

Spatially nested niche partitioning between syntopic grazers at foraging arena scale within overlapping home ranges

NORMAN OWEN-SMITH,[†] JODIE MARTIN, AND K. YOGANAND

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

Citation: Owen-Smith, N., J. Martin, and K. Yoganand. 2015. Spatially nested niche partitioning between syntopic grazers at foraging arena scale within overlapping home ranges. *Ecosphere* 6(9):152. <http://dx.doi.org/10.1890/ES14-00487.1>

Abstract. Niche separation among species with similar resource requirements can be expressed at various spatiotemporal scales, from the resource components selected at feeding sites to habitat and home range occupation and ultimately geographic distribution ranges. African large herbivores present a challenge to niche theory because multiple species commonly overlap both spatially and in vegetation components consumed. Aided by GPS telemetry, we investigated the space use patterns of two large grazers that are frequently associated in mixed-species aggregations. Specifically, we compared a generalist grazer with hindgut fermentation (plains zebra) with a similar-sized grazing ruminant (blue wildebeest) in west-central Kruger National Park, South Africa. We found that herds of the two species overlapped substantially in the home ranges that they occupied, but exploited spatially distinct foraging arenas for periods lasting several days or weeks within these ranges. Moreover, wildebeest and zebra differed in duration of settlement, extent of areas occupied during settlement, consequent exploitation intensity per unit area, proportion of time spent within foraging arenas relative to roaming interludes, and movement rates while within these arenas. In particular, wildebeest herds concentrated within small areas for prolonged periods, while zebra herds used more foraging arenas but exploited them for briefer periods. Both species overlapped substantially in habitat use, although wildebeest more strongly favored gabbro uplands and sodic sites presenting short grass lawns while zebra made greater use of areas with a taller grass cover. Hence resource partitioning was expressed mainly through behavioral distinctions in patch exploitation at foraging arena scale rather than in home range or habitat separation. Although zebra may have been partially excluded from the grasslands kept short by wildebeest, these sites formed only a small part of the wider ranges utilized by zebra, thereby restricting the competitive consequences. Hence spatially nested resource partitioning of this form contributes to the coexistence of these two grazers, and may be a mechanism enabling niche separation among other species.

Key words: competition; *Connochaetes taurinus*; *Equus zebra*; facilitation; foraging arena; GPS telemetry; home range; Kruger National Park; large mammalian herbivores; niche separation; spatial partitioning.

Received 5 December 2014; revised 2 February 2015; accepted 4 February 2015; **published** 17 September 2015.
Corresponding Editor: D. P. C. Peters.

Copyright: © 2015 Owen-Smith et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

[†] **E-mail:** norman.owen-smith@wits.ac.za

INTRODUCTION

The ecological niche concept expresses the functional outcomes of the anatomy, physiology

and behavior of a species for its distribution and abundance (Chase and Leibold 2003). These phenotypic attributes govern how individual organisms obtain shelter from thermal extremes

(Porter et al. 2000), locate and extract food resources (Stephens and Krebs 1986), digestively assimilate food (Codron and Clauss 2010), seek access to surface water (Cain et al. 2012), and evade becoming food for predators (Holt et al. 1994). While physiological tolerances and resource requirements govern broad-scale distributions (Guisan and Zimmermann 2000), biotic interactions become somewhat more important over finer spatiotemporal scales (Soberon 2007). According to niche theory, species with overlapping food requirements can coexist by seeking these resources in different places or at different times, or by exploiting them in different ways (Hardin 1960). Habitat partitioning can arise when species have distinct resource preferences, but may also occur when a generalist species is excluded from the most rewarding habitats by species specialized to exploit resource concentrations most effectively (Rosenzweig 1991). Distinct responses to the risk of predation can also lead to differences in habitat occupation between species with similar resource requirements (Kotler 1984). Mixed-species associations could reduce individual exposure to predation, but at the cost of heightened competition for shared resources (Stensland et al. 2003).

The coexistence of numerous species of grazing ungulates in African savanna ecosystems, dependent on the same vegetation components, has remained a challenge for niche theory (Owen-Smith 1985, Prins and Olf 1998). Niche partitioning among these species has been considered in terms of (1) how body size influences diet quality requirements (Jarman 1974), (2) how distinctions in digestive adaptations affect ability to cope with fibrous vegetation components (Hofmann 1989, Duncan et al. 1990), (3) how relative oral dimensions affect ability to handle grass swards differing in height (Bell 1970, Gordon and Illius 1988), and (4) how group size lowers the risk of predation (Jarman 1974). The general perception is that smaller species are superior competitors through being able to subsist on sparser resources than required to meet the greater quantitative needs of larger animals (Clutton-Brock and Harvey 1983, Prins and Olf 1998). However, larger ungulates may attain greater biomass densities through being able to exploit a wider quality range in food resources than is acceptable to smaller herbivores

(Owen-Smith 2002: Chapter 12). Furthermore, grazing by larger ungulates can enhance the amount of food available within the quality range required by smaller herbivores by reducing grass height and encouraging grass regrowth (Vesey-Fitzgerald 1960, McNaughton 1976). Whether competition or facilitation prevails may vary seasonally, with the consequences for relative abundance counterbalanced (Arsenault and Owen-Smith 2002). Nevertheless, there is substantial overlap among grazing ungulates in habitat conditions occupied (Murray and Illius 1996, Traill 2004), and grass species and height ranges exploited (Ben-Shahar 1991, Arsenault and Owen-Smith 2008, 2011, Kleynhans et al. 2011, Macandza et al. 2012a).

Current niche theory has not adequately addressed the consequences of environmental heterogeneity for spatial partitioning among mobile animals (Ritchie 2002). Within the geographic distribution range of the species, individual animals or groups commonly restrict their movements to bounded home ranges, and selectively occupy distinct habitats within these ranges (Spencer 2012). Different habitat features may be favored for different activities—places where animals are most secure from predation may differ from those where food is most readily available (Houston et al. 1993). The scale at which heterogeneity in these features is presented could potentially contribute to spatial partitioning and hence to niche separation among species differing in body size, which otherwise appear similar in their resource needs (Ritchie 2009). Nevertheless, an experimental test of this relationship found that the largest grazers did not avoid the finer grain plots (Cromsigt and Olf 2006). Observations on browsing ungulates showed that the smallest browser was restricted to the narrowest range in habitat conditions, while larger browsers occupied a wider range of habitats (du Toit and Owen-Smith 1989). Thus, spatial partitioning dependent on body size may operate at a larger scale than readily addressed experimentally.

Particularly perplexing is the co-existence of two of the most abundant grazers, wildebeest (*Connochaetes taurinus*) and plains zebra (*Equus quagga*), at spatial scales from regional and local distributions down to their frequent presence in mixed-species herds (Sinclair and Norton-Grif-

fiths 1982, de Boer and Prins 1990). While the hindgut digestion of zebra enables them to utilize taller and more fibrous grass than is generally selected by wildebeest, zebra also exploit short grass within the height and quality range favored by wildebeest (Voeten and Prins 1998, Arsenault and Owen-Smith 2008, 2011, Kleynhans et al. 2011). In the Serengeti ecosystem, zebra numbers have remained unaffected by the five-fold increase in the migratory wildebeest population that followed elimination of the rinderpest virus, suggesting little effective competition between these two grazers despite their spatial overlap (Sinclair et al. 2007). Both wildebeest and zebra aggregate on the Serengeti short-grass plains during the wet season, although wildebeest occur further east than zebra where the grass is shortest (Hopcraft et al. 2014). During the dry season when both of these grazers move into regions with taller grass, zebra are more widely distributed than wildebeest. Grazing by zebra could potentially facilitate food access by wildebeest through removing stemmy material and reducing grass height (Bell 1970).

Within the Kruger National Park (KNP), both wildebeest and zebra have distributions concentrated in the eastern basalt plains, but zebra are more widely present in the granitic west, where soils are generally less fertile, than wildebeest (Chirima et al. 2012). Wildebeest and zebra populations both show negative growth responses to annual variation in rainfall, apparently responding to changes in cover for their major predator rather than resource production (Smuts 1978, Ogutu and Owen-Smith 2005). Seasonal patterns of habitat occupation and movements by wildebeest in Kruger Park have been documented by Yoganand and Owen-Smith (2014) and Martin et al. (2015), while habitat use and forage selection by zebra have been described by Macandza et al. (2012a).

Opportunities to investigate space use patterns at scales intermediate between feeding sites and home ranges have been opened by developments in GPS tracking technology (Cagnacci et al. 2010; Owen-Smith and Martin 2015). We deployed GPS collars to document the comparative movement patterns of wildebeest and zebra herds in a region of KNP where the wildebeest subpopulation had formerly been migratory (Whyte and Joubert 1988). A fence constructed during the

1960s had blocked animal movements beyond the western park boundary, but was removed in 1994 (Joubert 2007). Hence at the time of our study animals were able to move westwards into private and provincial wildlife reserves adjoining the national park.

In this paper, we focus on distinctions in space use patterns within the home ranges of individual herds of wildebeest and zebra at the scale of foraging arenas (FAs) exploited for periods of several days or weeks during times of day when foraging activity predominates (Owen-Smith and Martin 2015). Having established periods of settlement at this scale, we investigated differences between herds of these two species in various metrics, including (1) settlement durations within FAs, (2) spatial extents of FAs exploited, (3) local intensities of exploitation in days spent per unit area, (4) proportions of time spent within FAs relative to roaming interludes between them, (5) rates of movement within and between FAs, and (6) relationships between the localities exploited by zebra and those of wildebeest. We show that the two grazers show niche distinctions in these features despite substantial overlap between them in home range and habitat occupation.

METHODS

Study area

We conducted our comparative study of wildebeest and zebra movements in the Orpen gate region of west-central KNP. A feature of this area is the presence of a gabbro sill within the granitic-gneiss geology that is typical of the western section of KNP. The gabbro generates clay-rich and hence relatively fertile soils, while the granite gives rise to sandy soils of lower fertility, except in bottomlands where mineral nutrients accumulate. Rainfall within the Orpen study area has averaged 570 mm (1960–2011), with ~80% received during the summer months October–March. Annual rainfall totals (July–June) were 619 mm in 2008/2009, 499 mm in 2009/2010, and 688 mm in 2010/2011 during the study period. Water was fairly widely available from pools in the Timbavati River and from dams elsewhere.

Various *Acacia* species were prevalent in the woody vegetation on gabbro, while granitic

landscapes supported mainly mixed *Combretum* savanna woodland. The prevalent bunch grasses on the gabbro were *Themeda triandra*, *Setaria incrassata*, and *Bothriochloa radicans*. On the granite, the most common grasses were various *Eragrostis* spp., *Heteropogon contortis*, and *Panicum maximum* growing mainly under tree canopies. Within regions of the gabbro uplands, short grasses predominated, representing grazing lawns maintained by herbivore pressure (Hempson et al. 2014). The main grass species in these localities were *Urochloa mosambicensis*, *Sporobolus nitens*, and *Chloris virgata*. The grazing lawns also lacked much tree and shrub cover. Habitat types distinguished by woody and herbaceous cover and geological substrate were mapped using a SPOT5 satellite image (Yoganand and Owen-Smith 2014).

Aerial counts of the larger ungulates conducted through the 1980s until 1995 yielded the following approximate species totals in the census blocks covering 535 km² encompassing the study area: impala (*Aepyceros melampus*), 6500; zebra, 900; wildebeest, 800; buffalo (*Synceurus caffer*), 400; kudu (*Tragelaphus strepsiceros*), 300; warthog (*Phacochoerus africanus*), 230; waterbuck (*Kobus ellipsiprymnus*), 80. No difference in the distribution of sightings of wildebeest and zebra within the study area was discernible from the aerial survey data.

GPS telemetry

Global Positioning System (GPS) collars transmitting data via the mobile telephone (GSM) network (supplier: <http://www.awt.co.za>) were placed on eight female wildebeest and four female zebra in separate herds in the Orpen Gate region in late March and early April 2009, and later replaced on the same individuals or in additional herds to extend the study duration over two years or longer. Animals were captured for collar placement using chemical immobilization by experienced veterinarians employed by South African National Parks following their established protocols, and no mortalities occurred during the capture process. Because of the herd structure of these two ungulate species, the movements of the collared females represent the movements of the herds with which they were associated. For wildebeest, herd sizes ranged from 12 to 35 animals, with temporary

splitting and joining, while zebra herd units varied narrowly between 6 and 8 animals. The collared wildebeest herds represented about 40% of the herds observed in the study area, while the collared zebra herds constituted a much smaller sample.

Data analysis

Broad patterns of space use by the collared wildebeest and zebra herds were documented in terms of (1) total annual range, indicated by 100% minimum convex polygons based on GPS locations gathered over 1–2 years, subsampled at six-hourly intervals to represent times of day when distinct activities prevailed; (2) seasonal home ranges, defined by 90% isopleths from local convex hulls (Getz et al. 2007); and (3) proportional occupation of habitat types in relation to the proportional extent of these habitats within the overall study area. Three seasonal divisions were made separating location records for the wet season months December–March from those for the early (April–July) and late (August–November) dry season months. Settlement periods within distinct FAs were defined by local change points in spatial location following the method described by Owen-Smith and Martin (2015). This assessment was based on GPS records representing the times of day when foraging activity typically predominates, specifically 07:00 in the morning and 19:00 in the evening (Owen-Smith and Goodall 2014). Change points were flagged when the GPS location of the collared animal was further than the mean plus two standard deviations from the centroid of prior or subsequent locations within 5-day or longer windows. Instances when an animal left a FA for ≤ 2 days were interpreted as temporary excursions. If the roaming interval lasted longer than 2 days, the settlement period was interpreted as broken, even if the animal returned to the same FA after the interruption. However, recursions were tallied only when settlement periods had been interrupted by occupation of another FA. To cover seasonal variation adequately, data sets used were limited to herds that supplied location records spanning 10 months or longer. In instances when two collared animals were closely associated for some time, data from only one of these collars were used to ensure independence. A full description

of the method is provided by Owen-Smith and Martin (2015).

After identifying settlement periods in FAs, we derived the following measures of the spatial patterns exhibited for each collared herd: (1) durations of periods when animals remained settled within particular FAs, from time of entry to time of departure, (2) areas encompassed by these FAs, excluding temporary excursions, (3) intensities of exploitation of resources within FAs in days (excluding excursions) spent per unit area, (4) proportions of locations assigned to periods of settlement within FAs relative to roaming interludes between them, (5) durations of roaming periods, (6) distances traversed between mid-points of successive FAs, (7) half-day displacements between morning and evening locations, comparing periods of settlement with roaming interludes, and (8) annual foraging ranges, from the combined extent of the distinct FAs exploited. Measures were assessed as mean values within blocks of months representing the wet season (December–March), early dry season (April–July) and late dry season (August–November). These blocks allowed for the lagged effects of rainfall on grass growth and senescence.

Statistical assessments establishing significant differences between the two ungulate species in these response measures were undertaken using function `lmer` in R (v3.1.1; R Development Core Team 2012), with “species” and “season” as fixed effects and individual animal identity as a random effect. The response measure was transformed to approximate a Gaussian distribution if appropriate.

Cases where the foraging arena of a zebra herd overlapped simultaneously with a foraging arena being exploited by a wildebeest herd were identified to establish whether there was attraction between the two grazers, indicating facilitation or shared preferences, or mutual repulsion, suggesting competitive displacement. We assessed whether the zebra herd involved was drawn to or inhibited from occupying the region being exploited by the wildebeest by comparing the proportion of zebra locations that fell within the FA of the wildebeest relative to the proportional extents of the two FAs.

RESULTS

Annual and seasonal home ranges

The annual ranges of the four collared zebra herds combined encompassed the entire study area (Fig. 1). Three of the zebra herds showed annual ranges (100% MCP) covering 150–250 km², while one herd extended its annual range to 450 km² by movements to the north and east (Table 1). Seasonal home ranges occupied by the zebra herds (90% convex hulls) covered 30–90 km² and were generally smallest in the wet season. Distinctions among these herds in the extent of the annual range were not reflected in the seasonal ranges. The annual ranges of the eight collared wildebeest herds lay within those of the collared zebra herds. Annual ranges of the five wildebeest herds that moved between seasonally separated home ranges encompassed 50–175 km², while those of three herds that showed little seasonal shift covered around 17–52 km². Within these limits the seasonal home ranges actually utilized within the 90% isopleth covered only 0.7–4 km² during the wet and early dry seasons, except for one wider-ranging herd (Table 1). Late dry season ranges were largest for the wildebeest herds that moved between separate FAs during the transitional months leading into the wet season.

Foraging arenas

Examples of the FAs delineated over one annual cycle are shown for two wildebeest herds and two zebra herds in Fig. 2. The two species differed strikingly in all metrics at this scale (Table 2). Wildebeest mostly settled within particular FAs for durations averaging from around 20 days to four months, while zebra showed mean settlement durations predominantly less than 20 days (Fig. 3A). One wildebeest herd showed short settlement durations similar to those of zebra. The longest settlement duration of a wildebeest herd was seven months (thus extended across seasons), while the maximum settlement period for a zebra herd was just over three months (Appendix: Fig. A1). Despite remaining settled for shorter periods, zebra herds moved over substantially larger FAs than the wildebeest during these periods: mean extent 3–6 km² versus 1–3 km² (Fig. 3A). For wildebeest, settlement durations tended to be shorter during

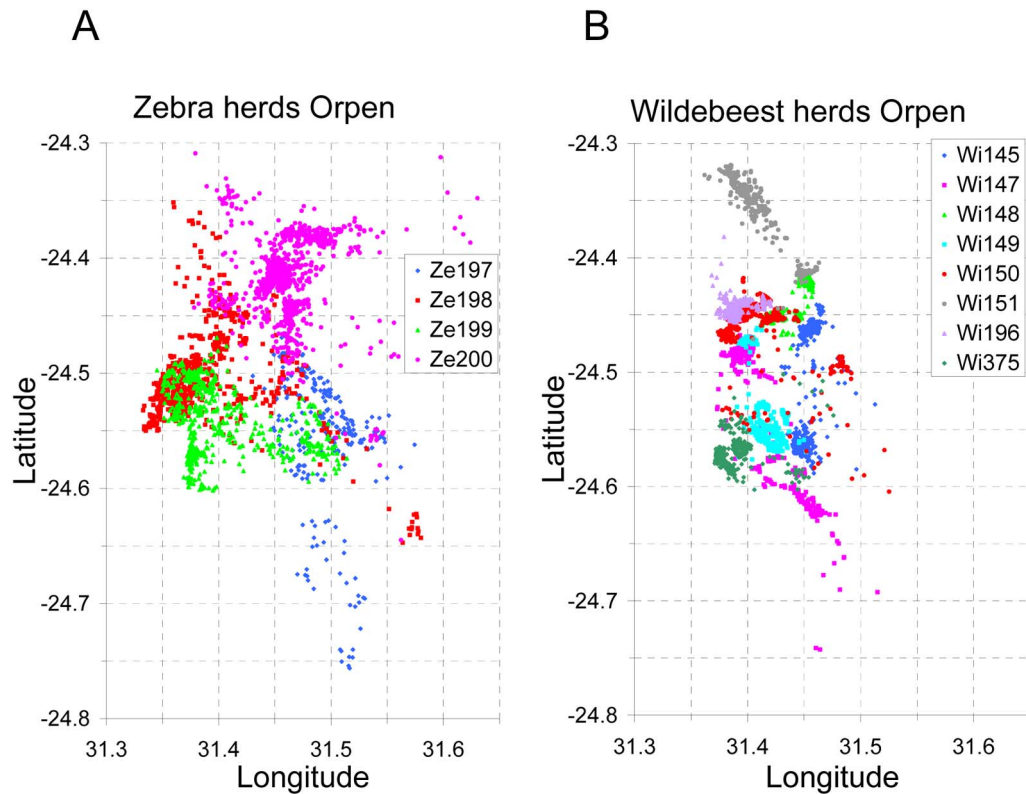


Fig. 1. Total ranges covered by zebra and wildebeest herds fitted with GPS collars in the Orpen region of west-central Kruger Park during the study period, as represented by GPS locations subsampled at 07:00 hours so as to restrict the overlap of symbols representing each individual herd. (A) The four zebra herds, (B) the eight wildebeest herds.

Table 1. Home range measures. Annual range limits were represented by 100% minimum convex polygons, seasonal home ranges by 90% local convex hulls. Mean extent, range and annually amalgamated extent of foraging arenas are also listed.

Species	Individual	Home ranges				Foraging arenas		
		Annual (km ²)	Wet season (km ²)	Early dry season (km ²)	Late dry season (km ²)	Mean (km ²)	Range (km ²)	Amalgamated (km ²)†
Zebra	#197	182	29.4	37.7	44.8	5.49	0.66–10.1	56.5
Zebra	#198	259	52.0	60.9	66.5	3.09	0.65–8.3	51.3, 36.7
Zebra	#199	148	49.2	91.1	47.5	3.69	0.64–7.4	50.1
Zebra	#200	446	35.7	80.3	80.1	4.05	0.74–11.2	37.4, 34.7
Wildebeest	#145	82	6.2	2.3	11.9	1.84	0.15–3.7	6.0, 8.2
Wildebeest	#147	131	4.2	1.6	23.5	1.43	0.22–3.3	6.7
Wildebeest	#148	17	0.7	2.3	3.7	1.37	0.25–3.2	4.6
Wildebeest	#149	50	3.9	3.0	8.1	1.89	0.22–5.8	11.0
Wildebeest	#150	176	2.9	3.2	31.3	1.82	0.18–4.5	15.8
Wildebeest	#151	52	8.8	9.8	19.1	3.81	1.0–8.8	11.3
Wildebeest	#196	30	2.3	3.3	4.0	1.90	0.34–3.6	3.9
Wildebeest	#375	67	1.5	1.8	20.4	1.94	0.58–3.2	6.9

† Separate estimates for each annual cycle are given, where available.

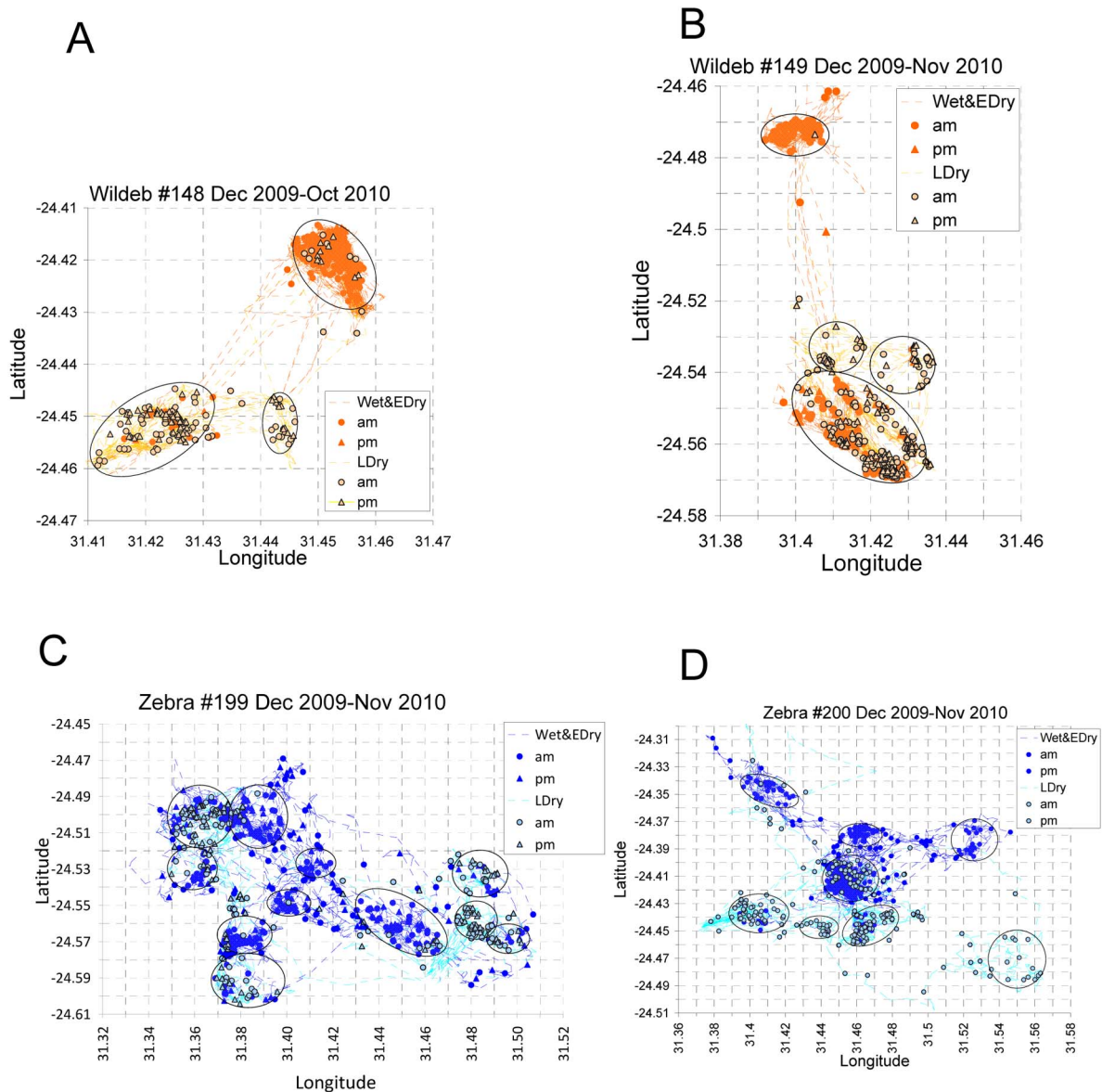


Fig. 2. Home ranges of representative wildebeest and zebra herds in the Orpen region over one annual cycle, showing the foraging arenas exploited. Symbols indicate morning (circles) or evening (triangles) locations during foraging periods, while dotted lines link sequential hourly records. Dark fill indicates locations during the wet season or early dry season months, and pale fill indicates locations during the late dry season. Ellipses enclose the foraging arenas. (A) Wildebeest herd #148, (B) wildebeest #149, (C) zebra #199, (D) zebra #200.

the late dry season than at other times of the year, but zebra showed no consistent seasonal pattern. Roaming interludes between FAs varied widely in duration with no consistent distinction between the two ungulate species. However, wildebeest more frequently showed zero roaming durations, indicating movements directly

from one FA to the next, than did zebra (Appendix: Fig. A2).

As a result of these differences, all except one of the wildebeest herds displayed grazing intensities within FAs that were vastly greater than those of zebra herds—between 10 and 40 days per km² for the wildebeest, compared with 5 or

Table 2. Statistical support for species and seasonal differences in various response measures at foraging arena scale.

Response	Transformation	Predictor	F	P
Settlement duration	log	Species	36.94	0.00012***
		Season	0.80	0.461
Extent	none	Species	25.00	0.00054***
		Season	1.69	0.207
Intensity	log	Species	37.50	0.00011***
		Season	5.76	0.0097**
Proportion in foraging arena	arcsin	Species	28.47	0.00033***
		Season	4.50	0.023*
Half-day displacement in foraging arena	log	Species	22.68	0.00077***
		Season	22.97	0.000004***
Half-day displacement while roaming		Species	2.44	0.151
		Season	1.60	0.226

fewer days per km² for the zebra, tending to be less in the late dry season than at other times of the year (Fig. 3B, Table 2). Correspondingly, the seasonal proportions of days that wildebeest spent within FAs were significantly greater than shown by zebra. Wildebeest showed shorter half-day shifts between their morning and evening locations than zebra while settled within FAs, and all three seasons differed significantly in this measure. However, there was no species or seasonal difference in half-day displacements during roaming interludes between FAs.

The combined annual extent of the FAs exploited by zebra herds varied from 35 km² to over 50 km², while most wildebeest herds exploited total areas of less than 5 km² and only one herd utilized >10 km². The annual proportion of days that zebra spent within FAs was less than shown by wildebeest. Most of the wildebeest herds exploited only two or three FAs, and concentrated particularly within one favored locality, while zebra herds occupied 8–12 FAs during the course of a year (Fig. 4). The annually summed intensity of use of the most favored FAs by wildebeest ranged from 25 to over 200 days per km², while for zebra the maximum annual intensity was just over 20 days per km². Zebra herds undertook 3–6 recursions to their most favored FAs during the course of a year, while wildebeest herds tended to undertake fewer recursions, because they remained in particular FAs for longer. The wildebeest herd that showed the least concentration of use within FAs was the one that tended to resemble zebra herds in other measures. This herd (#151) moved northwards from a section of grazing lawn towards more

diffuse localities occupied during the dry season. For herds of both species with location data spanning two years, patterns of FA occupation in successive years were similar.

Interactions and overlap

Relatively few of the FAs exploited by the collared zebra herds overlapped those of wildebeest herds, and rarely at the same time. When simultaneous overlap did occur during the wet season when the wildebeest occupied the gabbro uplands, the zebra moved over a substantially larger FA than occupied by the wildebeest, and a smaller proportion of zebra locations fell within the FA exploited by the wildebeest than expected if the zebra movements had been randomly distributed within the zebra FA (Appendix: Fig. A2). In the dry season when some of the wildebeest herds shifted to distinct dry season ranges, the nearest collared zebra herds occupied FAs largely separate from those occupied by nearest collared wildebeest herds.

Habitat occupation

There was much overlap in the habitats occupied by the wildebeest and zebra herds and also much variation in habitat occupation among the collared herds representing each species (Table 3). However, the wildebeest tended to make substantially greater use of the short grass lawns in gabbro uplands or sodic sites on granite, depending on the location of their home ranges, than did the zebra. Correspondingly, the zebra herds made proportionately more use of areas with a taller grass cover than did the wildebeest. Zebra as well as wildebeest

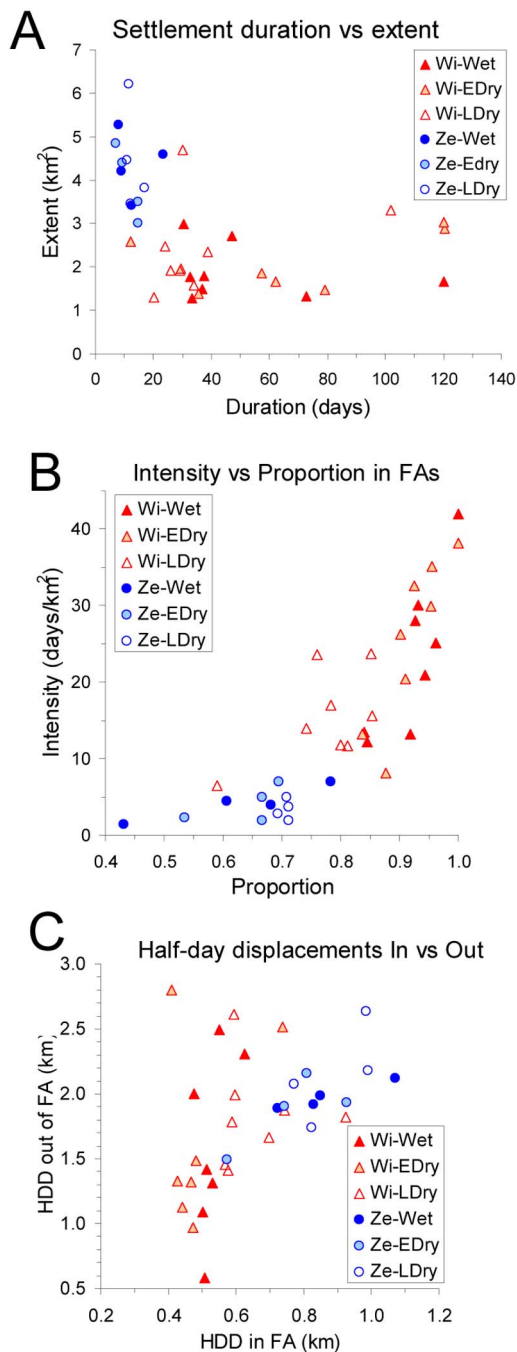


Fig. 3. Biplots of foraging arena metrics for wildebeest and zebra distinguished by season. (A) Mean seasonal extent of area covered (excluding excursions) during settlement within foraging arenas versus mean seasonal settlement duration. (B) Intensity of use of foraging arenas in days spent per unit area, versus the seasonal proportion of days occupied by settlement periods. (C) Half-day displacements between morning

and evening locations, comparing mean values while animals were settled within foraging arenas versus those shown during roaming interludes between them. Red triangles represent wildebeest, and blue circles, zebra. Dark fill = wet season, light fill = early dry season, no fill = late dry season.

DISCUSSION

The collared zebra and wildebeest herds overlapped both in home range occupation and in the habitats occupied within these ranges. Like wildebeest, zebra herds (1) favored habitat types associated with clay soils on gabbro substrates over those on less fertile granite, (2) preferred open grassy regions to those with denser woody cover, and (3) made proportionately greater use of the nutritional hotspots represented by gabbro and sodic lawns compared with the relative availability of these habitats. However, clear distinctions were evident between the two herbivore species in almost all measures of foraging behavior at the FA scale. The contrast was between opportunistic mobility in food procurement by the zebra, compared with locally intense utilization of specific sites by the wildebeest. Hence these two grazers exploited the heterogeneous and seasonally changing distribution of food resources in very different ways. Effectively, the wildebeest concentrated on localized patches of short grass that were nested within the wider ranges covered by the zebra. Although grazing lawn grasslands typically offer the best quality forage (Stock et al. 2010), the collared zebra herds at Orpen made less use of them than did the wildebeest, probably because wildebeest plus impala kept the grass in these localities too short to provide adequate rates of intake for zebra. Yoganand and Owen-Smith (2014) reported that the height of the lawn

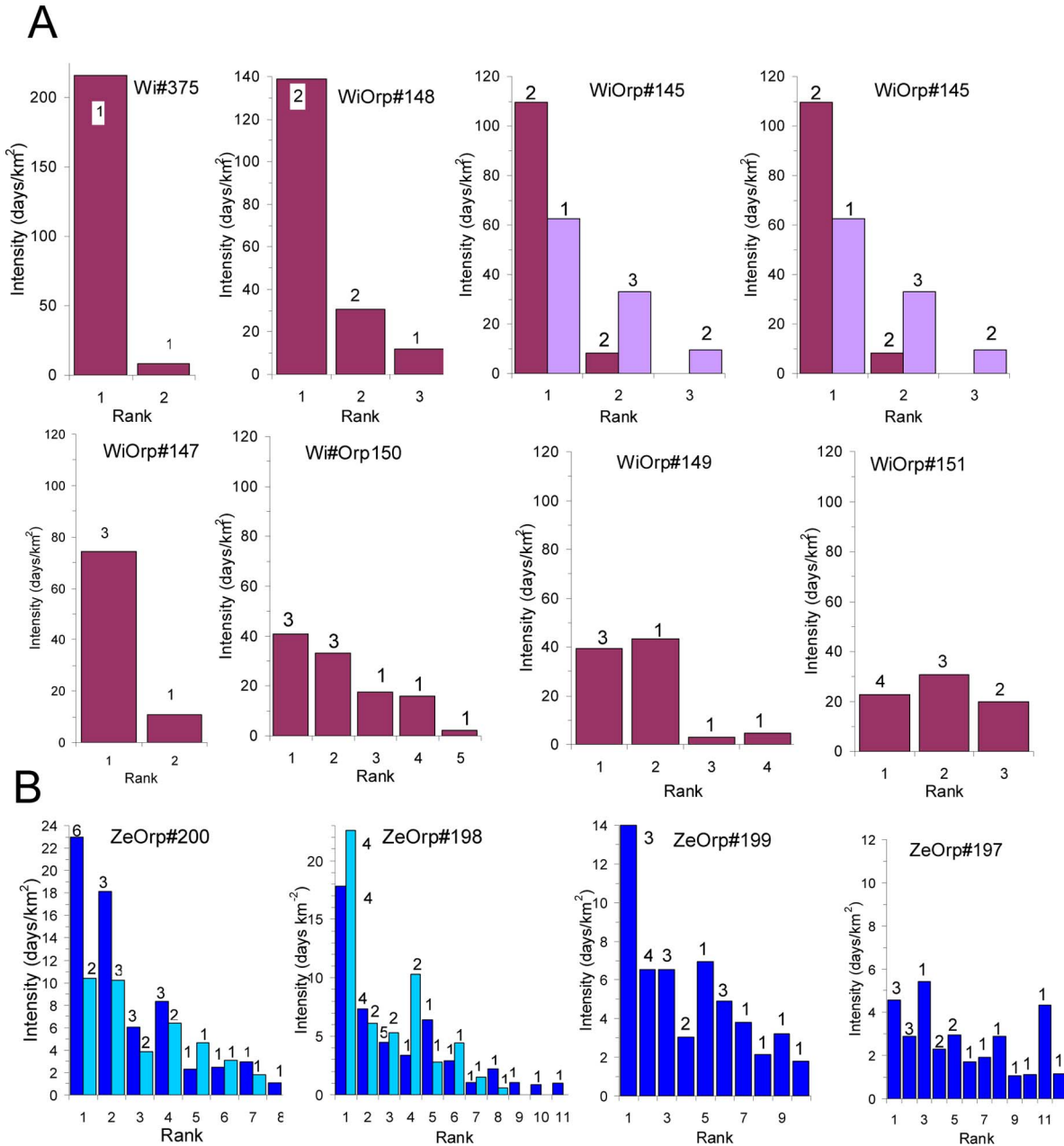


Fig. 4. Utilization intensity of the set of foraging arenas exploited annually by (A) wildebeest and (B) zebra herds, arranged in rank order of time spent within them. Separate bars for each year are distinguished by color when data for a particular herd span more than one complete year. Numbers above the bars represent the number of independent recursions made to each foraging arena over the course of the year.

grasslands at Orpen remained around 50 mm throughout the year. In the Hluhluwe-iMfolozi Park, zebra utilized grass ≤ 50 mm in height less than did wildebeest, and made less use of lawn grasslands in the drier of two years (Arsenault

and Owen-Smith 2011). Patterns of home range exploitation by the collared zebra herds at Orpen were similar to those of zebra herds further north in KNP where wildebeest were absent (Macandza et al. 2012a), and the annual extent of the

Table 3. Comparative habitat use of collared zebra and wildebeest herds by season in relation to the proportional availability of these habitat types in the overall study area. Range represents the range in values across herds and years.

Substrate and structure	Available (%)	Used					
		Wet season		Early dry season		Late dry season	
		Mean (%)	Range (%)	Mean (%)	Range (%)	Mean (%)	Range (%)
A) Zebra							
Granite							
Woodland	49.1	10.1	0.6–16.4	22.2	5.5–38.6	31.1	15.8–50.2
Grassland	27.8	24.8	4.4–43.4	33.1	12.8–54.2	30.0	15.6–41.2
Seep zone	7.2	13.2	1.9–30.8	13.4	4.9–19	8.7	5.9–19.0
Sodic lawn	2.4	7.4	5.0–10.4	6.0	1.1–11.7	3.9	1.0–10.1
Combined	86.5	55.5	15.6–97.4	74.8	36–100	73.7	51–100
Gabbro							
Woodland	3.9	5.8	0–12.3	4.3	0–14.7	6.9	0–12.2
Grassland	6.1	12.7	0.2–30.8	8.9	0–20.1	12.5	0–28.8
Gabbro lawn	3.5	26.0	2.4–80.3	12.0	0–48.6	6.9	0–20.7
Combined	13.5	44.5	2.6–84.4	25.2	0–64	26.3	0–49
B) Wildebeest							
Granite							
Woodland	49.1	6.8	0.5–15.7	8.0	0.4–18.4	17.9	5.0–33.6
Grassland	27.8	15.2	1.0–58.0	18.8	0.3–60.6	26.8	3.3–55.9
Seep zone	7.2	13.5	0.3–35.5	19.4	0.4–39.9	19.1	1.2–30.1
Sodic lawn	2.4	13.4	2.4–40.2	11.4	0.6–38.7	9.2	1.9–34.6
Combined	86.5	48.9	5.2–89.9	57.5	5.4–100	72.9	20.2–100
Gabbro							
Woodland	3.9	3.2	0.2–6.3	4.0	0.2–14.7	5.9	0–24.2
Grassland	6.1	5.3	0.6–20.3	7.9	0–28.9	8.2	0–31
Gabbro lawn	3.5	42.7	0–87.9	30.5	0–87.9	12.9	0–46
Combined	13.5	51.1	0–94.8	42.5	1.0–94.6	27.1	0–72.4

ranges of the Orpen zebra resembled those of zebra herds elsewhere in Kruger Park (Smuts 1975), and non-migratory zebra in the Ngorongoro Crater in Tanzania (Klingel 1969). Home range estimates for sedentary wildebeest herds elsewhere have not been published.

Although zebra and wildebeest are frequently observed in mixed herds, we did not find a positive association between them at Orpen. In instances when collared zebra herds utilized FAs overlapping simultaneously with those of wildebeest on gabbro uplands during the wet season, the zebra seemed to avoid the region where the wildebeest concentrated. In the dry season when the wildebeest had shifted to seep zones, collared zebra herds exploited adjacent regions with little or no overlap. This could indicate competitive displacement of the zebra by the wildebeest, coupled with impala, through keeping the grass too short for the quantitative food requirements of the zebra. However, the zebra were not completely excluded from the grazing lawns, and by foraging over a wider area they may have balanced the high quality but low bulk intake obtained from the lawns with the greater intake

that they could achieve in surrounding taller grasslands. Moreover, gabbro and sodic lawns combined covered only around 6% of the study area, including their fringing regions. Hence the area from which the zebra may have been partially excluded by the wildebeest was quite small. There was no indication that zebra facilitated later foraging by wildebeest in seep zone grasslands, but the sample of collared zebra herds was probably too small to detect this.

The foraging niche of the wildebeest observed at Orpen can be characterized as intensive exploitation of localities offering highest quality food. In contrast, through being more nutritionally tolerant on account of their hindgut digestion, zebra are able to forage more broadly over the landscape. In the Hluhluwe-Mfolozi Park, zebra were likewise more evenly distributed than similar-sized ruminants (Cromsigt et al. 2009). In Serengeti, zebra were spread more widely than the migratory wildebeest in the dry season, but occurred less far into the short grasslands than wildebeest during the wet season (Hopcraft et al. 2014). The situation resembles the shared-preference model of resource partitioning outlined by

Rosenzweig (1991), but is complicated by the seasonal variation in habitat occupation shown particularly by wildebeest in KNP. Both wildebeest and zebra prefer habitats offering better-quality forage, but differ in their ability to cope with circumstances in which either grass quantity or quality is inadequate, as occurs every winter or dry season. Habitat overlap between the two grazers is greatest in the wet season, when food is most abundant, but diminishes during the dry season when both the amount and quality of the remaining forage declines.

Behavioral niche partitioning at FA scale could be the aspect most effectively distinguishing other large herbivores differing in body size and digestive adaptations. Smaller ungulates are best able to exploit high-quality resources that are sparsely distributed within the broader range of habitats utilized by larger species, as described for browsing ruminants by du Toit and Owen-Smith (1989). Rather than avoiding the rich habitat patches favored by smaller species, larger herbivores make relatively less use of them because of local resource depression by the smaller herbivores. Although smaller herbivores may thus appear to be the superior competitors, the effect on the abundance of larger species could be immeasurable because of the restricted extent of the resource-rich patches. Moreover, spill-over by the greater biomass of larger more generalist herbivores into the habitats favored by the smaller specialists could potentially depress the abundance of the latter (Owen-Smith 2002: Chapter 12; Chase and Leibold 2003).

The effective scale of heterogeneity to which herbivores respond depends on the template presented by landscape features. The vast extent of lawn-like grasslands on the Serengeti plains (Hopcraft et al. 2014) contrasts with the patchy occurrence of lawns associated with gabbro uplands in west-central KNP (Yoganand and Owen-Smith 2014). Wildebeest are marginally less abundant than zebra in the Orpen region, but elsewhere where their requirements are extensively met, as in Serengeti, wildebeest greatly outnumber zebra. On the other hand, zebra are more widely distributed than wildebeest, meaning that their abundance could be greater than that of wildebeest at continental scale. In northwest KNP, sable antelope (*Hippotragus niger*) replace wildebeest and utilize

somewhat taller grass than zebra (Macandza et al. 2012a). Sable herds similarly restrict their foraging to localized arenas located within the annual ranges of more mobile zebra and buffalo herds (Owen-Smith and Martin 2015). Sable herds dynamically avoided close proximity to buffalo herds, but not zebra herds, but possibly due to avoidance of a shared predator rather than competitive displacement for resources (Macandza et al. 2012b). Moreover, the regional distribution of sable antelope (*Hippotragus niger*) herds within KNP appears to be governed primarily by how the abundance of wildebeest and impala affects the risk of predation (Chirima et al. 2013).

Spatially nested niche relationships have been described for small mammals, with a tradeoff between foraging efficiency and costs of travel enabling kangaroo rats (*Dipodomys* sp.) to exploit a wider range of seed patches more superficially than pocket mice (*Perognathus* sp.), which intensely exploit patches where seeds accumulate (Kotler and Brown 1988). With allowance for seasonal variation in these costs, this mechanism contributes to the coexistence of these granivores. A similar nested pattern has been described even for plants, with narrow-niche species more precisely exploiting local resource-rich patches within the depletion zones generated by more widely distributed and hence more abundant species (Campbell et al. 1991).

Food procurement is only one aspect of the niche, and other requirements must also be met in order for a population to be maintained, most importantly security from predation. Whether the concentration of wildebeest in grazing lawn grasslands is an outcome of narrow food requirements, or increased security from predation due to little vegetation cover for stalking lions, has still to be resolved (Smuts 1978, Yoganand and Owen-Smith 2014, Martin et al. 2015). In the Serengeti ecosystem, both food availability and predation risk influenced the regional distribution patterns of grazing ungulates (Hopcraft et al. 2012, 2014). Spatial separation among large mammalian herbivores based on distinct responses to the risk of predation is likely to be expressed on a larger scale than foraging arenas based on dietary distinctions.

Our findings demonstrate how large herbivores that overlap widely in space use at home

range scale and in habitat preferences within these ranges may nevertheless be separated behaviorally in their spatiotemporal patterns of resource exploitation at foraging arena scale. Distinctions in patterns of exploitation at this finer scale may partially negate the competitive interaction that might otherwise be expected between species with overlapping resource needs.

ACKNOWLEDGMENTS

Financial support for the study was provided by a South African National Research Foundation grant to N. Owen-Smith. J. Martin and K. Yoganand were supported by post-doctoral fellowships from the University of the Witwatersrand. Various staff members of South African National Parks helped with the capture of the animals for the placement of the collars and in various other ways. Lochran Traill assisted by providing the home range metrics. We acknowledge helpful comments on earlier drafts of this manuscript by Lochran Traill, James Cain and anonymous referees.

LITERATURE CITED

- Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97:313–318.
- Arsenault, R., and N. Owen-Smith. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos* 117:1711–1717.
- Arsenault, R., and 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.
- Bell, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. Pages 111–124 in A. Watson, editor. *Animal populations in relation to their food resources*. Blackwell, Oxford, UK.
- Ben-Shahar, R. 1991. Selectivity in large generalist herbivores: feeding patterns of African ungulates in a semi-arid habitat. *African Journal of Ecology* 29:302–315.
- Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B* 365:2157–2162.
- Cain, J. W. III, N. Owen-Smith, and V. Macandza. 2012. The costs of drinking: comparative water dependency of sable antelope and zebra. *Journal of Zoology* 286:58–67.
- Campbell, B. D., J. P. Grime, and J. M. L. Mackey. 1991. A tradeoff between scale and precision in resource foraging. *Oecologia* 87:532–538.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches. Linking classical and contemporary approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Chirima, G. J., N. Owen-Smith, and B. N. F. Erasmus. 2012. Recent distributions of larger ungulates in the Kruger National Park from ecological aerial survey data. *Koedoe* 54(1):art 1009.
- Chirima, G. J., N. Owen-Smith, B. N. F. Erasmus, and F. Parrini. 2013. Distributional niche of a relatively rare large herbivore: habitat template versus biotic interactions. *Ecography* 36:68–79.
- Clutton-Brock, T. H., and P. H. Harvey. 1983. The functional significance of variation in body size among mammals. *Special Publication of the American Society of Mammalogists* 7:632–663.
- Codron, D., and M. Clauss. 2010. Rumen physiology constraints diet niche: linking digestive physiology and food selection across wild ruminant species. *Canadian Journal of Zoology* 88:1129–1138.
- Cromsigt, J. P. G. M., and H. Olf. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology* 87:1532–1541.
- Cromsigt, J. P. G. M., H. H. T. Prins, and H. Olf. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. *Diversity and Distributions* 15:513–522.
- de Boer, W. F., and H. H. T. Prins. 1990. Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82:264–274.
- Duncan, P., T. J. Foote, I. J. Gordon, C. G. Gakahu, and M. Lloyd. 1990. Comparative nutrient extraction from forages by bovines and equids: a test of the nutritional model of equid/bovine competition and coexistence. *Oecologia* 84:411–418.
- du Toit, J. T., and N. Owen-Smith. 1989. Body size, population metabolism and habitat specialization among African large herbivores. *American Naturalist* 133:736–740.
- Getz, W. M., S. Fortmann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE* 2(2):e207.
- Gordon, I. J., and A. W. Illius. 1988. Incisor arcade structure and diet selection in ruminants. *Functional Ecology* 2:15–22.
- Guisan, A., and N. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modeling* 135:147–186.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131:1292–1297.
- Hempson, G., et al. 2014. Ecology of grazing lawns in

- Africa. *Biological Reviews* 90(3):979–994.
- Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative review of their digestive system. *Oecologia* 78:443–457.
- Holt, R. D., J. P. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144:741–771.
- Hopcraft, J. G. C., T. M. Anderson, S. Perez Vilo, E. Mayemba, and H. Olff. 2012. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology* 81:201–213.
- Hopcraft, J. G. C., J. M. Morales, H. L. Beyer, M. Borner, E. Mwangomo, A. R. E. Sinclair, H. Olff, and D. T. Haydon. 2014. Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs* 84:355–372.
- Houston, A. I., J. M. McNamar, and I. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B* 341:375–397.
- Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215–267.
- Joubert, S. 2007. *The Kruger National Park: a history*. High Branching, Johannesburg, South Africa.
- Kleynhans, E. J., A. E. Jolles, M. R. E. Bos, and H. Olff. 2011. Resource partitioning along multiple niche dimensions in different sized grazers. *Oikos* 120:591–600.
- Klingel, H. 1969. The social organization and population ecology of the plains zebra. *Zoologica Africana* 4:249–263.
- Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701.
- Kotler, B. P., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* 19:281–307.
- Macandza, V., N. Owen-Smith, and J. W. Cain III. 2012a. Habitat and resource partitioning between abundant and relatively rare grazing ungulates. *Journal of Zoology* 287:175–185.
- Macandza, V., N. Owen-Smith, and J. W. Cain III. 2012b. Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos* 121:891–898.
- Martin, J., S. Benhamou, K. Yoganand, and 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.
- McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* 191:92–93.
- Murray, M. G., and A. W. Illius. 1996. Multispecies grazing in the Serengeti. Pages 247–272 in J. Hodgson and A. W. Illius, editors. *The ecology and management of grazing systems*. CAB International, Wallingford, UK.
- Ogutu, J. O., and N. Owen-Smith. 2005. Oscillations in large herbivore populations: Are they related to predation or rainfall? *African Journal of Ecology* 43:332–339.
- Owen-Smith, N. 1985. Niche separation among African ungulates. Pages 167–171 in E. S. Vrba, editor. *Species and speciation*. Monograph number 4. Transvaal Museum, Pretoria, South Africa.
- Owen-Smith, N. 2002. *Adaptive herbivore ecology: from resources to populations in variable environments*. Cambridge University Press, Cambridge, UK.
- Owen-Smith, N., and V. Goodall. 2014. Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. *Journal of Zoology* 293(3):181–191.
- Owen-Smith, N., and J. Martin. 2015. Identifying space use at foraging arena scale within the home ranges of large herbivores. *PLoS ONE* 10(6):e0128821.
- Porter, W. P., S. Budaraju, W. E. Stewart, and N. Ramankutty. 2000. Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters and global community structure. *American Zoologist* 40:597–630.
- Prins, H. H. T., and H. Olff. 1998. Species richness of African grazer assemblages: towards a functional explanation. Pages 449–490 in D. M. Newbery, H. H. T. Prin, and N. D. Brown, editors. *Dynamics of tropical communities*. Blackwell, Oxford, UK.
- R Development Core Team. 2012. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ritchie, M. 2002. Competition and coexistence of mobile animals. Pages 110–131 in U. Sommer and B. Worm, editors. *Competition and coexistence*. Springer, Berlin, Germany.
- Ritchie, M. 2009. *Scale, heterogeneity, and the structure and diversity of ecological communities*. Princeton University Press, Princeton, New Jersey, USA.
- Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. *American Naturalist* 137(Supp):5–28.
- Sinclair, A. R. E., S. A. R. Mduma, J. G. C. Hopcraft, J. M. Fryxell, R. Hilborn, and S. Thirgood. 2007. Long-term ecosystem dynamics in the Serengeti: lessons for conservation. *Conservation Biology* 21:580–590.
- Sinclair, A. R. E., and M. Norton-Griffiths. 1982. Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of

- hypotheses. *Oecologia* 53:364–369.
- Smuts, G. L. 1975. Home range sizes for Burchell's zebra from the Kruger National Park. *Koedoe* 18:139–146.
- Smuts, G. L. 1978. Interrelations between predators, prey, and their environment. *BioScience* 28:316–320.
- Soberon, J. 2007. Grinnellian and Eltonian niches and geographic distribution of species. *Ecology Letters* 10:1115–1123.
- Spencer, W. D. 2012. Home ranges and the value of spatial information. *Journal of Mammalogy* 93:929–947.
- Stensland, E., A. Angerbjorn, and P. Berggren. 2003. Mixed species groups in mammals. *Mammal Review* 33:205–223.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- Stock, W. D., et al. 2010. Herbivore and nutrient control of lawn and bunch grass distribution in a southern African savannah. *Plant Ecology* 206:15–27.
- Traill, L. W. 2004. Seasonal utilization of habitat by large grazing herbivores in semi-arid Zimbabwe. *South African Journal of Wildlife Research* 34:13–24.
- Vesey-Fitzgerald, D. T. 1960. Grazing succession among East African game animals. *Journal of Mammalogy* 41:161–172.
- Voeten, M. N., and H. H. T. Prins. 1998. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120:287–294.
- Whyte, I. J., and S. C. J. Joubert. 1988. Blue wildebeest population trends in the Kruger National Park and the effects of fencing. *South African Journal of Wildlife Research* 18:78–87.
- Yoganand, K., and N. Owen-Smith. 2014. Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography* 37:969–982.

SUPPLEMENTAL MATERIAL

APPENDIX

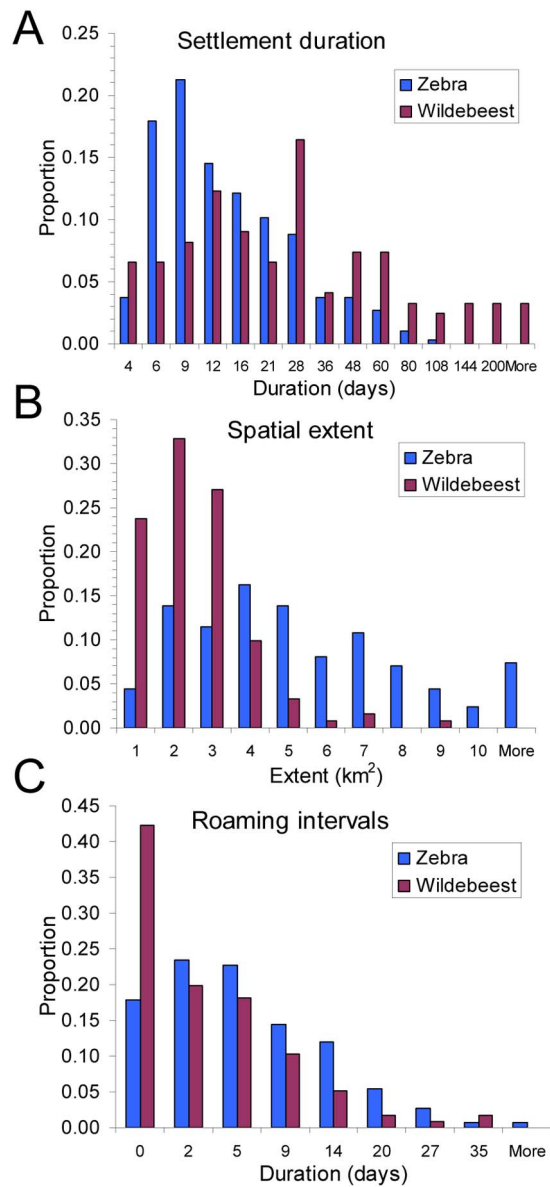


Fig. A1. Comparative statistical distributions of foraging arena metrics amalgamated over all collared wildebeest and zebra. (A) Settlement durations, (B) spatial extent, and (C) roaming intervals.

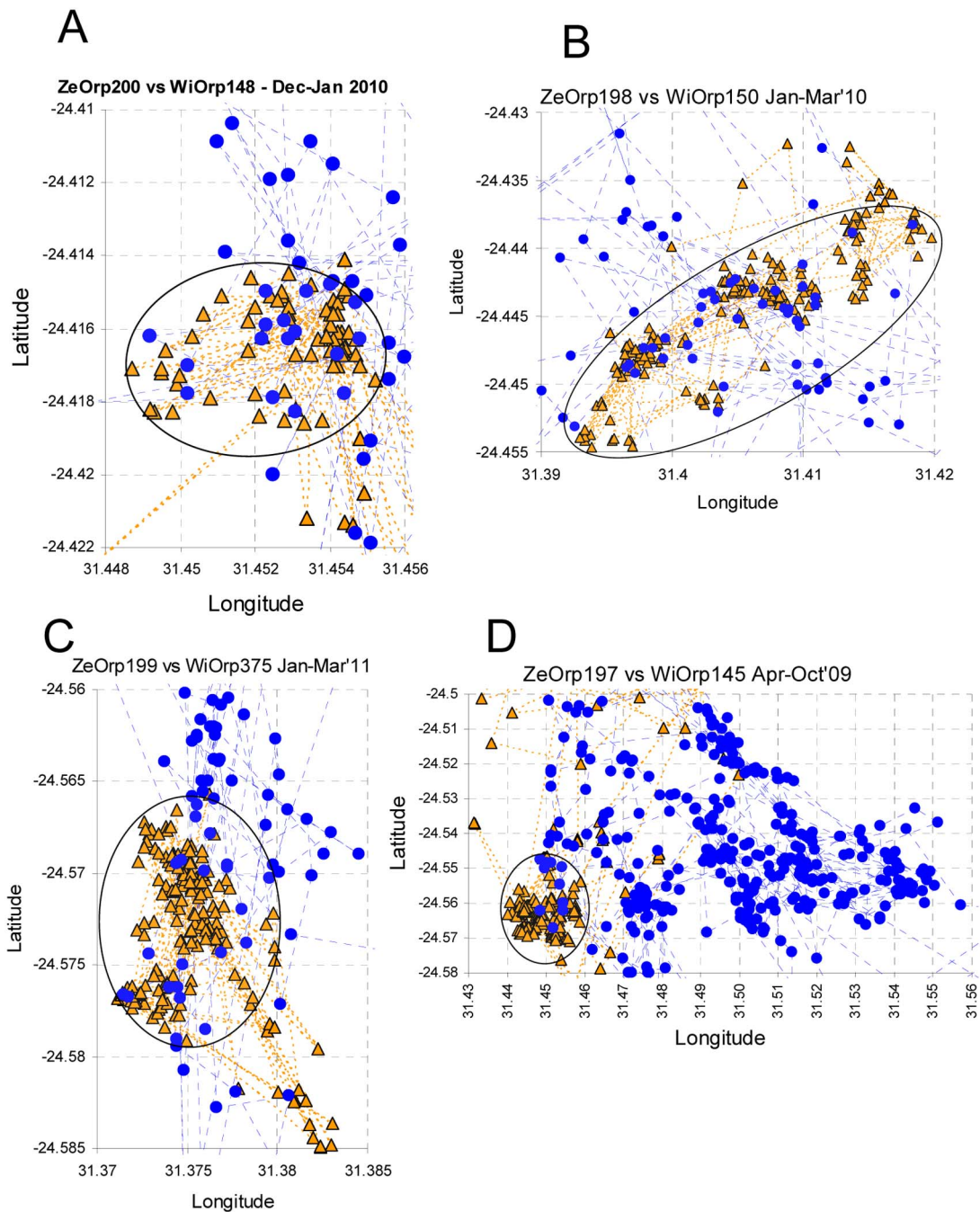


Fig. A2. Examples of the greatest spatial overlap between zebra and wildebeest in foraging arenas exploited that was observed. (A) and (B) Two examples of overlap in the wet season when wildebeest concentrated on grazing lawn grasslands in gabbro uplands. (C) Third wet season example where zebra and wildebeest overlapped in recently burned grassland in a gabbro landscape. (D) Example where foraging arena exploited by a zebra herd during the dry season was closest to the foraging arena on seep-zone grassland occupied by a wildebeest herd over the same period. Blue circles represent zebra, orange triangles represent wildebeest.