What grass characteristics drive large herbivore feeding patch selection? A case study from a South African grassland protected area

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Abstract

The coexistence of a large herbivore community depends on the degree of overlap in the resource used by the different species composing it. We investigated the role of grass greenness, height, biomass and feeding patch status on feeding patch selection by ruminant black and blue wildebeest (*Connochaetes gnu*, *C. taurinus*), red hartebeest (*Alcelaphus buselaphus*) and non-ruminant plains zebra (*Equus quagga*) in a protected grassland in South Africa. Selection by ruminants was associated with grass greenness and grass height, <10 cm for black and blue wildebeest, and >11 cm for red hartebeest. The non-ruminant zebra were more generalist but selected for wetlands in all seasons, as did red hartebeest and blue wildebeest. Each species modified its behaviour during the late dry season by searching more for biomass or accepting grass that was less green or longer. The presence of burnt patches did not affect patch selection by any study species. Thus, large herbivore resource use showed strong seasonal adaptations, wetlands were important for sustaining sympatric species in the study area, and none of the species used the exact same combination of resources.

Keywords: black wildebeest; blue wildebeest; plains zebra; red hartebeest; wetlands.

Introduction

Resource use by large herbivore is affected by forage quality, biomass and distribution (Sinclair et al. 1985; Bailey et al. 1996), which in turn interact in shaping large herbivore resource selection across different spatial and temporal scales (Senft et al. 1987; Bailey et al. 1996). Within a feeding patch (i.e. a cluster of feeding stations close enough to be reached by an herbivore during a feeding bout; Bailey et al. 1996) grass characteristics affect the amount of time a grazer spends in each patch and the moving rate between patches (Senft et al. 1987; Bailey et al. 1996; Owen-Smith 2002). In addition, the presence of competing species could influence the patch use behaviour of an herbivore. This is because two species cannot use the same set of resources at the same time (competitive exclusion principle, Schwartz and Ellis 1981; Day and Young 2004), thus when two coexisting species use a very similar resource along one niche dimension, they tend to differ along another (Pommerening and Grabarnik 2019).

To maximize energy, large herbivores start a feeding bout by selecting the best plants or plant parts from an accessible feeding patch (O’Reagain and Schwartz 1995; Bailey et al. 1996). They would exploit the feeding patch until its forage intake rate, which depends on quality and biomass of forage available, decreases below the level of the surrounding feeding patches (Charnov 1976). At this point, grazers would move to a neighbouring feeding patch that allow for the highest available forage intake rate (Senft et al. 1987; O’Reagain and Schwartz 1995). Forage characteristics, and consequent herbivore behavioural responses, vary seasonally. As grasses mature, the cell walls of leaves lignify and increase in fibre content, while decreasing in protein content (Meissner 1997). In the late dry season, grass quality is at its lowest and most of the grass has senesced (Owen-Smith 2002). During this period, the scarcity of proteins in forage may represent a serious constraint to large herbivore survival. Thus, grazers adapt their foraging behaviour to maximise forage energy intake (Moe et al. 1990) in different ways. They can allocate more time to foraging to compensate for the decreased grass quality (Demment and Van Soest 1985), widen their acceptance for grass species by including less palatable species or grasses of lower quality (Casebeer and Koss 1970; Owen-Smith 1994), or increase the use of key resources, i.e. resources available during a limiting period that can contribute to sustaining herbivore populations (Owen-Smith 2002). Different foraging adaptations lead to species-specific differences in resource selection across seasons.

Fire has often been used to alleviate nutritional stress for large grazers during the dry season (Moe et al. 1990; Gureja and Owen-Smith 2002). Indeed, fire destroys layers of low quality grass and stimulates the sprouting of new high quality grass (Moe et al. 1990; Hobbs et al. 1991), which results in burnt areas offering grass of higher quality than un-burnt areas (Archibald and Bond 2004). This makes burnt areas a key resource to grazers during the dry season. Several large grazers (including blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*)) are known to predominantly use burnt areas when available (Tomor and Owen-Smith 2002; Archibald and Bond 2004), thus improving the quality of their diet at a time when overall forage quality is relatively low (Hobbs and Spowart 1984; Parrini and Owen-Smith 2010). However, the presence of burnt areas in the dry season may not be enough to sustain all species present in an area. Because many species are simultaneously attracted to burnt feeding patches (Archibald and Bond 2004), competition can arise if broad-muzzled short-grass specialists, like blue and black wildebeest (*Connochaetes gnu*) keep the regrowth too short for tall-grass specialists to be able to exploit the burnt area (Gureja and Owen-Smith 2002). However, tall-grass specialists with narrow muzzles, such as red hartebeest (*Alcelaphus buselaphus*) (Janis and Ehrhardt 1988), could benefit over competitors by using patch types that offer tall grass, such as wetlands. Wetlands have higher plant productivity than dry-lands and offer water and nutrients in abundance (Thompson and Polet 2000). In addition, greenness and water content of dry-land vegetation decline considerably during the dry season, while remaining relatively constant in wetlands (Fynn et al. 2015), making them the best available source of tall grass of high quality by the late dry season (Thompson and Polet 2000). Several large herbivore species are known to use dry vegetation types (i.e. grasslands, woodlands) during the wet season and gradually increase the use of wetlands as the dry season progresses (Bell 1971; Parrini and Owen-Smith 2010; Macandza et al. 2012).

Resource selection by large herbivore does not only vary with season, but also depends on their digestive adaptations. Non-ruminants such as zebra have a fast passage rate of forage through the gut, allowing them to forage on high quantities of low quality grass and to be more generalist (Demment and Van Soest 1985; Duncan et al. 1990). On the other hand, ruminants rely on grass of high quality, due to the longer digestive process, which prevents them to ingest high quantities of forage (Demment and Van Soest 1985; Duncan et al. 1990). Due to these different digestion mechanisms, ruminants and non-ruminants should be able to avoid competition by selecting for different forage characteristics.

We investigated the role of grass quality, biomass, height and feeding patch status (burnt, un-burnt or wetland) on feeding patch selection by a sympatric guild of grazers inhabiting a fenced grassland reserve. We also assessed how selection varied by season and different vegetation communities of the study area (open grassland and wooded grassland). We expected ruminants to use feeding patches offering high quality grass, with blue and black wildebeest selecting short (< 10 cm) grass based on their broad muzzles. Red hartebeest were expected to prefer medium to tall grass (> 11 cm) because of their narrow muzzle (Janis and Ehrhardt 1988). We also expected zebra to use a wider variety of feeding patches, due to their non-ruminant nature, compared to ruminants. We predicted season to affect grass quality, biomass and feeding patch status in shaping feeding patch selection by each species. During the limiting dry season, ruminants would prefer key resources based on grass height preferences, i.e. wetlands for red hartebeest, and burnt patches for wildebeest; non-ruminant zebra would compensate for the reduced grass quality by ingesting more forage (Demment and Van Soest 1985; Duncan et al. 1990), and thus select for feeding patches offering more biomass than in the wet season. The different vegetation present in the two regions of the study area, namely the open grassland and the wooded grassland region, had a leading effect in large herbivore resource use at the landscape scale in the same study area (Mariotti et al. unpublished data). However, we did not expect the region to have an effect on herbivore feeding patch use, as the main difference between regions is the abundance of trees. We foresaw seasons and forage characteristics to be more important at the feeding patch spatial scale.

Materials and Methods

Study area

The study occurred at Telperion and Ezemvelo nature reserves which are fenced protected areas lying on the edge of the central inland plateau of northern South Africa (25˚38’ S - 25˚45’ S, 28˚55’ E-29˚03’ E)(Coetzee 2012). Perennial water is supplied by the Wilge River, supplemented by several temporary dams and streams. The Wilge River, the biggest water source in the area, runs from south to north dividing the study area into two regions: open grassland on the western side and wooded grassland on the eastern side. The mean annual rainfall is ca. 625 mm (Swanepoel and Bredenkamp 2007), with a wet season extending from November to March (ca. 462 mm of rain on average), and a dry season from April to October (ca. 163 mm of rain on average) (Swanepoel and Bredenkamp 2007). During the study period rainfall was lower than average: 105 mm of rain in the wet season 2017-2018, and 50 mm in the dry season 2018 (Ezemvelo Nature Reserve unpublished data). The vegetation in the area is classified as Rand Highveld Grassland and Loskop Mountain Bushveld (Mucina et al. 2005). The dominant grass species in the area are *Eragrostis curvula, Elionurus muticus* and *Setaria sphacelata* (Swanepoel and Bredenkamp 2007). The wetland is dominated by *Aristida junciformis, Eragrostis nindensis, Imperata cylindrica* and *Paspalum urvillei* (Helm 2007). The study area hosts more than 20 herbivores species, including large mammals such as blesbuck (*Damaliscus pygargus phillipsi*), common eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*), and the focal species black and blue wildebeest, red hartebeest, and plains zebra. Several small carnivores inhabit the study area, such as aardwolf (*Proteles cristata*), African civet (*Civettictis civetta*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) (Helm 2007). Leopards (*Panthera pardus*) have been seen moving through the study area, but no large carnivore is permanent.

Data collection

Data were collected from September 2017 to August 2018. We identified four seasons based on the Normalized Difference Vegetation Index (NDVI, a proxy for vegetation quality and primary productivity) and rainfall patterns: the late dry season (September-October 2017), the wet season (February 2018), the early dry season (May 2018) and the mid dry season (August 2018). In each season, we collected data over a period of three weeks, driving all the established roads of the study area twice per season. We searched for the focal species in the early morning and late afternoon, during peak grazing times (Gureja and Owen-Smith 2002). Each time we encountered a foraging individual or group of the study species, we recorded species, season, region of the study area, our geographic position (Garmin Montana 600 GPS), and the bearing and distance to the animals (military compass and Leica Rangemaster 1600B 7.0X rangefinder). We later calculated herbivore locations from the GPS location, bearing and distance. We estimated our accuracy to be ±5 m, tested in the field using a known fixed landmark. Herds of single species were considered as one sighting and data were collected for the foraging individual closest to the centre of the group.

Later the same day or the following day, we visited the calculated locations on foot using the GPS, to collect data on feeding patch use. We defined the feeding patch at each calculated location as a used feeding patch. We placed five 0.5 m^2 quadrats: one at the calculated location and four around it, one per cardinal direction, spaced 4 m from the central quadrat (adapted from Owen-Smith et al. 2013). In each quadrat we recorded: 1) grass height divided into 4 classes, namely: very short (<5 cm), short (6-10 cm), medium (11-30 cm) and tall (>30 cm); 2) the proportion of green leaves using Walker's (1976) eight-point scale (0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99% and 100% green); 3) standing crop biomass using a disk pasture meter (Zambatis et al. 2006; Arena et al. 2015); 4) the feeding patch status as ‘un-burnt’, ‘burnt’ or ‘wetland’. To estimate resource availability, we chose another random feeding patch for each used patch, 100 m away in a random direction. We conducted the same measurements in the used and available feeding patches.

Data analysis

To analyse feeding patch selection by the different ungulate species we fitted 19 generalized linear mixed models (GLMM) with a binomial error distribution. The response variable was ‘used’ versus ‘available’, with the mixed effect represented by the five quadrats in each feeding patch. We conducted the analysis using the ‘lme4 package’ (Bates et al. 2014) in R version 3.5.1 (R Development Core Team 2018). We tested six independent factors, five of which were categorical (grass greenness, grass height, feeding patch status, region and season) and one continuous (standing crop biomass). Interactions of season and region with all the other variables were also tested. When there was multicollinearity between different levels of a categorical variable, we merged them to create new combined levels. Thus, grass greenness in black and blue wildebeest analyses had four classes: <10%, 11-50%, 51-90%, and 91-100%, while grass height in red hartebeest and zebra analyses had three classes: <5 cm, 6-10 cm, and >11cm.

We conducted model selection using Akaike’s Information Criterion, corrected for small sample bias (AICc) (Anderson 2008), using the ‘AICcmodavg package’ (Mazerolle and Mazerolle 2017). The model with the smallest AICc value was considered as the best model (Anderson 2008). For the best model, we calculated the predicted logit and associated 95% confidence intervals for single categorical factors and the predicted degree of use expressed as the relative probability and associated 95% confidence intervals for interactions and the continuous variable. Results of categorical variables are presented as referred to the smallest category level of each variable. In plots of categorical variables, if confidence intervals of a category did not cross the reference category level, we interpreted there as a significant difference between the two levels (Godvik et al. 2009). Predictions and plots were made with the ‘jtools’ package (Long and Long 2017).

Results

We sampled 1544 feeding patches over four seasons, 328 in the late dry season, 416 in the wet season, 392 in the early dry season and 408 in the mid dry season. The total number of quadrats, from both used and available feeding patches, amounted to 1230 for black wildebeest, 2900 for blue

Table 1: AICc model results of the 3 best predictive models for each species probability of presence at feeding patch scale, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

#	Model	k	AICc	ΔAICc	w_i
Black wildebeest *n*(1230)					
1	Greenness + height + status + biomass*season	18	1477.92	0	0.73
2	Greenness + status + biomass + height*season	24	1479.89	1.97	0.27
3	Height + biomass + status + greenness*season	24	1492.29	14.37	<0.01
Blue wildebeest n(2900)					
1	Greenness + status + biomass + height*season	24	3044.21	0	1
2	Greenness + height + status + biomass*season	18	3079.62	35.41	<0.01
3	Height + biomass + status + greenness*season	24	3227.89	183.68	<0.01
Red hartebeest *n*(580)					
1	Greenness + height + status + biomass*season	19	774.11	0	0.98
2	Greenness + height + biomass + status*season	19	781.66	7.54	0.02
3	Greenness + status + biomass + height*season	22	790.02	15.9	<0.01
Zebra *n*(3010)					
1	Height + biomass + status + greenness*season	23	3998.13	0	1
2	Greenness + height + status + biomass*season	17	4027.11	28.97	<0.01
3	Greenness + height + biomass + status*section	14	4027.17	29.04	<0.01

= model identification number; *n* = no. observation; k = number of parameter in the model; AICc = Akaike's Information Criterion corrected for small-sample bias; ΔAICc = difference between model AICc and that of the lowest model; *wi* = model probability (Akaike weight); * = interaction.

wildebeest, 580 for red hartebeest and 3010 for zebra. For all species, the most parsimonious model included feeding patch status, grass greenness, grass height, biomass, and season in interaction with: biomass for black wildebeest and red hartebeest, height for blue wildebeest, and greenness for zebra (Table 1).

Black wildebeest

Black wildebeest selection for feeding patches was positively related to feeding patch greenness, with a preference for the greenest class (91-100%) over the least green one (log-odds = 1.19 ± 0.54) (Fig. 1). Black wildebeest avoided long grass and selected grasses <10 cm (Fig. 2). In addition, they selected burnt feeding patches less than the reference category ‘un-burnt’ (log-odds = -1.00 ± 0.64) (Fig. 3). The effect of grass biomass on feeding patch selection by black wildebeest depended on season. Indeed, black wildebeest selected patches with greater-than-average biomass in the late dry and wet seasons, but less-than-average biomass during the early dry and mid dry seasons (Fig. 4).

Blue wildebeest

Similar to black wildebeest, blue wildebeest selection for feeding patches increased with the greenness of the feeding patch (Fig. 1). Blue wildebeest selected burnt feeding patches less than un-burnt ones (log-odds = -0.72 ± 0.51) and selected wetlands significantly more than un-burnt patches (log-odds = 2.05 ± 1.71) (Fig. 3). Moreover, blue wildebeest favoured feeding patches offering less-than-average crop biomass (Fig. 5). The effect of grass height on feeding patch selection by blue wildebeest depended on season. In the late dry and wet seasons, blue wildebeest did not select a particular height class, but during the early dry and mid dry seasons, they favoured very short and short grass much more than medium and tall grass, and more than any height class in the other seasons (Fig. 4).

Red hartebeest

Red hartebeest avoided feeding patches with a greenness value <10% (Fig. 1) and selected grass >10 cm more than grass <5 cm (log-odds = 1.29 ± 0.94) (Fig. 2). They favoured wetlands slightly compared to un-burnt feeding patches and did not appear to distinguish between burnt and un-burnt feeding patches (Fig. 3). The effect of standing crop biomass depended on season. During the late dry season, red hartebeest selected feeding patches with greater-than-average biomass more than they did in any other season (Fig. 4).

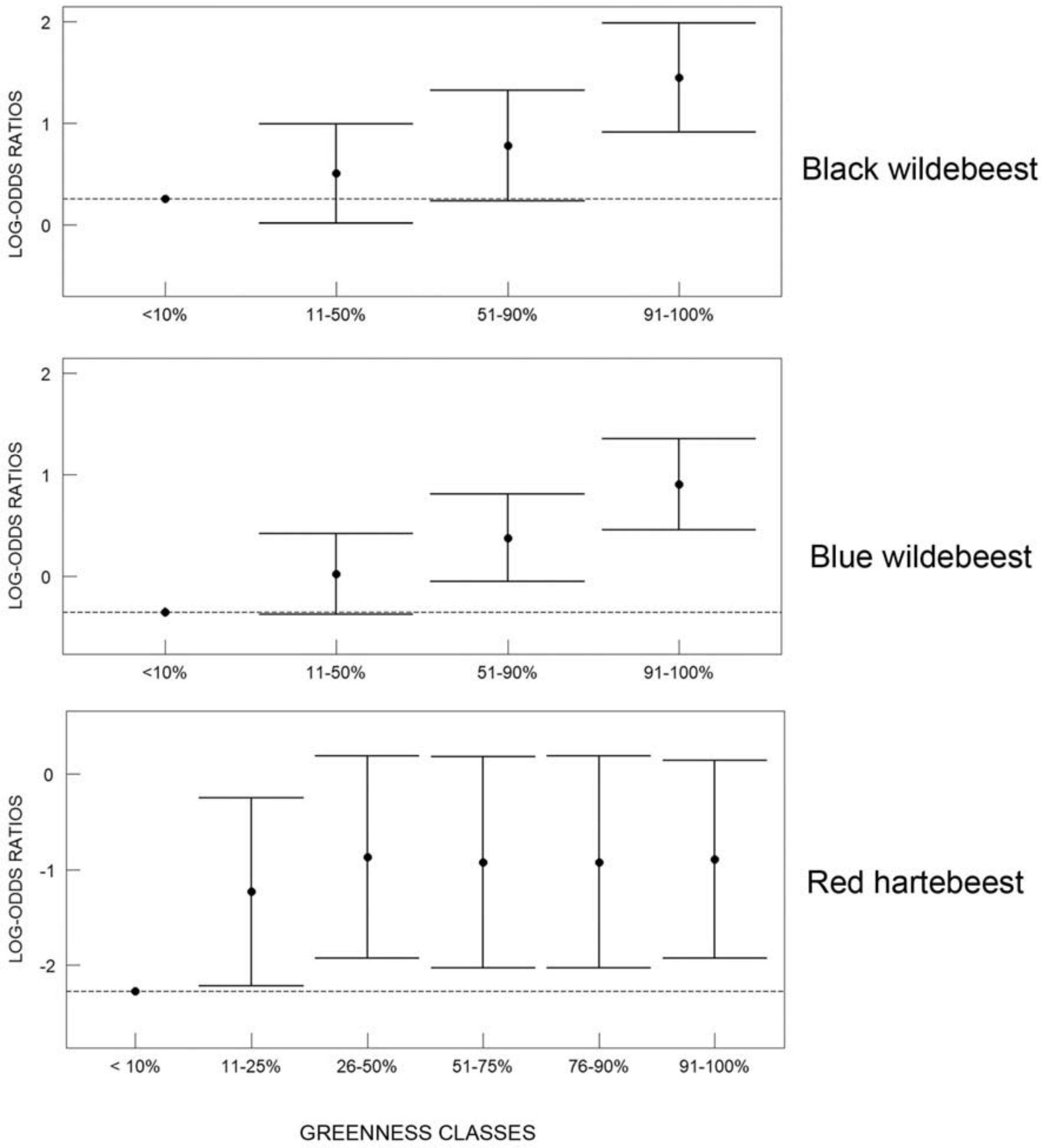

Figure 1: Predicted estimates (± 95% confidence interval) for feeding patch selection by black wildebeest, blue wildebeest and red hartebeest for grass greenness at telperion and Ezemvelo nature reserves, South Africa, 2018. the dashed line indicates the reference level: '<10%'

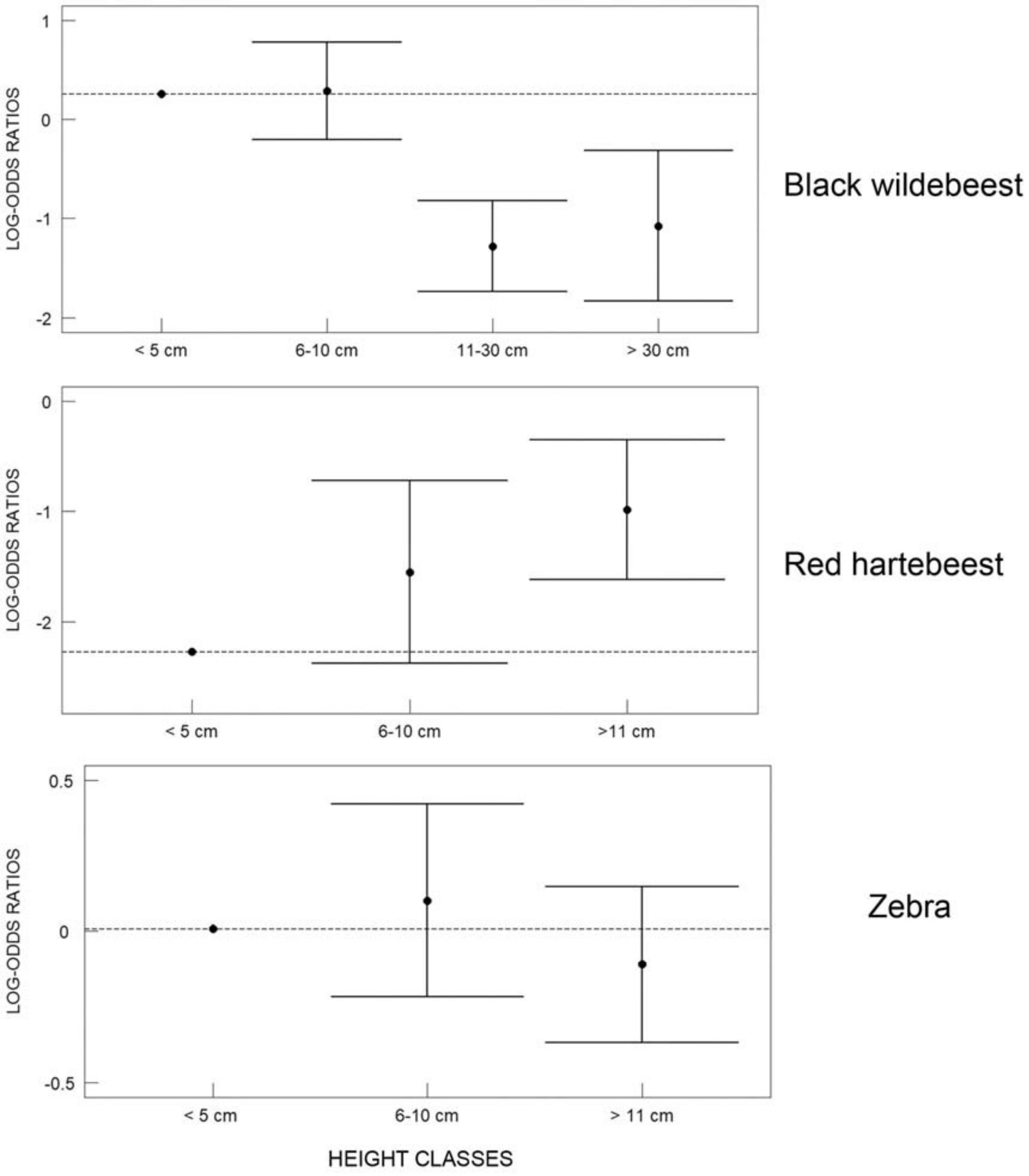

Figure 2: Predicted estimates (± 95% confidence interval) for feeding patch selection by black wildebeest, red hartebeest and zebra for grass height at telperion and Ezemvelo nature reserves, South Africa, 2018. the dashed line indicates the reference level: '<5 cm'

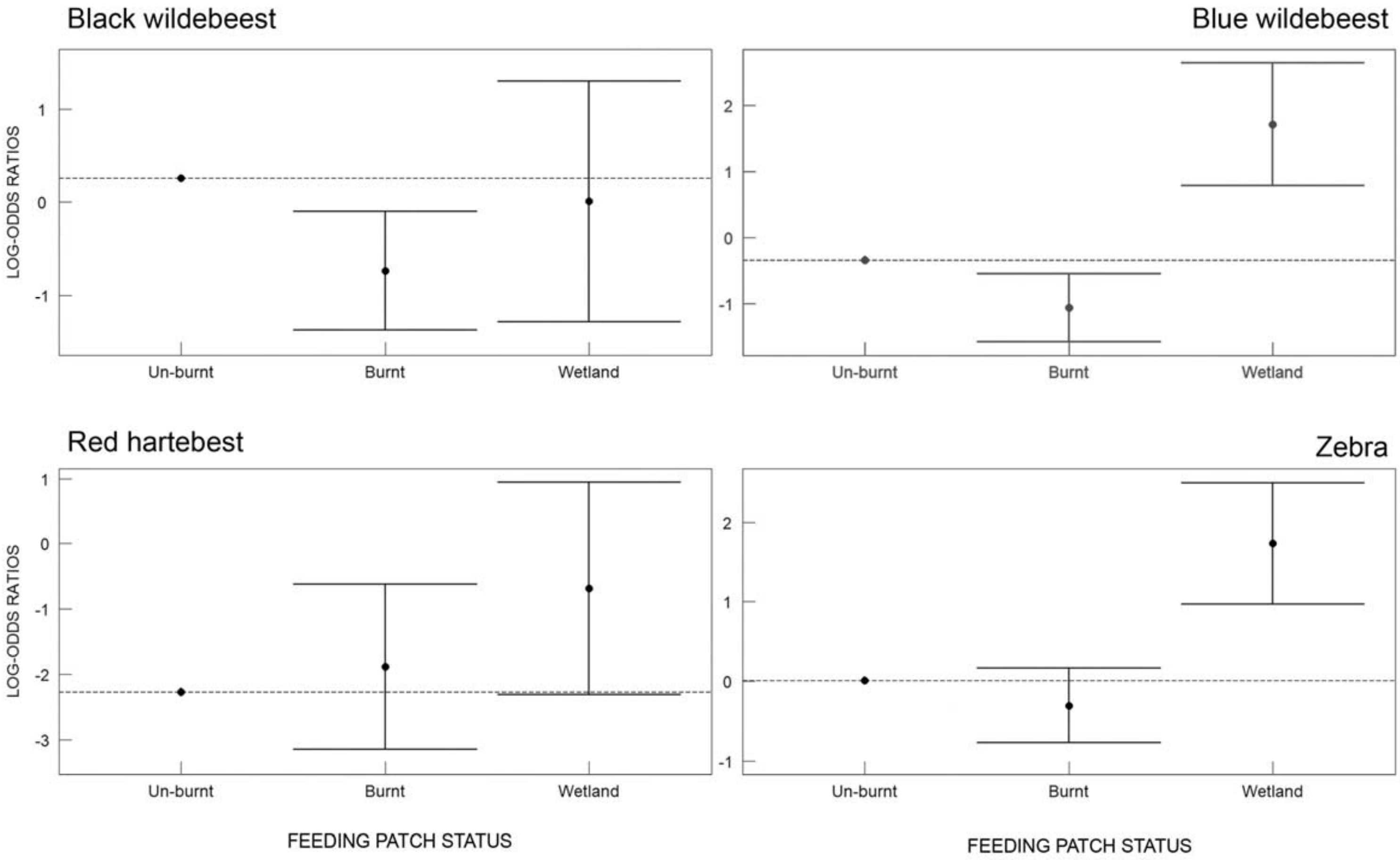

Figure 3: Predicted estimates (± 95% confidence interval) for feeding patch selection by black wildebeest, blue wildebeest, red hartebeest and zebra for feeding patch status at telperion and Ezemvelo nature reserves, South Africa, 2018. the dashed line indicates the reference level: 'Unburnt'

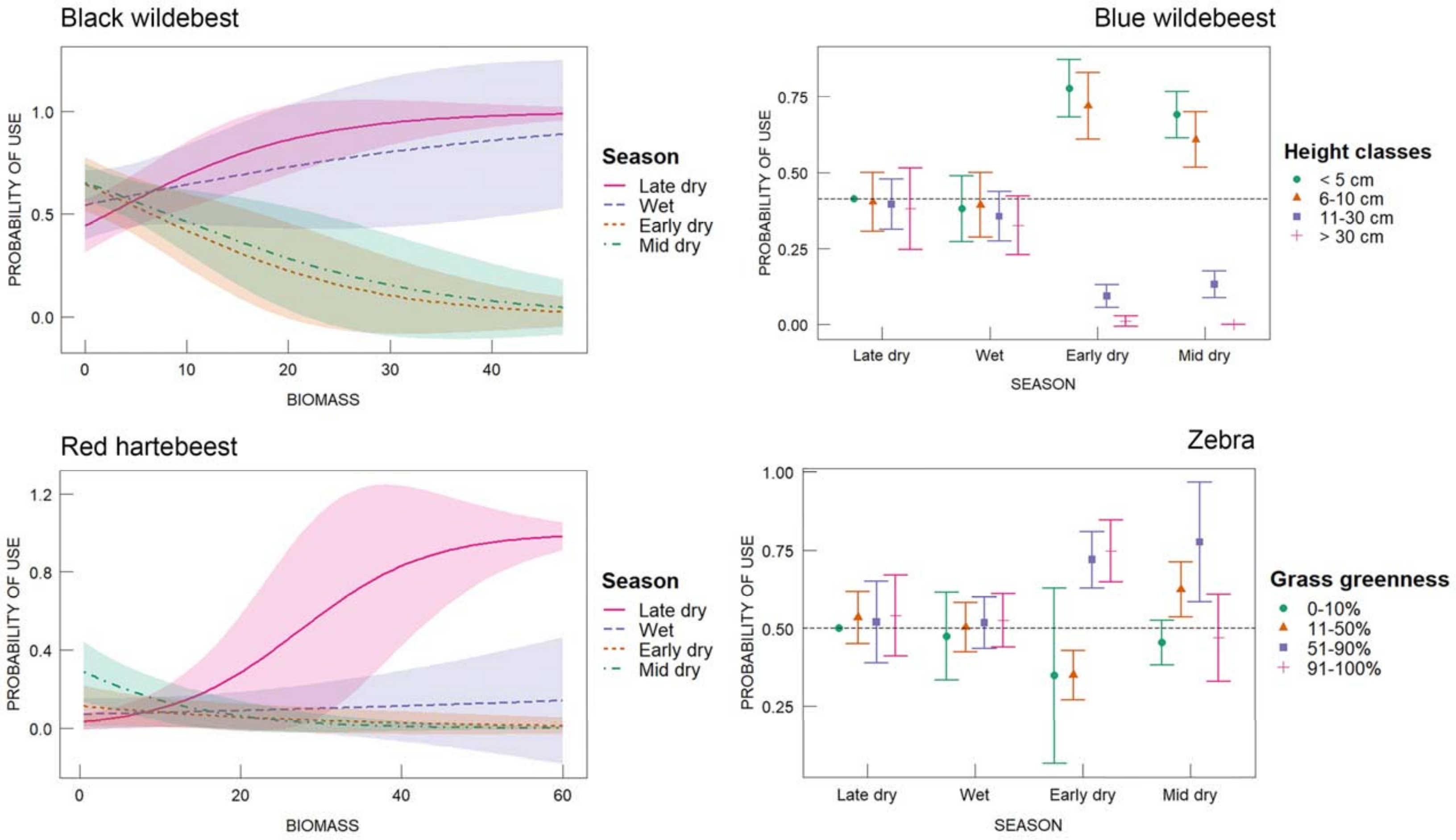

Figure 4: Predicted probability for feeding patch selection by each species, based on seasons at telperion and Ezemvelo nature reserves, South Africa, 2018. Predicted probability (± 95% confidence interval) for feeding patch selection by black wildebeest and red hartebeest for biomass over season. Predicted probability (± 95% confidence interval) for feeding patch selection by blue wildebeest for grass height over seasons, and by zebra for grass greenness over season. the dashed line indicates the reference level: '<5 cm' in late dry season for blue wildebeest and '0–10%' in late dry season for zebra

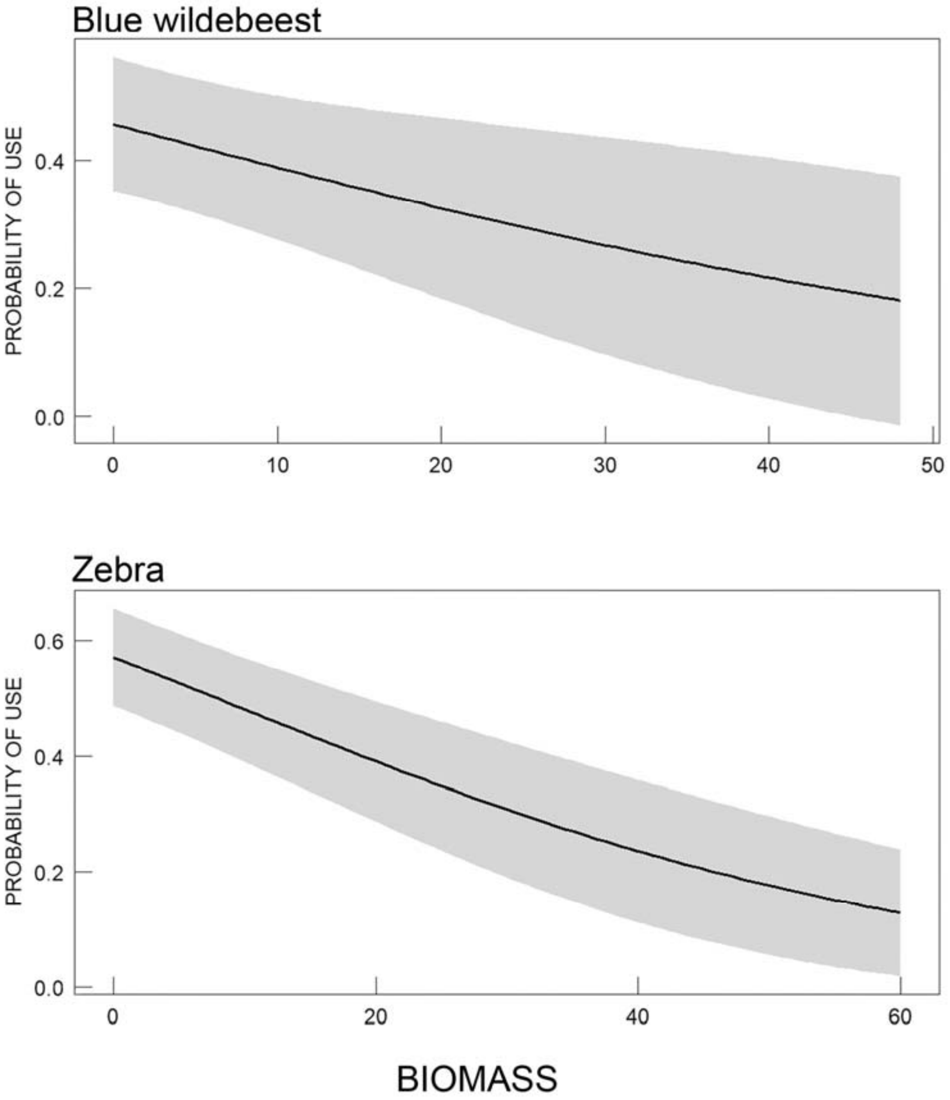

Figure 5: Predicted probability (± 95% confidence interval) for feeding patch selection by blue wildebeest and zebra for biomass at telperion and Ezemvelo nature reserves, South Africa, 2018

Zebra

Zebra selected wetlands significantly more than burnt and un-burnt patches (log-odds = 2.03 ± 1.53) (Fig. 3), and they selected feeding patches with less-than-average grass biomass (Fig. 5). Moreover, zebra selection for grass greenness depended on season: they did not show selection for greenness during the late dry and wet seasons (Fig. 4), but in the early dry season, zebra used the greenest classes of grass over the two least green. Furthermore, they selected grass of intermediate greenness (11-90%) more than both the greenest and the least green classes, during the mid dry season (Fig. 4). Grass height was part of the best model, but there was no evidence of selection based on height class of grass (Fig. 2).

Discussion

Our findings suggest that our study species partitioned feeding patch use with respect to some characteristics but overlapped with respect to others. Particularly interesting is the fact that blue wildebeest resource selection overlapped not only with black wildebeest, but also with zebra. As expected, feeding patch selection by ruminants was positively related to greenness, while zebra was less selective for greenness and more generalist. All species responded to seasonal changes: red hartebeest and black wildebeest modified their selection for grass biomass, blue wildebeest increased the use of short grass through the dry season and zebra selected more for greenness in the early and middle part of the dry season. Surprisingly, red hartebeest selected wetlands throughout the year, and black and blue wildebeest did not select burnt feeding patches.

Ruminant selection for very green feeding patches is common among large herbivores (Bergman et al. 2001; Odadi et al. 2011). In the same way, selection of grass height by all species followed what would be predicted based on their muzzle morphology (Owaga 1975; Janis and Ehrhardt 1988; Helm 2007; Arsenault and Owen-Smith 2008). Red hartebeest selected grass >11 cm, black wildebeest selected grass <10 cm and zebra did not select for any particular height of grass. Both blue wildebeest and zebra selected feeding patches with less-than-average biomass throughout the year. Moreover, blue wildebeest selected lower-biomass patches during the wet season than during the rest of the year, as also found in the same study area by Helm (2007).

Surprisingly, none of the species selected burnt feeding patches in any season, and black and blue wildebeest appeared even to avoid them. This suggests that, at the feeding patch scale, other forage characteristics were more important in feeding patch selection by wildebeest than being burnt.

Indeed, both wildebeest species favoured large burnt areas at a broader spatial level (Mariotti et al. unpublished data). The burnt feeding patches selected by wildebeest were often well inside the burnt area (>100 m form the closest un-burnt feeding patch), such that both used and available patches would have been recorded as ‘burnt’. Moreover, wildebeest frequently foraged in un-burnt feeding patches close to burnt ones (pers. obs.), in which case we could have chosen an available feeding patch inside the burnt area, resulting in wildebeest appearing to avoid burnt feeding patches. On the other hand, each species except for blue wildebeest favoured wetlands in every season. Wetlands often are sources of high quality grass and water, acting as a key resource and being attractive to herbivores (Parrini and Owen-Smith 2010; Fynn et al. 2015). Their use by three of the study species suggests that wetlands might have an important role in sustaining large herbivores in grassland-dominated environment. This strong selection for wetlands, even by species which we expected to rather use un-burnt patches (i.e. zebra) or burnt patches (i.e. blue wildebeest) may be favoured by the scarcity of rain during the study period.

Season had an important effect on the resource selection of all species, with the most interesting results being the different ways in which each species behaved during the late dry season. All the species modified their resource selection presumably to cope with the low quality of grass available in this season, and each species did it by widening their acceptance criteria.

Red hartebeest and black wildebeest selected feeding patches offering more biomass than in the other seasons. As grass greenness decreases in the dry season, these two species might have to increase the quantity of food ingested to satisfy their energetic needs (Day and Young 2004), with the result of selecting feeding patches with a higher biomass of forage compared to other seasons. Coke’s hartebeest (*Alcelaphus buselaphus cokii*), zebra and blue wildebeest, for example, prefer grass of both high biomass and greenness in the wet season, and they select for forage quantity in the dry season (Groom and Harris 2009). Groom and Harris (2009) affirmed that forage quantity is more important than forage quality in sustaining large herbivores in a resource-stressed environment, as was observed for red hartebeest and black wildebeest in the present study.

In contrast, blue wildebeest and zebra appeared to switch between low selectivity during the wet season, high selectivity in the early and late dry season, and no selectivity at the end of the dry season. Blue wildebeest selected grass <10 cm during the early and mid dry seasons, but showed no selection for height in the wet and late dry seasons; that is, blue wildebeest accepted medium to tall grass both when the quality was theoretically not limiting and when the quality was extremely limiting. A similar increase in grass height acceptance is common in the late dry season (Bell 1971; Arsenault and Owen-Smith 2008), but not during the wet season. This unexpected result may be due to the scarcity of precipitations experienced during the studied wet season: a quarter of the long-term mean. Because of it, the quality of forage could have been limiting even during the wet season, not allowing herbivores to be selective, but instead forcing them to forage on whatever was available.

In a similar way, zebra selected feeding patches of medium to high greenness during the early and mid dry seasons, but showed no particular selectivity for greenness in the wet season and late dry season. As the quality of grass decreased, zebra first became more selective for greenness but eventually started to forage on what was available. This behaviour is uncommon in literature, as zebras vary grass height and biomass selection with seasonal change (Bell 1971; Sinclair 1985) and can show selection for greenness only at the end of the dry season (Boyers 2011). This uncommon behaviour may be due to the peculiar characteristics of the study area. Indeed, available grass was on average taller than 11cm (Fig. 6) and rainfall was extremely low during the wet season. The eventual increased selection of taller grass by zebra during the late dry season may have been masked by the abundance of tall available grass. In addition, the wet season of 2018 was very dry, possibly explaining why both wildebeest and zebra behaviour was the same during the late dry and the wet season. Precipitations may have been too low for the vegetation to sprout, thus stretching the dry season. Consequently, grassland may have become greener only by the beginning of the next dry season, when blue wildebeest and zebra selected for height and greenness respectively, and black wildebeest and red hartebeest did not select for more biomass.

Feeding patch selection by blue wildebeest partially overlapped with patch selection by black wildebeest and zebra. Indeed, blue wildebeest selected for greenness and short grass, like black wildebeest, but they also favoured feeding patches with less biomass and wetlands, like zebra. Based on morphology, physiology and phylogeny, the very similar black and blue wildebeest should use very similar niches (Day and Young 2004). However, species using similar resources, i.e. overlapping along some niche dimensions, must partition in the use of another niche dimension to diminish the level of competition (Pommerening and Grabarnik 2019). Competition between black and blue wildebeest could be mitigated by the ability of blue wildebeest to use a wider set of resources. Indeed, black wildebeest are grassland specialists while blue wildebeest are common in a wider array of biomes (Codron and Brink 2007). Thus, blue wildebeest diet is likely more malleable, allowing them more

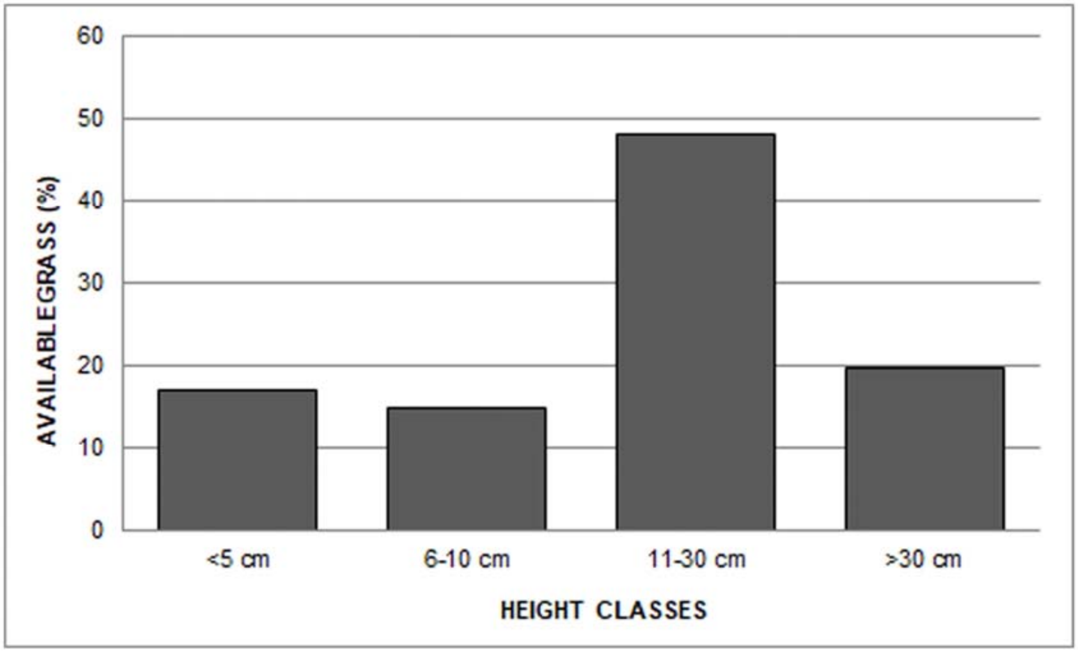

Figure 6: Percentage of availability of each class of grass height at telperion and Ezemvelo nature reserves, South Africa, 2018

flexible foraging compared to black wildebeest. In fact, the categorisation of blue wildebeest as specialist may not be accurate. For example, both blue wildebeest and zebras in Sabi-Sand Wiltuin reserve, South Africa, consumed grass species according to their availability, with the only difference being a shift in grass species acceptance between the dry and the wet season by blue wildebeest, a response that was not found in zebra (Ben-Shahar 1991). Ben-Shahar (1991) concluded that the definition of a species as generalist or specialist is highly influenced by the spatial and temporal scale of investigation. Shipley et al. (2009) suggested a more elastic definition of specialist and generalist: blue wildebeest could be facultative specialist, having the option of behaving as a generalist, while black wildebeest could be obligate specialist.

In conclusion, this study describes resource use and overlap of sympatric browsing herbivores at feeding patch scale, including black and blue wildebeest, which have seldom been studied together (Codron and Brink 2007; Helm 2007). In addition, this study highlights the critical importance of wetlands at this spatial scale in a grassland dominated landscape. Wetlands possibly are an essential key resource for grazers, especially during droughts which will be more frequent in the future with predicted climate change (Engelbrecht et al. 2015).

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