampling of the wet season range of the Eastern herd (Table 1). The Central herd covered the largest annual range despite being of similar size to the Eastern Herd and thus showed the lowest effective density of the three herds (Eastern herd: 0.7 km^{-2}, Western herd: 0.9 km^{-2}, Central herd: 0.4 km^{-2}). Certain pans that retained muddy pools of water into October in one or both years enabled occupation of the regions away from the inundated floodplain through the late dry season.

Habitat occupation

The area to the north of the home ranges of the Central and Eastern herds and beyond the eastern limit of the study area consisted predominantly of Mopane and apple-leaf woodland. The silver cluster-leaf woodland in the south-east of the study area where tourist camps were located was not used by any of the herds (Fig. 3). Between the annual *a*-LoCoH home ranges of the Western and Central herds was a large expanse of floodplain grassland and open savannah not utilized by either herd. Seasonally occupied ranges of the Eastern and Central herds were separated by regions with predominantly apple-leaf and mixed woodland. The area south of the airstrip consisting of floodplain grasslands intermingled with permanent water was avoided by the Central herd. Dryland grassland made up a larger proportion of the home ranges of all three

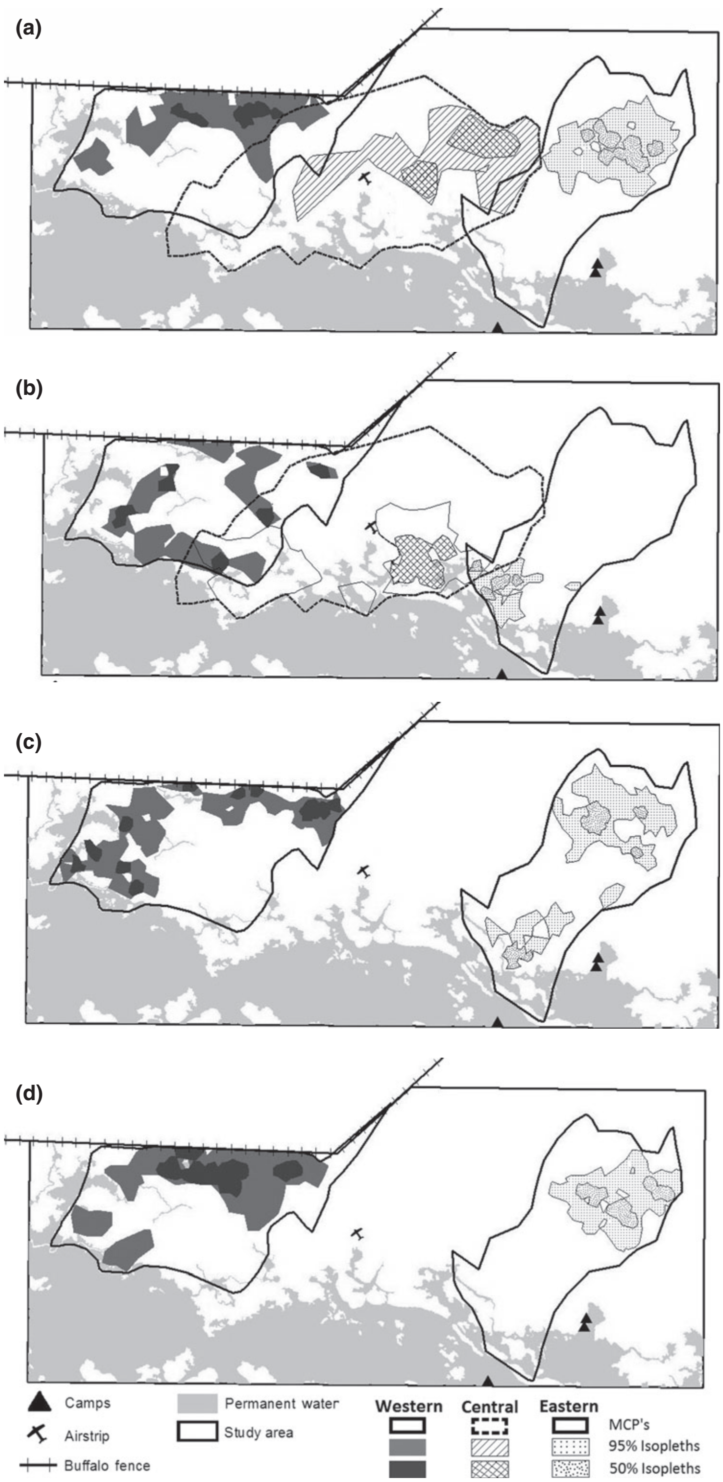

Fig 2 Total minimum convex polygons (MCP), seasonal (*a*-LoCoH, 95% isopleths) and core (*a*-LoCoH, 50% isopleths) home ranges of the three collared sable herds on the Kwedi study area, based on the number of days and hourly GPS records shown in Table 1. (a) Late dry season 2009, (b) wet season 2009/10, (c) early dry season 2010, (d) late dry season 2010

Table 1 Seasonal home range extents (95% isopleths) and seasonal core-range extents (50% isopleths) estimated using *a*-LoCoH, together with the number of days and number of hourly locations used for these estimates

Sable herd	Season	Period spanned	No. of days	Hourly GPS locations	Seasonal home range (km^2)	Seasonal core range (km^2)
Eastern	Late dry 2009	16/08–31/10	77	1833	10.6	2.2
	Wet 2010	07/03–31/03	24	587	3.4	0.8
	Early dry 2010	01/04–31/07	122	2922	11.3	1.7
	Late dry 2010	01/08–31/10	92	2204	9.3	2.0
Western	Late dry 2009	16/08–31/10	76	1823	11.8	1.5
	Wet 2009/10	1/12–31/03	44	1047	12.0	2.0
	Early dry 2010	01/04–31/07	122	2926	12.5	2.6
	Late dry 2010	01/08–31/10	92	2206	15.9	3.9
Central	Late dry 2009	12/10–31/10	20	470	17.2	3.8
	Wet 2009/10	1/12–25/03	112	2668	19.8	3.2

GPS, global positioning system.

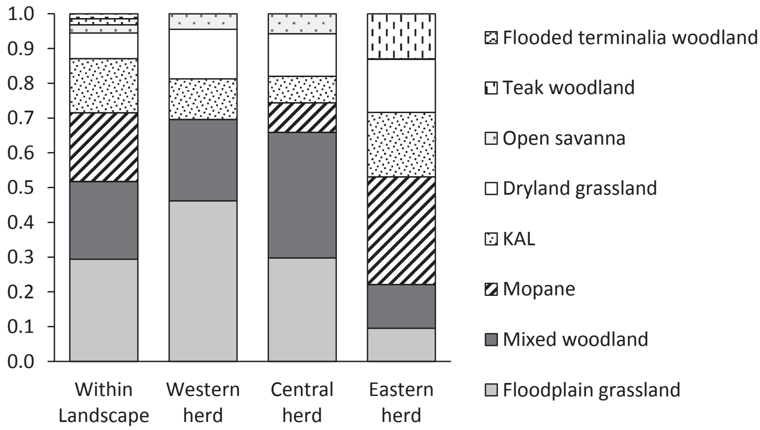

Fig 3 Overall availability of particular vegetation types within the study area compared with their proportional representation within the annual (*a*-LoCoH) home range of the three sable antelope herds

sable herds compared with its rather minor representation overall in the study area. Floodplain grassland constituted the largest proportion of the annual range of the Western herd, while Mopane woodland made up the greatest proportion of the annual range of the Eastern herd, and mixed woodland that of the Central herd.

The wet season range of the all three herds contained larger proportions of floodplain grassland and mixed woodland than the late dry season ranges they occupied in both 2009 and 2010 (Fig. 4). The dry season ranges of all three herds, and especially the core regions, contained more dryland grassland than utilized in the wet season. Teak woodland occupied an increased proportion of the dry season range of the Eastern herd in both years.

Discussion

Home range extents

Estimates of the total home range extents for the three sable herds at Kwedi obtained using MCP were around the upper end of the general range observed in other studies, while seasonal and core ranges excluding little-utilized sections were more in conformity with the range extents reported in other studies. Home ranges estimated for sable herds by minimum convex polygons varied from as little as 2.4 km^2 in Matopos National Park in Zimbabwe (Grobler, 1974) to over 100 km^2 in parts of the Kruger National Park (Henley, 2005; Owen-Smith & Cain, 2007), but with more usual values falling within the 7–45 km^2 range

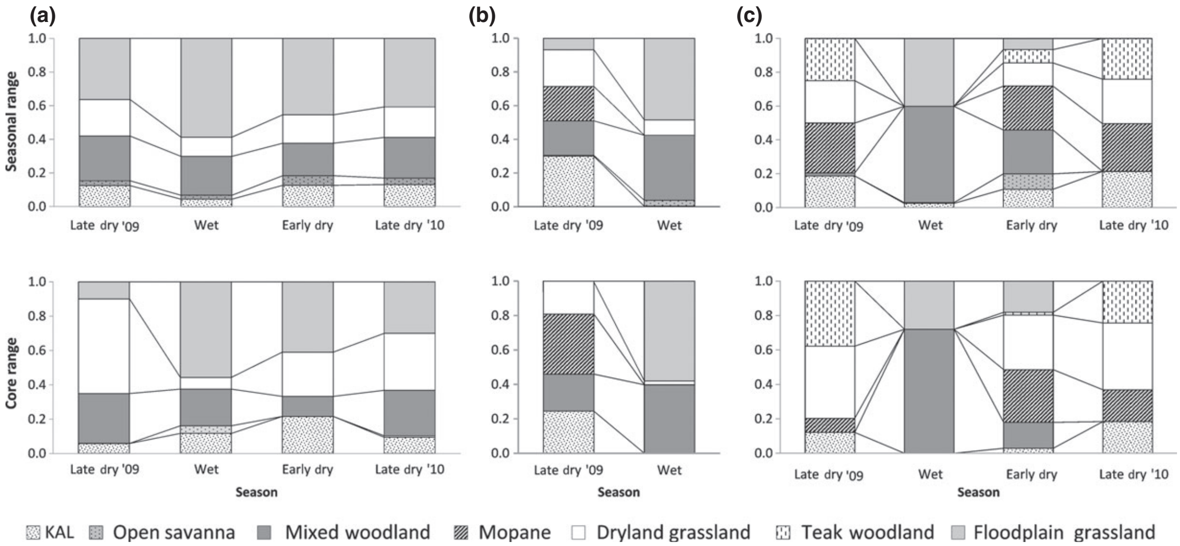

Fig 4 Seasonal trends in the relative use of different vegetation types within the seasonal home ranges and core ranges of the three sable antelope herds. (a) Western herd and (b) Central herd (c) Eastern herd

(Wilson & Hirst, 1977; Sekulic, 1981; Ross, 1984; Parrini, 2006; Magome *et al.*, 2008). Furthermore, the number of members of the three sable herds at Kwedi were towards the low end of the typical range for sable (Skinner & Chimimba, 2005). The regional density of sable in the Kwedi study area was only around 0.2 animals per km^2, from our total of 50 sables within the 250 km^2 study area. This meant that the effective sable density within the occupied range was not much higher than the maximum local densities reported for Kruger National Park (Chirima *et al.*, 2013) where the viability of the sable population appeared to be threatened (Owen-Smith *et al.*, 2012). Highest recorded sable densities exceeding 3 animals per km^2 have been recorded in Matopos National Park (Grobler, 1974) and in the Shimba Hills of Kenya (Ross, 1984). Hence, our expectation that we would be studying a thriving population of sable antelope was not supported by the local densities that we found.

Habitat use

The sable herds at Kwedi tended to favour dryland grassland during the dry season and floodplain grassland during the wet season. However, almost all of the vegetation types present in the study area were utilized by the sable, with differing habitat concentrations shown by the three herds. The only vegetation type that appeared to be strictly avoided was the seasonally inundated silver cluster-leaf woodland, restricted to a localized area near the tourist camp in the south-east, where human disturbance might have been an influence. Sable antelopes elsewhere have also been recorded as occupying a range of habitat types, from quite open grassland in some places (Ross, 1984; Parrini, 2006) to well-wooded savannah elsewhere (Estes & Estes, 1974). Seasonally, sable commonly concentrate in drainage line grasslands (dambos or vleis) retaining green foliage during the dry season (Grobler, 1981; Estes & Estes, 1974). Hence, we expected the Kwedi herds would make increased use of the newly exposed floodplains grassland during the late dry season when floodwaters had receded and green grass had become exposed, but this was not observed.

The restricted seasonal occurrence of sable herds in the Kwedi region appeared to be related to proximity to perennial surface water sources rather than by the unsuitability of vegetation features. The habitat types predominant to the north and east of the occupied home ranges – Mopane and Kalahari apple-leaf woodland – also occurred within these herd ranges and were utilized there. Sable herds within Kruger National Park have been recorded undertaking journeys of up to 7–8 km to drink during the late dry season (Cain, Owen-Smith & Macandza, 2012), and one herd shifted its seasonal range so as to maintain this maximum distance from water. Hence, longer journeys to and from water every few days in the dry season might become too costly. It was surprising that the sable herds at Kwedi generally occupied regions of their annual ranges furthest from permanent water during the late dry season, enabled by the persistence of water in pans. Rainfall conditions during the study period were close to average, and in years with low rainfall, these pans are likely to run dry and thus no longer enable the use of these regions. Instead of occupying the floodplain grasslands close to perennial water during the dry season, the sable shifted to these regions during November at the beginning of the wet season and persisted in using the floodplains well into the wet season. Surface water availability in the upland pans, or at least its muddy quality, might have influenced the shift. The regions of the floodplain occupied included a mosaic interspersion of woodland patches, providing some shade.

These patterns led us to believe that biotic interactions with competitors and predators were the predominant influences on local habitat occupation at Kwedi, in conformity with the situation identified in the Kruger National Park (Chirima *et al.*, 2013). We noted concentrations of buffalo, zebra and tsessebe in the floodplains grasslands during the late dry season, suggesting that the sable could have been avoiding these competitors by concentrating in more remote regions at this time of the year. Their shift to the floodplain grasslands following the start of the rains coincided with the general movement by other grazers to upland grassland during the wet season when grasses became predominantly green. Concentrations of abundant ungulates also draw predators, in particular lions (*Panthera leo*). Guides working in the concession noted that nine sables were killed on the floodplain (seven by lion, one by leopard *Panthera pardus* and one by cheetah *Acinonyx jubatus*) between August and November in 2007. Three more sables were killed by lions on the floodplain in August 2010, including one of the animals carrying a GPS collar. The small herd of four sables also present in the study area appeared to be a remnant of a larger herd, decimated by predation prior to our study. Because our study was not designed to document the importance of biotic interactions, we cannot substantiate these influences on the local distribution and abundance of sable at Kwedi. Further investigations are needed to establish how the spatial utilization patterns of sable herds are related to the presence of more abundant grazers, building on the findings reported by Macandza, Owen-Smith & Cain (2012).

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