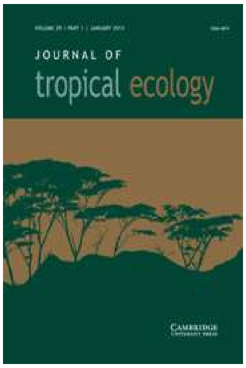

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Effects of resource limitation on habitat usage by the browser guild in Hluhluwe-iMfolozi Park, South Africa

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Abstract: Resource depletion and associated increases in interspecific competition are likely to influence differential habitat usage amongst a guild. We tested some prominent theoretical concepts using observed differences in seasonal habitat use amongst the savanna browser guild (elephant, giraffe, impala, kudu and nyala) in Hluhluwe-iMfolozi Park, South Africa. Herbivore locations ($n = 3108$) were recorded over 2 y using repeated road transects and, for elephant, GPS collars (187 254 downloads). Densities were calculated using a novel GIS approach designed to be a cost-effective method for annual censuses, but also able to cope with abrupt changes in visibility. Selectivity for (Manly's α) vegetation types, and overlap (Schoener's index) in vegetation type usage were calculated. Resource depletion in the dry season resulted in all members of the guild increasing selectivity for vegetation types (sum of absolute values away from the neutral value for Manly's alpha for the guild: dry seasons 3.97, 5.16; corresponding wet seasons 3.12, 3.68), but decreasing interspecific overlap (80% of Schoener's indices lower in dry season versus wet season). These effects were more marked over the second, more severe, dry season. We found support for the niche overlap hypothesis and the niche compression hypothesis. The Jarman–Bell principle was generally supported, although unexpectedly during the severe dry season elephant showed the most selectivity for vegetation type. The greater the resource depletion, the more relevant interspecific differences in habitat usage become in relation to the differential impacts of guild members.

Key Words: browsers, competition, elephant, giraffe, GIS, impala, kudu, niche, nyala, savanna, selectivity

INTRODUCTION

As resources decrease and competition increases amongst a guild, differences between species in their use of available habitats may alter. The resultant alteration in levels of impact across the range of habitats is likely to influence biodiversity. However studies from the guild perspective are rare – whether assessing the impacts of entire guilds on their habitats (Makhabu 2005, Olofsson *et al.* 2004), or the consequences of altering the density of part of a guild (Flecker 1997, Madhusudan 2004). Yet there is a considerable theoretical literature on the relationship between interspecific competition and niche use. Here we summarize these theories, which produce hypotheses and testable predictions. We then test these predictions using the savanna browser guild as a topical case study. Elephant (*Loxodonta africana* (Blumenbach)) densities are increasing, except where there is heavy poaching, in all areas (Scholes & Mennell 2008). It is uncertain how this will affect differences in use of habitat between elephant and other members of the guild.

Niche overlap has been demonstrated for omnivores, carnivores and herbivores in a wide range of systems including tropical (Bagchi *et al.* 2003), temperate (Bonesi *et al.* 2004), arctic (Elmhagen *et al.* 2002), desert (Jones & Barmuta 2000) and, perhaps most extensively, in African savannas (Ferrar & Walker 1974, Fritz *et al.* 1996, Lamprey 1963, Loveridge & Macdonald 2003). However niche overlap leads to competition only when resources are sparse, and maximum tolerable overlap would be expected to be lower if there is intense competition (Pianka 1972, 1976). Ideal free distribution theory (Fretwell & Lucas 1970) and centrifugal community organization theory (Rosenzweig 1981), suggest that interspecific niche overlap is reduced by competing individuals increasing their niche breadth, by being less selective and utilizing a wider range of resources. Conversely, the niche compression hypothesis (MacArthur & Pianka 1966) suggests that niche overlap is reduced by reducing

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niche breadth, with competitors increasing selection and utilizing a narrower range of resources.

The Jarman–Bell Principle (Bell 1971, Belovsky 1997, see also Demment & Van Soest 1985, Jarman 1974) predicts that larger animals can survive on relatively lower-quality foods, because of the interrelationships between body size, energy (Hungate *et al.* 1959) and protein turnover (Brody *et al.* 1934) and gut capacity (Illius & Gordon 1992). As a result of this wider food-quality tolerance, larger herbivores would be expected to utilize a higher proportion of habitat types than smaller herbivores (Cromsigt *et al.* 2009). The elephant is a non-ruminant, with most digestion occurring in the hind-gut (Van Hoven *et al.* 1981), and as such is adapted, compared with ruminants such as giraffe, kudu, nyala and impala, to process coarser forage at a rapid rate (Napier Bax & Sheldrick 1963).

These theories lead to the following hypotheses as to how resource limitation may influence habitat usage by the savanna browser guild: (1) with increasing resource limitation (a) interspecific habitat usage overlap will decrease (niche overlap hypothesis) and (b) selectivity for habitat types may either decrease (ideal free distribution theory and centrifugal community organization theory) or increase (niche compression hypothesis); (2) larger herbivores will be less selective of habitat type than smaller herbivores (Jarman–Bell principle); and (3) the elephant, as the largest member of the guild and its only non-ruminant, will be less selective of habitat type than other guild members (Jarman–Bell principle and digestive strategy).

METHODS

Community or vegetation type has been widely shown to be the principal influence on the habitat choice of large mammalian herbivores (Dekker *et al.* 1996, Ferrar & Walker 1974, Field & Laws 1970, Lamprey 1963). We assessed habitat usage, in terms of vegetation type usage, of elephant, giraffe (*Giraffa camelopardalis* (Linnaeus)), kudu (*Tragelaphus strepsiceros* (Pallas)), impala (*Aepyceros melampus* (Lichtenstein)) and nyala (*Tragelaphus angasii* (Gray)). We used observed differences in seasonal use to evaluate the described predictions from niche theory.

Study site

We conducted the study from September 2006 to October 2008 in Hluhluwe–iMfolozi Park (HiP), KwaZulu–Natal, South Africa (28°00′–28°26′S, 31°43′–32°09′E). HiP is a 900 km^2 completely fenced nature reserve, situated in the foothills of the first escarpment on the west side of the Zululand coastal plain (Whateley & Porter 1983). Mean annual rainfall and altitude decrease from Hluhluwe in the north (990 mm and 450 m asl), to iMfolozi in the south (635 mm and 60 m asl), with April to September being the dry season. During the study the second dry season was noticeably drier than the first, with the height of the second dry season (July–September) particularly dry (first year: wet season 569 mm, dry season 253 mm, July–September 51 mm; second year: wet season 577 mm, dry season 167 mm, July–September 19 mm). Terrain varies between valleys, hills and plains. The soils are mainly derived from sandstone, shale and dolerite intrusions and are generally eutrophic. In Hluhluwe during June and July (coldest months) the mean daily minimum temperature recorded over the study period was 12 °C, and during January and February (hottest months) 31 °C (Zululand Grass Project Weather Data, unpubl. data).

The national vegetation map of South Africa (Mucina & Rutherford 2006) recognizes three major vegetation types within HiP. These are Northern Zululand Sourveld (SVI22), Zululand Lowveld (SVI23) and Scarp Forest (FOz5). The vegetation is characterized by fine-leaved *Acacia* savanna with a continuous grass layer and a fairly open tree canopy. Hluhluwe is typified by *Acacia nilotica* woodlands, *Acacia karoo–Dichrostachys cinerea* thicket, *Euclea divinorum* woodlands and, at higher altitudes, *Celtis africana* forest communities. In the Corridor *A. nilotica* woodlands and *A. karroo–D. cinerea* thicket predominate; in iMfolozi *Acacia nigrescens* woodlands, *Acacia tortilis* woodlands and *Spirostachys africanus* woodlands (Whateley & Porter 1983). The *A. nilotica* woodlands and *A. karroo–D. cinerea* communities that dominate Hluhluwe and the Corridor are allied with dense, tall grass swards, consisting primarily of species of the tribe Andropogoneae such as *Themeda triandra* and *Cymbopogon excavatus* (Pooley 2003). HiP supports a large and diverse herbivore population. The principal browsers, and their current estimated average densities (K.Z.N.Wildlife 2008), are elephant 0.52 km^{-2} (increasing at 9% p.a.), giraffe 0.89 km^{-2}, black rhino (*Diceros bicornis* (Lichtenstein)) 0.35 km^{-2}, kudu 1.3 km^{-2}, nyala 7.3 km^{-2} and impala 26.1 km^{-2}.

Data collection

Management required a cheaper alternative to annual aerial censuses for monitoring population sizes amongst the browser guild. Previous use of distance sampling (Buckland *et al.* 2001) to analyse ground census data had produced unrealistic population estimates. This was probably due to the assumptions inherent in distance sampling being violated. Distance sampling assumes that sighting visibility falls off gradually as distance from the observer increases. The varied topography of HiP frequently results in visibility being abruptly cut off, leading to areas of dead ground where animals cannot be seen, between the observer and the limit of his vision. We therefore developed our own method, based on a GIS, for determining herbivore densities by habitat type, from which management could extrapolate to monitor reserve-wide population sizes.

We drove at 20 km h^{-1} on the same fixed route through a representative sample of the different vegetation types, using the reserve's road network, for 5 d mo^{-1} for 2 y (September 2006–September 2008). When study animals were seen the vehicle was stopped, and the species and number of animals recorded. At each sighting location we recorded the longitude/latitude of the vehicle using a GPS (Garmin 12XL), the distance from the vehicle to the (approximate) centre of the herd using a laser rangefinder (Yardage Pro 1000) and the compass bearing from the vehicle to the herd, using the GPS that was recording the direction of travel. The position of the individual animal or herd was then determined trigonometrically and imported into a GIS (ArcGIS 9). Although the elephant forms an estimated one-third of the reserve's browser biomass, its small numbers, comparative to the other browsers studied, result in comparatively few elephant sightings. Repeated transects relying on frequent sightings was therefore not an appropriate technique, and consequently an alternative approach was needed to determine elephant habitat usage. Over the study period six cow elephants, one in each of the reserve's six breeding herds, were fitted with GPS/mobile-phone collars set to record and download the wearer's position every 30 min. These records were then also imported into the GIS.

Data analyses

Data were analysed across the whole study period, by year and by separate seasons (Schooley 1994).

Ecological densities by vegetation type. The most recent vegetation community study and resultant GIS map of HiP is nearly 30 y old (Whateley & Porter 1983); it is also very detailed, consisting of 30 categories. To determine its current validity, three approaches were used. Ground (unpubl. data) used a series of fixed-point photographs taken over time (from 1975 onwards) at specific sites throughout HIP to develop a structural vegetation model. The outputs showed that although an overall thickening of the park had taken place over the past 33 y, changes were occurring at community rather than structural level (80% of predicted changes versus 10% respectively), with the majority of these shifts following successional pathways e.g. *Acacia caffra* wooded grassland to *A. nilotica*/*A. karroo* wooded grassland. Secondly, Google Earth satellite images were digitized and overlaid over the Whateley and Porter map in the form of polygons to verify habitat boundaries and, thirdly, all transects were re-driven and the nature and boundaries of communities directly compared with the Whateley and Porter map. Both these approaches also showed minimal structural changes in the park's vegetation communities. With the Whateley and Porter map thus structurally validated, a simplified GIS vegetation layer was constructed consisting of nine structural categories based on the original 30 categories. These were (with dominant woody species): broad-leaved thicket (*Euclea divinorum*), closed woodland (*Spirostachus africana*, *Euclea racemosa*, *Acacia grandicornuta*), dry forest (*Olea europa*, *Commiphora harveyi*), fine-leaved thicket (*Acacia* spp., *Dichrostachys cineria*), grassland, open woodland (*A. nigrescens*/*A. tortilis*, *A. nilotica*, *A. burkei*, *Commiphora apiculatum*), riparian (*A. robusta*, *Ficus* spp.), scarp forest (*Celtis* spp., *Harpephyllum* spp., *E. racemosa*) and wooded grassland (*A. karoo*, *A. caffra*, *D. cinerea*).

To determine the area sampled by the road transects, all transects were slowly re-driven with the observers recording, manually on large-scale maps, maximum sighting distances for the various herbivores, either side of the vehicle. In the GIS these results, together with the 3108 sighting records displayed in the GIS, were then used to construct polygons which were merged to produce one polygon of the area sampled. Using 'Intersect' from the 'Analysis Tools', the vegetation layer and the sampled area polygon as the 'input features', the resultant 'output' demarcated the area sampled by vegetation type. The 'XTools' routine was then used to calculate the area sampled by vegetation type. The number of animals sighted in each vegetation type was determined from the database and with the number of animals per vegetation type and the area of that vegetation type sampled known, ecological densities per vegetation type were obtained. To validate these ecological densities, total population estimates for each of the study herbivores were calculated and compared with available management population estimates (obtained by a mixture of aerial censuses and walked transects). Total population estimates were calculated here using the ecological densities and the total area of each vegetation type in the reserve (the latter obtained by applying the 'XTools' routine to the entire vegetation layer).

Densities for elephant were determined from their collar data. A concurrent study on the social behaviour of the six breeding herds in HiP showed that, over the period of this study, each collared cow remained with her herd and that membership of each herd varied little (Bodasing 2011). During the height of the dry season, breeding herds coalesced, typically into two large herds, with, again, the collared cows remaining with their core breeding herd within the larger dry-season herd. Thus movements of each collared cow can be taken as representative of their respective breeding herd. Overlaying the GPS downloads (n = 187 254) onto the GIS vegetation layer enabled the proportion of time spent in each vegetation type by each collared elephant to be calculated. Average numbers of elephants in each of the six herds for each of the four seasons were then used to weight these proportions. Knowing the total number of elephants in the reserve and total area of each vegetation type, these weighted proportions were used to produce densities for elephant by vegetation type across the reserve. The different methods used to determine densities per vegetation type for elephant versus other browsers, means one cannot directly compare the actual densities across these two groups. However, comparison of the proportional usage of different vegetation types by elephant versus other browsers is valid.

Vegetation types: preferences and overlaps. Krebs (1999) recommends Manly's α preference index (Manly *et al.* 1972) as a simple measure of preference derived from probability theory, that includes all the biological factors that may affect capture and encounter rates of prey, including availability. Manly's α (constant prey populations) may be adapted for habitat usage to:

$$\alpha_i = \frac{p_i}{P_i}\left(\frac{1}{\sum (p_j/P_j)}\right)$$

where α_i = Manly's α (preference index) for habitat type *i*, p_i, p_j = proportion of the overall habitat usage that usage of habitat type *i* or *j* forms (*i* and *j* = 1, 2, 3,.....n), P_i, P_j = proportion of habitat type *i* or *j* in the environment and n = number of habitat types. If α_i is > than (1/n) then habitat type *i* is preferred; if < than (1/n) habitat type *i* is avoided.

Seasonal differences in vegetation type preferences by the guild were assessed by calculating, and comparing, the sum of absolute values away from the neutral value for Manly's alpha (here 0.111) for the entire guild, and for each herbivore species, in each season. As obligate browsers (kudu and giraffe) experience different resource limitation between seasons compared with mixed feeders (impala, nyala and elephant), herbivores were grouped into obligate browsers or mixed feeders to assess the predictions of the Jarman–Bell principle. Weights of herbivores are the average of adult male and female, taken from Estes (1991).

As an additional measure of preference Ivlev's electivity index (1961), recommended by Lechowitz (1982), was calculated as:

$$E_i = (p_i - P_i)/(p_i + P_i)$$

where E_i = Ivlev's electivity index for habitat i, p_i = proportion of the overall habitat usage that usage of habitat type *i* forms, P_i = proportion of habitat type *i* in the environment. If $E_i = 0$, then no selection occurs. The closer E_i is to +1, the greater the preference; E_i of −1 represents complete avoidance.

Overlap of vegetation-type usage between all pairwise combinations of herbivores in the guild was assessed using Schoener's index (Schoener 1974), recommended by Abrams (1980) as a measure meeting the required criteria of an overlap measure. Where there is no use of the same resources this index is zero, and where completely identical resources are used to the same extent it is one; overlap is generally considered significant where the index ≥ 0.6 (Wallace 1981). Schoener's index for overlap of habitat usage was:

$$S_{ab} = 1 - \frac{1}{2}\sum_{i=1}^{n} |p_{ai} - p_{bi}|$$

where S_{ab} = Schoener's index for overlap of habitat usage between herbivore species *a* and *b*, p_{ai} = proportion of the overall habitat usage that usage of habitat type *i* by herbivore species *a* forms, p_{bi} = similarly for herbivore species *b*, *n* = number of habitat types. Seasonal differences in overlap of vegetation-type usage were assessed by applying the Wilcoxon rank-sum test to the wet and dry seasons $|p_{ai} - p_{bi}|$ part of Schoener's index equation. Schoener's index is relatively unaffected by sample size.

As an additional measure of overlap Morisita's index of similarity (1959), recommended by Wolda (1981) as 'the best overall measure of similarity for ecological use' but one affected by very small sample size (Krebs 1999), was calculated as:

$$M_{ab} = \frac{2\sum X_{ai}X_{bi}}{(\lambda_1 + \lambda_2)\,N_a N_b}$$

where M_{ab} = Morisita's index of similarity of habitat usage between herbivore species *a* and *b*, X_{ai} = number of individuals of herbivore species *a* in habitat type *i*, X_{bi} = number of individuals of herbivore species *b* in habitat type *i*, $N_a = \Sigma\ X_a$ = total number of individuals of herbivore species *a*, $N_b = \Sigma\ X_b$ = total number of individuals of herbivore species *b* and

$$\lambda_1 = \frac{\sum [X_{ai}\,(X_{ai} - 1)]}{N_a\,(N_a - 1)}$$

$$\lambda_2 = \frac{\sum [X_{bi}\,(X_{bi} - 1)]}{N_b\,(N_b - 1)}$$

The Morisita index of similarity varies from 0 (no similarity) to 1.0 (complete similarity). All statistical procedures were carried out in S-PLUS 2000.

Table 1. Occupancy of different vegetation types by members of the browser guild in Hluhluwe-iMfolozi Park, South Africa. Densities (number of animals km^{-2}) are shown for each member of the guild, in different wet and dry seasons.

Herbivore	Season	Broad-leaved thicket	Closed woodland	Dry forest	Fine-leaved thicket	Invaded grassland	Open woodland	Riparian	Scarp forest	Wooded grassland
Elephant	Wet 2007	0.7	0.4	0.6	0.4	0.2	0.5	0.5	0.4	0.5
Elephant	Wet 2008	0.1	0.6	0.7	0.2	0.1	0.5	0.5	0.1	0.6
Giraffe	Wet 2007	0.8	0.9	0.1	0.9	0	0.8	0.4	0	0.6
Giraffe	Wet 2008	2.7	0.3	1.0	1.6	0	1.7	0.3	0	1.5
Kudu	Wet 2007	0	0.7	0.6	0.3	0	0.7	0.1	0	1.0
Kudu	Wet 2008	0	0.1	1.2	0.2	0	0.8	0.2	0	0.5
Nyala	Wet 2007	7.0	2.2	1.3	0.7	0.8	1.7	1.3	2.4	2.1
Nyala	Wet 2008	4.7	3.0	0.7	1.6	0.2	2.0	0.1	1.1	1.5
Impala	Wet 2007	5.6	42.0	56.2	4.9	1.2	35.3	17.4	0	14.5
Impala	Wet 2008	2.0	33.3	35.3	2.8	5.3	40.1	10.5	1.1	19.0
Elephant	Dry 2007	1.3	0.2	0.3	1.0	0.4	0.4	0.7	1.1	0.4
Elephant	Dry 2008	1.1	0.3	0.4	0.8	0.6	0.4	0.7	1.6	0.5
Giraffe	Dry 2007	0.8	0.9	0.2	1.2	3.2	1.5	0.9	2.2	0.7
Giraffe	Dry 2008	0	0.6	0.8	1.7	3.2	0.9	0.5	2.0	0.8
Kudu	Dry 2007	0	0.4	0	0	0	0.7	0.2	0	0.8
Kudu	Dry 2008	0	0.9	1.0	0.2	1.0	0.8	0	0	0.6
Nyala	Dry 2007	5.3	2.5	0.7	1.2	0	2.8	3.2	0	1.4
Nyala	Dry 2008	1.8	3.1	0.4	0.8	0	1.8	2.1	0.6	1.5
Impala	Dry 2007	1.4	36.0	63.4	4.8	1.2	31.7	33.3	0	12.1
Impala	Dry 2008	5.6	38.9	40.1	3.9	2.8	32.4	32.5	0	8.4

RESULTS

Over the study period we obtained 3108 sighting records (totalling 27 947 animals). Data obtained on black rhino were too limited to form part of the analyses. Population estimates derived from aerial and walked censuses were available for impala (23 500) and for giraffe (800). Estimates derived from our GIS approach (impala: 23 600; giraffe: 900) compared favourably with these. In the wet season the guild members utilized a wide range of woodland vegetation types, with grassland, scarp forest and riparian communities generally avoided (Table 1). However, in the dry season there was a noticeable shift to these latter three vegetation types, with elephant and giraffe particularly preferring scarp forest and impala and nyala (and, to a lesser extent, kudu) riparian communities. The guild's reduced usage in the dry season of closed, open and grassed woodland was striking. Impala heavily preferred dry forest and nyala broad-leaved thicket in both seasons.

The sum of absolute values away from the neutral value for Manly's alpha for the entire guild was higher in both dry seasons (3.97, 5.16) compared with the preceding wet seasons (3.12, 3.68), indicating greater selection (whether avoidance or preference) of vegetation types occurred in the dry season. The higher value in the second dry season and the noticeably larger difference between the wet and dry season of the second year (1.48) compared with the first year (0.85), indicated greater selection was occurring in the more severe, drier, second dry season. Larger herbivores, within the category of obligate browser or mixed feeder, were generally less selective of habitat type than smaller herbivores (Figure 1). However over the first, less severe, dry season elephant showed a comparable degree of selectivity to the much smaller nyala, whilst over the second, severe dry season the elephant was the most selective mixed feeder. Similarly, amongst the obligate browsers, giraffe showed a comparable degree of selectivity to the smaller kudu over the second, severe dry season. Manly's alpha results were supported by Ivlev's electivity index results. The two

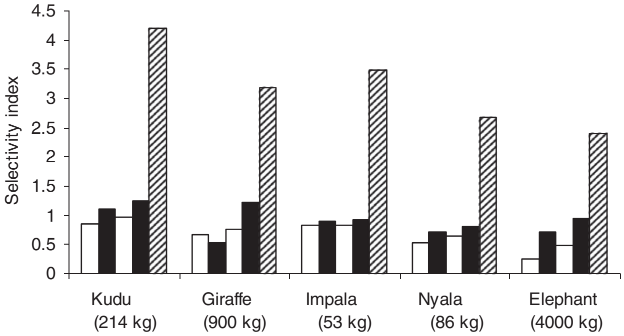

Figure 1. Selectivity for vegetation types amongst members of the browser guild in Hluhluwe-iMfolozi Park, South Africa. The sum of the absolute values away from the neutral value for Manly's alpha (here 0.111) are shown. The higher the value, the greater the degree of selectivity. Herbivore species are grouped into obligate browsers (kudu and giraffe) and mixed feeders (impala, nyala and elephant), and then ordered by mass (masses shown are the average of adult male and female, taken from Estes 1991). The first pair of columns for each herbivore species show values for the wet (open) and dry (black) seasons during the first year of the study, the second pair for the second year. The final columns (diagonal) show values for all four seasons combined.

Table 2. Overlap in vegetation type occupancy amongst members of the browser guild in Hluhluwe-iMfolozi Park, South Africa. Schoener's Index and Morisita's Index are shown for each herbivore species pair in each of the four seasons. For Schoener's Index, values ≥ 0.6 are considered significant. * Schoener's Indices which showed a significant change ($P < 0.05$, Wilcoxon rank sum test) from the wet to the corresponding dry season.

	Schoener's Index				Morisita's Index			
Species pair	Wet 2007	Dry 2007	Wet 2008	Dry 2008	Wet 2007	Dry 2007	Wet 2008	Dry 2008
Elephant/giraffe	0.85	0.77	0.77	0.80	0.97	0.93	0.92	0.93
Elephant/kudu	0.82*	0.58*	0.78	0.71	0.96	0.82	0.94	0.91
Elephant/nyala	0.85	0.77	0.82	0.79	0.96	0.92	0.97	0.91
Elephant/impala	0.80	0.62	0.86*	0.65*	0.96	0.82	0.97	0.85
Giraffe/kudu	0.81	0.72	0.80	0.70	0.94	0.90	0.96	0.87
Giraffe/nyala	0.79	0.83	0.77	0.69	0.94	0.98	0.90	0.84
Giraffe/impala	0.78	0.76	0.70*	0.60*	0.94	0.93	0.90	0.78
Kudu/nyala	0.83	0.76	0.84*	0.67*	0.96	0.93	0.98	0.87
Kudu/impala	0.76	0.75	0.85	0.84	0.91	0.91	0.97	0.97
Nyala/impala	0.73	0.85	0.76	0.81	0.90	0.97	0.92	0.95

indices closely agreed with each other, with 6% of results differing (marginally) in terms of showing a preference or avoidance.

Overlap was significant (Schoener's index ≥ 0.6) for all herbivore pairs in both wet seasons and for 95% of herbivore pairs in both dry seasons (Table 2). In the dry season 80% of overlap values were lower compared with the preceding wet season in both years. Significant seasonal reduction in overlap (Wilcoxon rank-sum statistic $W = 61$, $n_1 = n_2 = 9$, $P < 0.05$ two-tailed) was shown by only one herbivore pair in the first year, but by three herbivore pairs (Wilcoxon $W = 61, 60, 58$, $n_1 = n_2 = 9$, $P < 0.05$ two-tailed) in the second year with its more severe dry season. Similarly, across the guild as a whole significant seasonal reduction in overlap (Wilcoxon rank-sum normal statistic with correction $Z = -1.98$, $P < 0.05$ two-tailed) occurred between the wet and dry season in the second year, but not in the first. Schoener's index results were supported by Morisita's index of similarity results. The relative values of the two indices amongst the guild were similar and showed similar seasonal shifts (Table 2).

DISCUSSION

The similarity of our population estimates to those derived from aerial censuses, suggests our novel GIS approach to determining herbivore densities by vegetation type gives consistent values. Additionally, the finding of extensive utilization of woodland vegetation types by the guild's different members is in agreement with previous work on the habitat usage of elephant (Laws 1970), giraffe (Dagg & Foster 1976), impala (Jarman 1972), kudu (Grunow 1980), nyala (Anderson 1978) and black rhino (Tatman *et al.* 2000). This widely reported preference is probably because woodlands have both a physiognomy that maximizes the availability of food to browsers and mixed feeders of different sizes, and are likely to have a high nutritional status because of rapidly growing early-successional species, resulting from browsing, fire and wind disturbance. Increased usage of riparian habitats during the dry season has been specifically demonstrated by others for elephant (Mosugelo *et al.* 2002), giraffe (Pellew 1984), impala (Jarman 1972), kudu (Simpson & Cowrie 1967) and black rhino (Oloo *et al.* 1994); it corresponds to the dry-season movement down the catena that has been demonstrated for grazing ungulates (Bell 1970) and elephant (de Knegt *et al.* 2008). Whilst impala, nyala and, to a lesser extent, kudu showed this shift here, elephant and giraffe did not but, rather, showed a dry-season shift to scarp forests. This vegetation type only occurs in the considerably wetter north of the reserve and presumably retains, similar to riparian habitats, more nutritious plants through the dry season compared to other vegetation types.

The extensive overlap in vegetation type usage found amongst the guild implies that different guild members will broadly impact the same vegetation types. Pianka's niche overlap hypothesis was supported – in both dry seasons most guild members showed a decrease in interspecific overlap, whilst significant reductions in overlap were more numerous in the second, severer dry season, during which, uniquely, overlap across the guild as a whole also significantly declined. Thus interspecific habitat-usage overlap decreased with increasing resource limitation. The niche compression hypothesis was also supported – selectivity for vegetation types increased in both dry seasons, with this effect also more pronounced in the more severe of the two dry seasons, again implying a direct relationship with increasing resource limitation and, thus, competition. Conversely, the predictions of the ideal free distribution theory and centrifugal community organization theory, that selectivity decreases with increasing resource depletion, were not supported. Thus from the perspective of management, the greater the resource depletion (e.g. following increases in elephant density), the more relevant interspecific differences in habitat usage become in relation to the differential impact of guild members.

The Jarman–Bell principle was generally supported, with smaller herbivores showing decreased diversity of habitat use (i.e. increased selectivity) compared with larger herbivores. These findings directly support Cromsigt *et al.* (2009) who, working on the savanna grazing guild in HiP, found that larger ruminant grazers were more evenly distributed than smaller ruminants and had a more diverse use of habitats. However the dry-season selectivity of elephant, and to a lesser extent giraffe, did not support the Jarman–Bell principle, as these largest members of the guild showed comparable or, under marked resource-limitation conditions, greater selectivity than smaller guild members. The explanation for both species may be their greater mobility. Home ranges for both giraffe and elephant are markedly greater than those for smaller herbivores (du Toit 1990). By virtue of their size they are also less susceptible to predation (Owen-Smith 1988), and consequently less restricted by dense undergrowth which may conceal predators (Grand 2002). Dense undergrowth also supports higher densities of ticks; it has been suggested that larger ungulates may be better able to tolerate the metabolic cost of tick infestation than smaller ungulates (Gallivan & Horak 1997). Giraffes are also heavily attended by the tick-removing oxpecker (Hart *et al.* 1990). Elephant and giraffe might therefore be expected to alleviate resource depletion more successfully than smaller herbivores, by concentrating their foraging in whatever part of their larger range provides the best forage, relatively independent of predators or ticks. This appeared to be the case, with the relevant dry-season range of both elephant and giraffe being concentrated in the north-eastern part of the study area, which is characterized by thicker undergrowth and stands of *Acacia karoo* – a woody species heavily favoured by both herbivores (O'Kane *et al.* 2011). Elephants are also known to communicate over long distances (Poole *et al.* 1988), and thus the disparate but related herds that combine in the dry season (Bodasing 2008, Wittemyer *et al.* 2007) might inform one another where the best forage is to be found. The manner in which the smaller members of the guild were apparently unable to capitalize on these superior resources, emphasizes that factors other than efficiency in acquiring food sources of high nutritional value, as suggested by optimal foraging theory (Stephens & Krebs 1986), may also influence habitat and food selection (e.g. the giving-up-density theories (Brown 1988) suggest that both niche breadth and niche overlap may be influenced by factors such as predation). Additionally it is noteworthy that although the Jarman–Bell principle is widely accepted, some recent empirical evidence (Clauss & Hummel 2005, Franz *et al.* 2011, Weckerly 2009) questions this theoretically derived concept.

Conclusions

Amongst the savanna browser guild we found that with increasing resource depletion interspecific overlap in habitat usage decreased, whilst selectivity for habitat types increased. Smaller members of the guild generally showed greater selectivity for habitat types, but exceptions, noticeably elephant under marked resource depletion, were found. These principles may apply to other guilds and in other systems. However, the savanna browser guild has an unusually diverse range of browsers, and is thus likely to have a high degree of redundancy in the system, translating into heightened competitive effects amongst the guild. Guilds lacking these characteristics are likely to respond to resource limitation, in terms of the shifts in habitat usage overlap and selectivity discussed here, in a more muted manner.

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LITERATURE CITED

ABRAMS, P. 1980. Some comments on measuring niche overlap. *Ecology* 61:44–49.

ANDERSON, J. L. 1978. *Aspects of the ecology of the nyala* (Tragelaphus angasi *Gray 1849*) *in Zululand.* PhD dissertation. Imperial College, University of London, London.

BAGCHI, S., GOYAL, S. P. & SANKAR, K. 2003. Niche relationships of an ungulate assemblage in a dry tropical forest. *Journal of Mammalogy* 84:981–988.

BELL, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. Pp. 111–124 in Watson, A. (ed.). *Animal populations in relation to their food resources*. Blackwell Scientific Publications, Oxford.

BELL, R. H. V. 1971. A grazing system in the Serengeti. *Scientific American* 225:86–93.

BELOVSKY, G. E. 1997. Optimal foraging and community structure: the allometry of herbivore food selection and competition. *Evolutionary Ecology* 11:641–672.

BODASING, T. 2008. *Elephant movement and behaviour in Hluhluwe-iMfolozi Park*. KZN Wildlife, Hluhluwe. 18 pp.

BODASING, T. 2011. *Determinants of elephant spatial use, habitat selection and daily movement patterns in Hluhluwe-iMfolozi Park*. MSc dissertation. University of KwaZulu Natal, Durban. 120 pp.

BONESI, L., CHANIN, P. & MACDONALD, D. W. 2004. Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. *Oikos* 106:19–26.

BRODY, S., PROCTOR, R. C. & ASHWORTH, U. S. 1934. Growth and development with special reference to domestic animals, Part 34. *Research Bulletin. Missouri Agricultural Experiment Station* 220: 32.

BROWN, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22:37–47.

BUCKLAND, S. T., ANDERSON, D. R., BURNHAM, K. P., LAAKE, J. L., BORCHERS, D. L. & THOMAS, L. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford. 416 pp.

CLAUSS, M. & HUMMEL, J. 2005. The digestive performance of mammalian herbivores: why big may not be that much better. *Mammal Review* 35:174–187.

CROMSIGT, J., PRINS, H. H. T. & OLFF, H. 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.

DAGG, A. I. & FOSTER, J. B. 1976. *The giraffe: its biology, behaviour and ecology*. Van Nostrand Reinhold, New York. 210 pp.

DE KNEGT, H. J., GROEN, T. A., VAN DE VIJVER, C., PRINS, H. H. T. & VAN LANGEVELDE, F. 2008. Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. *Oikos* 117:543–554.

DEKKER, B., VAN ROOYEN, N. & BOTHMA, J. D. P. 1996. Habitat partitioning by ungulates on a game ranch in the Mopani veld. *South African Journal of Wildlife Research* 26:117–122.

DEMMENT, M. W. & VAN SOEST, P. J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641–672.

DU TOIT, J. T. 1990. Home range–body mass relations: a field study on African browsing ruminants. *Oecologia* 85:301–303.

ELMHAGEN, B., TANNERFELDT, M. & ANGERBJOERN, A. 2002. Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology* 80:1274–1285.

ESTES, R. D. 1991. *The behavior guide to African mammals*. University of California Press, Berkeley. 611 pp.

FERRAR, A. A. & WALKER, B. H. 1974. An analysis of herbivore–habitat relationships in Kyle National park, Rhodesia. *Journal of the South African Wildlife Management Association* 4:137–147.

FIELD, C. R. & LAWS, R. M. 1970. The distribution of the larger herbivores in the Queen Elizabeth National Park,Uganda. *Journal of Applied Ecology* 7:273–294.

FLECKER, A. S. 1997. Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. *Journal of the North American Benthological Society* 16:286–295.

FRANZ, R., HUMMEL, J., MULLER, D. W. H., BAUERT, M., HATT, J.-M. & CLAUSS, M. 2011. Herbivorous reptiles and body mass: effects on food intake, digesta retention, digestibility and gut capacity, and a comparison with mammals. *Comparative Biochemistry and Physiology* 158:94–101.

FRETWELL, S. D. & LUCAS, H. L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. 1. Theoretical development. *Acta Biotheoretica* 14:16–36.

FRITZ, H., DE GARINE-WICHATITSKY, M. & LETESSIER, G. 1996. Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. *Journal of Applied Ecology* 33:589–598.

GALLIVAN, G. J. & HORAK, I. G. 1997. Body size and habitat as determinants of tick infestations of wild ungulates in South Africa. *South African Journal of Wildlife Research* 27:63–70.

GRAND, T. C. 2002. Alternative forms of competition and predation dramatically affect habitat selection under foraging-predation-risk trade-offs. *Behavioural Ecology* 13:280–290.

GRUNOW, J. O. 1980. Feed and habitat preferences among some large herbivores on African veld. *Proceedings of the Grassland Society of South Africa* 15:141–146.

HART, B. L., HART, L. A. & MOORING, M. S. 1990. Differential foraging of oxpeckers on impala in comparison with sympatric antelope species. *African Journal of Ecology* 28:240–249.

HUNGATE, R. E., PHILLIPS, G. D., MCGREGOR, A., HUNGATE, D. P. & BUECHNER, H. K. 1959. Microbial fermentation in certain animals. *Science* 130:1192–1194.

ILLIUS, A. W. & GORDON, I. J. 1992. Modelling the nutritional ecology of ungulate herbivores – evolution of body size and competitive interactions. *Oecologia* 89:428–434.

IVLEV, V. S. 1961. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven. 302 pp.

JARMAN, P. J. 1972. Seasonal distribution of large mammal populations in the unflooded Middle Zambezi Valley. *Journal of Applied Ecology* 9:283–299.

JARMAN, P. J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour* 48:215–267.

JONES, M. E. & BARMUTA, L. A. 2000. Niche differentiation among sympatric Australian dasyurid carnivores. *Journal of Mammalogy* 81:434–447.

KREBS, J. R. 1999. *Ecological methodology*. Benjamin/Cummings, Menlo Park. 620 pp.

K.Z.N.WILDLIFE. 2008. *Population Estimates for Hluhluwe-iMfolozi Park*. K.Z.N. Wildlife, Hluhluwe. 14 pp.

LAMPREY, H. F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *East African Wildlife Journal* 1:63–92.

LAWS, R. M. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21:1–15.

LECHOWICZ, M. J. 1982. The sampling characteristics of electivity indices. *Oecologia* 52:22–30.

LOVERIDGE, A. J. & MACDONALD, D. W. 2003. Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). *Journal of Zoology* 259:143–153.

MACARTHUR, R. H. & PIANKA, E. R. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.

MADHUSUDAN, M. D. 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology* 41:858–869.

MAKHABU, S. W. 2005. Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana. *Journal of Tropical Ecology* 21:641–649.

MANLY, B. F. J., MILLER, P. & COOK, L. M. 1972. Analysis of a selective predation experiment. *American Naturalist* 106:719–736.

MORISITA, M. 1959. Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science Kyushu University series E* 3:65–80.

MOSUGELO, D., MOE, S. R., RINGROSE, S. & NELLEMAN, C. 2002. Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *African Journal of Ecology* 40:232–240.

MUCINA, L. & RUTHERFORD, M. C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria. 807 pp.

NAPIER BAX, P. & SHELDRICK, D. L. W. 1963. Some preliminary observations on the food of elephant in the Tsavo Royal National Park (East) of Kenya. *East African Wildlife Journal* 1:40–53.

O'KANE, C. A. J., DUFFY, K. J., PAGE, B. R. & MACDONALD, D. W. 2011. Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers. *Journal of Tropical Ecology* 27:249–258.

OLOFSSON, J., HULME, P. E., OKSANEN, L. & SUOMINEN, O. 2004. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* 106:324–334.

OLOO, T. W., BRETT, R. & YOUNG, T. P. 1994. Seasonal variation in the feeding ecology of the black rhinoceros (*Diceros bicornis* L.) in Laikipia, Kenya. *African Journal of Ecology* 32:142–157.

OWEN-SMITH, N. 1988. *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge. 300 pp.

PELLEW, R. A. 1984. The feeding ecology of a selective browser, the giraffe (*Giraffa camelopardalis*). *Journal of Zoology* (*London*) 202: 57–81.

PIANKA, E. R. 1972. *r* and *K*-selection or *b* and *d* selection? *American Naturalist* 106:581–588.

PIANKA, E. R. 1976. Competition and niche theory. Pp. 114–141 in May, R. M. (ed.). *Theoretical ecology. principles and applications*. Blackwell Scientific Publications, Oxford.

POOLE, J. H., PAYNE, K., LANGBAUER, W. R. & MOSS, C. J. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology* 22:385–392.

POOLEY, E. S. 2003. *The complete field guide to trees of Natal, Zululand & Transkei*. Natal Flora Publications Trust, Durban. 512 pp.

ROSENZWEIG, M. L. 1981. A theory of habitat selection. *Ecology* 62:327–335.

SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.

SCHOLES, R. J. & MENNELL, K. G. 2008. *Elephant management: a scientific assessment for South Africa*. Wits University Press, Johannesburg. 645 pp.

SCHOOLEY, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. *Journal of Wildlife Management* 58:367–374.

SIMPSON, C. D. & COWRIE, D. 1967. The seasonal distribution of kudu *Tragelaphus strepsiceros* Pallas on a southern lowveld ranch in Rhodesia. *Arnoldia* 3:1–13.

STEPHENS, D. W. & KREBS, J. R. 1986. *Foraging theory*. Princeton University Press, Princeton. 262 pp.

TATMAN, S. C., STEVENS-WOOD, B. & SMITH, V. B. T. 2000. Ranging behaviour and habitat usage in black rhinoceros *Diceros bicornis*, in a Kenyan sanctuary. *African Journal of Ecology* 38:163–172.

VAN HOVEN, W., PRINS, R. A. & LANKHORST, A. 1981. Fermentative digestion in the African elephant. *South African Journal of Wildlife Research* 11:78–86.

WALLACE, R. K. 1981. An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society* 110:72–76.

WECKERLY, F. W. 2009. Allometric scaling of rumen-reticulum capacity in white-tailed deer. *Journal of Zoology* 280:41–48.

WHATELEY, A. & PORTER, R. N. 1983. The woody vegetation communities of the Hluhluwe-Corridor-Umfolozi Game Reserve Complex. *Bothalia* 14:745–758.

WITTEMYER, G., GETZ, W. M., VOLLRATH, F. & DOUGLAS-HAMILTON, I. 2007. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology* 61:1919–1931.

WOLDA, H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50:296–302.