Owen-Smith, N and Traill, LW

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

http://researchonline.ljmu.ac.uk/id/eprint/11709/

Article

DRAFT 2016-03-30

Functional anatomy of space use by a large herbivore at home range scales: predation risk versus resource availability

Norman Owen-Smith and Lochran Traill

Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa

Introduction

The home range was classically defined as the space normally traversed by an animal in its routine activities (Burt 1943, Jewell 1966) and interpreted more recently as a utilization distribution in space through time (Van Winkle 1975). But assessments of space use have generally not taken into account how this space was utilized as indicated by the specific activities performed in different regions (Powell 2000, Getz & Wilmers 2004, Borger et al. 2006, Laver & Kelly 2008). Fitness is ultimately an outcome of resources obtained, security from predation provided and shelter from stressful conditions gained. Distinct contributions to fitness may be derived from different places and in aggregate determine the overall extent of the space occupied by individual animals or groups. How large an area is required to supply food needs? How is this area extended to access other resources besides food? How is space occupation modified by the risk of predation? How is it adjusted to alleviate thermal stresses? How is it restricted by the presence of potential competitors? Answers to these questions have ramifying consequences for local population densities, niche partitioning and social structuring (Owen-Smith, Martin & Yoganand 2015, Riotte-Lambert, Benhamou & Chamaille-Jammes 2015).

Mechanistically, space use patterns are generated by movements informed by an animal's cognitive memory of fitness landscapes (Van Moorter et al. 2009, Spencer 2012, Fagan et al. 2013, Avgar et al. 2015). Through persisting in particular localities and returning to these patches after some interval, movements generate regions of concentration at particular spatio-temporal scales (Benhamou. & Riotte-Lambert 2012, Owen-Smith 2014, Owen-Smith et al. 2015, Seidel and Boyce 2015). The overall extent of the home range occupied depends on whether the places contributing in various ways to fitness are spatially arranged; specifically, whether they are coincident, nested, overlapping, discrete or more widely separated.

A mechanistic model of home range emergence has been developed for mammalian carnivores that forage outwards from den sites (Moorcroft, Lewis & Crabtree 1999; see also Mitchell & Powell 2004, Moorcroft & Lewis 2006), but not yet for large mammalian herbivores. Such herbivores exploit a food resource that is widely dispersed, but rooted in space and temporally variable in quantity and nutritional value. Places where the most nutritious food is readily available should attract concentrations of herbivores through the plant growing season until plant regrowth fades and food resources in these places become depleted. Herbivores may then be prompted to shift their foraging range elsewhere to places where adequate food remains available. Temporary range shifts may occur while animals exploit ephemeral sources of high quality food generated after fires or local rainfall events (Yoganand & Owen-Smith 2014). When surface water is no longer available in places providing food, animals may need to undertake excursions beyond their usual ranges in order to drink (Cain et al. 2014).

While obtaining food and other resources, herbivores must also remain sufficiently secure from predation. Predators tend to hunt where they most frequently encounter potential prey under conditions where their chances of making a successful kill are greatest (Hopcraft et al.). Stalking predators, such as most felids, are more effectively concealed during conditions of darkness, meaning that the risk of being killed for their herbivore prey is elevated nocturnally (Prugh & Golden 2014). Hence large herbivores may be less mobile at night than during the day (Owen-Smith & Goodall 2014) and seek places where they are most secure from being ambushed. Cursorial predators hunt more frequently diurnally, but are least active during the midday period when conditions are hot, inhibiting long pursuits. This is also the time of day when the thermal

stress incurred by herbivores in tropical or subtropical regions is greatest, prompting these animals to cease foraging and seek shady sites, particularly while resting.

GPS telemetry has opened opportunities not only to track the sequential movements of animals (Kays et al. 2015), but also to infer their activity state from their movement patterns (Van Moorter et al. 2010, Wilson et al. 2012). Hence how the use of specific areas for particular activities defines the home range extent (Fieberg & Borger 2012) can now be investigated more thoroughly than was previously possible. Distinct movement states can be identified from displacement distances over hourly or finer time steps, and equated with the activities most likely to generate them (Owen-Smith, Goodall & Fatti 2012, Goodall 2014). While resting animals move little. For large herbivores, foraging activity generates slow, frequently tortuous movements because of the alternation of stationary feeding and intermittent relocation. Persistent travel, whether to and from water or between separate home range segments, generates longer, more directed movements. For large ungulates, foraging activity is most prevalent during the early morning and late afternoon periods (Owen-Smith 1998, Owen-Smith & Goodall 2014). Resting predominates during the night and through midday, although some foraging occurs even at these times of the diel cycle.

Our movement study was focussed on a relatively sedentary subpopulation of a grazing ruminant, the blue wildebeest (*Connochaetes taurinus*), in west-central Kruger National Park in South Africa. Habitat occupation patterns of these animals were documented by Yoganand and Owen-Smith (2014) and their fine-scale resource exploitation patterns within and between foraging arenas were described by Martin et al. (2015) and Owen-Smith et al. (2015). How these animals reacted following encounters with their major predator, the African lion (*Panthera leo*), was analysed by Martin and Owen-Smith (2016). A crux issue raised, not resolved by Yoganand & Owen-Smith (2014), is whether the narrow habitat occupation of wildebeest is governed by predation risk or by specific food requirements.

Our functional analysis of space use by wildebeest rests on assumptions about how the relative benefits and costs associated with particular activities are likely to vary both over the diel cycle and seasonally. We assumed that food needs would be the primary influence on places occupied by wildebeest herds during peaks in foraging activity during the early morning and late afternoon. Over midday when conditions are hot and lions are unlikely to be hunting, wildebeest might widen their foraging range into places where more ample food remained despite the greater concealment provided by taller grass for stalking lions. Their need for shade could also prompt them to occupy areas with greater tree cover especially while resting at this time of day. While foraging or resting during the night, space occupation by the wildebeest should become more narrowly restricted to places where they are least vulnerable to being killed by lions. As the dry season advances and food availability gets progressively reduced, wildebeest could shift their foraging activity towards places where sufficient grass of adequate quality remains. When travel to and from remaining sources of surface water sources becomes necessary, wildebeest should undertake such journeys towards midday when conditions are least favourable for hunting by lions.

Yoganand and Owen-Smith (2014) demonstrated that the foraging habitat selectively occupied by wildebeest herds in our study area through most of the year were associated with open woody cover and short grass, interpreted as grazing lawns. Accordingly, we expected to find the following spatial patterns manifested by the wildebeest herds that we tracked:

1. Foraging areas occupied during the prime-times in the morning and late afternoon would be largely coincident.

    2.   Foraging areas occupied over midday would be expanded somewhat into surrounding areas with taller grass.

    3.   Foraging activity undertaken during the night would be shifted away from the edges of the prime-times foraging areas where the risk of a lion ambush would be greatest.

    4.   Foraging ranges occupied during the dry season would be distinct from the wet season ranges.

    5.   Prime-times foraging ranges occupied in successive years by particular herds would be largely coincident.

    6.   Foraging ranges exploited by neighbouring herds competing for grass would overlap little.

    7.   Resting locations during midday would tend to be distributed beyond the limits of the prime-times foraging ranges.

    8.   Nocturnal resting sites would be located away from the edges of the prime-times foraging areas.

    9.   Travelling activity would be located mainly outside the prime-times foraging ranges in the direction of surface water or between separated foraging ranges.

Methods

Study area

The study was located in the west-central region of the Kruger National Park near the Orpen entrance gate plus adjoining regions of Manyaleti Game Reserve and Timbavati Private Nature Reserve. Geologically the area includes an intrusion of a gabbro sill into the surrounding granitic gneiss. Soils generated from gabbro contain more clay and hence are more fertile that the sandy soils typical of the granitic region. Woody vegetation consists of mixed thorn (*Acacia* spp) savanna on the gabbro and mixed bush willow (*Combretum* spp) savanna on the granite. Open areas with predominantly short grasses interpreted as grazing lawns maintained by the grazing pressure of wildebeest and other herbivores occur on the gabbro uplands. Bands of medium-height grassland with little tree cover are associated with seep zones in lower slope regions of granite landscapes, while sodic soils with a sparse short grass cover occur in bottomlands. Rainfall recorded at Kingfisherspruit ranger station within the study area has 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. The short grasslands on gabbro uplands and sodic bottomlands were the key resource areas occupied by wildebeest herds for most of the wet season. At some stage during the dry season, wildebeest herds shifted towards seep zones in the granitic region (Yoganand & Owen-Smith 2014). Some wildebeest herds occupied areas that temporarily offered short grass following burns during the transition period from the dry season into the wet season .Besides wildebeest, other common grazers in the study area included plains zebra (*Equus quagga*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*) and warthog (*Phacochoerus africanus*).

Data collection

In late March 2009, GPS collars supplied by Africa Wildlife Tracking (www.awt.co.za) were placed on 10 female wildebeest in separate herds numbering 12-35 animals and replaced when necessary to extend data collection for some herds until April 2012 (Yoganand & Owen-Smith 2014). Animals were immobilized by veterinary staff employed by South African National Parks following their ethical guidelines, and no fatalities occurred. GPS devices supplied location data through the GSM (mobile telephone) network on an hourly schedule. The GPS data are archived in the South African National Parks data depository (). Missing locations amounted to fewer than 5% of scheduled records, but for some herds there were gaps of a few months between collar failure and replacement. Two of the female wildebeest fitted with collars were associated together in the same herd for most of the study period, while one collar provided location data for less than a year. This reduced the sample of animals in independently moving herds with year-round location records to eight. The herds containing collared females represented around 40% of wildebeest herds in the approximately 500 km^2 study area. Male wildebeest not associated with herds of females and young were not considered in the study.

Data analysis

To establish the times of day when particular activities predominated, the daily activity schedule of the collared wildebeest was derived by fitting a mixture model to hourly displacements following the procedure outlined by Owen-Smith, Goodall and Fatti (2012; see Appendix A, Figs. A1 and A2). Four movement states were distinguished and associated with a predominance of these activities: (a) resting, identified by little or no movement (<55 m h^{-1}), (b) foraging, associated with slow movement (55-300 m h^{-1}), (c) mixed foraging and movement, indicated by intermediate rates of movement (300-1100 m h^{-1}), and (d) travel, typified by more substantial displacements (>1100 m h^{-1}). The hourly mixture of these activity states inferred from the statistical model was used to assign the predominant activity during each hourly interval, which was associated spatially with the mid-points between successive GPS fixes. This analysis also showed that peaks in foraging activity occurred in the early morning after dawn and from the late afternoon into the early evening, with a minor elevation in foraging around midnight (Appendix Fig. A3). Peak resting times were after midday, during the early evening and shortly before dawn. Travelling activity peaked around dawn and dusk. Overall, 60% of daylight hours and around 33% of the night was occupied by foraging activity or mixed foraging and movement. The daily activity pattern of the collared wildebeest was consistent across seasons, but with foraging commencing about an hour earlier during summer when the sun rose earlier (Appendix Fig. A3).

Seasonal divisions were made based on changes in movement patterns, which lagged behind rainfall, particularly with regard to the commencement of the wet season (Owen-Smith 2013). Accordingly, the following seasonal blocks were distinguished (a) wet season – December to March; (b) early (or cool) dry season – April to July; (c) late (or hot) dry season – August to November.

For analysis, the space occupied during the early morning and late afternoon foraging peaks was interpreted as representing the prime-times foraging range. The morning period when foraging prevailed extended from 05:00-08:00 during the summer wet season, shifting to 06:00-09:00 during the dry season months. Late afternoon foraging encompassed the period 16:00-19:00. The midday period when resting predominated extended from 12:00 to 15:00. Night-time was represented consistently by the period of darkness extending from 19:00 to 05:00.

The space-use measures we extracted were the spatial extent of the areas utilised for specific activities in different circumstances and the proportional overlaps between these ranges We distinguished these overlap patterns: (a) coincident – areas mostly overlapping; (b) nested – smaller range entirely enclosed within a larger one; (c) partial overlap – proportional overlap amounting to less than half of the respective areas; (d) separated – no overlap.

Areas encompassed by the overall herd home ranges encompassing all activities and seasons were assessed by both minimum convex polygon (MCP) and local convex hulls (LoCoH) methods using the package Adehabitat, comparing extents estimated within 50%, 90% and 99% isopleths. To define the specific areas occupied specifically for foraging, resting or travelling in particular circumstances, we used LoCoH, which most meaningfully delineated the edges of occupied regions and gaps within them, using the 90% isopleth (Getz et al. 2007). For statistically assessing central tendencies as well as range of variation in area and overlap, the eight collared herds formed the independent replicates. In particular we sought consistent patterns shown by all herds, bar one or two notable exceptions. Range estimates for seven of the eight herds encompassed two or three years in at least one season.

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

1. Between the prime morning and afternoon foraging ranges, to establish the extent to which they were spatially coincident and hence could be amalgamated;

2. Between prime-times foraging ranges in different seasons, to establish whether seasonal expansions or shifts occurred;

3. Between prime-times foraging ranges in different years for each season, to assess annual consistency;

4. Between places where midday foraging occurred relative to prime-times foraging ranges, to establish whether range expansion took place to seek more ample forage when predation risk was lowest;

5. Between resting sites occupied over midday and prime-times foraging ranges, to establish whether extensions occurred to seek more shady conditions;

6. Between prime-times foraging ranges of adjacent wildebeest herds, to establish whether there was competitive inhibition of much overlap;

7. Between resting sites occupied during the night and prime-times foraging ranges, to establish whether they were clustered away from the more risky edges of the latter;

8. Between locations of nocturnal foraging activity and prime-times foraging ranges, to establish whether more risky edges of the latter were still being avoided;

9. Between resting places occupied during daylight and sites occupied while resting at night, to assess shifts in location or contractions in spatial extent;

10. Between nocturnal resting sites and nocturnal foraging locations, to establish whether shifts in location or extent occurred;

11. Between locations of travelling activity and prime-times foraging ranges, to establish their distribution relative to the prime-times foraging range during different seasons and times of day or night.

Besides estimating range extents and overlaps, a more detailed analysis was conducted of the distribution of locations in different circumstances relative to the edges of the prime-times foraging ranges (LOCHRAN TO ADD DESCRIPTION OF HOW THIS WAS DONE)

Because one of the wildebeest herds (Wi151) had a somewhat diffuse range without a clear division between wet season and dry season segments, it was excluded from some of these comparisons.

Results

Annual home ranges
Total annual home range estimates obtained using 99% isopleths varied widely among herds depending on how far apart their seasonally occupied ranges were (Table 1). MCP vastly over-estimated the extent of the space occupied more than transiently by incorporating movement corridors between separate ranges, while LoCoH provided more parsimonious estimates of the space actually utilized. All except one of the wildebeest herds were recorded within an area of less than 1 km^2 for more than half of their time.

Diurnal space occupation
The areas occupied by each wildebeest herd during peak foraging periods in the morning and afternoon were largely coincident, and accordingly were amalgamated for further comparisons. Across all herds and years, the extent of these prime-times foraging ranges averaged about 2-3 km^2 (range 0.7-3.1 km^2) in the wet season and early dry season, expanding towards10 km^2 (range 3.6-17.4 km^2) during the late dry season (Table 2). All except one herd occupied distinct home range segments separated by several kilometres, one of them used mainly during the wet season and early part of the dry season and the other later in the dry season and early wet season (Fig. 1, Appendix Fig. B1). This range partitioning affected the proportional overlap between the foraging areas exploited within seasonal blocks, but in general the smaller of the seasonal ranges was nested within the larger one (Table 2).

　　Seasonal foraging ranges tended to be smaller within any individual year than when amalgamated across years, and encompassed only about 1 km^2 during the wet and early dry seasons in any particular year (Appendix Table B1). Late dry season ranges were somewhat larger, covering around 5-6 km^2 in individual years. Seasonal foraging ranges occupied in successive years largely overlapped. Low overlap indicated that the wildebeest herd had shifted occupation between its distinct home range segments between these paired years. The extent of foraging ranges utilised during the late dry season depended on whether there were extensions to utilise nearby areas that had been burned. The timing of the shifts between the seasonal range segments varied irregularly between years and among herds,indicating that there was no coordinated migration.

　　There was little or no overlap between the foraging ranges exploited in the same season by wildebeest herds occupying adjacent home ranges, except in three instances (Appendix Table B2). The exceptions were (a) overlap between the foraging ranges of herds Wi196 and herd Wi150 mainly in the wet season of 2009/10, although not occupied at the same time, (b) slight overlap between herds Wi148 and Wi151 in the wet season of 2009/10, and (c) overlap between herds Wi148 and herd Wi150 in the late dry season when both moved closer to pools remaining in a seasonal river. Additionally, there was brief overlap in the ranges occupied by herds Wi145 and Wi150 in the late dry season of 2009 when both were attracted to a section of newly burned grassland.

Movements consistent with foraging activity shown during the hot midday hours were located mostly within the area delineated by prime-times foraging during the early morning and late afternoon. This was shown by the smaller area encompassed and greater overlap with the prime-times ranges than vice versa (Appendix Table B3). However, there were some exceptions to this pattern, particularly during the late dry season, and one of the wildebeest herds (Wi196) consistently showed an expanded foraging range during the midday period in all seasons.

Sites occupied by wildebeest herds while resting through midday were located mostly within the prime-times foraging ranges, but with some herds showing a greater proportion of putative foraging records beyond the boundaries of the prime-time foraging ranges than within them (Fig. 2, Table 3, Appendix Fig. B2, Appendix Table B4). Midday resting sites tended to be less tightly concentrated within late dry season ranges than in wet season ranges.

Nocturnal space use
Nocturnal resting locations were clustered mostly in the interior of the prime-times foraging ranges utilized during the wet season for six out of seven wildebeest herds (Fig. 2 and Appendix Fig. B2) and hence encompassed a smaller area (Appendix Table B5). The exceptional herd occupied a home range abutting the fenced boundary of Manyaleti Game Reserve (Wi375) and shunted its nocturnal resting locations against this fence in the north-west corner of its home range (Appendix Fig. B2). A fence restriction on nocturnal resting, as well as other activities, was also evident for herd Wi145, which had its home range adjoining the fence around the ranger station in the north-west. There was little overlap between the places occupied while resting over midday and those used while resting during the night (Fig. 2, Appendix Fig. B2). Patterns were less consistent during the late dry season, because of disparities among the herds in how their time was partitioned between their seasonally distinct ranges. Nevertheless, if wildebeest herds were still in their wet season range during part of the late dry season their resting sites were coincident with those used earlier in the year.

Foraging activity taking place during the night was restricted to a smaller area in all seasons than the prime-times foraging range and largely coincided with the resting sites occupied during the night (Figure 2, Appendix Fig. B2, Table B6). For some herds nocturnal foraging was confined to an area as small as around 20 ha. Nocturnal resting and foraging activity were both consistently shifted away from the edge zone of the prime-times foraging range for six of the seven herds (Table 3).

Travelling activity
Travelling locations tended to fall more outside foraging ranges than within them during daytime in the wet season and early dry season. There was no consistent concentration in the direction of surface water sources at these times of the year. However, for some herds journeys to and from water were evident from the pattern of movement at 2-day intervals , undertaken from late morning through midday.. Relatively fewer nocturnal travel records fell beyond the prime-times foraging ranges. A higher proportion of travelling locations was located outside prime-times foraging ranges during the late dry season, but again these fell mainly between home range segments rather than being orientated towards surface water sources. In at least one instance, a wildebeest herd shifted between its seasonal ranges at night after an encounter with lions.

Excursions covering 10 km or more beyond normal home range limits over a few days were exhibited by certain wildebeest herds in October or November during the transition period between the dry season and the wet season. These wandering movements were largely

responsible for the difference in extent between the 90% home range and 99% annual range (Table 1).

Discussion
The home ranges exhibited by the collared wildebeest herds in our study area exhibited some of the complications of real situations that complicate the application of simple models like MCP or even kernel density distributions. These included seasonally separated ranges sometimes partitioned into distinct segments with abrupt boundaries and differential concentrations of use within these ranges dependent on the activity being performed. Travelling movements between separate foraging ranges and between foraging areas and water sources greatly extended the total area traversed with which the animals have some familiarity. Wandering excursions extended the annual range traversed by some of the wildebeest herds to over 100 km^2, more than an order of magnitude greater than the space actually used for 90% of their needs. Resting sites concentrated a large fraction of time within small areas. Excluding locations where animals remained immobile form the estimation of utilization distributions, as is sometimes done (), assumes that the pattern of use is governed primarily by food requirements. Security from predation, or shelter from environmental stress, can become the overriding considerations while animals are resting. Certain animals seek seclusion in burrows or otherwise enclosed sites. Large herbivores like wildebeest remain exposed and hence seek places where approaching predators are most readily detected (open habitat), or conditions where it is more difficult for the predator to detect them (e.g. thick bush, REF). Places occupied for particular activities by wildebeest differed between daytime and night-time, governed by when their major predator hunts most actively (Martin & Owen-Smith 2016). Movements between separated ranges were irregularly timed and could not be interpreted as migratory in the sense of coordinated population movements. Nevertheless, the home ranges of all of the collared wildebeest herds ranges were mostly consistent between successive years. Amalgamating location records across all times of day for assessing home ranges blurs functional relationships because of the strong daily rhythms in activities typical of most animals.

For the Orpen wildebeest herds, it was striking how small an area was utilized for foraging activity for most of the year, from the wet season into the early part of the dry season. Foraging areas were associated mostly with short grasslands with sparse woody canopy cover on gabbro uplands, providing both high quality food and little concealment for stalking lions (Yoganand & Owen-Smith 2014). At some stage during the dry season most of the collared herds shifted to separated dry season ranges associated with seep zones on lower slopes, likewise lacking woody vegetation cover but with less short grass. Temporary range shifts were also undertaken during the transition months into the early wet season and associated with the flushing of nutritious short grass following dry season fires. Some shifts back and forth between the seasonal ranges were made as the dry season advanced as well as later around the transition into the wet season. Nevertheless, some wildebeest herds remained continuously within foraging arenas coincident with the wet season range for periods of up to seven months, before shifting elsewhere (Owen-Smith & Martin 2015). Within the seasonal foraging ranges the spatial utilization by the wildebeest herds was also spatially heterogeneous in terms of residence times and frequency of visits (Martin et al. 2015).

During the night the places occupied for both resting and foraging activity were contracted substantially away from the edges of the daytime foraging ranges, where vegetation cover potentially concealing stalking lions increases. Home ranges of most large herbivores are

generally assumed to be only vaguely bounded, but those of the Orpen wildebeest herds were surprisingly abrupt. Presumably this is because of the transition from grazing lawn grasses maintained by the grazing pressure of the wildebeest to tall, more fibrous and hence less nutritious grass. Nevertheless, these boundaries were mostly respected whatever the activity being performed by the wildebeest herds. They were not tempted to forage outwards where more grass remained, nor to seek more shady conditions for resting over midday when lions are least active. Excursions to and from water were taken towards midday when high visibility and high temperatures would make attacks by lions lurking near waterholes least likely to be successful.

Strikingly, the places occupied by the wildebeest herds for the same activity, resting, were spatially disparate between day and night. Furthermore, the localities occupied for two distinct activities, resting and foraging, at night were spatially coincident. This indicates the overwhelming influence of the risk of predation in governing nocturnal movements. At least some of the instances when wildebeest herds were recorded resting or supposedly foraging outside their prime range limits during the night were associated with encounters with lions (Martin & Owen-Smith 2016). Unlike zebra, which commonly flee following encounters with lions, wildebeest herds tend to stay within their foraging ranges, where they are least vulnerable to being killed should an attack be launched, more often than not (Martin & Owen-Smith submitted). This helps explain the occurrence of travelling activity with the foraging ranges, especially at night.

There was also surprisingly little overlap in the ranges covered by neighbouring wildebeest herds, suggesting competitive partitioning of resources without signs of any overt aggression. This pattern needs to be confirmed by focused observations on more individually identifiable animals than encompassed by our sample. However, it is consistent with patterns described for other herd-forming ungulates, including African buffalo (), greater kudu () and sable antelope (). Spatial partitioning could be generated by resource exploitation patterns dependent on cognitive memory of previously used patches (Riotte-Lambert et al).

The area enclosed within the prime foraging ranges of the Orpen wildebeest herds evidently provided adequate shade, even if only from a few trees, and the lack of much screening cover from trees and grass was advantageous for detecting stalking lions and evading capture. Places were resident grazers concentrated in Serengeti similarly conferred both nutritional and anti-predator benefits (Anderson et al. 2010). For other ungulates elsewhere, adequate food, shelter and security may be provided in distinct places. Kudus () seek shelter from cold, wet and woody conditions in patches of dense shrubbery providing little food (N. Owen-Smith unpublished observations). Sable antelope () herds that are dependent on taller grass in more densely wooded savanna as their food source occupied more open patches at night (Cain pers comm.), but zebra () moved into denser woody cover at night where they were less visible (). Norwegian red deer () subject to human hunting occupied pastures offering abundant forage during the night and remained settled in forested habitats providing more cover during the day (Godvik et al. 2009). For other large herbivores, the places most favourable for food resources are often those where animals are most vulnerable to predation. This seems to be the case for North American elk () in Canada (Kittle et al. 2008)), as well as for certain African ungulates (Thaker), necessitating dynamic trade-offs.

The relative contributions of food resources and security from predation to habitat occupation are difficult to disentangle, because both contribute fundamentally to fitness. We have attempted to do this by distinguishing the predominant activities undertaken in different places and at particular times of day or night. Most informative are the places NOT used by the wildebeest

herds under particular conditions. Food resources falling outside the grazing lawn or seep zone grasslands were mostly ignored, however abundant. Wildebeest herds moved rapidly through areas with greater tree cover and taller grass while transferring between their separate foraging ranges, and while travelling to and from water sources. In contrast, zebra herds foraged quite widely through the taller-grass habitats, indicating that the grass quality there was adequate for them. During the night when hunting conditions became more favourable for lions, wildebeest shunned large sections of the areas where they had foraged during daylight. Hence the risk of predation seemed to be the prime consideration of space occupation by wildebeest, which are generally the prime prey species selected by lions (Owen-Smith & Mills 2008). By occupying open habitats with little impediment to vision or escape speed, even sedentary wildebeest are able to survive alongside abundant lions, as in KNP. The locations of the wildebeest herds are highly predictable within their small home ranges. But it is comparatively difficult for lions to capture and kill them while they remain in such habitats, even at night.

Our observations were made in years when seasonal rainfall did not deviate much from the long term average, meaning that the collared wildebeest herds were under little pressure to wander beyond their preferred open habitats. In years with much lower rainfall, the reduced grass growth could reduce the period of their exploitation of the grazing lawns and extend that of the seep zone grasslands, forcing them to spend longer periods in the surrounding savanna landscape with taller grass. Under these conditions their exposure to predation would potentially become elevated. Hence risk-sensitive foraging as exhibited by our collared herds restricts not only the local population density attained by the wildebeest, but also their population dynamics.

Within the habitats where wildebeest concentrate to alleviate the risk of predation, they must also obtain adequate food. Their special trophic adaptation is their exceptionally broad muzzle, enabling them to crop very short grass effectively and thus remain within the grazing lawn grasslands that they cultivate for prolonged periods (Murray & Brown, Arsenault & Owen-Smith 2011, Owen-Smith). Where nutritious short grass is more widely available, as in the vast Serengeti ecosystem, wildebeest attain vastly greater population densities than shown in Kruger Park (Hopcraft et al).

Our interpretation of the synergistic operation of food needs and security from predation on the home range occupation, population dynamics and local population density levels attained wildebeest rests on our ability to relate seasonally and daily varying space use to the specific activities performed in particular places. Home range utilisation distributions need to be considered not merely in terms of statistical probability levels, but informed by the prevalent activities undertaken in particular places and hence the fitness contributions derived. This functional approach needs to be extended to other animal species enabled by technological advances in remote tracking of space use patterns.

Conclusions

Need to distinguish activity states generating movement rates for functional interpretation. Basic home range extent is set by area needed for foraging while food remains plentiful. Extended to accommodate dry season resources and seasonal water restrictions but simultaneously constrained to varying extent by risks of predation.

Actual space required by wildebeest herds for >90% of food requirements is only ~5-10 km^2 year-round. Journeys to and from water and between separate seasonal ranges extend the annual range traversed.

Local abundance is limited by synergistic interaction between contributions to fitness of bottom-up (resources) and top-down (risks) at every stage.

Identifying place-specific activities performed linked to time of day and season enables functional interpretations of utilisation distributions.

References

Anderson, T.M., Hopcraft, J.G.C., Eby, S., Ritchie, M., Grace, J.B. & Olff, H. (2010) Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology* **91**, 1519-1529.

Arsenault, R. & N. Owen-Smith. 2011. Competition and coexistence among short grass grazers in the Hluhluwe-iMfolozi Park, South Africa. *Canadian Journal of Zoology* 89:900-907.

Avgar, T., Baker, J.A., Brown, G.S. et al. (2015) Space-use behaviour of woodland caribou based on a cognitive movement model. *Journal of Animal Ecology* **84**, 1059-1070.

Benhamou, S. & Cornelis, D. (2010) Incorporating movement behaviour and barriers to improve kernel home range space use estimates. *Journal of Wildlife Management* **74**, 1353-1360.

Benhamou, S. & Riotte-Lambert, L. (2012) Beyond the utilization distribution: identifying home range areas that are intensely exploited or repeatedly visited. *Ecological Modelling* **227**, 112-116.

Borger, L., Francconi, 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. *American Naturalist* **168**, 471-485.

Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* **24**, 346-352.

Cain, J. W. III, N. Owen-Smith & V. Macandza. 2012. The costs of drinking: comparative water dependency of sable antelope and zebra. *Journal of Zoology* 286:58-67.

Estes (wildebeest territoriality)

Fagan, W.F., Lewis, M.A., Auger-Methe, M. et al. (2013) Spatial memory and animal movement. *Ecology Letters* **16**, 1316-1329.

Fieberg, J. & Borger, L. (2012) Could you please phrase 'home range' as a question? *Journal of Mammalogy* **93**, 890-902.

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**(2), e207, 11pp.

Godvik, I.M.R., Loe, L.E., Vik, J.O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009) Temporal scales, tradeoffs, and functional responses in red deer habitat selection. *Ecology* **90**, 699-710.

Hopcraft, J.G.C., Morales, J.M., Beyer, H.L., Borner, M., Sinclair, A.R.E., Olff, H. &Haydon, D.T., (2014) Competition, predation and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs* **84**, 355-372.

Jewell, P.A. (1966) The concept of home range in mammals. *Symposium of the Zoological Society of London* **18**, 85-109.

Kays, R., M.C. Crofoot, W. Jetz & M. Wikeski (2015) Terrestrial animal tracking as an eye on life and planet. *Science* **348**, aaa2478.

Laver, P.N. & Kelly, M.J. (2008) A critical review of home range studies. *Journal of Wildlife Management* **72**, 290-298.

Lottker, P., A. Rummel, M. Traube, A. Stache, P. Sustr, J. Muller & M. Heurich (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. *Wildlife Biology* **15**, 425-434.

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.

Martin, J., S. Benhamou, K. Yoganand & N. Owen-Smith. 2015. Coping with spatial heterogeneity and temporal variability in resources and risks: adaptive movement behaviour by a large grazing herbivore. *PLoS ONE* 10(2):e0118461, 19pp

Martin, J. & N. Owen-Smith (submitted Nov 2015) Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Animal Behaviour*

Mitchell, M.S. & Powell, R.A. (2004) A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling* **177**, 209-232.

Moorcroft, P.R., Lewis, M.A. & Crabtree, R.L. (1999) Home range analysis using a mechanistic home range model. *Ecology* **80**, 1656-1665.

Moorcroft, P.R. & Lewis, M.A. (2006) *Mechanistic Home Range Analysis.* Princeton University Press, Princeton.

Murray & Brown

Owen-Smith, N. 2002. *Adaptive Herbivore Ecology. From Resources to Populations in Variable Environments*. 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. *Journal of Zoology, London* 246:183-192.

Owen-Smith, N. 2013. Daily movement responses by an African savanna ungulate as an indicator of seasonal and annual food stress. *Wildlife Research* 40:232-240.

Owen-Smith, N. 2014. Spatial ecology of large herbivore populations. *Ecography* 37:416-430.

Owen-Smith, N., V. Goodall & P. Fatti. 2012. Applying mixture models to derive activity states from movement rates of large herbivores obtained using GPS telemetry. *Wildlife Research* 39:452-462.

Owen-Smith, N. & V. Goodall. 2014. Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. Journal of Zoology 293:181-191.

Owen-Smith, N. & J. Martin. 2015 Identifying space use at foraging arena scale within the home ranges of large herbivores. *PloS ONE* 10(6):e0128821, 21pp

Owen-Smith, N., J. Martin & K. Yoganand. 2015. Spatially nested niche partitioning between syntopic grazers at foraging arena scale within overlapping home ranges. *Ecosphere* 6(9):152.

Owen-Smith, N. & M. G. L. Mills. 2008. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77:173-183.

Powell, R.A. (2000) Animal home ranges and territories and home range estimators. *Research Techniques in Animal Ecology* (eds. L. Boitani & T.K. Fuller), pp. 65-110. Columbia University Press, New York.

Prugh, L.R. & Golden, C.D. (2014) Does moonlight increase predation risk? Meta-analysis reveals divergen esponses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology* **83**, 504-514.

Radloff & du Toit

Riotte-Lambert, L., Benhamou, S. & Chamaille-Jammes, S. (2015) How memory-based movement leads to nonterritorial spatial segregation. *American Naturalist* **185**, E

Spencer, W.D. (2012) Home ranges and the value of spatial information. *Journal of Mammalogy* **93**, 929-947.

Thaker

Van Moorter, B., Visscher, D., Benhamou, S., Borger, L., Boyce, M.S. & Gaillard, J.-M. (2009) Memory keeps you at home: a mechanistic model for home range emergence. *Oikos* **118**, 641-652.

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. *Journal of Wildlife Management* **74**, 588-594.

Van Winkle, W. (1975) Comparison of several probabilistic home range models. *Journal of Wildlife Management* **39**, 118-123

Wilson, R.R., Gilbert-Norton, L. & Gese, E.M. (2012) Beyond use versus availability: behaviour-specific resource selection. *Wildlife Biology* **18**, 424-430.

Yoganand, K. & N. Owen-Smith. 2014. Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography* 37:969-982

Table 1 Estimates of annual home range extents in km^2 including all seasons and activities for the eight wildebeest herds, as provided by minimum convex polygon (MCP) and local convex hull (LoCoH) methods for 50%, 90% and 99% isopleths

Table 2 Comparative extents of seasonal foraging ranges (all years combined) and their overlap

Table 3. Shifts in the distribution of location records relative to the edges of prime-times foraging ranges for midday resting, nocturnal resting and nocturnal foraging activity during wet and early dry season conditions for seven wildebeest herds (for full distributions, see Fig. 3

Figures

Fig. 1 A. Overall space occupation patterns of two representative wildebeest herds (Wi145 & Wi147) distinguished by season (see legend at bottom). Symbols represent positions at 6-h intervals (01:00, 07:00, 13:00, 19:00) to restrict the overlay. Dotted lines connect hourly positions. Grid is approximately 1 km^2. B. Representation of the seasonal home ranges of these two wildebeest herds obtained using 90% isopleths in LoCoH. Grey shaded region represents Kruger NP, white region the adjoining provincial and private wildlife reserves, blue lines two seasonal rivers

Fig. 2. Mapped distributions of midday resting, nocturnal resting and nocturnal foraging locations of two representative wildebeest herds (Wi145 & Wi147) during the wet season into the early dry season overlain on prime-times foraging ranges in the wet season for all years combined.

Fig. 3 Distribution of locations relative to the edge limits of prime-times foraging ranges during the wet season and early dry season (as defined by 90% LoCoH isopleths) for seven wildebeest herds for all years combined. A Comparison between midday resting and nocturnal resting locations, B Comparison between nocturnal resting and nocturnal foraging locations