'Remote' behavioural ecology: do megaherbivores consume vegetation in proportion to its presence in the landscape?

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ABSTRACT

Examination of the feeding habits of mammalian species such as the African elephant (*Loxodonta africana*) that range over large seasonally dynamic areas is exceptionally challenging using field-based methods alone. Although much is known of their feeding preferences from field studies, conclusions, especially in relation to differing habits in wet and dry seasons, are often contradictory. Here, two remote approaches, stable carbon isotope analysis and remote sensing, were combined to investigate dietary changes in relation to tree and grass abundances to better understand elephant dietary choice in the Kruger National Park, South Africa. A composited pair of Landsat Enhanced Thematic Mapper satellite images characterising flushed and senescent vegetation states, typical of wet and dry seasons respectively, were used to generate land-cover maps focusing on the forest to grassland gradient. Stable carbon isotope analysis of elephant faecal samples identified the proportion of C_3 (typically browse)/C_4 (typically grass) in elephant diets in the 1–2 days prior to faecal deposition. The proportion of surrounding C_4 land-cover was extracted using concentric buffers centred on faecal sample locations, and related to the faecal %C_4 content. Results indicate that elephants consume C_4 vegetation in proportion to its availability in the surrounding area during the dry season, but during the rainy season there was less of a relationship between C_4 intake and availability, as elephants targeted grasses in these periods. This study illustrates the utility of coupling isotope and cost-free remote sensing data to conduct complementary landscape analysis at highly-detailed, biologically meaningful resolutions, offering an improved ability to monitor animal behavioural patterns at broad geographical scales. This is increasingly important due to potential impacts of climate change and woody encroachment on broad-scale landscape habitat composition, allowing the tracking of shifts in species utilisation of these changing landscapes in a way impractical using field based methods alone.

INTRODUCTION

The manner in which large mammal herbivores interact with the plants they consume is central to the functioning of many terrestrial ecosystems (*De La Dantas et al., 2016*; *Gordon & Prins, 2019*). Plant consumption varies as a function of multiple processes including nutrient composition, phenological changes in availability, and life history traits of the consumer species. Such variation is often studied at fine scales ranging from habitat and patch quality down to bite size. However, large animals necessarily require information over large spatial scales as well (*Senft et al., 1987*). Furthermore, the processes that operate at, for instance, landscape levels may differ markedly from more proximate causes like plant nutrient content. This can be methodologically challenging. African savannas are characterised by still having mammalian megafaunal communities—at least in some protected areas—unlike most parts of the world where these communities are extinct (*Shorrocks & Bates, 2015*). Past work studying behavioural ecology of vertebrate communities often involved extensive field-based observations (*Kruuk, 2003*; *Birkhead, Wimpenny & Montgomerie, 2014*), and while this is a valuable research strategy it is time consuming and limited in the geographical extent over which these observations can be conducted. However, advances in technology allow other complimentary approaches to be applied over far larger areas, in greater detail and increasingly cost-effectively. Here, the power of such approaches is illustrated with a study combining remote sensing of vegetation and stable carbon isotope evidence designed to test the relationship between habitat and diet for the African savanna elephant (*Loxodonta africana*).

Megaherbivores in general, and elephants in particular, process large quantities of vegetation (often of poorer quality compared to the diets of smaller taxa sharing the same habitat) rather than being selective feeders (*Owen-Smith, 1988*). Indeed, such herbivores may play a considerable, and often underestimated, role in plant ecology (*Pausas & Bond, 2019*). These large animals require substantial quantities of vegetation, but in processing this bulk biomass are able to tolerate lower plant nutrient levels than most smaller herbivores (*Olff, Ritchie & Prins, 2002*; *Müller et al., 2013*; *Schmitt, Ward & Shrader, 2016*; *Schmitt et al., 2019*). This helps elephants tolerate a broad environmental range from desert to forest because they eat both browse and grass-based foods and can therefore maintain sufficient dry matter intake in a variety of habitats. Given the need to maintain very high intake rates, and their ability to eat both grass and tree products, one might expect elephant diets to reflect the availability of grass and browse in local environments. Indeed, there is evidence that more grass is eaten in open grassy environments, while browse is favoured in more wooded habitats (*De Boer et al., 2000*; *Scholes, Bond & Eckhardt, 2003*). Other studies, by contrast, did not find that elephant diets reflect the relative abundance of local vegetation (*Wing & Buss, 1970*; *Laws, Parker & Johnstone, 1974*; *Codron et al., 2011*), and suggest that elephants pursue strategies tending towards optimal foraging, that is those that maximise energy consumption and/or

minimise exposure to potentially toxic secondary compounds (*Jachmann & Bell, 1985*; *Stokke & Du Toit, 2000*; *Codron et al., 2011*; *Kos et al., 2012*; *Pretorius et al., 2012*; *Schmitt et al., 2019*).

One potential reason for such contradictions in the studies above is that it is difficult, if not nearly impossible, to track diet and habitat at the spatial and temporal scales necessary to address the question. For instance, broad-scale habitat data, which are frequently used for such studies (*Codron et al., 2011*), may be too coarse to capture the scale at which elephants make foraging decisions (*Shrader et al., 2012*; *Schmitt, Ward & Shrader, 2016*; *Schmitt et al., 2019*). By contrast, one can get highly detailed habitat descriptions from spatially restricted sites, but it would be impractical to do this at a great many sites, especially while obtaining feeding data from each. Remote sensing, however, offers unique opportunities for mapping land-cover and quantifying vegetation characteristics over broad geographical areas at a variety of spatial, temporal and spectral scales. The increasing availability of cost-free satellite imagery means that it is now possible to conduct complementary landscape analysis linking forage availability to megafauna feeding behaviour over a large number of sites at multiple scales. Here, reanalysis of the isotope data in *Codron et al. (2011)* was performed using more detailed vegetation data than was available in the original study (the original study used ground-based estimates of biomass from routine ongoing monitoring programmes, which had limited spatial resolution). This investigation coupled carbon isotope analysis of faeces from the Kruger National Park (KNP), South Africa, which quickly and inexpensively provided information on proportions of browse: grass (C_3:C_4 plant biomass) eaten within the last 1–2 days, with remote sensing, which provided data on relative amounts of grassy vegetation at scales relevant to the daily foraging of elephants, as a way to explore links between foraging behaviour and habitat.

MATERIALS AND METHODS

Remote sensing

African savanna vegetation often exhibits large contrasts between dry and wet seasons. Herbaceous vegetation is generally only green during the rainy season with senescence occurring shortly afterwards, whereas most woody plants remain photosynthetically active over larger parts of the year (*Brandt et al., 2016*). Analysis using single-date imagery alone can have limitations in discriminating between woody and herbaceous vegetation, which can be spectrally similar at certain times of year (*Marston et al., 2017*). To overcome this, and to quantify the varying levels of grassy vs. woody cover within the KNP study area, a pair of Landsat Enhanced Thematic Mapper (ETM+) satellite images (path 168 row 77), one acquired while herbaceous vegetation was senescent (18 June 2002) and one when grasses remained flushed (3 May 2003), were used in combination to generate a 30 m resolution land-cover map of the study area. Using a pair of images characterising vegetation state in both senescent and flushed states offered improved discrimination of woody and herbaceous vegetation based on their phenological differences. Both these image-acquisition dates fell within the period of faecal field sampling. Although the Landsat ETM+ 30 m spatial resolution precludes identification of individual trees and

shrubs, *Marston et al. (2017)* illustrated that land-cover classifications of African savannas generated using Landsat ETM+ imagery are remarkably congruent with classifications of the same locations generated from very high resolution IKONOS and WorldView-2 imagery (which can identify individual shrubs and trees), despite some loss of spatial detail. Medium resolution Landsat ETM+ imagery is, therefore, considered appropriate for broad-scale land-cover mapping of heterogeneous African savannas.

The Landsat ETM+ surface reflectance data product, which is pre-orthorectified and atmospherically corrected, was used for this study. Further image pre-processing steps were performed using ERDAS Imagine to ensure data quality was maintained. These included: error detection and recording; cloud and cloud shadow masking; and finally compositing of the senescent and flushed vegetation images into a single dual-date composite image (*Morton et al., 2011*). For both images spectral bands 1 (blue, 0.45–0.52 μm wavelength), 2 (green, 0.52–0.60 μm), 3 (red, 0.63–0.69 μm), 4 (near infra-red 1, 0.77–0.90 μm), 5 (short-wave infra-red 1, 1.55–1.75 μm) and 7 (short-wave infra-red 2, 2.09–2.35 μm) were used. The composite image was projected in the Universal Transverse Mercator WGS84 zone 36 south coordinate system.

To generate training and validation data for the image classification, expert interpretation of high-resolution reference satellite imagery of the study area available via public portals such as Google Earth was used to identify locations of known land-cover types. The use of very high-resolution imagery such as that available via Google Earth as a data source for the training and validation of land-cover classifications derived from coarser resolution satellite data (such as the Landsat ETM+ imagery used here) has become an established technique (*Cihlar et al., 2003*; *Xie, Sha & Yu, 2008*; *Duro, Franklin & Dube, 2012*). As the acquisition dates of the Landsat ETM+ imagery and the high-resolution imagery used as a reference data source are not coincident, any areas where suspected temporal change or disturbance had occurred in the time-period between Landsat and high-resolution imagery acquisition were disregarded as a source of reference data.

For each land-cover class, the reference data points were allocated on an alternating basis as training or validation locations, which created two equal-sized datasets providing 410 locations for both the training and validation datasets (820 in total) distributed across all land-cover classes. Both training and validation datasets comprised 50 locations for each land-cover class except agriculture and closed coniferous woodland, which had 30 locations each. These two classes had lower availability of reference data due to their more restricted coverage when compared to the other land-cover classes. Although these classes were present within the Landsat image extent, they were not present within the KNP boundary which is of interest in this study. For the training data, training locations were used to generate reference polygons where spectral homogeneity allowed. Validation data was retained as point locations for classification accuracy assessment.

The classification nomenclature employed was based on a modified version of the Global Land Cover 2000 Land Cover Map of Africa classification system (*Mayaux et al., 2004*), classifying the forest–grassland gradient into 25% intervals (Table 1). Given the particular focus on the proportion of woody cover and grassland, the classification nomenclature followed the approach of *Torello-Raventos et al. (2013)*, which stratified

Table 1 Land cover map classification nomenclature.

General habitat	Land cover class and code
Woodland	Closed deciduous woodland (CDW) (75–100% woody cover)
	Open deciduous woodland (ODW) (50–75% woody cover)
Grassland	Discontinuous grassland (DG) (25–50% woody cover)
	Continuous grassland (CG) (0–25% woody cover)
Anthropogenic classes	Agriculture (AG)
	Built-up (BU)
	Closed coniferous woodland (CCW) (non-indigenous forestry plantations)
Bare	Bare ground (BA)
Water	Water (W)

this gradient into five forest to grassland categories at 25% intervals, with the final interval at 0–5% forest. Here, the 0–5% class was amalgamated with the 5–25% class, forming a 0–25% interval class. Although not all of the land-cover classes in the classification nomenclature were used for subsequent analysis given the focus on the woodland–grassland gradient, these classes were included at the classification stage to be representative of the land-cover types found across the extent of the imagery coverage, including areas outside the KNP boundary. The land-cover classifications were performed using a random forest classifier in R, using the random Forest package (*Liaw & Wiener, 2002*). Classification accuracy assessment was subsequently performed using the validation dataset.

Land-cover data were extracted for a series of concentric circular buffers surrounding each isotope sample site (see below) of radius sizes 2, 4, 8 and 12 km. The proportion of each land-cover class was calculated using the ArcMap 10.2 and Geospatial Modelling Environment software packages.

Stable isotopes

Faecal isotope data for elephants are derived from specimens collected from south of the Olifants River in the KNP, South Africa, from June 2002 until January 2005–a period of average rainfall, falling outside climatically extreme periods of severe drought (1991–1992 and 2014–2016), or high rainfall years (1999–2000) in the park (*MacFadyen et al., 2018*; *Staver, Wigley-Coetsee & Botha, 2019*). Faecal sampling protocols were permitted by South African National Parks and carried out in accordance with their guidelines for fieldwork. Specimens were obtained across four sub-regions representing a variety of savanna landscape types across the southern portion of Kruger Park (Fig. 1), and include collections made at monthly and at seasonal (biannual) resolutions (*Codron et al., 2011*). For the first 2 years, collections were made biannually, once in the dry season and once in the wet. Thereafter, sampling was carried out at monthly intervals, with the aim of collecting at least 10 individual faecal specimens per study region per month. Only recent faeces (i.e. fresh or damp) were collected. Each specimen encountered was assumed to represent a separate individual, a reasonable assumption because no more than a single sub-region was sampled per day. Further, because only fresh material was collected, it is
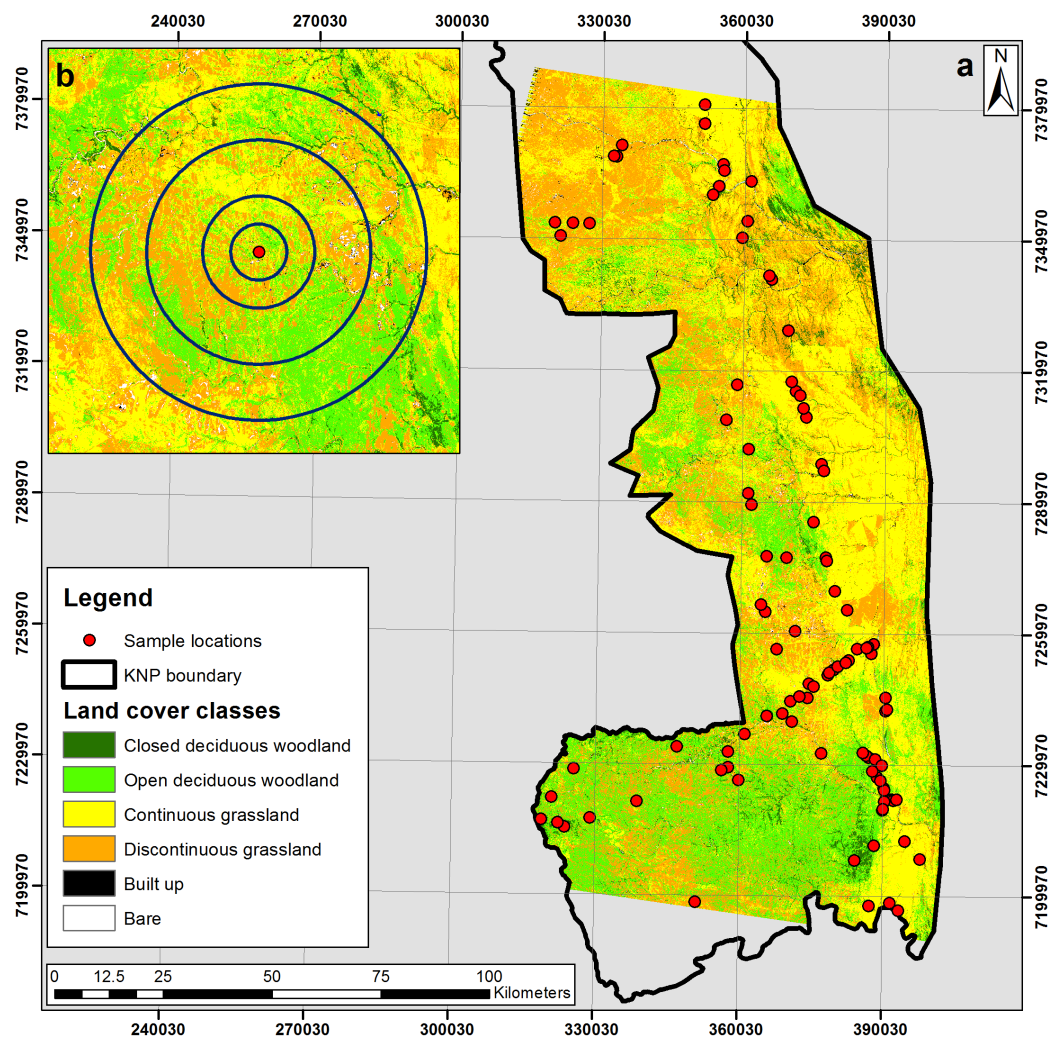
Figure 1 (A) Land cover classification of the southern Kruger National Park study area; and (B) inset image displaying 2 km, 4 km, 8 km and 12 km concentric buffers surrounding an isotope sample location. Full-size ▣ DOI: 10.7717/peerj.8622/fig-1

unlikely that sampling of multiple individuals per day was a frequent occurrence. However, because sampling was opportunistic, the demographic status of individuals could not be ascertained.

Faeces were oven-dried at 60 °C for 24 h and then ground through a one mm sieve to a homogeneous powder. Samples were combusted individually in an automated elemental analyser (Carlo–Erba, Milan, Italy), and the resultant CO_2 gas introduced to a mass spectrometer (MAT 252 or DELTA XP; Finnigan, Bremen, Germany) using a continuous flow-through inlet system. $^{13}C/^{12}C$ ratios were presented in delta (δ) notation, in per mill (‰) relative to the VPDB (Venice Pee Dee Belemnite) standard (Table S1). Standard deviations of repeated measurements of internal and interlaboratory plant and protein standards were less than 0.1%. The results were converted to estimates of %C_4 food intake using a linear mixing model that accounted for predicted diet-faeces isotopic

discrimination effects and known spatial and temporal changes in plant carbon isotope compositions (see *Codron et al., 2011* for full methodology).

Range sizes

Elephants feed throughout the day, with gut retention time in captive African elephants recorded as less than 30 h (*Hackenberger, 1987*; *Clauss et al., 2007*). *Thomas, Holland & Minot (2012)* presented several years of GPS data collected on three female elephants in the southern KNP, which gave a mean minimum daily distance moved of about 4 km. These values were used to analyse the land-cover within a series of concentric buffers related to the likely range from which the faecal samples were derived over the course of a day (4 km) as well as smaller (2 km) and larger (8 and 12 km) range sizes (Fig. 1). The land-cover data were then correlated with the stable isotope results with permutation tests performed to determine whether or not there is any relationship between the proportion of C_4 in the environment and the proportion of C_4 in the diet.

Grassiness index

As the Landsat imagery is medium resolution (30×30 m per pixel) it is not possible to discriminate individual trees. Therefore, the land-cover classification calculated the proportion of woody cover within each pixel on a 4-point scale: closed deciduous woodland (>75% woody cover), open deciduous woodland (50–75% woody cover), discontinuous grassland (25–50% woody cover) and continuous grassland (<25% woody cover). A 'grassiness index' was calculated by multiplying the percentage of relevant land-covers per buffer by a modifier (from ×1 for closed woodland to ×4 for open grassland) and then summing them together. Therefore for a given percentage of pixels in a buffer 'continuous grassland' would contribute four times more to the index than would closed deciduous woodland; so buffers with higher values contain more grass than those with lower values. Of the many potential indices that could be devised this one has the virtue of simplicity (*Murtaugh, 2007*), and importantly was decided on in advance of any quantitative analyses to avoid the danger of trying multiple indices before settling on the one with the most interesting results (*Amrhein, Trafimow & Greenland, 2019*). Once calculated, the grassiness index for each sample and buffer size was plotted against the %C_4 from the faecal samples.

The hypothesis that elephant %C_4 intake is related to grassiness in the landscape was tested using simple linear regressions of estimated %C_4 in the diet on the grassiness index for each sampling locality and time interval (month). However, this analysis may not be robust to bias introduced by the fact that most localities (128 of 194) are represented by more than one faecal specimen (in fact, more than a third of localities were presented by four or more faecal specimens, in any given sampling interval). Therefore, permutations tests were used, by randomising the data for each locality and sampling interval, and summarising the regression results over 10^3 iterations. This allowed us to compute permuted means and 95% confidence limits for the regression parameters r^2, the intercept (a), and slope (b) that were unbiased with respect to repeated collections at a

Table 2 Land cover classification confusion matrix. The land cover classification is compared to validation locations of known land cover type ($n = 410$), with overall classification accuracy high at 90.73%. For the key woodland and grassland classes of interest, class-specific accuracies were generally high with closed deciduous woodland, open deciduous woodland and continuous grassland all displaying producer's accuracies at or over 90%, and user's accuracies over 83%. Discontinuous grassland had lower accuracies of 76% and 77.55% for producer's and user's accuracies respectively. Land cover class abbreviations: CDW, closed deciduous woodland; ODW, open deciduous woodland; CG, continuous grassland; DG, discontinuous grassland; AG, agriculture; BU, built-up; CCW, closed coniferous woodland; BA, bare; and W, water. UA, Users Accuracy; PA, Producers accuracy.

Classified data	Reference data									
	CDW	ODW	CG	DG	AG	BU	CCW	BA	W	UA (%)
CDW	49	3	0	2	3	0	0	0	0	85.96
ODW	0	45	0	5	2	0	2	0	0	83.33
CG	0	0	48	5	0	2	0	0	0	87.27
DG	0	2	2	38	0	7	0	0	0	77.55
AG	1	0	0	0	25	0	0	0	0	96.15
BU	0	0	0	0	0	40	0	1	0	97.56
CCW	0	0	0	0	0	0	28	0	0	100.00
BA	0	0	0	0	0	0	0	49	0	100.00
W	0	0	0	0	0	1	0	0	50	98.04
PA (%)	98.00	90.00	96.00	76.00	83.33	80.00	93.33	98.00	100.00	
Overall accuracy (%) = 90.73										

given locality. Significance tests were based on Monte Carlo analysis of resultant model p-values, where (with α-level set at 0.05):

$$\hat{p} = 1 - \frac{\text{sum of models with } p < 0.05}{10^3}$$

Models were repeated for all the data combined, as well as for wet and dry season data separately. A similar Monte Carlo approach was used to compare r^2 and b of the two seasons, but in this case the resultant p-values were divided by two for a one-tailed test, with the null hypothesis: dry ≤ wet season. These procedures were repeated for grassiness values obtained from each of the four buffer sizes for comparison. Regression models and the permutation algorithm were carried out using R v 3.5.2 (*R Core Team, 2015*).

RESULTS

The land-cover classification generated, clipped to the area of the KNP, is displayed in Fig. 1. The land-cover class coverages within this clipped area comprised 40.69% continuous grassland, 32.58% discontinuous grassland, 21.56% open deciduous woodland, 4.10% closed deciduous woodland, 0.57% bare ground, 0.36% built-up and 0.13% water. The overall accuracy of the classification was 90.73%, with a detailed confusion matrix presented in Table 2.

Monte Carlo one-tailed permutation tests showed relationships between %C_4 intake and grassiness to be positive regardless of season (Fig. 2). However, models only met the conventional significance level ($p < 0.05$) when using data for dry seasons or, usually, both
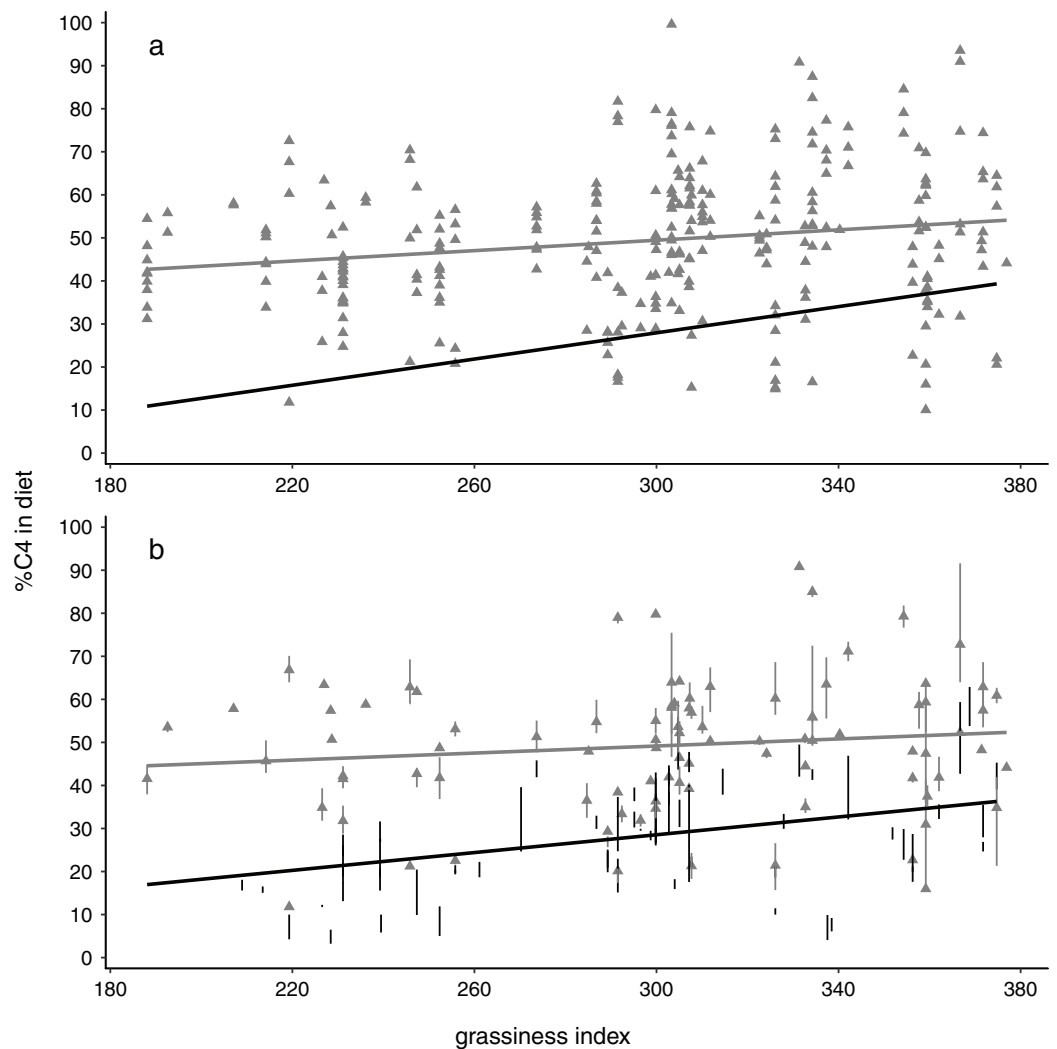
Figure 2 Relationships between %C₄ grass in elephant diets with availability of grass in the landscape, depicted showing (A) all data points and (B) means and interquartile ranges for each collection locality. Note the steeper slopes and stronger relationships for dry season data (black circles, black regression lines) compared with wet season data (grey triangles, grey lines). All results shown here are for the 4 km buffer size. Full-size ⬛ DOI: 10.7717/peerj.8622/fig-2

seasons combined (Table 3). Wet-season models were non-significant and concomitantly had substantially smaller slopes and r^2 values than models for the dry season. Interestingly, the slopes of these models tended to increase with increases in buffer size, at least in the case of dry season data (non-overlapping confidence estimates in Table 3). This implies that, in terms of the predicted relationship between diet and habitat structure, the effect becomes increasingly apparent over larger spatial scales. Note that the size of the effects (slope and r^2) are likely much more biologically meaningful than the p-values (significance values) (*Nakagawa & Cuthill, 2007*).

A possible factor in the analysis is the presence of water (such as boreholes or waterholes) within the buffer. These are more likely to have more grass surrounding them, contrasting with rivers which are more likely to have riparian woodlands.

Table 3 **Permutation test permuted means and 95% confidence limits for the regression parameters r^2, intercept, and slope (b) and significance test p-values.** n = number of observations per location; regression parameters are shown as means with 95% confidence intervals in parentheses; p-values are derived from Monte Carlo simulations of 10^3 randomised permutations, adjusted to one-tailed equivalents for the last two columns; significant models are shown in bold.

Buffer size (km)	Season	n	r^2	Intercept	Slope (b)	model	$r^2_{dry > wet}$	$b_{dry > wet}$
2	Both	194	**0.0359 (0.0353–0.0364)**	**17.0890 (16.9196–17.2584)**	**0.0710 (0.0704–0.0716)**	**0.022**		
2	Dry	101	0.0613 (0.0602–0.0624)	8.0449 (7.8404–8.2494)	0.0687 (0.0681–0.0694)	0.086		
2	Wet	93	0.0172 (0.0165–0.0179)	36.7310 (36.4762–36.9858)	0.0413 (0.0404–0.0422)	0.962	<0.0001	<0.0001
4	Both	194	**0.0424 (0.0418–0.0430)**	**13.7514 (13.5721–13.9308)**	**0.0819 (0.0813–0.0826)**	**<0.01**		
4	Dry	101	**0.1202 (0.1187–0.1218)**	**−2.3335 (−2.5697–2.0973)**	**0.1029 (0.1021–0.1037)**	**<0.0001**		
4	Wet	93	0.0160 (0.0153–0.0167)	36.7965 (36.5121–37.0810)	0.0412 (0.0402–0.0422)	0.969	<0.01	0.036
8	Both	194	**0.0373 (0.0367–0.0379)**	**12.1572 (11.9360–12.3785)**	**0.0881 (0.0873–0.0889)**	**0.026**		
8	Dry	101	**0.1349 (0.1333–0.1365)**	**−9.3957 (−9.6741–9.1174)**	**0.1271 (0.1262–0.1281)**	**<0.0001**		
8	Wet	93	0.0141 (0.0135–0.0148)	36.3013 (35.9753–36.6273)	0.0434 (0.0422–0.0446)	0.988	<0.0001	<0.01
12	Both	194	0.0257 (0.0252–0.0261)	14.9687 (14.7473–15.1901)	0.0803 (0.0795–0.0811)	0.237		
12	Dry	101	**0.1189 (0.1176–0.1203)**	**−10.9163 (−11.1901–10.6424)**	**0.1341 (0.1331–0.1350)**	**<0.0001**		
12	Wet	93	0.0235 (0.0227–0.0244)	30.8930 (30.5453–31.2408)	0.0634 (0.0621–0.0647)	0.890	<0.0001	<0.0001

Significance tests (p-values) span the last three columns (model, $r^2_{dry > wet}$, $b_{dry > wet}$).

DISCUSSION

These results are consistent with elephant diets tracking the proportion of grass in the habitat, but only during periods where grass quality and/or availability is low, that is during the dry season. This potentially harmonises seemingly contrasting suggestions that elephants select vegetation in proportion to its abundance (*De Boer et al., 2000*; *Scholes, Bond & Eckhardt, 2003*; *Owen-Smith & Chafota, 2012*; *Schmitt, Ward & Shrader, 2016*; *Schmitt et al., 2019*) with reports that they selectively consume grass (*Guy, 1976*; *Owen-Smith, 1988*). It appears that both assertions are true in the KNP depending on season. On balance, however, it may be best to categorise these elephants as selective feeders that are capable of maintaining broader diets when dealing with some form of constraint–in this case the low quality and/or abundance of grass in the dry season. This is also broadly consistent with other reports that elephants are selective feeders that eat large quantities of grass in the wet season and switch to woody plant species, and a variety of low-quality plant parts, in the dry season (*Barnes, 1982*; *Owen-Smith & Chafota, 2012*). More proximate factors such as soil geochemistry (and its effects on plant nutrient content) and avoidance of secondary metabolites in woody vegetation (*Schmitt, Ward & Shrader, 2016*; *Schmitt et al., 2019*) may also play a role in food selection, although it is unclear that such fine-scale foraging decisions occur over landscape scales—the scale of our study. Moreover, we observed that the influence of grass availability on grass intake became increasingly apparent over broader spatial scales, which could imply that decisions about whether to eat browse or grass are constrained only by relative availability, whereas finer-scale decisions determine which plant species or organs are consumed.

The idea that animals may forage in an optimal manner—or at least tend towards optimal foraging—dates back to the mid 1960's but was developed in more theoretical

detail during the 1970's (*Krebs & McCleery, 1984*). In this context, the tendency towards higher grass consumption with increased availability might be expected, at least across woodland to grassland environments, as grasses tend to be fairly continuously distributed across such landscapes (hence available in bulk), are probably more consistent in nutritional value (i.e. they have no indigestible woody parts), and probably allow higher harvesting rates. These qualities outweigh, or at least match, potential losses of grazing given the low nutrient content of grasses (*Hummel et al., 2006*). Because grasses can be consumed without the woody stems that often accompany elephant tree-leaf consumption (*Owen-Smith & Chafota, 2012*), digestible dry-matter intake should typically be higher when elephants consume grasses. The non-preference for grasses during the dry season implies that nutritional and harvesting benefits for grass relative to browse becomes neutral during this time, resulting in diets which are largely a function of relative availability of the resource, that is encounter rate. Thus, one might predict, for instance, that in areas where grass stays green for the greater part of the year due to close proximity to permanent water, there may be no relationship between diet and habitat even seasonally. A strong preference for grasses makes sense given that the elephant dental morphology appears to be an adaptation for grass consumption (*Lister, 2013*), and that carbon isotope evidence from the enamel of post-Miocene fossil elephantids from Africa shows a strong preference for C_4 grasses (*Cerling, Harris & Leakey, 1999*). In this light, the high levels of browse consumption by many modern elephant populations seem puzzling (for example, in our study C_3 browsing is a major part of the diet—Fig. 2). Evidently, elephants readily bulk up their diets with grasses when this resource is available, seemingly favouring this feeding style when resources are not limiting, as in our rainy season data.

Nonetheless, it is worth noting that our results are somewhat different from those presented in *Codron et al. (2011)* which, using the same carbon isotope dataset, found no evidence that elephant browse and grass consumption tracked local availability. One possible reason for this is that the current study focused on the southern portion of KNP, whereas the former included the northern region in which the tree communities are dominated by a single-species: mopane *Colophospermum mopane*. Given the high concentration of defensive secondary compounds in mopane (*Styles & Skinner, 2000*; *Kohi et al., 2010*), and the tendency of many (but certainly not all) animals to avoid high loads of such anti-feedants by diversifying their diets (*Freeland & Janzen, 1974*; *Wiggins, McArthur & Davies, 2006*; *Torregrossa, Azzara & Dearing, 2011*; *Wilkinson & Sherratt, 2016*), elephants might under-utilize mopane. Such a foraging behaviour would necessitate greater consumption of grasses in habitats such as the northern KNP, and consequently reduce any relationship between browse/graze consumption and availability for the park as a whole. Indeed, *Codron et al. (2011)* suggested a limited effect of mopane on increasing grass consumption—the effect size in this case was probably reduced by including data from southern KNP. *Kos et al. (2012)*, however, found no evidence that elephants restricted their use of mopane in a study in a reserve adjacent to KNP–speculating that the extent to which elephants avoid this tree may be affected by the availability of other plants in the area. One possibility is that elephants may in some

situations need to include other plant species to access micro-nutrients which may be scarce in the dominant plant species (*Westoby, 1978*).

Another reason for the difference between the current study and that of *Codron et al. (2011)* is that for the latter, vegetation-cover data were based on calculated averages across large areas, so may not have reflected the actual areas in which the elephants were feeding and depositing the faecal samples, while the present study used habitat data at a much finer resolution. This illustrates the importance of coupling isotope and remote-sensing data. Carrying out ground-based vegetation surveys for the more than 1,000 faecal samples from 149 collection sites in *Codron et al. (2011)* would have been extremely impractical, time intensive and expensive. Here, by contrast, once the satellite imagery had been classified and the models were validated, extracting grassiness index data from the land-cover classification for each site was comparatively trivial. It is, however, acknowledged that further work is also needed to investigate how variations in ranging patterns may influence observed results.

The increasing availability of cost-free remote sensing imagery, along with the improving image spatial resolution and temporal repeat coverage, means that future work could enable the characterisation of land-cover, and therefore food resources (using the methods presented here), at multiple dates throughout the year where cloud-free imagery allows. Therefore, seasonal changes in the relative C_3 and C_4 availability within a landscape can potentially be quantified, and in turn related to isotopic values derived from faecal sampling conducted in different seasons. Along with the ability to perform multi-scale examination of the landscape around faecal sampling points using different buffer sizes, this creates a highly flexible tool which, complementary to existing methods, offers an improved ability to monitor and predict animal behavioural patterns at broad geographical scales. This is increasingly important due to the potential impacts of climate and other environmental changes such as woody encroachment on broad-scale landscape habitat composition (*Warren et al., 2001*; *Huntley et al., 2016*), as the use of isotope data in combination with remote-sensing analysis will be able to track shifts in species utilisation of these changing landscapes. These methods are also transferable both to other geographical areas, and to other species. The ability to apply multiple scales of observation guided by established species-specific home ranges is also useful where there is a potential disconnect between where animals are feeding and defaecating. For example, in our study the massive size and large daily ranging pattern of elephants creates a potential disconnect between foraging and defaecation sites which could lead to ambiguity in linking diet with habitat. Despite this, significant correlations were found between grassiness and C_4 intake at all buffer sizes, with the strongest correlations observed for the 4 and 8 km buffer sizes. We would argue that this result is robust given that it persists across buffer sizes. This result suggests that the uncertain relationship between where the elephants ate and where they defaecated does not present a confounding factor at least for this species and/or at this spatial scale of sampling. It can thus be predicted that our approach would yield even more accurate results for smaller-bodied species that travel over shorter distances than elephants.

CONCLUSIONS

Our results suggest that one reason for the sometimes contradictory results in studies of feeding selectivity in elephants is that there is variation in preference throughout the year. In our study, elephants consumed C_4 vegetation in proportion to its availability in the surrounding area during the dry season, but during the rainy season there was less of a relationship between C_4 intake and availability as elephants targeted grasses in these periods. Over the last few decades various technological advances (for example, GPS collars, camera traps, DNA technology) have greatly added to the ease of collecting some types of data in behavioural ecology and conservation biology (*Schaller, 2012*). Here, we demonstrated the utility of comparing isotopes and remote sensing. Clearly, any study utilising isotopes is considering diet in a very coarse way compared to direct observational studies or models which make use of data on plant consumption at the species level (*Schmitt, Ward & Shrader, 2016*), which can focus on both species and plant part consumed. Studies such as the above will never supplant these traditional studies given the rich detail they provide, and the very different questions they can address. However, the importance of the approach outlined in this paper is that it allows us to address diets of wildlife species over a very large and vegetationally heterogeneous area—greatly increasing the data available to inform management in the face of an often rapidly changing world. The potential of this approach is shown by the way it potentially explains contradictory results in previous studies of elephant foraging.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

Matt Sponheimer is an Academic Editor for PeerJ.

Author Contributions

- Christopher G. Marston conceived and designed the experiments, performed the experiments, analysed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- David M. Wilkinson conceived and designed the experiments, analysed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Matt Sponheimer conceived and designed the experiments, performed the experiments, analysed the data, authored or reviewed drafts of the paper, and approved the final draft.

- Daryl Codron conceived and designed the experiments, performed the experiments, analysed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Jacqui Codron conceived and designed the experiments, performed the experiments, analysed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Hannah J. O'Regan conceived and designed the experiments, analysed the data, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw data are available as a Supplemental File. This includes stable carbon isotope data, sampling locations and proportional land cover class coverage within 2, 4, 8 and 12 km buffered areas centred on each sampling location respectively.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.8622#supplemental-information.

REFERENCES

Amrhein V, Trafimow D, Greenland S. 2019. Inferential statistics as descriptive statistics: there is no replication crisis if we don't expect replication. *American Statistician* **73(Suppl. 1)**:262–270 DOI 10.1080/00031305.2018.1543137.

Barnes RFW. 1982. Elephant feeding behaviour in Ruaha National Park, Tanzania. *African Journal of Ecology* **20(2)**:123–136 DOI 10.1111/j.1365-2028.1982.tb00282.x.

Birkhead T, Wimpenny J, Montgomerie B. 2014. *Ten thousand birds; ornithology since Darwin.* Princeton: Princeton University Press.

Brandt M, Hiernaux P, Tagesson T, Verger A, Rasmussen K, Diouf AA, Mbow C, Mougin E, Fensholt R. 2016. Woody plant cover estimation in drylands from Earth Observation based seasonal metrics. *Remote Sensing of Environment* **172**:28–38 DOI 10.1016/j.rse.2015.10.036.

Cerling TE, Harris JM, Leakey MG. 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Oecologia* **120(3)**:364–374 DOI 10.1007/s004420050869.

Cihlar J, Latifovic R, Beaubien J, Guindon B, Palmer M. 2003. Thematic mapper (TM) based accuracy assessment of a land cover product for Canada derived from SPOT VEGETATION (VGT) data. *Canadian Journal of Remote Sensing* **29(2)**:154–170 DOI 10.5589/m02-091.

Clauss M, Streich WJ, Schwarm A, Ortmann S, Hummel J. 2007. The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. *Oikos* **116(2)**:209–216 DOI 10.1111/j.0030-1299.2007.15461.x.

Codron J, Codron D, Lee-Thorp JA, Sponheimer M, Kirkman K, Duffy KJ, Sealy J. 2011. Landscape-scale feeding patterns of African elephant inferred from carbon isotope analysis of feces. *Oecologia* **165(1)**:89–99 DOI 10.1007/s00442-010-1835-6.

De Boer WF, Ntumi CP, Correia AU, Mafuca JM. 2000. Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology* **38(3)**:188–201 DOI 10.1046/j.1365-2028.2000.00243.x.

De La Dantas V, Hirota M, Oliveira RS, Pausas JG. 2016. Disturbance maintains alternative biome states. *Ecology Letters* **19(1)**:12–19 DOI 10.1111/ele.12537.

Duro DC, Franklin SE, Dube MG. 2012. Multi-scale object-based image analysis and feature selection of multi-sensor earth observation imagery using random forests. *International Journal of Remote Sensing* **33(14)**:4502–4526 DOI 10.1080/01431161.2011.649864.

Freeland WJ, Janzen DH. 1974. Strategies in herbivory in mammals: the role of plant secondary compounds. *American Naturalist* **108(961)**:269–289 DOI 10.1086/282907.

Gordon IJ, Prins HHT. 2019. *The ecology of browsing and grazing II*. Cham: Springer.

Guy PR. 1976. The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa area, Rhodesia. *South African Journal of Wildlife Research* **6**:55–63.

Hackenberger MK. 1987. Diet digestibilities and ingesta transit times of captive Asian and African elephants. M.Sc thesis, The University of Guelph, Guelph.

Hummel J, Südekum K-H, Streich WJ, Clauss M. 2006. Forage fermentation patterns and their implications for herbivore ingesta retention times. *Functional Ecology* **20(6)**:989–1002 DOI 10.1111/j.1365-2435.2006.01206.x.

Huntley B, Collingham YC, Singarayer JS, Valdes PJ, Barnard P, Midgley GF, Altwegg R, Ohlemuller R. 2016. Explaining patterns of avian diversity and endemicity: climate and biomes of southern Africa over the last 140,000 years. *Journal of Biogeography* **43(5)**:874–886 DOI 10.1111/jbi.12714.

Jachmann H, Bell RHV. 1985. Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology* **23(4)**:245–258 DOI 10.1111/j.1365-2028.1985.tb00955.x.

Kohi EM, De Boer FW, Slot M, Van Wieren SE, Ferwerda JG, Grant RC, Heitkonig IMA, De Knegt HJ, Van Der Waal C, Prins HHT. 2010. Effects of simulated browsing on growth and leaf chemical properties in *Colophospermum mopane* saplings. *African Journal of Ecology* **48(1)**:190–196 DOI 10.1111/j.1365-2028.2009.01099.x.

Kos M, Hoetmer AJ, Pretorius Y, De Boer WF, De Knegt H, Grant CC, Kohi E, Page B, Peel M, Slotow R, Van Der Waal C, Van Wieren SE, Prins HHT, Van Langevelde F. 2012. Seasonal diet changes in elephant and impala in mopane woodland. *European Journal of Wildlife Research* **58(1)**:279–287 DOI 10.1007/s10344-011-0575-1.

Krebs JR, McCleery RH. 1984. Optimization in behavioural ecology. In: Krebs JR, Davies NB, eds. *Behavoural Ecology: An Evolutionary Approach*. Second Edition. Oxford: Blackwell, 91–121.

Kruuk H. 2003. *Niko's nature*. Oxford: Oxford University Press.

Laws RM, Parker ISC, Johnstone RCB. 1974. *Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda*. Oxford: Clarendon.

Liaw A, Wiener M. 2002. Classification and regression by random Forest. *R News* **2**:18–22.

Lister AM. 2013. The role of behaviour in adaptive morphological evolution of African proboscideans. *Nature* **500(7462)**:331–334 DOI 10.1038/nature12275.

MacFadyen S, Zambatis N, Van Teefelen AJA, Hui C. 2018. Long-term rainfall regression surfaces for the Kruger National Park, South Africa: a spatio-temporal review of patterns from 1981 to 2015. *International Journal of Climatology* **38(5)**:2506–2519 DOI 10.1002/joc.5394.

Marston CG, Aplin P, Wilkinson DM, Field R, O'Regan H. 2017. Scrubbing up: multi-scale investigation of woody encroachment in a Southern African Savannah. *Remote Sensing* **9(5)**:419 DOI 10.3390/rs9050419.

Mayaux P, Bartholome E, Fritz S, Belward A. 2004. A new land-cover map of Africa for the year 2000. *Journal of Biogeography* **31(6)**:861–877 DOI 10.1111/j.1365-2699.2004.01073.x.

Morton D, Rowland C, Wood C, Meek L, Marston C, Smith G, Wadsworth R, Simpson IC. 2011. Final Report for LCM2007 - the new UK land cover map. Countryside Survey Technical Report No 11/07 NERC/Centre for Ecology & Hydrology (CEH Project Number: C03259) 112.

Murtaugh PA. 2007. Simplicity and complexity in ecological data analyses. *Ecology* **88(1)**:56–62 DOI 10.1890/0012-9658(2007)88[56:SACIED]2.0.CO;2.

Müller DWH, Codron D, Meloro C, Munn A, Schwarm A, Hummel J, Clauss M. 2013. Assessing the Jarman–Bell Principle: Scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **164(1)**:129–140 DOI 10.1016/j.cbpa.2012.09.018.

Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews of the Cambridge Philosophical Society* **82(4)**:591–605 DOI 10.1111/j.1469-185X.2007.00027.x.

Olff H, Ritchie ME, Prins HHT. 2002. Global environmental controls of diversity in large herbivores. *Nature* **415(6874)**:901–904 DOI 10.1038/415901a.

Owen-Smith N. 1988. *Megaherbivores: the influence of large body size in ecology*. Cambridge: Cambridge University Press.

Owen-Smith N, Chafota J. 2012. Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). *Journal of Mammalogy* **93(3)**:698–705 DOI 10.1644/11-MAMM-A-350.1.

Pausas JG, Bond WJ. 2019. Humboldt and the reinvention of nature. *Journal of Ecology* **107(3)**:1031–1037 DOI 10.1111/1365-2745.13109.

Pretorius Y, Stigter JD, De Boer WF, Van Wieren SE, De Jong CB, De Knegt HJ, Grant CC, Heitkönig I, Knox N, Kohi E, Mwakiwa E, Peel MJS, Skidmore AK, Slotow R, Van Der Waal C, Van Langevelde F, Prins HHT. 2012. Diet selection of African elephant over time shows changing optimization currency. *Oikos* **121(12)**:2110–2120 DOI 10.1111/j.1600-0706.2012.19680.x.

R Core Team. 2015. *R: A language and environment for statistical computing*. Vienna: The R Foundation for Statistical Computing. *Available at* http://www.R-project.org/.

Schaller GB. 2012. *Tibet wild*. Washington: Island Press.

Schmitt MH, Shuttleworth A, Shrader AM, Ward AM. 2019. The role of volatile secondary metabolites as pre-ingestive cues and potential toxins dictating diet selection by African elephants. *Oikos* **129(1)**:24–34 DOI 10.1111/oik.06665.

Schmitt MH, Ward D, Shrader AM. 2016. Incorporating secondary metabolites, tannin-binding proteins, and diet breadth into carrying-capacity models for African elephants. *Ecological Modelling* **332**:8–18 DOI 10.1016/j.ecolmodel.2016.03.016.

Scholes RJ, Bond WJ, Eckhardt HC. 2003. Vegetation dynamics in the Kruger ecosystem. In: du Toit JT, Rogers KH, Biggs HC, eds. *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Washington, D.C.: Island Press, 242–262.

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* **37(11)**:789–799 DOI 10.2307/1310545.

Shorrocks B, Bates W. 2015. *The biology of African savannahs*. Second Edition. Oxford: Oxford University Press.

Shrader AM, Bell C, Bertolli L, Ward D. 2012. Forest or the trees: at what scale do elephants make foraging decisions? *Acta Oecologica* **42**:3–10 DOI 10.1016/j.actao.2011.09.009.

Staver AC, Wigley-Coetsee C, Botha J. 2019. Grazer movements exacerbate grass declines during drought in an African savanna. *Journal of Ecology* **107(3)**:1482–1491 DOI 10.1111/1365-2745.13106.

Stokke S, Du Toit JT. 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* **23(1)**:70–80 DOI 10.1111/j.1600-0587.2000.tb00262.x.

Styles CV, Skinner JD. 2000. The influence of large mammalian herbivores on growth form and utilization of mopane trees, *Colophospermum mopane*, in Botswana's Northern Tuli Game Reserve. *African Journal of Ecology* **38(2)**:95–101 DOI 10.1046/j.1365-2028.2000.00216.x.

Thomas B, Holland JD, Minot EO. 2012. Seasonal home ranges of elephants (*Loxodonta africana*) and their movements between Sabi Sand Reserve and Kruger National Park. *African Journal of Ecology* **50(2)**:131–139 DOI 10.1111/j.1365-2028.2011.01300.x.

Torello-Raventos M, Feldpausch TR, Veenendaal E, Schrodt F, Saiz G, Domingues TF, Djagbletey G, Ford A, Kemp J, Marimon BS, Marimon BH Jr, Lenza E, Ratter JA, Maracahipes L, Quesada CA, Ishida FY, Nardoto GB, Affum-Baffoe K, Arroyo L, Bowman DMJS, Compaore H, Davies K, Diallo A, Fyllas NM, Gilpin M, Hein F, Johnson M, Killeen TJ, Metcalfe D, Miranda HS, Steininger M, Thomson J, Sykora K, Mougin E, Hieraux P, Bird MI, Grace J, Lewis SL, Phillips OL, Lloyd J. 2013. On the delineation of tropical vegetation types with an emphasis on forest/savannah transitions. *Plant Ecology and Diversity* **6(1)**:101–137 DOI 10.1080/17550874.2012.762812.

Torregrossa A-M, Azzara AV, Dearing MD. 2011. Differential regulation of plant secondary compounds by herbivorous rodents. *Functional Ecology* **25(6)**:1232–1240 DOI 10.1111/j.1365-2435.2011.01896.x.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414(6859)**:65–69 DOI 10.1038/35102054.

Westoby M. 1978. What are the biological bases of varied diets? *American Naturalist* **112(985)**:627–631 DOI 10.1086/283303.

Wiggins NL, McArthur C, Davies N. 2006. Diet switching in a generalist mammalian folivore: fundamental to maximising intake. *Oecologia* **147(4)**:650–657 DOI 10.1007/s00442-005-0305-z.

Wilkinson DM, Sherratt TN. 2016. Why is the world green? The interactions of top–down and bottom–up processes in terrestrial vegetation ecology. *Plant Ecology & Diversity* **9(2)**:127–140 DOI 10.1080/17550874.2016.1178353.

Wing LD, Buss IO. 1970. Elephants and forests. *Wildlife Monographs* **19**:3–92.

Xie Y, Sha Z, Yu M. 2008. Remote sensing imagery in vegetation mapping: a review. *Journal of Plant Ecology* **1(1)**:9–23 DOI 10.1093/jpe/rtm005.