Hierarchical resource selection by impala in a savanna environment

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Abstract The factors that affect resource selection by a foraging herbivore can vary according to the resources or conditions associated with particular levels of organization in the environment, and to the scales over which the herbivore perceives and responds to those resources and conditions. To investigate the role of forage in this hierarchical process, we studied resource selection by a mixed-feeding large herbivore, the impala (*Aepyceros melampus*). We focussed on three spatial scales: plant species, feeding station and feeding patch. In paired sites where impala were and were not observed, we identified the plant species from which animals fed, the attributes of the plants, and the characteristics of the broader site. Across all three scales, plant species available as forage was central in determining resource selection by impala. At the species level, that effect was modified by the nutritional quality (greenness) and whether it was during a period of forage abundance or scarcity (season). At the feeding-station level, overall greenness and biomass of the station were important, but their effects were modified by the season. At the feeding-patch level, broader-scale factors such as the type of vegetation cover had an important influence on resource selection. The grass *Panicum maximum* was a preferred forage species and a key resource determining the locations of feeding impala. Our findings support the idea that selection by a foraging herbivore at fine scales (i.e. diet selection) can have consequences for broader-scale selection that result in observed patterns of habitat use and animal distribution.

Key words: bushveld savanna, forage selection, foraging behaviour, foraging hierarchy, South Africa.

INTRODUCTION

Forage selection and the factors that influence selection are crucial aspects of large herbivore ecology through their role in determining distribution and abundance (Owen-Smith 2005). Contributing to that influence is whether the herbivore is a browser, grazer or mixed feeder (Hofmann 1989). Mixed or intermediate feeders can be classified broadly into two additional groups based on whether they prefer grass or browse (Jarman 1974; McNaughton & Georgiadis 1986). Part of the decision about whether to select grass or browse, and then what to eat within those groups, depends on whether the resources are preferred, reserve, buffer or key resources (Owen-Smith 2005). Preferred resources are plant species that are highly palatable and most readily eaten by herbivores whenever available and nutritionally acceptable. Reserve resources are used to supplement the diet when preferred resources are declining in availability and nutrition. Buffer resources are used only to sustain

herbivores through periods of forage scarcity when very little other forage is available or palatable. Key resources are any resource (preferred, reserve or buffer) that are essential to the survival of herbivores during resource-limited periods (Varley & Gradwell 1960; Illius & O'Connor 2000). Temporal variability in rainfall, temperature and light induce changes in nutrient content of forage plants (Van Soest 1994), which in turn influences whether a forage species is perceived by the herbivore as a preferred, reserve or buffer resource. It is that variability that requires the herbivore to switch between species or forage types when favoured species are insufficiently available (Albon & Langvatn 1992; Wilmshurst *et al.* 1999b; Mysterud *et al.* 2001), and it also influences the distribution of key resources that affect herbivore distribution at local and regional scales (Seagle & McNaughton 1992).

Contributing further to decisions about forage selection is nutritional quality and acceptability of plants, determined by the ratio of cell walls to cell contents and by the concentration of nutrients (e.g. protein, minerals and soluble carbohydrates) of the cell contents (Owen-Smith 2005; Codron *et al.* 2007). The ratios and concentrations differ between plant species and plant parts (Arzani *et al.* 2004; Codron *et al.* 2007), change with season, differ considerably between grass and browse, and ultimately influence palatability (Jarman

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1974; McNaughton & Georgiadis 1986; Cooper *et al.* 1988). For example, total fibre content negatively influences selection of mature leaves by kudu (*Tragelaphus strepsiceros*) and of new and mature leaves by impala (*Aepyceros melampus*; Cooper *et al.* 1988). Acceptability of browse species also can be affected by plant defence compounds (Freeland & Janzen 1974), such as condensed tannins which can deter herbivory by kudu, impala and domestic goats (Cooper & Owen-Smith 1985).

While forage characteristics can influence fine-scale resource (i.e. diet) selection, broader-scale factors can affect selection of feeding stations, patches, or regions of the landscape (Senft *et al.* 1987), such as vegetation cover, terrain or locations of water sources. As such, resource selection occurs as a nested hierarchy of choices, with some factors being relevant at broader scales and others at finer scales. Moreover, choices made by a foraging herbivore at one scale can limit the options available at finer scales (Johnson 1980). For example, choice of vegetation community subsequently affects options available for feeding stations and plant species, and consequently can contribute to effects on herbivore distribution that arise through scale-dependent influences of environmental factors.

The objectives for this study were to identify factors influencing resource selection by a mixed-feeding large herbivore at three spatial scales, to identify resources that were preferred, reserve or buffer, and to identify which resources might be defined as key resources. Our investigation focussed on impala (*Aepyceros melampus*), which prefer grass, but also consume varying percentages of non-grass forages (i.e. stems and leaves from dicotyledonous plants or dicots, fruits, seeds) ranging from 5% (Stewart 1971) to >30% (Meissner *et al.* 1996). They also switch between grass and browse in response to changing resource conditions as a consequence of environmental factors such as decreasing rainfall (Du Toit 1988; Van Rooyen 1992; Skinner & Chimimba 2005). Greenness of vegetation is generally an indication of forage quality (O'Reagain & Owen-Smith 1996) and is negatively related to grass maturity, digestibility, and fibre content (Van Soest 1994). We predicted therefore that (i) impala would select the greenest and youngest forage, but that they would demonstrate greater fine-scale selection for certain species, regardless of the greenness of those species (i.e. because of their role as key resources). Resource selection at a larger scale can be influenced by tree canopy cover, with *Acacia* spp. in particular being known to increase the nutritional value of sub-canopy grasses (Belsky 1994; Ludwig *et al.* 2004; Treydte *et al.* 2007). Moreover, impala have a relatively small body size (45–55 kg; Skinner & Chimimba 2005), and thus a relatively small rumen volume to body mass ratio (Hofmann 1989). As a consequence, impala should have high energy requirements for their size

(McNaughton & Georgiadis 1986) and should be selective of forage high in cell contents to meet those requirements (Illius & Gordon 1992; Van Soest 1994). Thus, we predicted that (ii) larger-scale resource selection would be driven by nutritional quality of forage available at the level of feeding station or patch.

METHODS

Study area

The study was conducted in two savanna reserves in north-eastern South Africa (Manyeleti Game Reserve (Manyeleti; 24°36′S, 31°28′E) and Wits Rural Facility (WRF; 24°33′S, 31°06′E)), May–October 2009. The area has a wet season (November–April) and a dry season (May–October). Our sampling focussed on the dry season, the period over which forage resources died back owing to low rainfall and foraging pressure by herbivores, and when increasing scarcity of forage would more clearly elicit behavioural responses of a foraging herbivore during a nutritionally critical period. We divided the dry season into early-dry (May–July) and late-dry (August–October) periods by comparing weekly greenness levels of vegetation; the late-dry season began when there was a sudden drop in greenness.

Wits Rural Facility (350 ha) is 30 km from the Orpen gate, Kruger National Park, and mean annual rainfall is 670 mm. The main gate for Manyeleti is 5 km from Orpen gate, and its mean annual rainfall is 507 mm. Manyeleti is contiguous with Kruger National Park, so animals can move freely between the two areas, whereas WRF is a fenced area allowing limited movement to neighbouring reserves. Dominant tree species in both areas include *Terminalia sericea*, *Acacia* spp. and *Combretum* spp. (Schmidt *et al.* 2002). Dominant grasses include *Panicum maximum*, *Aristida* spp., *Urochloa mosambicensis*, *Pogonathria squarrosa*, *Heteropogon contortus*, *Eragrostis* spp. and *Cynodon dactylon* (Shackleton 1993). Large mammals occurring in WRF include impala, kudu, common duiker (*Sylvicapra grimmia*), reed buck (*Redunca fulvorufula*), water buck (*Kobus ellipsiprymnus*) and warthog (*Phacochoerus aethiopicus*). Hyaena (*Crocuta crocuta*) and leopard (*Panthera pardus*) are occasionally observed passing through WRF from neighbouring reserves. The Greater Kruger National Park (including Manyeleti) has approximately 147 mammal species including most of the large savanna predators (Mbunda 2003).

Data collection

We compared the characteristics of used and unused resources at three levels: plant species, feeding station, and feeding patch (Bailey *et al.* 1996). We sampled each study area three times a week, alternating daily between areas. On each day's sampling, we covered most of the study area by vehicle in search of herds of feeding impala. A feeding patch was identified as an area where impala spent 1–30 min feeding (Bailey *et al.* 1996). Once the herd had moved away from the patch we approached on foot to search for plants

that showed fresh bites (i.e. bites that had no dried edge; Parrini 2006; Macandza 2009).

We placed a 0.5×0.5-m plot over the vegetation where we first identified fresh bites, and extended the plot vertically to 1.5 m to include browse within reach of impala. Each such plot was classified as a feeding station (i.e. the area that can be used by a herbivore without moving its feet; Novellie 1978). At each feeding patch we sampled four additional feeding stations, each one 2 m apart. The plots were placed in the four cardinal directions relative to the first. If on inspection it became apparent that a distinct feeding path was followed, then the plots were placed 2 m apart along the feeding path (Parrini 2006).

Within each feeding station we recorded all plants species present and identified whether any species had fresh bites. Species with fresh bites were defined as 'used'; otherwise, they were 'unused'. A feeding station was 'used' if there were plant species within it with fresh bites, and a feeding patch was 'used' if any of the feeding stations within had been used. For each species present in a feeding station, we ranked both greenness and basal cover according to an 8-point scale (Walker 1976): 0 (0% green), 1 (1–10%), 2 (11–25%), 3 (26–50%), 4 (51–75%), 5 (76–90%), 6 (91–99%), 7 (100%). We estimated biomass for the feeding station by a modification of the comparative yield method (Haydock & Shaw 1975). We ranked each plot 0–5 according to the percentage of edible forage present within the plot: 0 (0%; i.e. bare plot, or plot with no edible forage), 1 (1–25%), 2 (26–50%), 3 (51–75%), 4 (76–99%), 5 (100%; i.e. a plot filled with grass up to 1.5 m). To convert the ranks into biomass, we clipped 20 plots representing each rank, dried the clippings at 60°C for two days and weighed the clippings. We used linear regression to find the relationship between plot ranks and biomass, and we used that relationship to convert ranked numbers into biomass (g m^{-2}). We also measured the midpoint of sward height of each species.

For each patch used by impala, we also sampled an unused patch. We located the unused patch by walking 40 m in a randomly selected compass direction and collecting the same data that were collected for the used patch (Matson *et al.* 2005). Both used and unused patches were ranked according to the dominant cover type: short grass (≤0.5 m), tall grass or shrubs (>0.5 m), short grass with canopy cover, and tall grass or shrubs with canopy cover.

Data analysis

We based our analysis on methods for estimating resource selection functions (Manly *et al.* 2002). Using multi-model inference (Anderson 2008), we developed four to eight logistic regression models for each level of selection in each study area. Each model had 'used' or 'not used' as binary response variables. For plant species models, we used mixed-effects regression with identifiers for feeding station and feeding patch as nested random effects. For feeding station models, only the patch identifier was the random effect. The models for the feeding patch level had fixed effects only. For species selection models, we analysed grass and dicot species separately. Explanatory variables included the individual species (categorical), species basal cover (categorical), season (early dry, late dry), height of leaves (continuous), greenness

of the species (categorical), and sward height (continuous). We also included interactions to determine whether selection was based solely on the species available, or if the effect of species was modified by the other explanatory variables.

To determine whether particular forage species played the role of key resources for impala at broader scales, we evaluated whether their presence influenced the selection of a feeding station or patch. For those scales, presence or absence of individual species were represented as binomial explanatory variables. The other explanatory variables for the feeding station analysis were season, feeding station biomass (continuous), greenness (categorical) and average sward height (continuous). For the feeding patch analysis, other explanatory variables were season, average patch biomass (continuous), average patch greenness (categorical), average sward height (continuous) and cover type (categorical).

Because of the distributional characteristics of our data, we had frequent problems with false convergence. Such errors occur when a model-fitting algorithm fails to converge on a maximum likelihood estimate for a given data set (Allison 2004). This can happen if there are substantial gaps in the distributions of continuous data, or if some levels of a categorical variable have few observations relative to other levels (Allison 2004). A solution to the first problem is to create a categorical variable from a continuous one, such that one level of the categorical variable encompasses a gap in distribution (Allison 2004). Thus, variables such as basal species cover, which were measured originally on a continuous scale, were analysed as categorical variables. A solution to the second problem is to combine levels containing few observations (Allison 2004). Thus, to produce maximum likelihood estimates from our analyses, we combined categories of greenness (e.g. >25 % or >75%, depending on the distribution of observations for a particular analysis), we grouped use of plant parts into whether any part of the species as a whole was used, we grouped rarely used species into 'other grasses' (i.e. herbaceous monocots) and 'other dicots' (i.e. forbs and other non-grass species not analysed as a separate category), and we conducted separate analyses on subsets of the data (e.g. grasses separate from dicots).

Models were compared using Akaike's Information Criterion, corrected for small sample bias (AICc). Of all the candidate models, the one with the lowest AICc value was considered the most parsimonious (Anderson 2008). Models within two AIC units were considered to have similar support from the data; in such cases, the models with fewer parameters were considered more parsimonious. Further model comparison was carried out by calculating the relative likelihoods (w_i) of the candidate models (i.e. the probability that the model was closest to reality, given the set of candidate models). We calculated evidence ratios (E_{ij}) using the relative likelihoods (w_i/w_j) to compare weights of evidence between models of the same set, where a higher evidence ratio indicates better support for model i over model j (Anderson 2008).

We calculated log-odds ratios (±95% confidence intervals) for the explanatory variables from each of the best models. For categorical variables, a coefficient was calculated for each level of the category beyond a reference category (Godvik *et al.* 2009; Van Beest *et al.* 2010), and each coefficient was an estimate of the difference between that category and the reference category (Zuur *et al.* 2009). Choice of the reference categories did not affect the outcome of the analysis

(i.e. the estimated differences between levels did not change), but were chosen to aid interpretation. Thus, we usually set the lowest level as the reference category and interpreted changes in selection relative to that lowest level. When interpreting those differences, values >0 indicate selection of a category that is higher than the reference category, and values <0 indicate selection of a category that is lower than the reference category (Godvik *et al.* 2009). Confidence intervals that overlap the reference category indicated no difference to the reference category. We conducted all analyses in R version 2.10.1 (R development Core Team 2008), using function 'lmer' for mixed-effects models with binomial errors, and function 'glm' for fixed-effects models with binomial errors.

RESULTS

Species selection

We recorded 80 different plant species in feeding stations, of which 46 were grass and 34 were woody. Of those, impala fed from 26 grass species and 26 woody species. At both Manyeleti and WRF, >80% of the grass diet was made up of *P. maximum* and *U. mosambicensis*. The bulk of the non-grass diet was *Acacia* spp. and 'forbs' at Manyeleti and *D. cinerea* and 'forbs' at WRF.

The highest-ranked model for dicot species selection at Manyeleti ($w_i = 0.76$) included species only as a categorical explanatory variable (Table 1), which contained 'forbs', *Acacia* spp., *Euclea* spp. and 'other dicots' as categories. Based on that model, 'forbs' were favoured more (log-odds = 2.966 ± 0.54), and *Euclea* spp. was favoured less (log-odds = -3.392 ± 0.74), than *Acacia* spp. (reference category). At WRF, there was evidence for selection based on species (containing two levels for WRF: *D. cinerea* and 'other dicots'; $E_{1,2} = 1.6$), but there was also evidence of an interaction with season (Table 1). Using 'other dicots' in the early-dry season as the reference class, selection of both *D. cinerea* in the early-dry season (log-odds = -5.17 ± 3.04) and 'other dicots' in the late-dry season

Table 1. Species selection: candidate models to test the importance of plant species and other explanatory variables on forage selection by impala, Manyeleti Game Reserve and Wits Rural Facility (WRF), South Africa, May–October 2009

Explanatory variables	AICc	ΔAICc	k	w_i
Dicots, Manyeleti ($n = 239$)				
Species	260.3	0.0	5	0.76
Species × Season	264.4	4.1	9	0.10
Species × Greenness	265.0	4.7	9	0.07
Species × Basal cover	265.3	5.0	9	0.06
Species × Season + Species × Greenness	269.8	9.5	13	0.01
Dicots, WRF ($n = 130$)				
Species × Season	117.0	0.0	5	0.44
Species	118.0	1.0	3	0.27
Species × Season + Species × Greenness	119.3	2.3	7	0.14
Species × Season + Species × Basal cover	120.1	3.1	6	0.09
Species × Basal cover	121.5	4.5	5	0.05
Species × Season + Species × Basal cover	127.8	10.8	5	<0.01
Grass, Manyeleti ($n = 4018$)				
Species × Season + Species × Greenness	3933	0	22	0.99
Species × Greenness + Species × Basal cover	3967	34	25	<0.01
Species × Greenness	4021	88	19	<0.01
Species × Basal cover + Species × Season	4375	442	13	<0.01
Species × Basal cover	4421	488	10	<0.01
Species × Season	4450	517	7	<0.01
Species × Leaf height	4483	550	7	<0.01
Species	4499	566	4	<0.01
Grass, WRF ($n = 1959$)				
Species × Season + Species × Greenness	1846	0	22	0.99
Species × Greenness	1879	33	19	<0.01
Species × Leaf height	1960	114	8	<0.01
Species × Season + Species × Leaf height	1961	115	10	<0.01
Species × Season + Species × Basal cover	1979	133	13	<0.01
Species	1986	140	4	<0.01
Species × Season	1989	143	7	<0.01

All models with interacting variables (×) also contained linear terms for those variables. Because of convergence problems during model fitting, the list of candidate models differs between sites. n, no. plots; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AIC and that of the lowest model; k, number of parameters in the model; w_i, model probability (Akaike weight).

(log-odds = −3.94 ± 3.20) were lower. An additional model having similar support contained an interaction between species and greenness ($E_{1,3}$ = 3.1; Table 1).
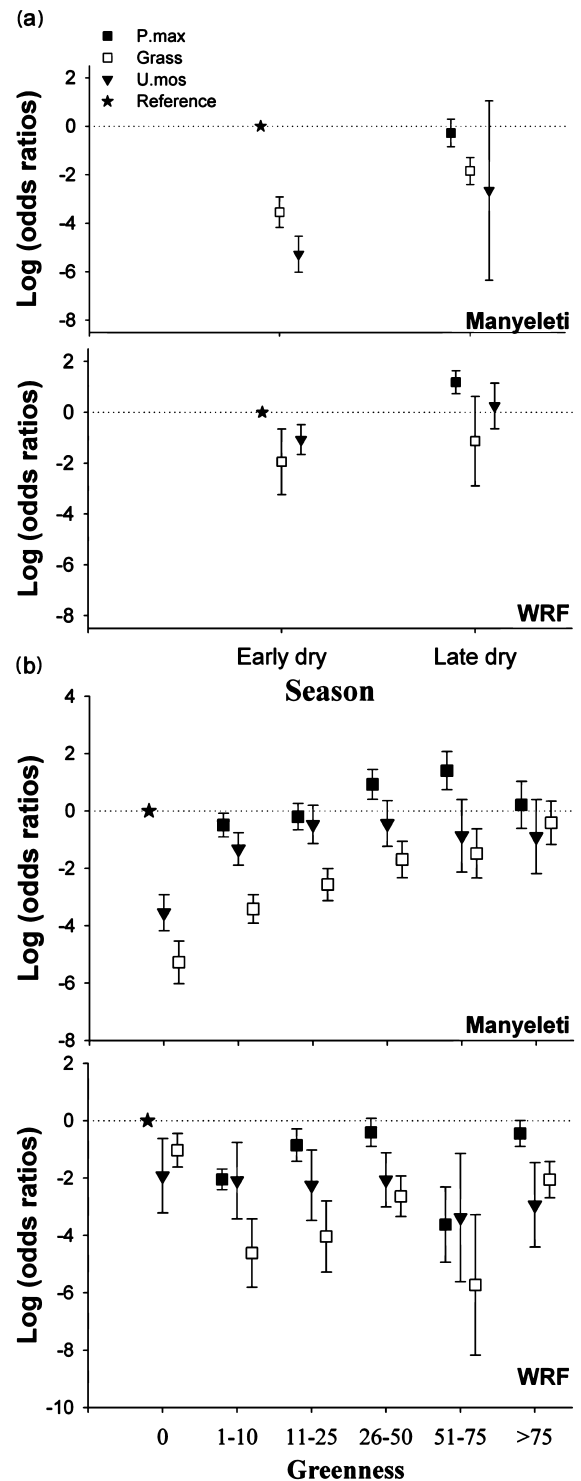
Selection of grass species at Manyeleti and WRF depended on the greenness of the species and whether it was early- or late-dry season (Table 1). At Manyeleti, the highest selection was for *P. maximum* in the early-dry season (reference category), followed by *U. mosambicensis*, and 'other grass' during both seasons, although selection of 'other grass' was highly variable in the late-dry season (Fig. 1a). *Urochloa mosambicensis* was avoided less during the late-dry than during the early-dry season, and 'other grass' was roughly similar between seasons (Fig. 1a). At WRF, selection of *P. maximum* increased from early- to late-dry season. Selection of *U. mosambicensis* and 'other grass' in the early-dry season was lower than *P. maximum* in the same season, but selection of those two groups increased by the late-dry season to be similar to early-dry *P. maximum* selection (Fig. 1a).

At Manyeleti, selection based on greenness varied by grass group (Fig. 1b). Impala tended to select *P. maximum* the most, regardless of greenness, and selection varied little across greenness categories (Fig. 1b). Selection of *U. mosambicensis* was substantially lower than that of *P. maximum* at low greenness levels, but impala showed higher selection as greenness increased, until selection of both species were approximately equal at intermediate greenness (Fig. 1b). 'Other grass' showed the lowest selection of the grass groups; its selection also increased with greenness, but impala demonstrated similar selection to *U. mosambicensis* and *P. maximum* only at the highest levels of greenness (Fig. 1b). At WRF selection of the three grass groups changed little with greenness. Overall, impala tended to favour *P. maximum* most, followed by *U. mosambicensis*, and 'other grass' (Fig. 1b).

Feeding station selection

Based on the highest-ranked candidate model at Manyeleti, selection by impala was strongly influenced by plant groups occurring within the feeding station (Table 2). It was further influenced by the overall greenness, but its effect on selection depended on the season (Table 2). The highest-ranked model for WRF (w_i = 0.95) included plant group, an interaction between season and greenness, and an interaction between season and biomass (Table 2).

At Manyeleti, the presence of 'forbs', *Acacia* spp. or 'other dicots' resulted in greater selection of a feeding station, relative to a station containing no plant groups at all (i.e. the reference category; Fig. 2). 'Forbs' increased selection most, followed by *Acacia* spp. and 'other dicots' (Fig. 2). The only grass species that resulted in greater selection of a feeding station was

Fig. 1. Species selection estimates (±95% confidence interval) for *Panicum maximum* (P.max), *Urochloa mosambicensis* (U.mos) and all other grasses (Grass) at Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), South Africa, May–October 2009. (a) Selection based on season (early dry, late dry), with the reference category (Reference) being *P. maximum* in ED; (b) selection based on greenness, with the reference category being *P. maximum* with 0% greenness. The dashed line indicates the reference level.

Table 2. Feeding station selection: candidate models to test the importance of plant species and other explanatory variables on forage selection by impala, Manyeleti Game Reserve and Wits Rural Facility (WRF), South Africa, May–October 2009

Model	AICc	ΔAICc	k	w_i
Manyeleti ($n = 2620$)				
Acacia spp. + Pmax + Umos + Other grass + Other dicots + Forbs + Deriantha + Greenness × Season	2864	0	19	0.62
Acacia spp. + Pmax + Umos + Other grass + Other dicots + Forbs + Deriantha + Greenness × Season + Biomass × Season	2865	1	21	0.38
Acacia spp. + Pmax + Umos + Other grass + Other dicots + Forbs + Deriantha + Biomass × Season	3142	278	11	<0.01
Acacia spp. + Pmax + Umos + Other grass + Other dicots + Forbs + Deriantha	3152	288	8	<0.01
WRF ($n = 1294$)				
Pmax + Umos + Other grass + Other dicots + Forbs + Dcinerea + Greenness × Season + Biomass × Season	1494	0	21	0.95
Pmax + Umos + Other grass + Other dicots + Forbs + Dcinerea + Greenness × Season	1500	6	19	0.05
Pmax + Umos + Other grass + Other dicots + Forbs + Dcinerea + Biomass × Season	1601	107	11	<0.01
Pmax + Umos + Other grass + Other dicots + Forbs + Dcinerea	1602	108	8	<0.01

All models with interacting variables (×) also contained linear terms for those variables. n, no. plots; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AIC and that of the lowest model; k, number of parameters in the model; w_i, model probability (Akaike weight); Pmax, *Panicum maximum*; Umos, *Urochloa mosambicensis*; Forbs, all forb species combined; Deriantha, *Digitaria eriantha;* Dcinerea, *Dichrostachys cinerea*.

P. maximum. Urochloa mosambicensis resulted in selection similar to that of a species-absent station, while impala demonstrated lower selection for feeding stations containing 'other grass' and *D. eriantha* (Fig. 2). At WRF, impala selected feeding stations containing any dicot similarly to one containing no forage species (Fig. 2). The presence of *P. maximum*, followed by *U. mosambicensis*, resulted in greater selection, while those containing 'other grass' resulted in selection similar to one absent of forage species (Fig. 2).

The influence of greenness on selection of feeding stations varied between the early- and late-dry seasons (Fig. 3). At Manyeleti, impala showed little difference in selection among greenness categories in the early-dry season. In the late-dry season, there was decreased selection for feeding stations of the lowest greenness category, but increased selection of feeding stations of intermediate and high greenness, relative to stations of 0% average greenness in the early-dry season. There was a similar trend at WRF: during the early-dry season, selection varied little between greenness categories, although there was weak evidence of using lower greenness categories less and higher greenness categories more than the reference category (Fig. 3). Late-dry-season selection, however, showed a more prominent pattern of using low-greenness feeding stations less than the early-dry-season reference category (Fig. 3). The highest-ranked model for WRF also contained an interaction between season and biomass, which indicated that the relationship between selection and biomass became more negative when shifting from the early-

(log-odds = −3.647 ± 0.001) to the late-dry season (log-odds = −3.956 ± 0.001).

Feeding patch selection

At patch level, species presence influenced selection at Manyeleti only, but greenness and dominant cover type were important drivers for patch selection in both study areas. The highest-ranked model for patch selection in Manyeleti ($w_i = 0.99$) included species (*Acacia* spp., 'forbs', 'other dicots', *P. maximum*, *U. mosambicensis*, 'other grass' and *D. erianta*) and interactions between mean patch greenness and season, and between cover type and season (Table 3). For WRF, the highest-ranked model included interactions between greenness and season, and cover and season ($w_i = 0.99$; Table 3). There was no evidence that species played an important role in patch selection at WRF ($E_{1,2} = 77$; Table 3).
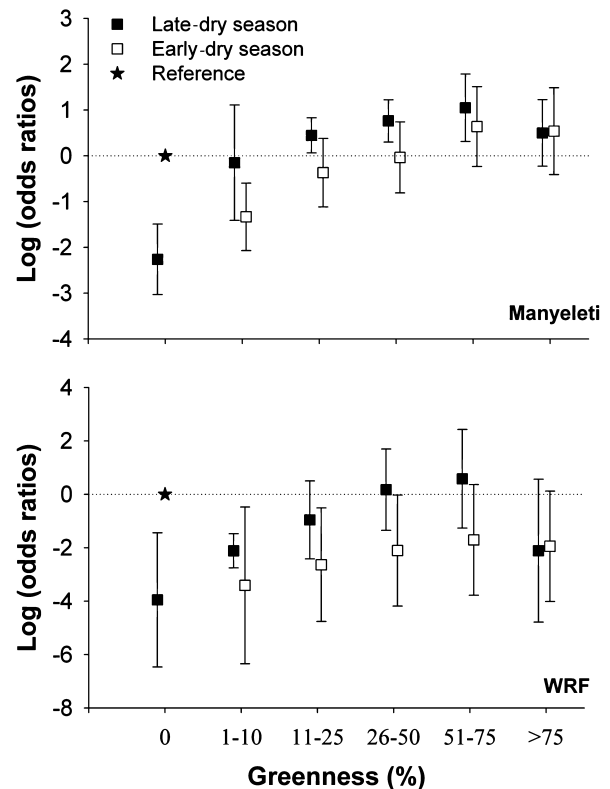
At Manyeleti and compared with patches with an absence of forage species, impala showed greater selection for patches with *Acacia* spp., 'forbs' and 'other dicots', in descending order (Fig. 4). The only grass species that increased patch selection was *P. maximum*. Selection of patches was no different with presence of *U. mosambicensis* than patches with an absence of forage species, and patches with *D. eriantha* or 'other grass' were selected less (Fig. 4). At WRF, there was no evidence that forage species played a role in patch selection by impala (Fig. 4).
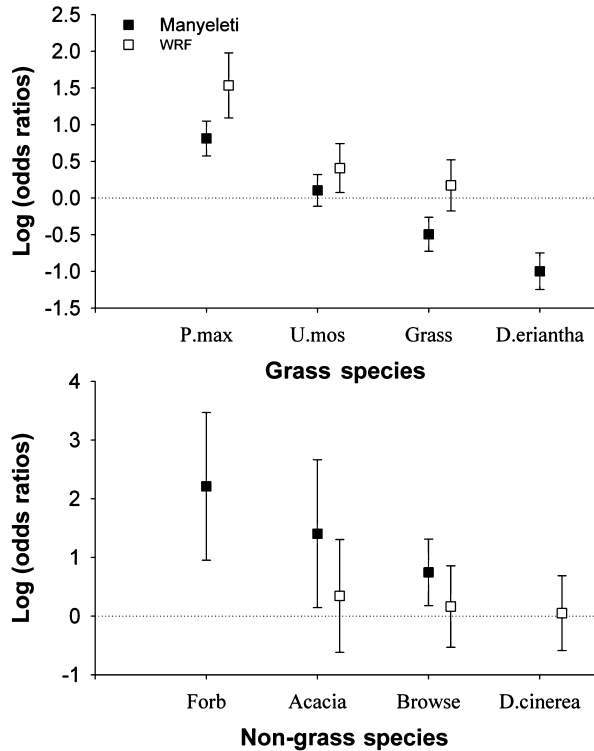
Fig. 2. Feeding station selection estimates (±95% confidence interval) based on forage species at Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), South Africa, May–October 2009. Reference category is the absence of species (horizontal dashed line). Forbs = all forb species, Acacias = *Acacia* spp., Dicots = other dicot species, D.cine = *Dichrostachys cinerea*, P.max = *Panicum maximum*, U.mos = *Urochloa mosambicensis*, Grass = other grass species, D.eriantha = *Digitaria eriantha*. Forbs were rare in feeding stations at WRF, and thus are not represented in the figure.

Fig. 3. Feeding station selection estimates (±95% confidence interval), based on the mean greenness of a feeding station in the early-dry and late-dry seasons, for Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), South Africa, May–October 2009. Reference category (Reference) is feeding stations with greenness of 0% in the early-dry season.

The highest-ranked model for both study areas contained greenness as a variable (Table 3). Based on two greenness classes (>25% and <25%), patches of high and low greenness at Manyeleti showed similar selection in the early-dry season (Fig. 5a). During the late-dry season, impala showed greater selection of high-greenness patches (Fig. 5a). Although the highest-ranking model for WRF also included a interaction between greenness and season (Table 3), wide confidence intervals around the log odds-ratios suggested similar selection of patches based on greenness (Fig. 5a). The same model without the greenness-by-season interaction (Table 3), however, had substantially lower support ($E_{1,3} = 2122$), providing suggestive but inconclusive evidence of a role of greenness at WRF.

For Manyeleti, the highest-ranked model included an interaction between cover type and season, but in this instance as well, wide confidence intervals suggested that impala showed similar selection of different cover types across seasons (Fig. 5b). A role of cover type at Manyeleti was suggestive, however, because the same model without the cover-type-by-season interaction had substantially lower support ($E_{1,2} = 4316$). In the early-dry season, impala at WRF selected patches of all other cover types less than those of short grass, with patches dominated by tall grasses and shrubs being avoided most. There was no evidence that cover type played a role in patch selection during the late-dry season (Fig. 5b).

DISCUSSION

Species selection

Impala used a range of grasses and dicots throughout the dry season, and selection of these species was influenced by season and greenness. The effects of species and greenness depended on season. Greenness

Table 3. Feeding patch selection: candidate models to test the importance of plant species and other explanatory variables on forage selection by impala, Manyeleti Game Reserve and Wits Rural Facility (WRF), South Africa, May–October 2009

Model	AICc	ΔAICc	k	w_i
Manyeleti (n = 526)				
Acacia spp. + Pmax + Umos + Other grass + Other dicots + Forbs + Deriantha + Greenness × Season + Cover type × Season	537.77	0.00	9	0.99
Acacia spp. + Pmax + Umos + Other grass + Other dicots + Forbs + Deriantha + Greenness × Season	554.51	16.74	12	<0.01
Acacia spp. + Pmax + Umos + Other grass + Other dicots + Forbs + Deriantha + Cover type × Season	562.39	24.62	16	<0.01
Acacia spp. + Pmax + Umos + Other grass + Other dicots + Forbs + Deriantha	582.45	44.68	9	<0.01
Greenness × Season + Cover type × Season	609.88	72.11	11	<0.01
WRF (n = 260)				
Greenness × Season + Cover type × Season	321.70	0.00	10	0.98
Pmax + Umos + Other grass + Other dicots + Forbs + Dcinerea + Greenness × Season + Cover type × Season	330.25	8.55	17	0.01
Cover type × Season	337.02	15.32	9	<0.01
Pmax + Umos + Other grass + Other dicots + Forbs + Dcinerea + Cover type × Season	346.96	25.26	15	<0.01
Pmax + Umos + Other grass + Other dicots + Forbs + Dcinerea + Greenness × Season	356.74	35.04	11	<0.01
Pmax + Umos + Other grass + Other dicots + Forbs + Dcinerea	371.18	49.48	8	<0.01

All models with interacting variables (×) also contained linear terms for those variables. Because of convergence problems during model fitting, the list of candidate models differs between sites. n, no. patches; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AIC and that of the lowest model; k, number of parameters in the model; w_i, model probability (Akaike weight); Pmax, *Panicum maximum*; Umos, *Urochloa mosambicensis*; Forbs, all forb species combined; Deriantha, *Digitaria eriantha*; Dcinerea, *Dichrostachys cinerea*.

of vegetation is associated with its nutritional value as forage for herbivores (Van Soest 1994; O'Reagain & Owen-Smith 1996), with younger grasses being greener and more nutritious, and mature grasses being higher in fibre (Jarman 1974; Short *et al.* 1974; Van Soest 1994). Young foliage often has less resins and oils (Jarman 1974), and impala likely chose leaves from trees or forbs that were most palatable (i.e. >50% green). These seasonal changes in plant phenology thus likely led to changes in selection of dicot species and grass species that were seasonal, with impala feeding on forage when defence compounds, resins, or fibre were least (Jarman 1974; Short *et al.* 1974; Van Soest 1994).

We observed impala to feed from 58 plant species in total, but the bulk of their diet consisted of *P. maximum* and *U. mosambicensis*. *Panicum maximum* was the species selected most during poor-forage conditions (i.e. overall greenness <10%, late-dry season), followed by *U. mosambicensis*. Both grasses are nutritious to herbivores (Ben-Shahar & Coe 1992; Murray & Illius 2000; Mutanga *et al.* 2004; Van Oudtshoorn 2004; Codron *et al.* 2007; Van Niekerk & Hassen 2009), but *P. maximum* stays green for longer (Grant *et al.* 2000) and therefore is more favoured by herbivores well into the dry season (Mutanga *et al.* 2004; Van Oudtshoorn 2004). Strong selection of a small number for forage species is not common to all impala populations. Other populations experiencing drought conditions in the region of our

study used four to six grass species in lower amounts (5–15% per species), with dicots comprising up to 20% of their diet (Meissner *et al.* 1996). We observed dicots to comprise only a small portion of their diet, but important dicots included *Acacia* spp. and forbs at Manyeleti, and *D. cinerea* and forbs at WRF. Many forb species have nutritional values close to those of many grasses, and they remain greener for longer than most grasses (Arthun *et al.* 1992; Kallah *et al.* 2000; Codron *et al.* 2007); thus, impala might supplement their diet with forbs, especially during the late-dry season (Du Toit 1988).

We recognize that different plant tissues within the same species can represent substantially different resources to a foraging herbivore (Owen-Smith 2005); however, because of model-fitting problems with analysing plant parts separately, our finest scale of analysis was limited to plant species within a feeding station. Nonetheless, whereas selection of a species through most of the dry season concentrated on foliage or stems, a switch to other plant parts was apparent as forage became more scarce. For example, selection of flowers from *Euclea* spp. was noticeable towards the end of the the dry season. Also, consumption of seed pods increased through the dry season, primarily from *D. cinerea* at WRF and *Acacia* spp. at Manyeleti. Seed pods are consumed by a number of large herbivore species when alternative food sources are scarce (Coppock *et al.* 1986; McNaughton & Georgiadis 1986; Miller 1994, 1996). Impala commonly consume
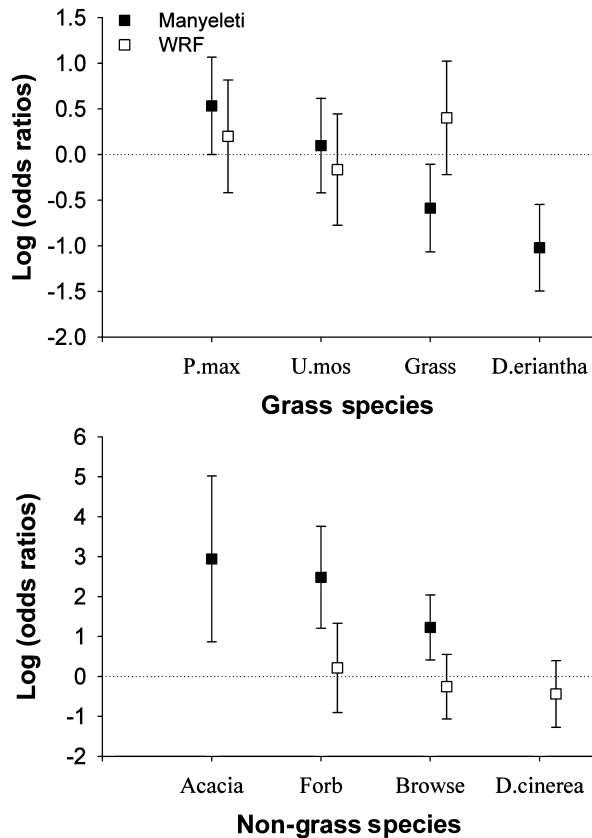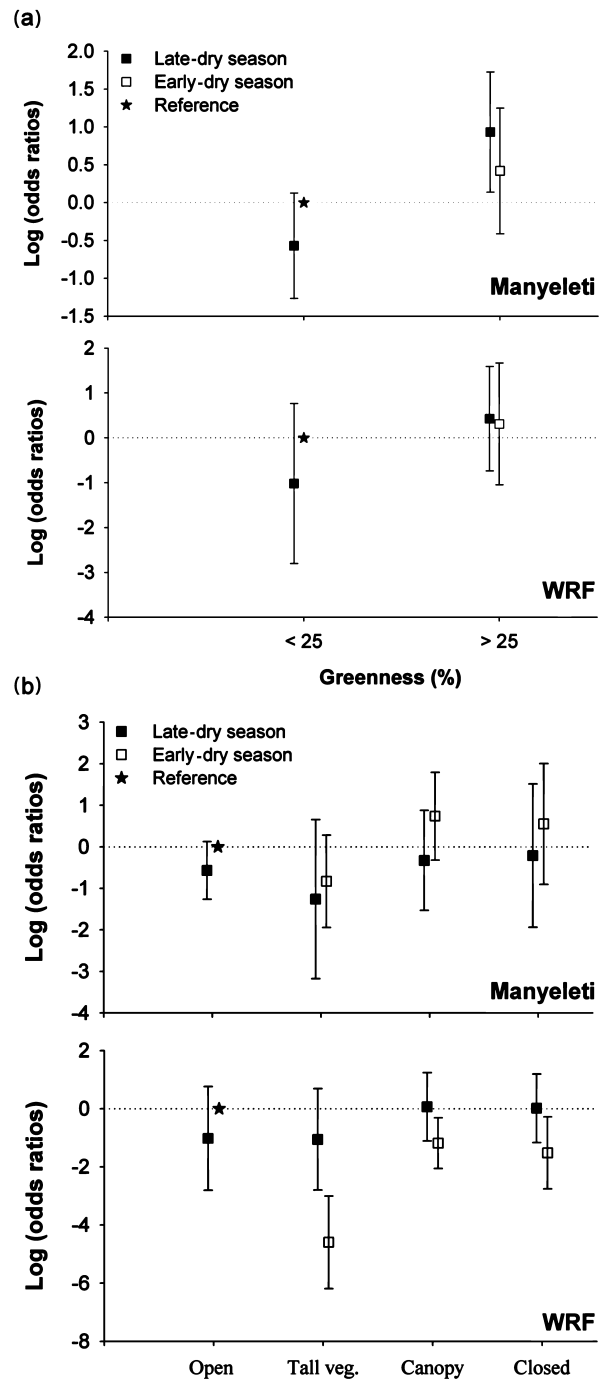
Fig. 4. Patch selection estimates (±95% confidence interval) based on forage species in Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), South Africa, May–October 2009. Reference category is the absence of species (horizontal dashed line). Acacias = *Acacia* spp., Forbs = all forbs, Dicots = other dicot species, D.cine = *Dichrostachys cinerea*, P.max = *Panicum maximum*, U.mos = *Urochloa mosambicensis*, Grass = other grass species, D.eriantha = *Digitaria eriantha*. *Acacia* spp. were rare in patches at WRF, and thus are not represented in the figure.

and disperse seed pods from *Acacia* spp., and their diet consists in large part of this food source during the dry season (Miller 1996).

Feeding station selection

Selection of feeding stations increased with the presence of non-grass forage species and *P. maximum* at Manyeleti, and with *P. maximum* and *U. mosambicensis* at WRF, likely as a consequence of those grass species being both abundant and highly nutritious. Large trees can influence the nutritional composition of sub-canopy grasses (Belsky *et al.* 1993; Belsky 1994; Treydte *et al.* 2007), with *Acacia* spp. having the largest effect on nutrient content of vegetation (Ludwig *et al.* 2004); this pattern could contribute to impala selecting patches containing trees. We found that forbs also

Fig. 5. Patch selection estimates (±95% confidence interval) for Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), South Africa, May–October 2009. Selection during the early-dry and late-dry seasons based on (a) greenness with the reference category (Reference) being patches with 0% greenness in the early-dry season, and (b) dominant cover type, with the reference category (Reference) being short grass in the early-dry season. Open = short grass only, Tall veg. = tall grass or shrubs >0.5 m, Canopy = short grass with canopy cover, Closed = tall vegetation with canopy cover.

play an important role in selection of feeding stations, likely because of their contribution to the diet during the late-dry season.

The highest-ranked model for feeding station selection at WRF, and the second-ranked model at Manyeleti, both indicated a decrease in selection with an increase in biomass. Because grass of high biomass is also high in structural compounds that are difficult to digest (Demment & Van Soest 1985), ruminants should avoid high-biomass feeding stations. But selection of feeding stations with forage of high quality and low biomass can result in reduced herbivore intake rate (Langvatn & Hanley 1993). The solution is to balance intake rate and digestibility by selecting feeding stations of intermediate biomass (Wilmshurst *et al.* 2000). For example, Thompson's gazelle (*Gazella thompsonii*) prefer areas of short grasses and intermediate biomass, which allows them access to a moderate abundance of higher-quality forage with relatively high digestibility (Wilmshurst *et al.* 1999a). Impala should similarly select a diet that limits fibre intake, because of their relatively small body size and short retention time (Demment & Van Soest 1985; McNaughton & Georgiadis 1986). The change in fibre of maturing grasses could explain the role of plant biomass on selection of feeding stations.

Feeding patch selection

Most factors that influence selection of feeding stations could potentially influence feeding patch selection, including the presence of forage plants, and forage quality and abundance (Bailey *et al.* 1996). The presence of particular forage species did not influence patch selection at WRF. At Manyeleti, however, selection of patches and feeding stations were both influenced by available forage species. Dicots likely had a similar influence on selection at both levels of the foraging hierarchy: trees alter nutritional quality subcanopy grasses (Belsky *et al.* 1993; Belsky 1994; Ludwig *et al.* 2004; Treydte *et al.* 2007). The relatively high nutritional quality of forbs and their persistence during dry conditions (Arthun *et al.* 1992; Kallah *et al.* 2000; Codron *et al.* 2007) are likely to make patches containing them appealing to impala. We also found similarities in the importance of factors between levels of the foraging hierarchy for greenness: selection by impala in the dry season was influenced by the overall greenness of feeding stations and feeding patches, further demonstrating the importance of forage quality in determining resource selection by and distribution of impala and multiple scales.

Predation has been recognized to play an important role in influencing the distribution of animals, and consequently the resources that are available (Sinclair and Arcese 1995; Laundré *et al.* 2001). Although not an objective of this study, we recognize that predation could play a role in selection of broad-scale landscape attributes (i.e. cover) that in turn could affect availability and selection of resources at finer scales. A role of predation could have contributed to differences in foraging between Manyeleti and WRF; however, isolating that effect from those of other differences between study sites is difficult. Predator communities differ substantially between areas, but so do the sizes of areas over which impala can range freely, the abundances of other species of large herbivores (as competitors or as facilitators), and the relative proportions of open and closed vegetation types. All of these can have consequences on foraging behaviour and anti-predator behaviour that are difficult to separate from each other. Direct measurement anti-predator behaviour (e.g. vigilance, group size) would assist to clarify the role of predation in affecting resource selection.

Palatability classes

Because of their role in influencing resource selection at all three foraging levels, we concluded that *P. maximum* and *U. mosambicensis* were preferred resources for impala, being both highly palatable to herbivores and strongly selected by impala when overall forage quality was low. *Panicum maximum*, in particular, contributed most to the diets of impala in both study areas; thus, *P. maximum* is likely a key resource for impala. Such resources influence habitat selection and distribution, especially during the resource-limited periods, and have a strong effect on survival and reproduction (Varley & Gradwell 1960; Illius & O'Connor 2000).

Reserve resources are eaten less often than preferred resources and are used to supplement the diet when preferred resources are unavailable or insufficient to satisfy nutritional requirements (Owen-Smith 2005). Foliage from *Acacia* spp. and forbs at Manyeleti, and *D. cinerea* at WRF, appeared to fill such a role for impala. *Acacia* spp. and forbs increased selection of patches and feeding stations, but selection of these species was mostly confined to the late-dry season. Impala fed from *D. cinerea* during the late-dry season only. Seed pods of *Acacia* spp. and *D. cinerea* also played an important role, but only when other food sources were scarce. Hence, although impala are preferential grazers (Skinner & Chimimba 2005), their seasonal switch to seed pods might make this an important reserve resource.

Unpalatable evergreen species are consumed by browsers and mixed feeders towards the end of the dry season, when more palatable deciduous woody species and nutritious grasses are unavailable (Owen-Smith & Cooper 1987; Owen-Smith 1994), and thus are buffer resources for herbivores (Owen-Smith

2005). The only species that was clearly observed as a buffer resource was *Euclea* spp. This taxon was abundant at both study areas (present at 10% of patches at WRF and 30% of patches at Manyeleti), yet impala fed from them only at the very end of the dry season. Impala, however, rarely fed from *Euclea* spp., because the previous rainy season had higher-than-average rainfall, and many grasses maintained green stems towards the end of the dry season. Consumption of *Euclea* spp. was more common only where alternative resources were depleted. Thus, although impala fed from a several different species, their preferred, reserve and buffer resources consisted of a few essential forage species.

CONCLUSION

These results support our predictions that forage quality, as indicated by greenness, has an important influence on resource selection at multiple spatial scales. Nonetheless, forage species present played a central role in determining where impala foraged. Impala fed on a wide variety of species, but only a few species influenced selection across scales. *Panicum maximum* was perhaps the most important of these, and was likely a key resource determining impala movements and foraging patterns. Furthermore, evidence from Manyeleti suggests that forage species played a role in selection of patches (Table 3), supporting the idea that selection by a foraging herbivore at fine scales (i.e. diet selection) might have consequences for broader-scale selection that results in observed patterns of habitat use and animal distribution.

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