Environmental controls on African herbivore responses to landscapes of fear

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Abstract

Herbivores balance forage acquisition with the need to avoid predation, often leading to tradeoffs between forgoing resources to avoid areas of high predation risk, or tolerating increased risk in exchange for improved forage. The outcome of these decisions is likely to change with varying resource levels, with herbivores altering their response to predation risk across heterogeneous landscapes. Such contrasting responses will alter the strength of non-consumptive predation effects, but are poorly understood in multiple-predator/multiple-prey systems. We combined fine-scaled spatial information on two predator and 11 herbivore species with remotely-sensed measurements of forage quantity and vegetation structure to assess variation in herbivore response to predation risk with changing environmental context, herbivore body size, herbivore foraging strategy (browsers versus grazers), predator type (ambush versus coursing hunters) and group size across a South African savanna landscape. Medium-sized herbivore species were more likely to adjust their response to risk with a changing resource landscape: warthog, nyala and wildebeest tolerated increased long-term predator encounter risk in exchange for abundant (warthog and nyala) or preferred (wildebeest) forage, and nyala selected areas with higher visibility only in landscapes where food was abundant. Impala were more likely to be observed in areas of high visibility where wild dog risk was high. In addition, although buffalo did not avoid areas of high lion encounter risk, large buffalo groups were more

frequently observed in open areas where lion encounter risk was high, whereas small groups did not alter their space use across varying levels of risk. Our findings suggest that risk effects are not uniform across landscapes for medium-sized herbivores and large buffalo groups, instead varying with environmental context and leading to a dynamic landscape of fear. However, responses among these and other prey species were variable and not consistent, highlighting the complexities inherent to multi-predator/multi-prey systems.

Introduction

Herbivores are not evenly distributed across landscapes. Instead, individual animals choose to occupy some areas more frequently than others based on spatial and temporal variation in resources and risks. Herbivores need to find and consume sufficient food to meet nutritional requirements, while simultaneously avoiding being killed by predators (Houston et al. 1993, Sinclair and Arcese 1995, Anderson et al. 2010). These often-conflicting needs lead to tradeoffs between forage acquisition and tolerance of real or perceived predation risk, with herbivores inhabiting a resulting landscape of fear (Laundré et al. 2001, Gaynor et al. 2019). Accordingly, prey perceive the landscape as consisting of varying levels of risk and make decisions to either avoid risky areas and times or to tolerate increased risk in exchange for improved food availability (Hebblewhite and Merrill 2009, Riginos 2015). Such indirect effects of predation risk avoidance, or of increased antipredator behaviour in high-risk areas (e.g. vigilance), can have large effects on herbivore dynamics that can be even stronger than the direct (consumptive) effects of predation (Creel and Christianson 2008).

Antipredator behaviour amongst herbivores is almost always in the form of behavioural tradeoffs. Herbivores must balance activities such as foraging with those of vigilance and other antipredator behaviours, such that they might be expected to allocate more time to antipredator behaviour when risk is high and more to feeding when risk is low (Lima and Bednekoff 1999). The outcome of this balancing act depends not only on temporally varying levels of risk, but also on changing environmental conditions that dictate herbivore foraging needs (Hayward et al. 2015, Owen-Smith 2015, Lone et al. 2017). For example, mammalian herbivores in east Africa selected habitats with lower predation risk during normal rainfall years, but shifted into more dangerous, but nutritionally-rich, habitats during drought years when high quality food was in short supply over much of the landscape (Riginos 2015). Spatial variation in resource availability might similarly influence herbivore responses to risk, but is poorly understood relative to temporal variation, partly because most studies are limited in spatial scale and resolution, or are focused on investigating individual drivers of herbivore behaviour and/or distributions (Anderson et al. 2010). Moreover, although variation in resource–risk tradeoffs are relatively well established for invertebrates (Preisser et al. 2009, Matassa et al. 2016), limited empirical evidence is available for large vertebrates, especially at ecologically relevant landscape scales and in multiple-predator/multiple-prey systems (Montgomery et al. 2019).

The effects of predation risk also vary with predator and prey attributes. Prey are expected to respond more strongly to risk from ambush predators, which use predictable habitat features to stalk and ambush prey, than to coursing predators that are less predictable (Thaker et al. 2011). Attributes of the prey, such as body size and foraging strategy, also affect prey responses and are potentially even more important than predator attributes because they affect all aspects of prey response to risk (Creel 2011). Herbivores require more food and become increasingly difficult to capture and handle by predators as body size increases, with large-bodied herbivore populations regulated more by resource availability than predation (Hopcraft et al. 2010). In contrast, small-bodied herbivores require less food (being more sensitive to forage quality) and are vulnerable to a greater number of predators (Sinclair et al. 2003, Hopcraft et al. 2010). Small herbivores are therefore expected to be more responsive to predation risk (Hopcraft et al. 2012). Differences in herbivore foraging strategy also affect response strength. African savanna browsers were more responsive to predation risk from ambush-hunting lions *Panthera leo* than grazers because they were able to move away from woodland areas (where they forage) into open habitats when predation risk was high; grazers, however, foraged in open habitats already and could not make further spatial adjustments in response to increased risk (Valeix et al. 2009a). Similarly, prey defence strategies, such as running, hiding or group formation, can affect responses to risk. Smaller species might hide more often given their smaller size, whereas larger prey are more likely to flee (Jarman 1974, Brashares et al. 2000). Large species, particularly those with horns, sometimes rely on defence tactics to resist predators by attacking them (Tambling et al. 2012), and many herbivore species form groups in response to increased predation risk (Valeix et al. 2009b, Creel et al. 2014)

African ecosystems are of particular interest in predator–prey studies due to their inherent complexity resulting from diverse communities of predator and prey species. However, much of our understanding of vertebrate predator–prey dynamics is derived from studies on single predator–prey dyads in northern temperate zones (Montgomery et al. 2019, Say-Sallaz et al. 2019), which are increasingly found to differ from dynamics in African ecosystems (Owen-Smith 2015). Moreover, few studies anywhere, including in Africa, have attempted to capture the complexities of multiple-predator/multiple-prey communities, resulting in a simplified understanding of vertebrate predator–prey dynamics (Montgomery et al. 2019, Say-Sallaz et al. 2019).

Here, we aimed to understand how fine-scaled habitat selection of African herbivores varies in response to predation risk across savanna landscapes with differing forage availability during the late dry season when food is limited. We investigated variation in the spatial distribution of five grazers and six browsers of varying body size in response to predation risk from ambush (lions) and coursing (African wild dogs, *Lycaon pictus*) predators, while also accounting for group size effects. We expected smaller, more vulnerable herbivores to be more responsive to predation risk than larger herbivores whose distributions would be driven by forage quantity. Nested within this body size framework, we predicted weaker responses to predation risk in areas of greater forage quantity because herbivores would prioritize nutritional needs at this time of year (late dry season), tolerating increased risk in exchange for access to greater forage availability. Alternatively, herbivores could be expected to avoid risk more when forage was abundant because they could do so and still find sufficient forage in the surrounding landscape. In areas of limited forage, however,

herbivores would be required to prioritize food resources over risk avoidance. We also predicted stronger responses to risk from ambush predators (lions), particularly among browsers that were expected to be more common in areas of dense vegetation due to their foraging requirements, but to move out of these areas and be observed in more open locations in landscapes where lion predation risk was high.

Methods

Study area

We carried out our study in the 89 600 ha Hluhluwe-iMfolozi Park (HiP), South Africa (Fig. 1). The park consists mostly of undulating hills and savanna vegetation, with some forest and open grassland patches in the north. There is a wide range of elevation (60–580 m a.s.l.) and precipitation (650–1000 mm year^{-1}), with summer rainfall occurring primarily between October and April. The park is completely fenced and almost no artificial water is provided (Cromsigt et al. 2017). We studied the spatial distribution of five grazers (warthog *Phacochoerus africanus*, blue wildebeest *Connochaetes taurinus*, plains zebra *Equus quagga*, African buffalo *Syncerus caffer* and white rhinoceros *Ceratotherium simum*) and six browsers (red duiker *Cephalophus natalensis*, grey duiker *Sylvicapra grimmia*, impala *Aepyceros melampus* (although impala is a mixed-feeder, it is predominantly a browser during the dry season), nyala *Tragelaphus angasii*, kudu *Tragelaphus strepsiceros* and giraffe *Giraffa camelopardalis*) in response to risk of predation imposed by lions, wild dogs and habitat structure (measured as visibility) across environments varying in forage quantity over a ten week period (July to September 2014). These herbivore species represent substantial variation in body size (Table 1). Diet data from HiP indicate that lions consume all these species apart from red duiker, whereas wild dogs consume all apart from white rhinoceros, although impala and nyala comprise ~ 95% of recorded wild dog kills (Somers et al. 2017). The lion population at the time of the study was estimated at 110 individuals in 10 prides, rendering a density of 12.3 lions/100 km^2 (Ezemvelo KZN Wildlife unpubl.). An estimated 52 adult and yearling wild dogs were present in six packs, with a density of 5.8 adult and yearling wild dogs/100 km^2 (Ezemvelo KZN Wildlife unpubl.). An estimated 106 spotted hyena *Crocuta crocuta* were resident in the park in 2013 and 126 in 2015 (Ezemvelo KZN Wildlife unpubl.), 67 leopards *Panthera pardus* were estimated in 2014 (Somers et al. 2017) and six adult cheetah *Acinonyx jubatus* were known to be resident in December 2014 (Ezemvelo KZN Wildlife unpubl.). However, no accurate spatial data on spotted hyenas, leopards or cheetahs were available for use in this study. Lions and wild dogs together, however, contribute the majority of mammal herbivore mortality in HiP (> 80% of recorded carcasses, Supporting information) across a wide range of body sizes (Somers et al. 2017) and were thus expected to exert a detectable influence on the behaviour of most herbivores. Moreover, lions, spotted hyenas, leopards and cheetahs display significant spatial overlap in their ranges (Vanak et al. 2013, Darnell et al. 2014, Dröge et al. 2017, Green et al. 2019) and by including both ambush (lions) and cursorial (wild dogs) predators, we were able to measure herbivore responses to predators employing opposing hunting strategies.
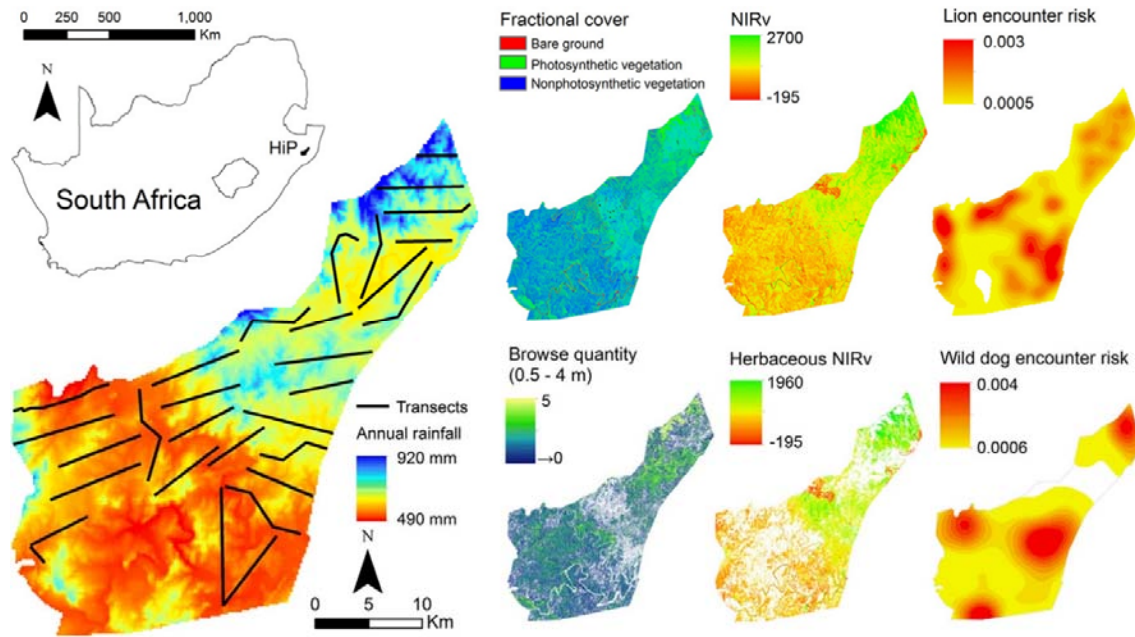
Figure 1. The spatial distribution of forage and predation risk covariates used in the logistic regression models describing herbivore distributions in Hluhluwe-iMfolozi Park (HiP), South Africa, as well as the location of the park in relation to South Africa (upper-left panel) and the 30 census transects used in the study (main left panel).

Table 1. Browsing height and eye level estimates used for each herbivore species. Foraging height estimates for browsers are taken from du Toit (1990) and, for nyala, Kirby et al. (2008). Mass (three-quarters of mean adult female body mass) follows Clements et al. (2014)

	Species (mass)	Browse height (m)	Eye level (m)
Browsers	Red duiker (10 kg)	1*	0.5
	Grey duiker (16 kg)	1*	0.7
	Impala (30 kg)	1.5	1
	Nyala (47 kg)	1.5	1
	Kudu (135 kg)	2	1.5
	Giraffe (550 kg)	4	4.5
Grazers	Warthog (45 kg)		0.7
	Wildebeest (136 kg)		1.5
	Zebra (175 kg)		1.5
	Buffalo (432 kg)		1.5
	White rhinoceros (1400 kg)		1.5

* Based on measurements from similar sized steenbok *Raphicerus campestris*.

Herbivore observations

From 12 July to 18 September 2014, which is the late dry season, groups of two trained observers (one field ranger paired with a volunteer) walked 30 line transects ranging in length from 2 to 11 km, for a total of 232 km (Fig. 1), and recorded the locations and group sizes of all herbivores encountered with the use of binoculars, a GPS unit, compass and Bushnell Yardage Pro 1000 range finder (see le Roux et al. 2017 for a detailed description of the census method). The field ranger was largely responsible for the observations, while the volunteer recorded them into the database. This census is performed biennially in HiP and is

highly standardized across years and between transects, making consistent observer bias highly unlikely. The bearing of, and distance to, each sighting (using herd centres when groups were encountered) were recorded to calculate the location of each observation relative to the transect line. In cases where animals moved after they had been sighted, observations were recorded where the animal (or herd) was first seen. If an animal (or herd) was not initially observed, but rather disturbed by the observers and then seen running off, it was not recorded. Effects of detectability and distance on group counts were accounted for using Distance software. Each transect was walked between five and thirteen times over the course of the survey, yielding a total survey distance of 2715 km. To avoid potential detection bias across different habitat types and vegetation densities, we only used the observations recorded within 100 m of the observer (number of observations per species: red duiker = 52, grey duiker = 105, impala = 266, nyala = 287, kudu = 41, giraffe = 59, warthog = 101, wildebeest = 37, zebra = 82, buffalo = 145 and white rhinoceros = 326). Transects were evenly distributed throughout the park, encompassing all main vegetation types and variability in rainfall and elevation (Fig. 1). The access-limited, south-western wilderness area of HiP was excluded from the study due to no available lion spatial data. An equal number of random points, matching the maximum number of observations for any one herbivore species (i.e. 326), were generated within 100 m buffers around the surveyed transects to represent available habitat.

Airborne LiDAR

We surveyed all of HiP with discrete-return airborne light detection and ranging (LiDAR) in March 2015 using the Global Airborne Observatory (GAO), formally known as the Carnegie Airborne Observatory (Asner et al. 2012). The GAO LiDAR subsystem provides three-dimensional structural information of vegetation canopies and the underlying terrain surface. The GPS-IMU subsystem provides position and orientation data for the GAO sensors, allowing for highly precise and accurate positioning of LiDAR observations on the ground. For this study, the GAO data were collected from 2000 m above ground level, using a scan angle of 36° and a side overlap of 50%. The aircraft velocity was 130 knots, and the LiDAR pulse frequency was 250 kHz, resulting in an average point density of 5.81 pulses (7.47 points) per m^2. Horizontal and vertical error estimates were 16 and 7 cm RMSE, respectively. The LiDAR data provided maps of ground elevation, woody canopy height and three-dimensional structure at 1 m spatial resolution. Measurements of vegetation height from the GAO have been field-validated for savanna vegetation, with LiDAR derived measurements closely matching field values (Asner et al. 2009a). We did not expect seasonal variation in vegetation between the LiDAR collection and transect sampling to substantively affect our results because the density of seasonally varying vegetation, such as leaves, is roughly proportional to woody vegetation (Lefsky et al. 1999). Moreover, perennial woody biomass accounts for a large proportion of savanna vegetation (Venter et al. 2003), and the general vegetation structure would therefore remain largely unchanged over the course of the study. In addition, browsers forage on both leaves and shoots during the dry season, with shoots being especially well correlated with woody structure. Vegetation structure therefore serves as a proxy for both leaves and shoots, especially when changes in the relative amount of browse (leaves and shoots together) across space are of most interest, as was the case in our study.

Predation risk

Long-term predation risk was defined as the aggregate predator encounter risk from three months of predator GPS location data and was assessed at each herbivore observation and random point by using a combination of the long-term probability of a predator being present and visibility, from the perspective of the herbivore. The probability of predator presence was calculated using spatial data from lions and wild dogs obtained from GPS collars between July and September 2014 (GPS satellite units, African Wildlife Tracking, Pretoria, South Africa and Sirtrack Iridium, New Zealand). Collars were placed on at least one female member of each known lion pride (n = 9), a subordinate adult in each wild dog pack (n = 6) and three resident male lion coalitions. This collar distribution encompassed all known lion prides and wild dog packs within the study area (i.e. excluding the south-western wilderness section) at the time. Download frequencies varied between 16 and 24 fixes per day for the lions, with hourly fixes available for all lions between 5 p.m. and 6 a.m., and at 10 a.m. and 2 p.m. All lion datasets were therefore subsampled to match this latter download schedule of 16 fixes (i.e. we used hourly GPS fixes recorded between 5 p.m. and 6 a.m. as well as daily fixes at 10 a.m. and 2 p.m. in the analysis). There was more variability in the wild dog GPS fix schedule. For the three packs in the southern part of the study region, more data were available and we first subsampled these fixes to four standard readings per day to match the southern pack with the fewest recordings. We then randomly subsampled 167 fixes from each of the six packs to match the minimum number available for any one pack across the park, ensuring equal representation across packs.

Two lion prides were only collared toward the end or soon after the study period, resulting in little or no overlapping spatial data from these prides. To counteract this, we used data from the same time period the following year, July–September 2015, for these two prides. An analysis of range overlap between these time periods for lions that had data from two years (July–September 2014 and either 2015 or 2013) revealed high levels of overlap in both their overall (95% kernel, 78–100% overlap with a mean of 94%) and core (50% kernel, 34–100% overlap with a mean of 73%) ranges. We also compared range overlap between adjacent time periods, i.e. July–September with October–December, finding substantially less overlap (95% kernel, mean overlap 87%; 50% kernel, mean overlap 50%). We therefore used data from matching time periods (seasons) for these two prides, and regarded the overlap high enough to render these data reliable for characterizing broad distribution patterns.

Using the combined datasets for each predator, we approximated the risk of lion and, separately, wild dog encounter at a given location by an index proportional to the probability of predator presence, following Valeix et al. (2009a). Consecutive 10% kernel isopleths were calculated from the spatial data using the R package *adehabitatHR* (Calenge 2006). We used 0.6 times the reference smoothing factor *href* because *href* tends to over-smooth data when locations are clumped and therefore does not result in a range estimate that accurately identifies high-use areas (Bertrand et al. 1996). We then approximated the probability of a lion or wild dog being present by $0.1/(A_i - A_{i-1})$; with A_i being the surface area of the isopleths i and 0.1 because 10% of all locations are located between two consecutive isopleths (Fig. 1). Predator encounter risk was then estimated at each herbivore observation and random point by calculating the mean value of each in a 50 m radius

around each point, matching the spatial scale of the viewshed analysis. Although lions live in fission–fusion societies, with prides dividing into smaller sub-groups fairly regularly (Packer et al. 1990, Mbizah et al. 2020), we did not consider this to substantively effect our maps of lion utilization and therefore lion encounter risk for several reasons. First, the time period of our study was relatively short (three months of lion spatial data were used) and conducted over a single season, the late dry season. This short time period increases the likelihood of lion group stability during the study. Second, fission–fusion dynamics in lions are driven primarily by variation in ecological factors, including inter-seasonal variation (Mbizah et al. 2020). Because our study was conducted over part of a single season, the likelihood of changing ecological factors over the time period that could drive a change in lion group structure was unlikely. Third, lion groups are larger and more stable when hunting larger prey (Mbizah et al. 2020), and the majority of lion diet in HiP during the study period consisted of large bodied prey species, and especially buffalo (Barnardo et al. 2020), implying that lion groups would be large and stable. Fourth, lion groups maintain high levels of connectedness when prey are abundant (Mbizah et al. 2020), as was the case in HiP during our study (Barnardo et al. 2020). Lastly, the same individuals were frequently observed together over the study period, suggesting high levels of group stability (Ezemvelo KZN Wildlife unpubl.).

To characterize risk associated with habitat characteristics, we used LiDAR data to measure visibility in the form of viewsheds (Aben et al. 2018) at each site (herbivore observations and random points) following Davies et al. (2016a, b2016b). Viewsheds were modelled by calculating the visible area (including terrain and vegetation) within a 50 m radius of each point in a three-dimensional field of view (i.e. viewsheds did not only capture horizontal line of sight, but also included lower vegetation strata and below canopy area), assuming a height approximating the eye level of each herbivore species (Table 1). Visible area also included areas up and/or downslope and could be obstructed by both vegetation and terrain. While all visible vegetation and terrain within this area was initially included, yielding three-dimensional viewshed area calculations, visible pixels within tree canopies above 1 m were excluded because these places would not be occupied by lions or wild dogs, resulting in visibility being a two-dimensional measurement of visible surface area at a 1-m^2 resolution.

Landscape forage quantity

Metrics of landscape-level forage quantity for browsers and grazers were derived using remotely-sensed vegetation cover. For browse quantity, we first measured woody vegetation volume at herbivore-specific heights (Table 1) across the landscape following Asner et al. (2015). We computed a metric of vegetation density from the LiDAR data by first binning and counting the LiDAR returns in a three-dimensional grid with a step size of 5 × 5 × 0.5 m (defined as voxels), where the first two dimensions of the grid are east and north coordinates and the third is height above ground. For each voxel, we computed a metric of vegetation density (z_i) from the LiDAR returns within its associated 5 × 5 m vertical column ($x_1 - x_n$):

$$z_i = \frac{x_i}{\sum_{j=1}^{i} X_j}$$

where z_i represents vegetation density within a window of 0.5_i to $0.5_{(i+1)}$ m above ground, n is the highest voxel containing LIDAR returns in each column. In using the proportion of LiDAR returns relative to the total number of returns at or below each voxel, we reset the fraction of radiation that reached each voxel, thereby controlling for vegetation above each voxel that could have reflected incoming radiation. Any returns below 0.5 m were classified as ground returns and excluded from these calculations, ensuring that all returns used measured only woody vegetation. We then summed the vegetation density measurements within height bands appropriate for each browser based on their browsing range (Table 1) and quantified the amount of woody vegetation available within each species-specific height band across the landscape at a 5 m resolution (Fig. 1). However, because not all woody vegetation is edible (i.e. wood and very dry leaves), we multiplied vegetation density by the proportion of photosynthetic vegetation in each 5 m cell. We used the Carnegie Landsat Analysis System-lite (CLASlite) to produce estimates of the proportion of photosynthetic vegetation (PV), non-photosynthetic vegetation (NPV) and bare soil across the landscape at 30 m resolution using Landsat 8 surface reflectance images collected on 22 July and 23 August 2014, when cloud-free images over the entire study area were available (Fig. 1). CLASlite automates radiometric correction and uses automated Monte Carlo unmixing (AutoMCU) to produce estimates of vegetation fractional cover in each 30 m image pixel (Asner et al. 2009b). Each 30 m pixel was subsampled to a 5 m resolution to match the woody density measurements.

For grazing quantity, we calculated the near-infrared reflectance of terrestrial vegetation (NIRv) from the same Landsat 8 surface reflectance images (22 July and 23 August 2014). NIRv estimates gross primary productivity (GPP) across landscapes by measuring photosynthetic reflectance while accounting for spectral mixing, leaf area and vegetation canopy depth, and has been shown to correlate strongly with chlorophyll florescence (a direct index of photons intercepted by chlorophyll) and ground-based measures of GPP (Badgley et al. 2017). We considered NIRv a better measurement for herbaceous vegetation than fractional cover because it more directly measures GPP and therefore herbaceous biomass and grazing quantity. However, we did not use it for browse quantity because we had a more direct and height stratified measurement of woody biomass from the LiDAR data. To distinguish herbaceous NIRv from that of woody vegetation, we classified each 30-m cell in the landscape as being either woody- or herbaceous-dominated using LiDAR-derived vegetation height. Because vegetation height data were available at a 1-m resolution and NIRv at a 30-m resolution, we calculated the proportion of 1-m cells per 30-m cell that were above or below 0.5 m in height, with vegetation < 0.5 m regarded as herbaceous and > 0.5 m as woody. We then classified each 30-m cell as being dominated by herbaceous vegetation when > 75% of the 1-m cells were < 0.5 m in height. We were therefore able to mask out portions of the landscape that were clearly dominated by woody vegetation when deriving measurements of graze quantity, reducing the impact of trees on our measurement of graze quantity.

A circular buffer with a radius of 1 km was then generated around each herbivore observation and random site, and the mean browse and graze quantity within the buffer measured as a metric of forage availability in the surrounding landscape. These buffers were larger than those used for predator encounter risk (50 m) because we were interested in how herbivore responses to risk would change across landscapes with varying resource

conditions (forage availability). We also assessed buffers with a radius of 500 m and 1.5 km, with similar results.

Analysis

We used logistic regression models to develop resource selection functions (RSF, proportional to the probability of resource use by an animal) for each herbivore species with the dependent variable being herbivore presence, 1, contrasted with random points that represented available habitat, 0. Because vegetation condition would have changed over the ten weeks of the census, including a fire that burnt part of the area in mid-August, each herbivore observation was paired with forage quantity data from the temporally corresponding Landsat image (22 July or 23 August 2014), and each species set of herbivore observations paired with an equal number of random points with temporally matching fractional cover or NIRv data. We then modelled the probability of a herbivore selecting a site (1 versus 0) as a function of landscape-level forage quantity (either browse or graze quantity depending on herbivore foraging strategy), visibility (viewshed area), lion encounter risk (probability of encountering a lion, i.e. long-term lion risk) and wild dog encounter risk (probability of encountering a wild dog, i.e. long-term wild dog risk). We included interactions between forage quantity and the three measures of risk (visibility, lion risk and wild dog risk), as well as between viewshed and lion and wild dog encounter risk because we were interested in how responses to predation risk might vary across landscapes of varying resource availability and predator encounter probability. Wild dog risk was excluded from models for giraffe, buffalo and white rhinoceros because wild dogs are unlikely to hunt these species (Hayward et al. 2006). We initially included metrics of both browse and graze quantity for mixed-feeding impala RSFs, but models with browse metrics performed better than those with graze (lower AICc values), and we therefore retained only browse metrics in these models. Model selection was performed using Akaike information criteria corrected for sample size (AICc) and the model Akaike weights (AICwi) using the R package *MuMIn* (Barton 2019). There was close convergence between top models for all species (small changes in AICc scores and AICwi between models), and conditional model averaging was therefore implemented using the coefficients from the models with a delta AICc ≤ 2 relative to the most parsimonious model (Burnham and Anderson 2002). Collinearity between main effects for each species dataset was assessed prior to analysis using variance inflation factors (VIF), with VIF scores for all variables across all models being < 2. All predictor variables were scaled and centred before analysis. To visually assess the influence of each predictor variable on the probability of herbivore presence, we varied each covariate considered important (relative importance value ≥ 0.8) in the model averaging output across its range of values while keeping all other variables constant at their mean. Since we were particularly interested in how responses to risk varied with environmental context and predation risk, we repeated this procedure for each important (relative importance value ≥ 0.8) interaction term, holding either the forage quantity or encounter risk covariate in the interaction term at its minimum and, separately, maximum value while keeping all other predictor variables constant at their mean, to illustrate how herbivore responses to predation risk might vary in contrasting environments.

We further assessed effects of group size on resource selection for two browsers (nyala and impala) and two grazers (zebra and buffalo). We chose these four species because they are

known to form groups varying in size from singletons to large groups and because we had a sufficient number of observations for large and small groups from each of them. For each species, we divided the census observations into roughly equal pairs of small and large groups. This resulted in 189 small groups (1–2 individuals) and 98 large groups (ranging from 3 to 12 individuals) for nyala, 146 small groups (1–5 individuals) and 120 large groups (ranging from 6 to 50 individuals) for impala, 47 small groups (1–3 individuals) and 35 large groups (ranging from 4 to 9 individuals) for zebra, and 68 small groups (1–2 individuals) and 77 large groups (ranging from 3 to 140 individuals) for buffalo. We then paired these known observations with random points following the same procedures described above, repeated the RSF analysis for each set of observations (i.e. group size class) for each species and compared effect sizes between group size classes.

Table 2. Model-averaged parameter estimates from browser occurrence models that had a ΔAICc ≤ 2 compared with the top performing model

Species	Covariate	$\hat{\beta}$	SE ($\hat{\beta}$)	p	Importance
Red duiker	Browse	1.25	0.40	< 0.01	1.00
	Viewshed	−0.73	0.30	< 0.05	1.00
	Lion risk	0.52	0.36	0.15	0.58
	Browse: Lion risk	0.72	0.44	0.10	0.40
	Browse: Viewshed	0.35	0.46	0.44	0.13
	Lion risk: Viewshed	−0.34	0.39	0.38	0.13
Grey duiker	Wild dog risk	0.28	0.14	0.05	0.89
	Lion risk	0.16	0.14	0.25	0.32
	Browse	0.16	0.15	0.28	0.30
	Viewshed	0.06	0.14	0.67	0.11
Nyala	Browse	0.14	0.10	0.17	1.00
	Lion risk	0.21	0.11	0.06	1.00
	Viewshed	−0.44	0.10	< 0.001	1.00
	Wild dog risk	−0.31	0.09	< 0.001	1.00
	Browse: Lion risk	0.38	0.13	< 0.01	1.00
	Browse: Wild dog risk	−0.19	0.10	0.06	0.81
	Browse: Viewshed	0.20	0.10	< 0.05	0.80
	Lion risk: viewshed	0.17	0.11	0.13	0.53
	Viewshed: Wild dog risk	−0.08	0.11	0.44	0.20
Impala	Browse	−0.61	0.13	< 0.001	1.00
	Lion risk	0.35	0.10	< 0.001	1.00
	Viewshed	−0.25	0.10	< 0.05	1.00
	Wild dog risk	0.21	0.09	< 0.05	1.00
	Viewshed: Wild dog risk	0.15	0.09	0.09	0.81
	Browse: Lion risk	−0.12	0.17	0.50	0.14
	Browse: Wild dog risk	0.08	0.13	0.55	0.13
	Lion risk: Viewshed	0.05	0.11	0.65	0.12
	Browse: Viewshed	0.05	0.12	0.68	0.12
Kudu	Wild dog risk	−0.40	0.24	0.10	0.80
	Lion risk	−0.14	0.25	0.58	0.25
	Viewshed	−0.17	0.26	0.52	0.24
	Lion risk: Viewshed	−0.58	0.31	0.07	0.13
	Browse	−0.13	0.23	0.57	0.12
Giraffe	Viewshed	−0.32	0.23	0.17	0.69
	Browse	−0.25	0.26	0.33	0.57
	Browse: Viewshed	0.41	0.20	< 0.05	0.57
	Lion risk	−0.32	0.22	0.14	0.55
	Wild dog risk	−0.31	0.23	0.18	0.40
	Browse: Lion risk	0.20	0.26	0.45	0.11
	Wild dog risk: Viewshed	−0.15	0.24	0.54	0.05

Results

Browsers

Forage quantity was among the most important drivers of site selection for red duiker, impala and nyala (Table 2). Red duiker and nyala were observed more frequently in areas of higher browse quantity, whereas impala observations were negatively associated with browse quantity (Fig. 2a–c).
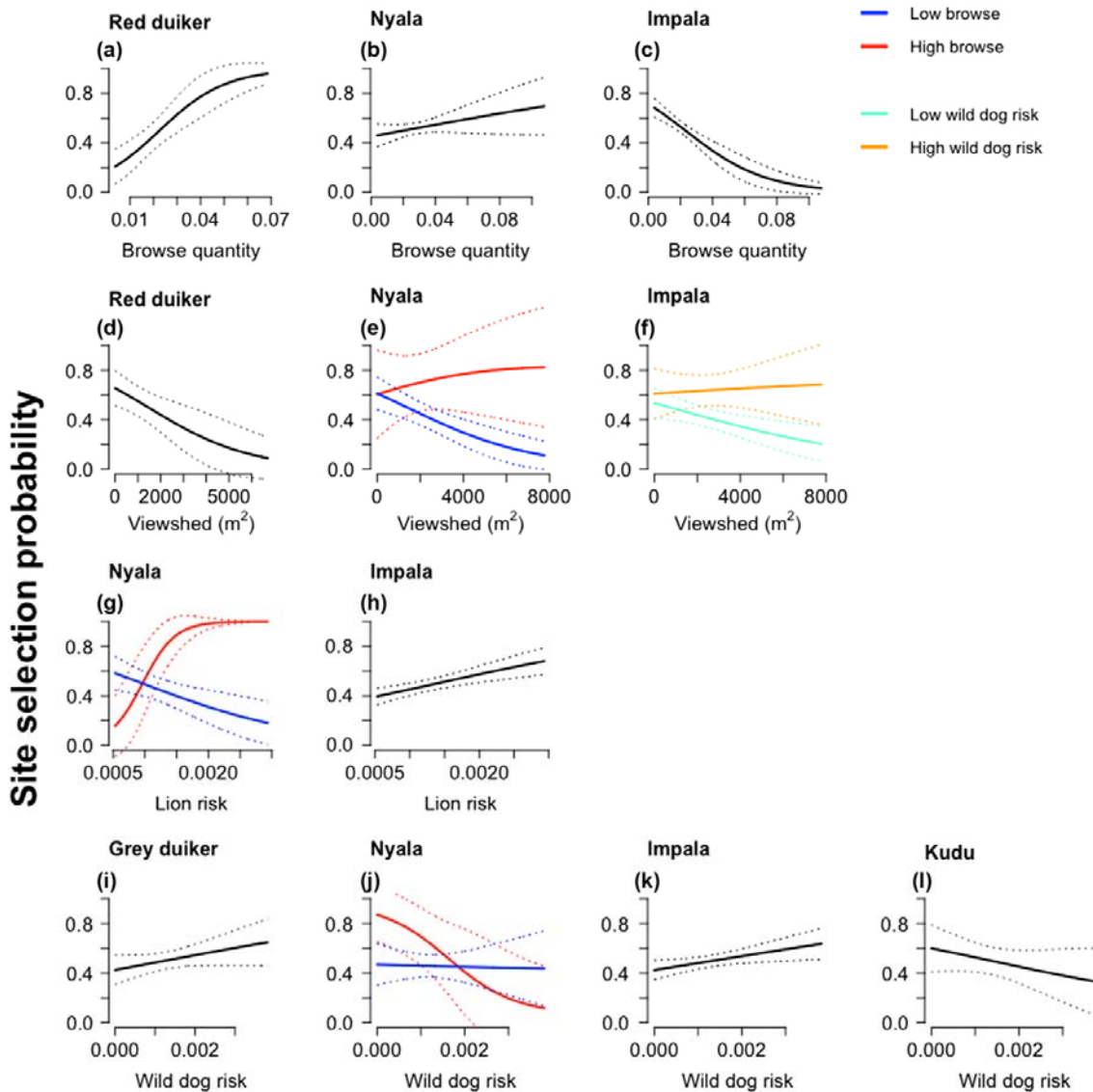

Figure 2. Relationships between the probability of selecting a site and important covariates (relative importance ≥ 0.8) for browsing herbivores in Hluhluwe-iMfolozi Park, South Africa. Results are derived from averaged predictions from logistic models. Dotted lines represent 95% confidence errors around predictions.

All browsers, apart from grey duiker, were observed more frequently in areas with small viewsheds, and viewshed area was one of the most important drivers of occurrence for all other browsers apart from kudu and grey duiker (Table 2, Fig. 2d–f). The interaction between viewshed area and forage quantity was important for nyala site selection. In areas where forage was limited, nyala were more likely to occupy patches with small viewsheds. However, in areas where forage was abundant, the likelihood of nyala using larger viewsheds increased (Fig. 2e). The interaction between viewshed area and predator encounter risk was important for impala, with impala displaying no selection for varying viewshed area where wild dog encounter risk was high, but were observed more often in areas with small viewsheds when wild dog encounter risk was low (Fig. 2f).

Impala were also more likely to occur in areas with greater lion encounter risk (Table 2, Fig. 2h), while nyala presence was influenced by the interaction between lion risk and forage quantity. Nyala were more likely found in areas of greater lion encounter risk when food was abundant, but avoided lion risk when food was limited (Fig. 2g).

Grey duiker and impala were observed more frequently where wild dog encounter risk was high (Fig. 2i, k), whereas kudu presence was negatively associated with wild dog risk (Fig. 2l). Nyala varied their response to wild dog risk with changing forage availability; their likelihood of occurrence being more than three times greater where wild dog risk was low and browse quantity high. In contrast, nyala presence was largely unaffected by wild dog risk when browse was limited (Fig. 2j).

None of our measured variables were important (relative importance value ≥ 0.8) for giraffe resource selection (Table 2).

Grazers

Grazing quantity, lion encounter risk and their interaction were equally the most important drivers of warthog and wildebeest presence (Table 3). Both these grazers were observed more frequently where forage was limited (Fig. 3a–b), but they displayed opposite responses to lion encounter risk. Warthog were more frequently observed in areas with high lion encounter risk where forage was abundant (Fig. 3f), whereas wildebeest were more frequently observed in areas with high lion encounter risk where forage was limited (Fig. 3g).
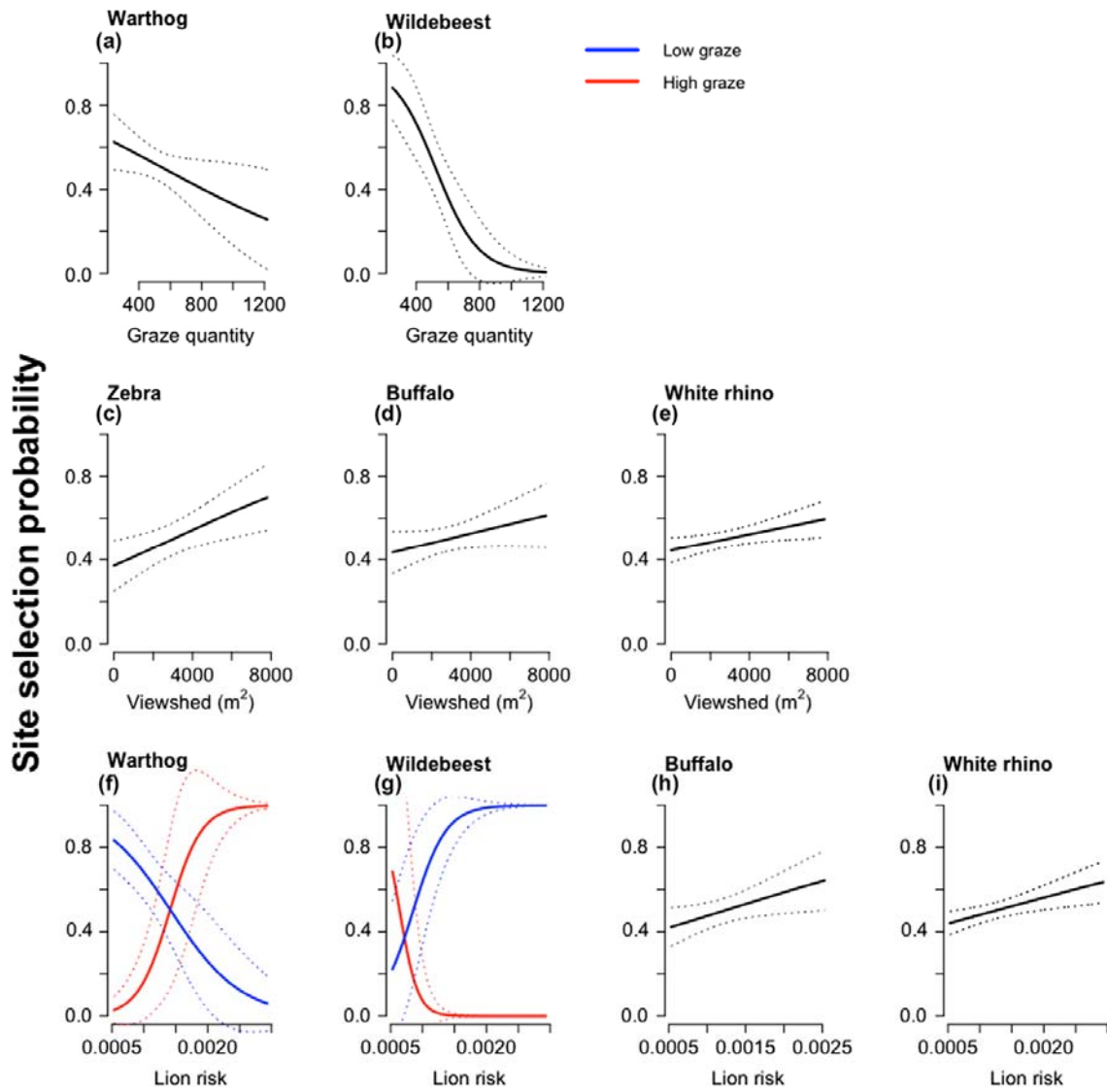
Figure 3. Relationships between the probability of selecting a site and important covariates (relative importance ≥ 0.8) for grazing herbivores in Hluhluwe-iMfolozi Park, South Africa. Results are derived from averaged predictions from logistic models. Dotted lines represent 95% confidence errors around predictions.

Table 3. Model-averaged parameter estimates from grazer occurrence models that had a ΔAICc ≤ 2 compared with the top performing model

Species	Covariate	$\hat{\beta}$	SE $(\hat{\beta})$	p	Importance
Warthog	Graze	−0.29	0.16	0.07	1.00
	Lion risk	−0.07	0.15	0.64	1.00
	Graze: Lion risk	0.63	0.23	< 0.01	1.00
	Wild dog risk	0.15	0.15	0.33	0.36
Wildebeest	Graze	−1.31	0.45	< 0.01	1.00
	Lion risk	0.47	0.29	0.11	1.00
	Graze: Lion risk	−1.44	0.56	< 0.05	1.00
	Wild dog risk	0.43	0.28	0.12	0.60
	Graze: Wild dog risk	−0.33	0.41	0.43	0.18
Zebra	Viewshed	0.41	0.17	0.01	1.00
	Lion risk	−0.12	0.16	0.44	0.20
	Wild dog risk	−0.10	0.16	0.52	0.19
	Graze	−0.10	0.17	0.57	0.18
Buffalo	Lion risk	0.27	0.13	0.04	1.00
	Viewshed	0.23	0.12	0.06	0.90
	Graze	0.21	0.13	0.10	0.72
	Lion risk: Viewshed	0.20	0.13	0.22	0.55
	Graze: Lion risk	−0.10	0.21	0.72	0.09
	Graze: Viewshed	0.04	0.13	0.72	0.09
White rhinoceros	Lion risk	0.22	0.08	0.01	1.00
	Viewshed	0.18	0.08	0.02	1.00
	Lion risk: Viewshed	−0.04	0.08	0.65	0.22
	Graze	0.03	0.08	0.68	0.22

The three largest grazers (zebra, buffalo and white rhinoceros) were observed more frequently in areas with large, open viewsheds (Table 3, Fig. 3c–e). None of these larger grazers demonstrated avoidance of areas with high lion encounter risk (Table 3), and buffalo and white rhinoceros were more often observed where lion risk was high (Fig. 3h–i).

No grazers responded to wild dog encounter risk (Table 3).

Group size effects

Small groups of nyala showed stronger selection for small viewshed area compared with large groups (non-overlapping confidence intervals, Fig. 4a), whereas large groups of impala displayed stronger selection for areas of decreased browse quantity relative to small groups (Fig. 4b). No other differences in selection across group size classes were recorded for these two browsers.
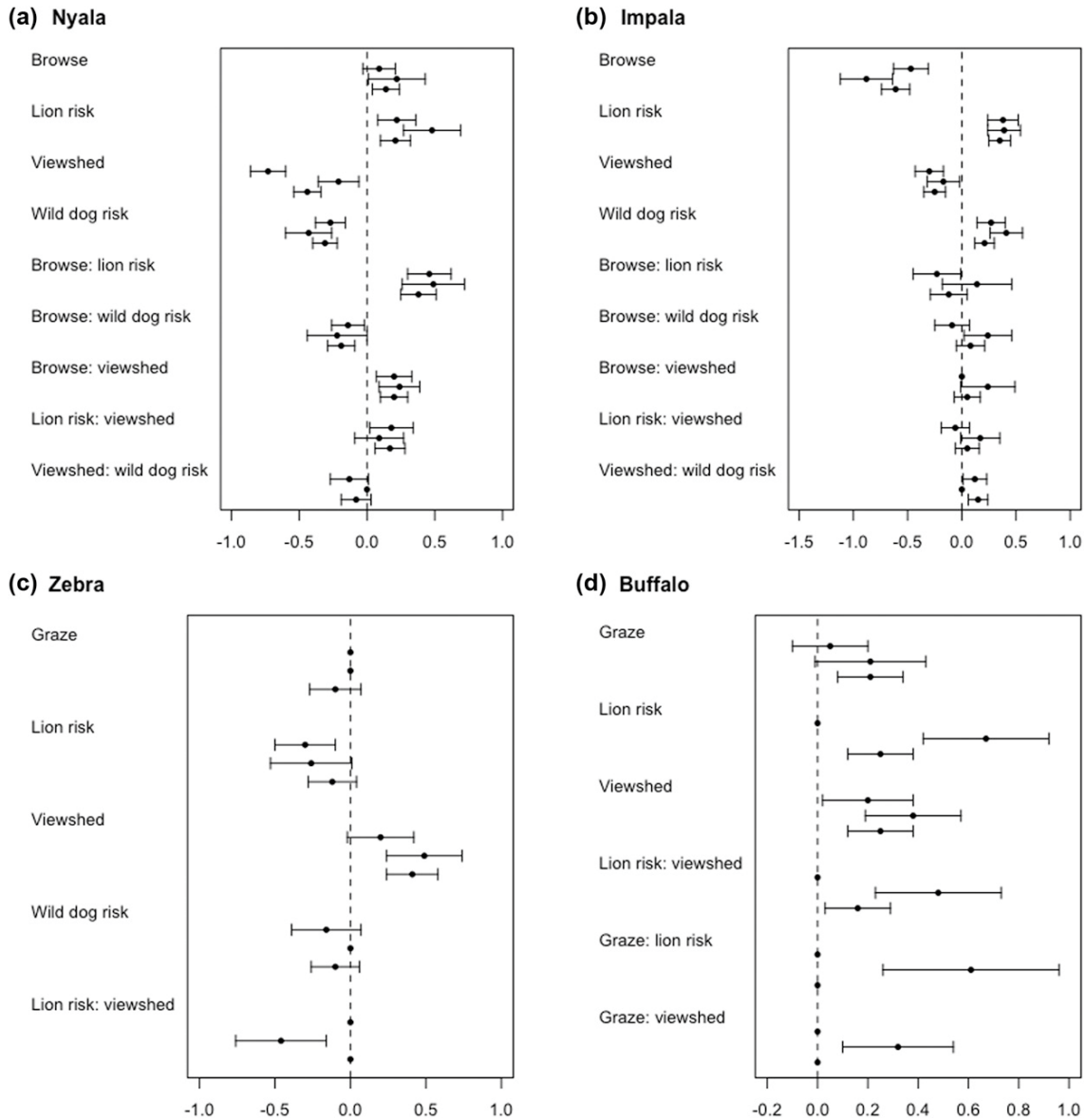
Figure 4. Comparison of effect sizes of drivers of habitat selection for small groups (top data point for each variable), large groups (middle data point) and the overall population (bottom data point for each variable) for four herbivore species in Hluhluwe-iMfolozi Park, South Africa. Solid black dots represent modelled coefficients from averaged predictions from logistic models, while error bars represent 95% confidence intervals. The dotted vertical line represents zero, i.e. no selection.

Large groups of zebra appeared to vary their selection of viewshed area with lion encounter risk (Fig. 4c), however, small sample sizes of large zebra groups in areas of high lion risk precluded further inference. Buffalo were the only herbivore species to display clear differences in habitat selection across group size and levels of risk (i.e. differences in an interaction between habitat use and risk between group sizes). Although large buffalo groups were more frequently observed in areas of high lion risk, these large groups also displayed variable behavioural responses in relation to lion encounter risk (Fig. 4d), selecting more open areas (larger viewsheds) when in areas of high lion encounter risk (Fig. 5).
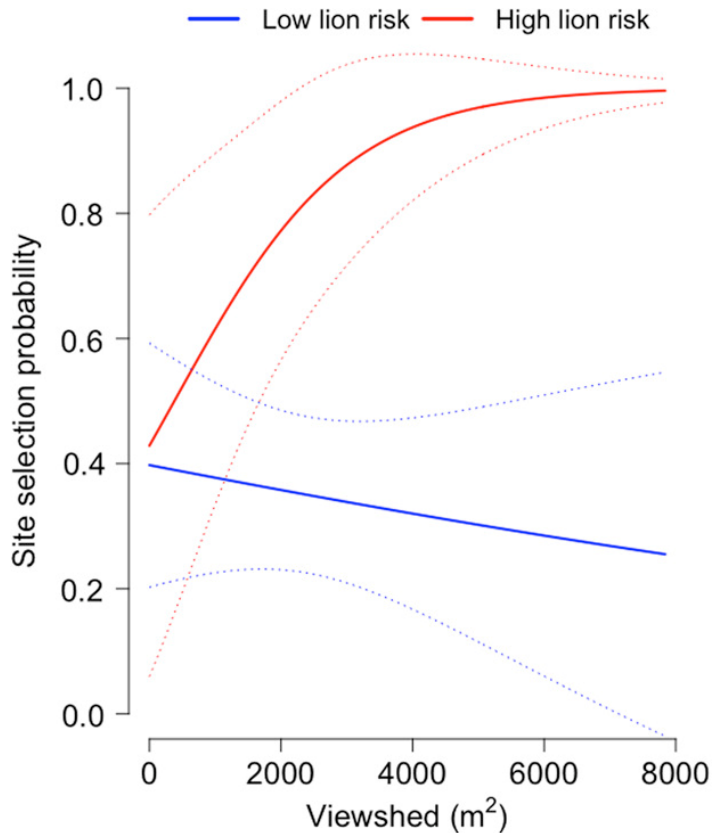
Figure 5.Relationship between the probability of selecting a site and viewshed area in places of contrasting lion encounter risk for buffalo groups (≥ 3 individuals) in Hluhluwe-iMfolozi Park, South Africa. Results are derived from averaged predictions from logistic models. Dotted lines represent 95% confidence errors around predictions.

Discussion

Our results reveal that landscape context can mediate response strength to predation risk among some herbivore species. While patterns across prey species were variable and not well defined, with responses to predation risk being limited for several species and not varying with resource availability, medium-sized herbivores, comprising the two smallest grazers (warthog and wildebeest) and two browsers (nyala and impala) demonstrated variable responses to risk with changing forage availability or vegetation structure. Furthermore, although buffalo (a large grazer) did not demonstrate variable responses to risk at the population level, large groups (representing mixed herds of males, females and juveniles) modified their use of vegetation structure with varying lion encounter risk. However, even among these species, we found variation in response to predation risk with changes in landscape context, particularly with varying resource quantity. Warthog and nyala were both observed more frequently in areas of high lion encounter risk where forage was abundant, but avoided areas of high lion risk where resources were limited (Fig. 2g, 3f), suggesting that these species tolerate greater risk in exchange for abundant food (although warthog are also able to take refuge in underground burrows at night when lions are most active). Wildebeest, however, were observed more frequently where forage quantity was

limited even where long-term lion encounter risk was high (Fig. 3g). Wildebeest prefer to forage on short (lower quantity) grass patches (Wilmshurst et al. 1999), and their increased tolerance of lion encounter risk in these low quantity, but preferred, areas suggests that the drivers of response to risk in wildebeest are similar to those of warthog and nyala, i.e. all three species tolerate greater risk in exchange for preferred foraging areas. However, areas with increased graze quantity contain high levels of grass biomass that likely aid ambush-hunting lions, and wildebeest might also avoid these environments because they represent areas of high catchability for lions (Davidson et al. 2012, Davies et al. 2016a). Short grass patches (i.e. low quantity forage) therefore likely represent both preferred forage and low risk habitat for wildebeest.

Responses of nyala to risk imposed by habitat features (viewshed) also varied with resource availability. Although nyala were more frequently observed in areas with small viewsheds regardless of forage quantity, they were more likely to be observed in areas with small viewsheds where forage was limited (Fig. 2e). This result suggests that nyala select open, likely safer, habitats when they are not resource-stressed (i.e. food-stressed), but need to prioritize resource acquisition where food is limited and are then forced to accept greater risk in exchange for food, being consistently observed in areas of dense vegetation. Impala similarly varied their response to viewshed area, but in response to wild dog encounter risk, being more frequently observed in open areas where wild dog risk was high (Fig. 2f), suggesting selection for safer areas where risk was high for this frequently consumed prey species (Somers et al. 2017).

That food availability can affect the strength of responses to predation risk for medium-sized herbivores is an important finding that expands on recent results documenting herbivore risk avoidance only during times of relative food abundance (Riginos 2015). When food is limited (such as during drought or the dry season), herbivores place a higher priority on obtaining sufficient forage, tolerating higher risk in exchange for improved forage availability (Owen-Smith 2015, Riginos 2015). In our late dry season study, several herbivore species demonstrated similar results on a spatial level, tolerating greater risk in places with more abundant forage (e.g. warthog and nyala for lion encounter risk), or alternatively being less able to avoid risk when food was limited (e.g. nyala avoided areas with high wild dog encounter risk only where forage was abundant, but showed no response to risk where food was limited, Fig. 2j). In both cases, herbivores demonstrate a need to balance risk avoidance with foraging requirements, which is likely heightened in times of food shortage (e.g. the late dry season). These results, together with previous findings (Valeix et al. 2009a, Riginos 2015), suggest that some African herbivores adjust their spatial distributions in response to predation risk only when they can afford to do so, conforming to the risk allocation hypothesis (Lima and Bednekoff 1999). Avoiding predation risk can carry substantive costs for herbivores, reducing nutritional intake, body condition and fecundity (Creel et al. 2007, Christianson and Creel 2010), and they can likely only incur these costs when conditions allow, i.e. when resources are in relative abundance. When resources, such as food or water, are limited, physiological needs are prioritized and herbivores embark on riskier behaviour to meet them, increasing their vulnerability to predation (Riginos 2015).

Variability in response to predation risk with herbivore body size did not align closely with our prediction that smaller species would show stronger responses because they are more

vulnerable to predation (Hopcraft et al. 2012). Instead, the two smallest species, red and grey duiker, were unaffected by predation risk regardless of forage quantity, with grey duiker even being observed more often in areas with higher wild dog encounter risk. Moreover, red duiker were found much more frequently in places with small viewsheds and did not adjust their use of dense habitat with changing predation risk. Both these duiker species are seldom consumed by lions or wild dogs in HiP (Somers et al. 2017), and are below or close to the lower end of the accessible prey weight range for these predators (Clements et al. 2014). Being small in size and solitary, they are also more likely to rely on hiding when threatened by a predator, which could further result in them employing different risk avoidance strategies (Jarman 1974, Brashares et al. 2000). The species that did respond the strongest to long-term risk, and that varied their response strength with environmental context, were mostly medium in size (i.e. warthog, wildebeest and nyala), placing them within the optimal prey weight range of lions and wild dogs. Herbivores within a similar size range (Grant's gazelle *Gazella granti* and Coke's hartebeest *Alcelaphus buselaphus*) also showed the clearest shifts in risk tolerance in relation to drought-induced changes in environmental conditions (Riginos 2015). However, apart from varied use of dense vegetation by impala in response to wild dog encounter risk, impala responses to predator encounter risk were surprisingly weak considering that they comprise a large proportion of lion and wild dog diet in HiP (Somers et al. 2017). Impala observations even increased with both lion and wild dog encounter risk. Impala are mixed feeders, which could confound results when considering forage availability (although we did consider herbaceous forage quantity in models for impala). Moreover, impala are frequently consumed by other predators, particularly leopards, in fairly equal numbers in HiP (Somers et al. 2017) and they could be balancing risk responses to both our measured and unmeasured predators. Increased impala observations in areas of increased predation risk could also stem from lions and wild dogs selectively hunting in areas where impala are most abundant.

Responses of grazers to predation risk were more similar to our body size predictions, with the two largest species, buffalo and white rhinoceros, displaying no avoidance of their primary predator, lions, and even being observed more frequently where lion encounter risk was high. The large size of these herbivores and their ability to defend themselves against predator attack results in them being less vulnerable to predation and therefore less likely to avoid risk (Hopcraft et al. 2012, Tambling et al. 2012), which could be especially pertinent for male buffalo that are known to take increased risks in exchange for quality forage (Hay et al. 2008). Indeed, large buffalo groups, representing mixed herds, were found to use large viewsheds when lion encounter risk was high, but small groups (primarily males) did not alter their landscape use with changing predator risk (Fig. 4, 5). Despite buffalo being the primary prey species of lions in HiP (Somers et al. 2017, Barnardo et al. 2020), buffalo attempts to avoid areas of high lion encounter risk could be thwarted by lions actively selecting areas with high prey (buffalo) abundance, leading to an apparent selection of high lion risk areas by buffalo (Davidson et al. 2012). Buffalo could then be expected to use alternative strategies, such as selecting open areas where lion risk is high to reduce the likelihood of an ambush attack, as was the case for large groups. Buffalo elsewhere have also been shown to rely on defence tactics when attacked by lions (Tambling et al. 2012), and they could similarly utilize such behaviour in HiP instead of lion avoidance, especially in the case of small, presumably male, groups that are known to more frequently use risky habitats (Hay et al. 2008). Large herbivores also have a wider dietary tolerance than smaller

species, allowing them to be more widespread in the landscape, which could further explain the apparent lack of habitat selection in response to predation risk by large grazers as well as giraffe, the largest browser (Cromsigt et al. 2009). White rhinoceros are almost invulnerable to predation from lions, and it is therefore not unexpected for them to be unresponsive to lion encounter risk (le Roux et al. 2018).

Site selection in terms of visibility varied with herbivore foraging strategy, which could be due to different predation risk avoidance strategies as well as foraging requirements. All browsers, apart from grey duiker, were found more often in areas with small viewsheds (dense vegetation), whereas all grazers were associated more often with large, open viewsheds, with large buffalo groups being the only grazer to vary their response to viewshed selection with changing long-term predation risk. Grazers might select open areas to facilitate vigilance and lower predation risk, but also need to be in these areas to forage. Accordingly, grazers are likely unable to move into open, safer areas when predation risk increases because they are already in such areas, whereas browsers can adjust their spatial location to open areas when predation risk is high (as evidenced by impala), or forage availability allows (as was the case for nyala) (Fig. 2e–f). These findings corroborate those from Hwange National Park where browsers were found in open habitats where lion risk was high, presumably having moved out of woodland areas, whereas grazers foraged in the open already and could not make further adjustments in response to increased lion presence (Valeix et al. 2009a).

In contrast to our predictions and previous findings (Thaker et al. 2011), we did not record overall stronger responses to ambush predators (lions) than to cursorial ones (wild dogs). Nyala and kudu were instead more responsive to wild dog encounter risk than that of lions, and impala altered their response to visibility with changing wild dog, but not lion, risk. Krüger et al. (1999) suggested that wild dogs in HiP have adapted to hunt in dense cover, which could perhaps explain the similar responses to lion and wild dog risk we recorded. Wild dogs are also more diurnal than lions (Hayward and Slotow 2009) and likely pose a greater threat to prey species during the day when observations were recorded, potentially driving stronger responses than lions. However, nyala, which are strongly selected by both lions and wild dogs (Somers et al. 2017), varied their response to both predators in response to changing resource availability. Nyala only avoided wild dogs where forage was abundant, but tolerated greater lion risk in the same areas (abundant food). Nyala possibly do not tolerate increased wild dog risk in exchange for improved forage as they do for lions because there are few options available to reduce risk from wild dogs other than avoidance. In contrast, nyala could exploit the hunting predictability of lions, in terms of both habitat and nocturnal activity, and select safer foraging locations (open viewsheds) when in areas of high lion risk, as well as forage in these riskier areas during the day. Such alternate risk avoidance strategies to ambush and cursorial predators have been documented in northern temperate prey species, where contrasting risk landscapes squeeze prey because risk from ambush hunters is exacerbated when prey seek dense cover to escape detection by cursorial predators (Atwood et al. 2009, Lone et al. 2014), which could explain why nyala are so heavily consumed by both lions and wild dogs in HiP.

Although we recorded some response of prey species to predation risk that varied with environmental context, particularly for medium-sized herbivores and large buffalo groups,

clear and consistent patterns for other species were limited. Multi-predator/multi-prey systems are inherently complex and prey responses to risk depend on a multitude of competing factors. Studies that encompass multi-predator/multi-prey dynamics are therefore extremely challenging and rare, especially for vertebrates (Montgomery et al. 2019, Say-Sallaz et al. 2019). Although we measured multiple components of the system, using a range of techniques including field surveys, GPS telemetry and remote sensing, generalizable patterns across species were difficult to detect. This could be due to missing measurements, such as risk posed by spotted hyenas, cheetahs and leopards, as well as the effects of forage quality or water availability on herbivore habitat selection, but also suggest that general patterns of prey response to risk are not straightforward or easily predictable (Cusack et al. 2020). Similarly, recent studies have shown that trophic cascades can fail to emerge despite predator impacts on prey populations (Ford et al. 2015) and that they can be diluted by megaherbivore behaviour (le Roux et al. 2018). Inconsistent and weak responses by prey to risk will further dampen ecosystem level effects. Moreover, the existence of spatially-varied responses to predation risk among medium-sized prey species and large buffalo groups suggest that risk effects are not uniform across landscapes and that some areas will likely be affected more by herbivores than others. When such spatial variation in risk is combined with varying response strength through time, shifting landscapes of fear can result, further diluting trophic cascades (Riginos 2015). It is clear that much remains to be uncovered, especially in spatially varied and complex multi-predator/multi-prey systems, before firm conclusions can be made about the ecosystem-level effects of predation risk.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.kprr4xh3g> (Davies et al. 2020).

Author contributions

Andrew B. Davies: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and

editing (lead). **Joris P. G. M. Cromsigt**: Conceptualization (supporting); Formal analysis (supporting); Resources (supporting); Writing – review and editing (supporting). **Craig J. Tambling**: Formal analysis (supporting); Writing – review and editing (supporting). **Elizabeth le Roux**: Formal analysis (supporting); Writing – review and editing (supporting). **Nick Vaughn**: Data curation (equal); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). **Dave J. Druce**: Project administration (supporting); Resources (supporting); Writing – review and editing (supporting). **David G. Marneweck**: Resources (supporting); Writing – review and editing (supporting). **Gregory P. Asner**: Conceptualization (supporting); Data curation (supporting); Funding acquisition (lead); Methodology (supporting); Resources (lead); Writing – review and editing (supporting).

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