

Space use patterns of a large mammalian herbivore distinguished by activity state: fear versus food?

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Abstract

Space use patterns have generally been interpreted using home-range concepts without distinguishing the particular activities performed in different regions. The relative influences of food resources, security from predation and shelter from thermal extremes on space occupation are likely to vary with time of day and changing conditions over the seasonal cycle. We used hourly movement rates obtained from GPS telemetry to infer the predominant activity states of blue wildebeest in the Kruger National Park, South Africa, at different times of day. Food procurement was assumed to be the primary consideration during the morning and late afternoon, shade seeking to become important over midday, and security from predation to be the overriding factor at night when stalking predators are most active. Traveling excursions were expected to occur mostly during daylight when lurking predators are most readily detected. Movements beyond the preferred range should occur more frequently in the late dry season when food has been depleted and surface water sources become restricted. As anticipated, we observed shifts in space occupation by the collared wildebeest herds with time of day and activity state. During the night, wildebeest herds remained within the ranges they occupied during prime foraging times in the early morning and late afternoon. However, they contracted their space occupation away from habitat edges where concealment for stalking lions increased, both while resting and while foraging. Herds inconsistently expanded their space use into surrounding areas with more shade but taller grass over midday. Risky excursions beyond the prime foraging ranges became more frequent late in the dry season. Security from predation seemed to be the overriding influence and restricted access to food resources. By taking into account temporal variation in prevailing activity states and other influences, space occupation patterns can be related to particular vital needs and their interactions.

Introduction

Space occupation patterns have generally been interpreted in terms of the concept of a home range, defined as the space normally traversed by an animal in its routine activities (Burt, 1943; Jewell, 1966). How these various activities contribute towards generating the area traversed under different conditions has rarely been explored. Home-range estimators typically do not distinguish the forms of use that generate the space occupation patterns manifested (Powell, 2000; Getz & Wilmers, 2004; Borger *et al.*, 2006; Laver & Kelly, 2008; Fieberg & Borger, 2012). Locations obtained using VHF collars have usually been restricted to daylight conditions, for logistic reasons, while places where animals were apparently resting may be either included or omitted from the spatial analysis (Cornelis *et al.*, 2011). Functional interpretations of home-range extents have been focussed largely on resource requirements (Kelt &

Van Vuuren, 1999; Tamburello, Cote & Dulvy, 2015), without taking into account constraints imposed by vulnerability to predation.

Besides procuring food and other resources, animals must remain sufficiently secure from predation, and might at times need to seek shelter from thermal extremes. Our analysis is premised on the expectation that the relative influences of these needs will change over the day-night cycle in illumination and temperature and through the seasonal progression in resource availability, generating shifts in space occupation. During the morning and afternoon while conditions are neither too hot nor too dark, food needs should be the primary consideration influencing space occupation, except when surface water is restricted and animals must travel elsewhere to drink. During the midday period when conditions are hottest, animals might need to move into shaded sites, especially while resting. For species hunted primarily by stalking carnivores benefitting

from concealment, sites where the risk of being ambushed is least should be sought nocturnally, most strictly while animals are resting. Furthermore, trade-offs for fitness between resource deprivation and vulnerability to predation will shift through the seasonal cycle, as the availability of nutritionally adequate food and accessible surface water diminishes and temperature regimes change. What the consequences are for the resultant home-range extent will depend on whether places providing the best food, shelter or security are coincident, nested, partially overlapping, discrete or widely separated in space.

Consistent with expectations, studies have shown that large mammalian herbivores subject to predation mainly by stalking felids typically show peaks in foraging activity during the early morning and late afternoon, and are least active during the night and over midday (Berry, Siegfried & Crowe, 1982; Owen-Smith, 1988, 1998; Owen-Smith & Goodall, 2014). However, how space occupation varies with the activity being performed and time of day has rarely been investigated. Following the advent of GPS telemetry, it has now become possible to document the space use patterns of animals precisely throughout the night as well as during the day and under all conditions (Kays *et al.*, 2015).

Furthermore, the prevailing activity state of animals can be inferred from movement rates (Morales *et al.*, 2004; Lottker *et al.*, 2009; Van Moorter *et al.*, 2010; Wilson, Gilbert-Norton & Gese, 2012). Distinct movement modes can be identified from displacement distances over hourly or finer time steps, and related to the activities most likely to generate them (Owen-Smith, Fryxell & Merrill, 2010; Owen-Smith, Goodall & Fatti, 2012; Goodall, 2013). Resting is associated with minimal movement. For large herbivores, foraging activity generates slow, frequently tortuous movements due to the alternation of stationary feeding and intermittent relocation (Owen-Smith, 2002). Persistent travel, whether to and from water sources or between home-range sections, generates longer, more directed movements.

Our study was undertaken on a relatively sedentary sub-population of a large grazing ruminant, the blue wildebeest (*Connochaetes taurinus*), in west-central Kruger National Park (KNP) in South Africa. Wildebeest are the prime prey species of lions (*Panthera leo*) in this park, and relatively few are killed by carnivores besides lions (Owen-Smith & Mills, 2008a,b). A prior analysis documented how the habitat occupation of these wildebeest herds during times of day when foraging activity predominated was concentrated in localized habitats typified by sparse woody vegetation cover and short grass, providing both high quality forage and comparative security from predation (Yoganand & Owen-Smith, 2014). Martin *et al.* (2015) reported how residence times within foraging patches extending over several hours (allowing excursions shorter than 6 h) increased with the proportion of lawn grassland in the vicinity and with distance from the nearest wooded area, indicating influences of both high quality food and predation risk. Furthermore, wildebeest showed shorter residence times and moved more frequently between foraging patches in the late dry season when movements to and from surface water became necessary. Owen-Smith, Martin & Yoganand (2015) described how wildebeest herds exploited particular foraging

arenas covering 1–3 km² for periods of several weeks within their home ranges, before relocating to a new area, while zebra (*Equus quagga*) herds showed shorter settlement durations and more frequent relocations. Following encounters with lions taking place mainly at night, wildebeest tended to remain within their preferred open habitat rather than moving elsewhere as zebra did (Martin & Owen-Smith, 2016), and Traill, Martin & Owen-Smith (2016) showed that moon phase did not influence the nocturnal activity of wildebeest unless lions were nearby.

In this article, we expand our spatial assessment of habitat use to consider also the places occupied at times of day beside the main foraging periods and for activities besides foraging. We will interpret the area occupied during the peak foraging periods in the early morning and late afternoon, as established below, to represent the prime-times foraging range (PFR). We anticipated that PFRs would expand or shift seasonally as food availability diminished through the dry season months. We expected that places occupied nocturnally would either be shifted or contracted into more secure locations, especially while animals were resting. We anticipated that during the hot midday period, space occupation might be expanded into nearby areas providing more shade, and perhaps also more food, noting that predators were also likely to be resting at this time. We expected that travelling excursions beyond the PFRs would take place mainly during daylight and mostly during the late dry season, and be orientated mainly towards nearby surface water sources.

Materials and methods

Study area

The study was located in west-central KNP near the Orpen entrance plus adjoining regions of Manyeleti Game Reserve and Timbavati Private Nature Reserve. Geologically the area includes an intrusion of a gabbro sill into the surrounding granitic gneiss (Venter, Scholes & Eckhardt, 2003). Woody vegetation consisted of mixed thorn (*Acacia* spp) savanna with short grass on gabbro uplands and mixed bush willow (*Combretum* spp) savanna with taller grass in the surrounding granitic region. The annual rainfall total within the study area averaged 572 mm (1965–2005) with over 80% received during the wet summer extending from November through April. Annual rainfall (July–June) during the study period was 8% above average in 2009/2010, 13% below average in 2010/2011, and 20% above average in 2011/2012. Besides wildebeest, other common grazers in the study area include plains zebra (*Equus quagga*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*) and warthog (*Phacochoerus africanus*). Lion, leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*) all occurred in the study area.

Data collection

The database of animal locations we used is lodged with the data repository of South African National Parks (<http://dataknp.sanparks.org>), where it may be obtained upon request. It was

derived from GPS collars (supplier Africa Wildlife Tracking: <www.awt.co.za>) placed on 10 female wildebeest in separate herds numbering 12–35 animals in late March 2009, and replaced when necessary on the same animals to extend data collection until April 2012 for some herds. GPS devices supplied location data on an hourly schedule. Because female wildebeest were always associated in distinct breeding herds, the movements of the collared animals represent the movements of the herds with which they were associated. We used data provided by eight collars on independently moving herds spanning a full year or longer, while six of these collars covered two successive years in at least two seasons (Table S1).

Data interpretation

While Hidden Markov models have frequently been used to infer activity states from movement tendencies, following Morales *et al.* (2004), we found that independent mixture models were simpler to apply and the output more easily interpreted with little loss in precision (Goodall, 2013; Goodall, Fatti & Owen-Smith, in press). Accordingly, we followed the procedure outlined by Owen-Smith *et al.* (2012) to establish the distinct movement tendencies contributing to the overall statistical distribution of hourly step displacements. Four movement modes emerged from the model output (see Appendix S1): (a) step displacements $<55 \text{ m h}^{-1}$, consistent with predominantly stationary resting; (b) slow movement of $55\text{--}300 \text{ m h}^{-1}$, consistent with primarily foraging activity; (c) intermediate rates of movement of $300\text{--}1100 \text{ m h}^{-1}$, interpreted as mixed mobility; and (d) displacements $>1100 \text{ m h}^{-1}$, assumed to represent persistent travel. Consistency with foraging behaviour was judged from the typical proportion of foraging time spent walking by grazing ungulates and rate of travel while walking (Owen-Smith, 2002; : page 48; see also Cain, Owen-Smith & Macandza, 2012). Obviously other activity states generating slow movements, such as social interactions, will be subsumed within the foraging mode, but these make a minor contribution relative to the time taken up with foraging by large herbivores (Owen-Smith, 1988). The model assigned the most likely proportional contributions from the distinct movement modes to each hourly displacement, from which we extracted the predominant state for spatial plotting. This was associated with mid-points between successive GPS fixes.

The temporal distribution of movement mode contributions was used to establish the times of day when particular activity states predominated, separately by season. The following seasonal blocks were distinguished, following Owen-Smith (2013): (a) wet season – December to March; (b) early (or cool) dry season – April to July; (c) late (or hot) dry season – August to November. This analysis confirmed that the wildebeest herds showed peaks in movement consistent with foraging activity during the early morning after dawn and from the late afternoon into the early evening, with a minor elevation in foraging around midnight (Appendix S1 Fig. A3). Resting peaked after midday, during the early evening and shortly before dawn. Travelling showed peaks around dawn and dusk. Overall, 60% of daylight hours and around 33% of the night was associated with primarily foraging activity or mixed mobility.

The derived activity pattern of the collared wildebeest matched that documented by direct observations on wildebeest herds by Berry *et al.* (1982), and changed little across seasons.

The space occupied by primarily foraging activity during the early morning and late afternoon was interpreted as the prime-times foraging range (PFR). The morning foraging period extended from 05:00 to 08:00 during the summer wet season, shifting to 06:00–09:00 during the winter dry season when the sun rose later. Late afternoon foraging prevailed from 16:00 to 19:00. Resting predominated through the midday period from 12:00 to 15:00. For temporal comparisons, night-time encompassed 19:00–05:00, while diurnal conditions spanned 07:00–17:00, excluding transitional periods between night and day.

Spatial analysis

The eight collared herds providing year-round data formed the independent replicates for all analyses. Range estimates spanning two or three successive years in at least one season were available for seven of the eight herds.

For comparing the annual home ranges encompassing all activities defined by various procedures, we used the Adehabitat package within the R language (R Core Team 2014). Specifically, the areas broadly enclosed by minimum convex polygons (MCP) were compared with those defined by kernel utilization densities (KUD) and local convex hulls (LoCoH) for 99%, 90% and 50% isopleths. To delineate the areas occupied for specific activities in different circumstances, we used the package LoCoH, which best demarcates edges of occupied regions and gaps within them (Getz *et al.*, 2007). We chose the 90% isopleth for consistency, following Borger *et al.* (2006). PFRs generated initially for each herd, year and season were amalgamated across years for each herd because their locations generally remained consistent between years.

Within ArcMap (ESRI, 2014), we used the ‘overlay’ and ‘union’ analysis tools, and the Spatial Statistics tool to determine the reciprocal range overlaps in addition to the range extents in km^2 . Distinctions in range extents and overlaps were supported by standard errors of mean values across all herds providing relevant data (i.e. the herds are the replicates). Reciprocal overlaps represent the proportion of range A enclosed within range B, and vice versa. We distinguished these overlap patterns: (1) coincident – $>50\%$ reciprocal overlap; (2) nested – smaller range almost entirely enclosed within the larger range; (3) partially overlapping – reciprocal overlaps both amounting to $<50\%$ of the respective areas; (4) separated – $<5\%$ overlap.

We also established the distance of each location from edges of the PFRs under specific conditions of activity state and time of day, and imported the location co-ordinates into ArcMap. We assumed that these edges were closely associated with the habitat transition towards taller grass and greater woody vegetation cover as established by Yoganand & Owen-Smith (2014). We then created a Raster polygon of PFR limits for each collar ID, and generated a base Raster layer of distance to edge in metres from mid-points of each polygon. The Spatial Analyst tool was used to extract distance-from-edge for each location point. Using the Select Features tool, we subdivided the location data as falling either within or outside of

each foraging range, and then exported each of these split data frames to derive a breakdown of the distribution of location data inside and outside of PFRs.

The following spatial comparisons were undertaken, usually separately by season:

- 1 Between PFRs in different seasons, to establish whether seasonal expansions or shifts occurred;
- 2 Between places where midday foraging occurred and PFRs, to establish whether range expansion took place to seek more ample forage or shade;
- 3 Between resting sites occupied over midday and PFRs, to establish whether extensions occurred to seek more shady conditions;
- 4 Between resting sites occupied during the night and PFRs, to establish whether these were shifted away from the more risky edges;
- 5 Between resting sites occupied during daylight and places occupied while resting at night, to assess shifts in location or contractions in spatial extent in response to contrasting risks of predation and thermal conditions;
- 6 Between nocturnal resting sites and nocturnal foraging locations, to establish whether shifts in location or extent occurred dependent on food needs;
- 7 Between locations of travelling activity and PFRs, to establish their relative distribution during different seasons and day versus night.

Results

Annual home ranges

Total annual home ranges obtained using LoCoH were substantially smaller than those estimated from MCP or KUD, irrespective of the isopleth used to define the bounds (Table 1).

Diurnal space use

Combining all herds and years, PFRs obtained using LoCoH averaged 2–3 km² in extent through the wet and early dry seasons, expanding to 9 km² during the late dry season (Table 2). For most wildebeest herds, the PFR was constituted by two or more segments separated by several kilometres, one occupied

mainly during the wet season and early part of the dry season, and the other later in the dry season and sometimes into the start of the wet season (Fig. 1b, Fig. S1). The wet season segment, occupied for the major portion of the year, averaged $1.55 \pm \text{SE}0.16 \text{ km}^2$. Proportional overlaps between PFRs exploited within each seasonal block depended on the time apportionment between the separate range segments within each season, and were influenced by the greater extent of the dry season range (Table 2). Seasonal PFRs of individual herds were consistent in their location in successive years, except when herds expanded their late dry season ranges to exploit nearby burnt areas. The PFRs of individual wildebeest herds remained largely distinct.

Movements indicative of foraging activity during the midday period fell almost entirely within the PFRs during the wet season and early dry season, except for one herd. In the late dry season, only three of the eight herds expanded their foraging ranges over midday, by 1–2 km². Resting sites occupied over midday were similarly located mostly within the PFRs, but again less so in the late dry season than during other times of the year (Fig. 2, Fig. S2).

Nocturnal space use

Nocturnal resting locations of all except one herd were nested within the PFRs and shifted away from edges of the PFRs towards the interior during both the wet and early dry seasons (Fig. 2, Figs S2 and S3). The exceptional herd (Wi375) had its home-range abutting the fenced western boundary of Manyaleti Game Reserve and rested close to this fence. Places occupied for resting at night and those where resting occurred over midday showed relatively little overlap (Table 3). Patterns were less consistent during the late dry season, because of disparities in how space occupation was partitioned between the seasonally distinct ranges. Nevertheless, when wildebeest herds were still within their wet season ranges during some portion of the late dry season, their nocturnal resting locations were coincident with those used earlier in the seasonal progression.

Movements indicating foraging activity occurring during the night were largely coincident with nocturnal resting places (Fig. 2, Table 3; Fig. S2). Nocturnal foraging activity was likewise shifted away from the edge zones of the PFRs (Fig. 2, Table 3; Fig. S2). Wildebeest herds spent only half as much time within 50 m of the PFR edges at night than while

Table 1 Estimates of annual home-range extents in km² encompassing all seasons and activities for the eight collared wildebeest herds, provided by minimum convex polygons (MCP), kernel utilization density (KUD) and local convex hulls (LoCoH) for 50%, 90% and 99% isopleths

Method	Isopleth (%)	Wi145	Wi147	Wi148	Wi149	Wi150	Wi151	Wi196	Wi375	Mean	SE
MCP	50	64.5	39.4	7.1	11.0	9.1	14.7	1.0	5.2	19.0	7.7
	90	80.0	110.8	20.4	52.4	79.2	58.1	7.9	14.4	52.9	12.9
	99	95.9	124.2	24.7	55.7	156.0	68.1	18.0	58.8	75.2	16.8
KUD	50	7.5	7.3	1.9	6.0	6.0	8.8	0.4	2.7	5.1	1.1
	90	32.8	53.8	10.1	23.2	33.6	34.5	4.8	12.4	25.7	6.1
	99	91.7	166.8	23.9	50.4	137.9	81.8	12.6	40.5	75.7	20.7
LoCoH	50	0.5	0.5	0.4	0.8	0.8	1.7	0.3	0.5	0.7	0.2
	90	7.8	8.3	2.8	7.1	14.1	14.7	3.9	5.9	8.1	1.5
	99	44.4	77.2	11.9	25.4	94.6	44.6	14.3	35.7	43.5	10.3

Table 2 Extent of prime foraging ranges within each season (all years combined obtained using LoCoH and 90% isopleths) and their proportional overlap for the eight collared wildebeest herds

Season	Extent (km ²)		Mean overlap (% ±SE)	
Wet	Mean ± SE	2.12 ± 0.30	Early dry in wet	47.3 ± 4.9
	Range	0.69–3.10	Wet in early dry	58.0 ± 6.2
Early dry	Mean ± SE	2.75 ± 0.70	Late dry in wet	14.7 ± 1.6
	Range	1.42–7.41	Wet in late dry	66.9 ± 6.3
Late dry	Mean ± SE	8.98 ± 1.54	Late dry in early dry	23.6 ± 3.5
	Range	3.62–17.35	Early dry in late dry	82.8 ± 5.5

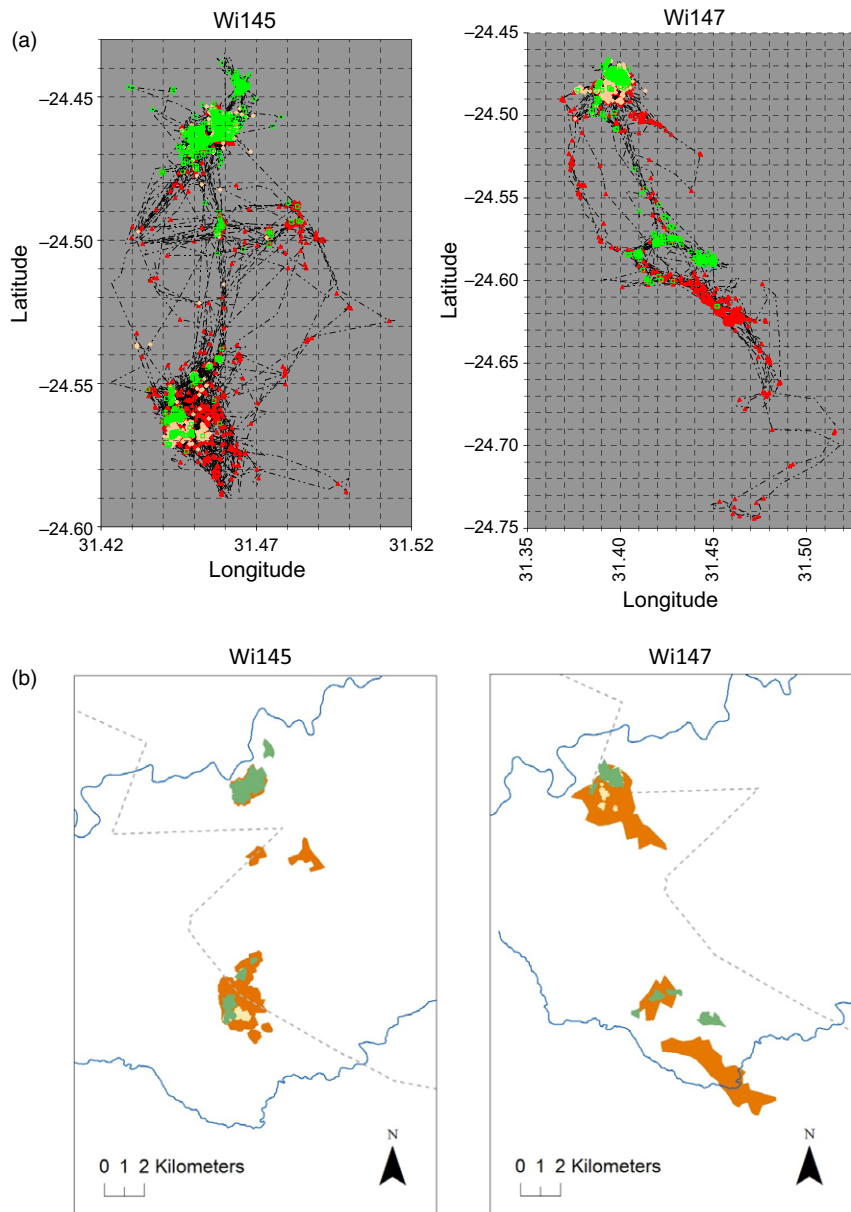


Figure 1 (a) Complete space occupation data plotted for two wildebeest herds, distinguished by season. Symbols represent positions at 6-h intervals (01:00, 07:00, 13:00 and 19:00) in order to restrict their overlay. Green = wet season, tan = early dry season, red = late dry season. Dashed lines connect sequential hourly locations. Grid is approximately 1 km². (b) Seasonal home ranges derived using 90% isopleths in LoCoH for these same two wildebeest herds. Dashed grey line indicates the unfenced Kruger NP boundary; wavy blue lines the two seasonal rivers traversing the region. Green = wet season range, tan = early dry season range, and red = late dry season range.

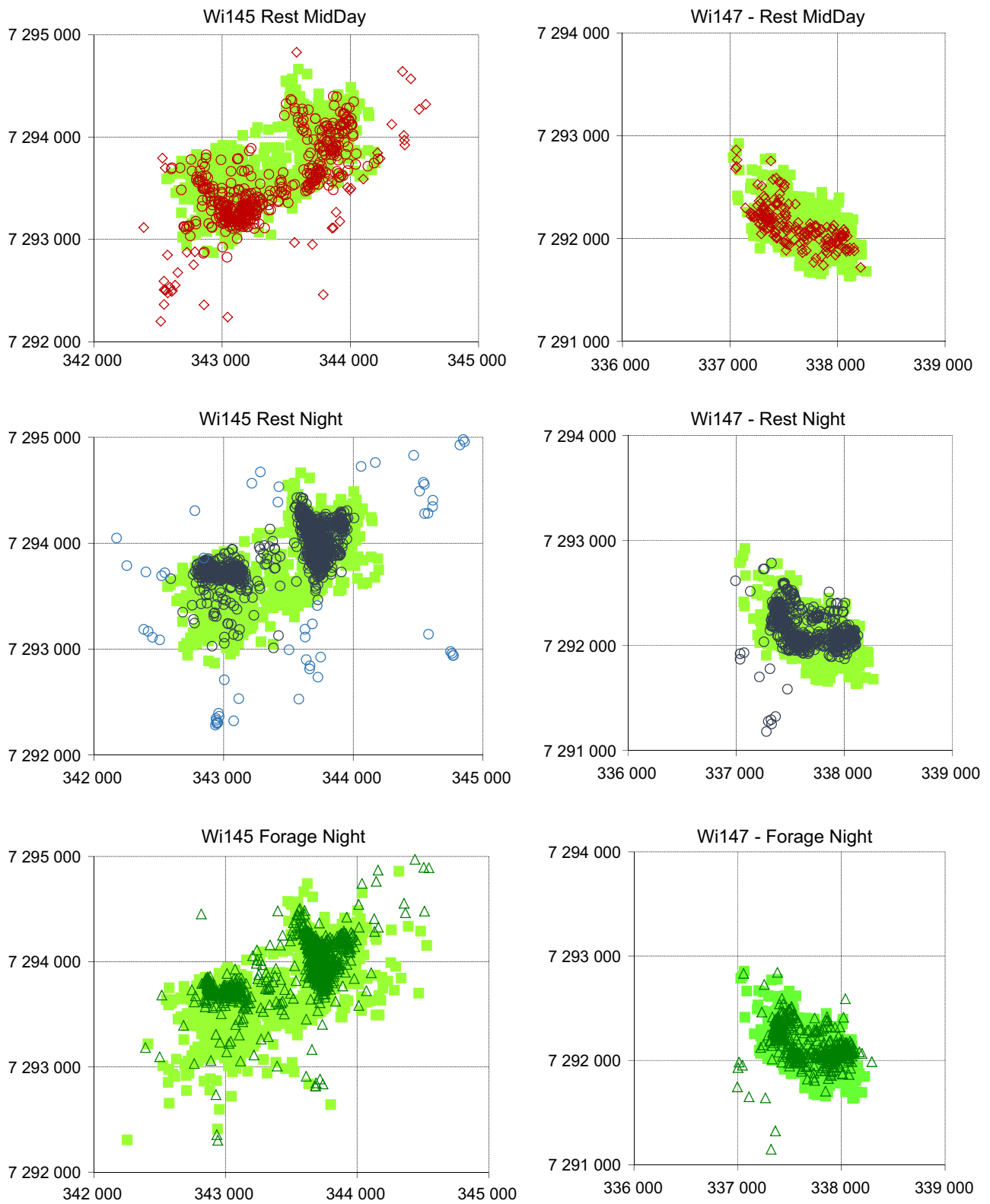


Figure 2 Mapped distributions of midday resting, nocturnal resting and nocturnal foraging locations of two wildebeest herds (open symbols) during the wet season and early dry season, overlain on prime foraging ranges in the wet season (filled symbols), for all years combined.

Table 3 Spatial extent of the areas occupied by the collared wildebeest herds while resting over midday and while resting or foraging during the night plus the proportional overlap between these areas

Activity and period	Season	Extent (km ²)	Overlap (% ±SE)
Midday resting	Wet	Mean ± SE	1.20 ± 0.21
		Range	0.19–1.81
Midday resting	Early Dry	Mean ± SE	1.77 ± 0.27
		Range	0.54–2.26
Midday resting	Late Dry	Mean ± SE	5.47 ± 1.40
		Range	0.95–11.88
Nocturnal resting	Wet	Mean ± SE	0.28 ± 0.06
		Range	0.12–0.49
Nocturnal resting	Early dry	Mean ± SE	0.34 ± 0.07
		Range	0.13–0.64
Nocturnal resting	Late dry	Mean ± SE	2.64 ± 0.79
		Range	0.72–6.14
Nocturnal foraging	Wet	Mean ± SE	0.44 ± 0.12
		Range	0.09–0.95
Nocturnal foraging	Early dry	Mean ± SE	0.54 ± 0.13
		Range	0.17–1.14
Nocturnal foraging	Late dry	Mean ± SE	2.84 ± 0.64
		Range	0.86–6.07

Table 4 Proportion of location records for the collared wildebeest herds that were <50 m from edge inside prime foraging ranges and up to 500 m beyond the edge for different activity states and times of day under wet and early dry season conditions

Activity state	Proportion <50 m from edge (%)	Proportion up to 500 m beyond edge (%)
Prime-time foraging	Mean	13.7
	Range	5.1–23.7
Midday resting	Mean	10.7
	Range	3.9–23.9
Nocturnal foraging	Mean	4.7
	Range	0.4–9.4
Nocturnal resting	Mean	5.2
	Range	0.9–11.6

Table 5 Number and proportions of travelling records of the collared wildebeest herds that fell outside of their prime foraging ranges, amalgamated over seasons

	Number of records	Proportion outside (%)
Day	Mean ± SE	70 ± 12
	Range	20–109
Night	Mean ± SE	32 ± 5
	Range	11–52

foraging during the day, and generally spent more time beyond the bounds of the PFRs while resting over midday than under other conditions (Table 4). Correspondingly, the extent of the area occupied at night, whether for resting or foraging, represented only a small fraction of the area utilized during the prime foraging times (Tables 2 and 3).

Travelling activity

Movements indicating travelling activity fell mostly outside the PFRs during both diurnal and nocturnal conditions in all

seasons (Table 5; dawn and dusk periods when conditions were intermediate between daylight and darkness excluded). Travelling occurred about twice as frequently during the day as at night, but showed no consistent orientation in any direction. The movement state interpreted as mixed mobility also occurred much less frequently at night than during the day, and was more prevalent outside PFRs than within them.

Excursions extending several kilometres beyond PFR limits over several successive days were shown by certain wildebeest herds in October or November during the transition period between the dry season and the wet season (see Fig. 1). These roaming movements were largely responsible for the difference in extent between the 90% annual home range and 99% total range traversed (Table 1).

Discussion

Annual home ranges encompassing all activity states, whether defined by minimum convex polygons or kernel utilization densities, greatly over-estimated the extent of the area where foraging activity was mostly concentrated because they encompassed

outlying travel. Areas obtained using LoCoH proved most parsimonious. The extent of the area enclosed within the 50% isopleth, commonly used to identify core areas, coincided mostly with the places where resting took place. These discrepancies help explain why conventional home-range estimators provide such vague indications of the metabolic scaling of space use (Kelt & Van Vuuren, 2001; Ofstad *et al.*, 2016).

The PFRs occupied by the wildebeest herds during early morning and late afternoon periods coincided with the open habitats with comparatively short grass identified by Yoganand & Owen-Smith (2014) as representing either gabbro uplands, favoured during the wet season, or seep zones in granitic landscapes, occupied during the dry season. PFRs occupied by individual wildebeest herds remained consistent from 1 year to the next, and overlapped little or not at all with those of neighbouring herds (Owen-Smith *et al.*, 2015). While providing high quality grazing, the PFRs also presented low cover for predators, making it difficult to separate these two influences on habitat occupation during these times of day (Yoganand & Owen-Smith, 2014).

Our expectations that space occupation would shift somewhat with time of day and with the predominant activity, as well as seasonally, were largely confirmed. We found no consistent tendency for the collared wildebeest herds to expand their space use into surrounding areas presenting greater woody canopy cover during the midday period when thermal stress was likely to be greatest. During the night when lions hunted most actively, the collared wildebeest herds remained within their PFRs, but contracted their space occupation centrally and spent less time in the edge zone in proximity to more trees and taller grass (as documented by Yoganand & Owen-Smith, 2014), both while resting and while apparently foraging. When accosted by lions at night, the wildebeest tended to dodge the lions and returned to the more secure habitat after the lions had moved on (Martin & Owen-Smith, 2016).

Excursions beyond the PFRs were undertaken more frequently during daylight than at night, especially later in the dry season when travel to seek water became necessary. Some of the nocturnal movement was associated with evading capture attempts by threatening lions (Martin & Owen-Smith, 2016). Prolonged excursions beyond PFRs occurred during the transitional period around the end of the dry season when both food and water supplies were at their minimum.

Localities where resident grazers concentrate in the Serengeti ecosystem in Tanzania likewise confer both nutritional and anti-predator benefits (Anderson *et al.*, 2010). As well as providing high-quality food, the short-grass plains where migratory wildebeest concentrate during the wet season provide little cover for stalking lions (Hopcraft *et al.*, 2014).

Relatively broad muzzles enable wildebeest to persist within areas of short grass until little forage remains (Murray & Brown, 1993). Nevertheless, at some stage during the dry season the amount of grass left in their preferred habitat becomes insufficient, prompting them to forage more widely and thereby incur an increased risk of predation. Such excursions occurred mainly during the transition period between the dry season and the wet season. During our study period, annual rainfall deviated little from the long-term average. Under lower rainfall

conditions, reduced grass growth could curtail exploitation of the gabbro uplands earlier in the dry season and lengthen it within seep zone grasslands. These circumstances could force the wildebeest to spend more time in denser vegetation during the critical period of the year. The elevated susceptibility of wildebeest to predation in these circumstances could contribute towards regulating the local population density (Owen-Smith, 2015).

For other ungulate species elsewhere, adequate food, security and shelter may be obtained in different places. Within Kruger Park, sable antelope herds are not found where the best quality grazing exists, but rather where there are few wildebeest and impala and hence relatively few lions (Chirima *et al.*, 2013). Zebra move into places with denser woody cover at night where they are less readily detected by hunting lions (Fischhoff *et al.*, 2007). In contrast, impala aggregate in open glades, where their prime predator, the leopard, has less cover, especially at night (Ford *et al.*, 2014). For other large herbivores, the places with most favourable food resources are often those where animals are most vulnerable to predation (e.g. North American elk *Cervus elaphus canadensis* in Canada: Kittle *et al.*, 2008; and some African ungulates: Thaker *et al.*, 2011), necessitating dynamic trade-offs.

Our findings indicate the pervasive influence that the risk of predation can have on space occupation in different circumstances (Laundré *et al.*, 2014). Further studies are needed on how this “landscape of fear” affects the space use patterns of other animal species, drawing on the location data supplied by GPS telemetry covering all times of day, activity states and seasons.

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References

- Anderson, T.M., Hopcraft, J.G.C., Eby, S., Ritchie, M., Grace, J.B. & Olf, H. (2010). Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology* **91**, 1519–1529.
- Berry, H.H., Siegfried, W.R. & Crowe, T.M. (1982). Activity patterns in a population of free-ranging wildebeest at Etosha National Park. *Z. Tierpsychol.* **59**, 229–246.
- Borger, L., Franconi, N., Feretti, F., Mesche, F., De Michele, G., Gantz, A. & Coulson, T. (2006). An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am. Nat.* **168**, 471–485.
- Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24**, 346–352.
- Cain, J.W. III, Owen-Smith, N. & Macandza, V. (2012). The costs of drinking: comparative water dependency of sable antelope and zebra. *J. Zool.* **286**, 58–67.

- Chirima, G.J., Owen-Smith, N., Erasmus, B.F.N. & Parrini, F. (2013). Distributional niche of a relatively rare large herbivore: habitat template versus biotic interactions. *Ecography* **36**, 68–79.
- Cornelis, D.S., Benhamou, S., Janeau, G., Morrellet, N., Oudraogo, M. & de Visscher, M.N. (2011). Spatiotemporal dynamics of forage and water resources shape space use of West African savanna buffalos. *J. Mammal.* **92**, 1287–1297.
- ESRI. (2014). *ArcGIS desktop: release 10.3*. Redlands: Environmental Systems Research Institute.
- Fieberg, J. & Borger, L. (2012). Could you please phrase “home range” as a question? *J. Mammal.* **93**, 890–902.
- Fischhoff, I.R., Sundaresan, S.R., Cordingley, J. & Rubenstein, D.R. (2007). Habitat use and movements of plains zebra in response to predation danger from lions. *Behav. Ecol.* **18**, 725–729.
- Ford, A.T., Goheen, J.R., Otieno, T.O., Biddner, L., Isbell, L.A., Palmer, T.L., Ward, D., Woodroffe, R. & Pringle, R.M. (2014). Large carnivores make savanna trees less thorny. *Science* **346**, 346–349.
- Getz, W.M. & Wilmers, C.C. (2004). A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* **27**, 489–505.
- Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C. (2007). LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE* **2**, e207, 11 pp.
- Goodall, V. (2013). *Statistical time series analyses of the ungulate movement patterns in the Kruger National Park*. PhD thesis, University of the Witwatersrand, Johannesburg.
- Goodall, V., Fatti, P. & Owen-Smith, N. (in press). Animal movement modelling – independent or dependent models? *S. Afr. Statistics J.*
- Hopcraft, J.G.C., Morales, J.M., Beyer, H.L., Borner, M., Sinclair, A.R.E., Olf, H. & Haydon, D.T. (2014). Competition, predation and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecol. Monogr.* **84**, 355–372.
- Jewell, P.A. (1966). The concept of home range in mammals. *Symp. Zool. Soc. London* **18**, 85–109.
- Kays, R., Crofoot, M.C., Jetz, W. and Wikeski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science* **348**, aaa2478.
- Kelt, D.A. & Van Vuuren, K. (1999). Energetic constraints and the relationship between body size and home range area in mammals. *Ecology* **80**, 337–340.
- Kelt, D.A. & Van Vuuren, D.H. (2001). The ecology and macroecology of mammalian home range area. *Am. Nat.* **157**, 637–645.
- Kittle, A.M., Fryxell, J.M., Desy, G.E. & Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia* **57**, 163–175.
- Laundré, J.W., Hernández, L., López Medina, P., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P. & Browning, D.M. (2014). The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* **95**, 1141–1152.
- Laver, P.N. & Kelly, M.J. (2008). A critical review of home range studies. *J. Wildl. Manag.* **72**, 290–298.
- Lottker, P., Rummel, A., Traube, M., Stache, A., Sustr, P., Muller, J. & Heurich, M. (2009). New possibilities of observing animal behaviour from a distance using activity sensors in GPS collars: an attempt to calibrate remotely collared activity data with direct observation in red deer. *Wildl. Biol.* **15**, 425–434.
- Martin, J. & Owen-Smith, N. (2016). Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Anim. Behav.* **116**, 163–170.
- Martin, J., Benhamou, S., Yoganand, K. & Owen-Smith, N. (2015). Coping with spatial heterogeneity and temporal variability in resources and risks: adaptive movement behaviour by a large grazing herbivore. *PLoS ONE* **10**, e0118461, 19 pp.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**, 2436–2445.
- Murray, M.G. & Brown, D. (1993). Niche separation of grazing ungulates in the Serengeti: an experimental test. *J. Anim. Ecol.* **62**, 380–389.
- Ofstad, E.G., Herfindal, I., Solberg, E.J. & Saether, B.-E. (2016). Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proc. R. Soc. B* **283**, 20161234.
- Owen-Smith, N. (1988). *Megaherbivores. The influence of very large body size on ecology*. Cambridge: Cambridge University Press.
- Owen-Smith, N. (1998). How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu. *J. Zool.* **246**, 183–192.
- Owen-Smith, N. (2002). *Adaptive herbivore ecology. From resources to populations in variable environments*. Cambridge: Cambridge University Press.
- Owen-Smith, N. (2013). Daily movement responses by an African savanna ungulate as an indicator of seasonal and annual food stress. *Wildl. Res.* **40**, 232–240.
- Owen-Smith, N. (2015). How diverse large herbivores coexist with multiple large carnivores in African savanna ecosystems: demographic, temporal and spatial influences on prey vulnerability. *Oikos* **124**, 1417–1426.
- Owen-Smith, N. & Goodall, V. (2014). Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. *J. Zool.* **293**, 181–191.
- Owen-Smith, N. & Mills, M.G.L. (2008a). Predator-prey size relationships in an African large-mammal food web. *J. Anim. Ecol.* **77**, 173–183.
- Owen-Smith, N. & Mills, M.G.L. (2008b). Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology* **89**, 1120–1133.

- Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movement. *Phil. Trans. R. Soc. B* **365**, 2267–2278.
- Owen-Smith, N., Goodall, V. & Fatti, P. (2012). Applying mixture models to derive activity states from movement rates of large herbivores obtained using GPS telemetry. *Wildl. Res.* **39**, 452–462.
- Owen-Smith, N., Martin, J. & Yoganand, K. (2015). Spatially nested niche partitioning between syntopic grazers at foraging arena scale within overlapping home ranges. *Ecosphere* **6**, 152, 15 pp.
- Powell, R.A. (2000). Animal home ranges and territories and home range estimators. In *Research techniques in animal ecology*: 65–110. Boitani, L. & Fuller, T.K. (Eds). New York: Columbia University Press.
- R Core Team. (2014). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Tamburello, N., Cote, I.M. & Dulvy, N.K. (2015). Energy and the scaling of animal space use. *Am. Nat.* **186**, 196–211.
- Thaker, M., Vanak, A.B., Owen, C.R., Ogden, M.B., Niemann, S.M. & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* **92**, 398–407.
- Traill, L.W., Martin, J. & Owen-Smith, N. (2016). Lion proximity, not moon phase, affects the nocturnal movement behaviour of zebra and wildebeest. *J. Zool.* **299**, 221–227.
- Van Moorter, B., Visscher, D.R., Jerde, D.R., Frair, J.L. & Merrill, E.H. (2010). Identifying movement states from location data using cluster analysis. *J. Wildl. Manage.* **74**, 588–594.
- Venter, F.J., Scholes, R.J. & Eckhardt, H.C. (2003). The abiotic template and its associated vegetation pattern. In *The Kruger experience*: 83–129. du Toit, J.T., Rogers, K.H. & Biggs, H.C. (Eds). Washington: Island Press.
- Wilson, R.R., Gilbert-Norton, L. & Gese, E.M. (2012). Beyond use versus availability: behaviour-specific resource selection. *Wildl. Biol.* **18**, 424–430.
- Yoganand, K. & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography* **37**, 969–982.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Application of a mixture model to translate hourly displacements into predominant activity states during the intervals between successive hourly GPS locations and thereby establish the daily activity schedule of wildebeest in the study area.

Figure S1. Seasonal home ranges of six collared wildebeest herds in the Orpen gate region of Kruger National Park as defined by 90% convex hulls.

Figure S2. Mapped distributions of midday resting, nocturnal resting and nocturnal foraging locations for five wildebeest herds through the wet season into the early dry season.

Figure S3. Distribution of resting locations through midday and at night relative to the edge limits of prime foraging ranges through the wet season and early dry season (as defined by 90% LoCoH isopleths) for seven wildebeest herds for all years combined.

Table S1. Summary of the data provided by the GPS collars placed on wildebeest herds in the Orpen region of Kruger National Park.