

Diet selection of African elephant over time shows changing optimization currency

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Multiple factors determine diet selection of herbivores. However, in many diet studies selection of single nutrients is studied or optimization models are developed using only one currency. In this paper, we use linear programming to explain diet selection by African elephant based on plant availability and nutrient and deterrent content over time. Our results indicate that elephant at our study area maximized intake of phosphorus throughout the year, possibly in response to the deficiency of this nutrient in the region. After adjusting the model to incorporate the effects of this deficiency, elephant were found to maximize nitrogen intake during the wet season and energy during the dry season. We reason that the increased energy requirements during the dry season can be explained by seasonal changes in water availability and forage abundance. As forage abundance decrease into the dry season, elephant struggle to satisfy their large absolute food requirements. Adding to this restriction is the simultaneous decrease in plant and surface water availability, which force the elephant to seek out scarce surface water sources at high energy costs. During the wet season when food becomes more abundant and energy requirements are satisfied easier, elephant aim to maximize nitrogen intake for growth and reproduction. Our study contributes to the emerging theory on understanding foraging for multiple resources.

How abundant does a plant species need to be and what nutrient content does it have to have in order to be included in a free ranging herbivore's diet? Theoretically, this depends on the physiological and morphological forage adaptations and nutrient requirements of the animal, which in turn depend on the animal's body size, life history stage and current nutritional status (Hanley 1997, Shipley et al. 1999, Brown et al. 2004). However, due to the difficulty in determining these parameters, the theoretical considerations are hardly supported by field data. Scientific knowledge on nutrition of large herbivores mostly comes from studies on livestock under controlled conditions (McDonald et al. 1995, Robbins 1993). Whereas the animal's ideal diet is in the hands of the nutritionist in agriculture, what wild herbivores eat is a result of natural selection and adaptation to the environment. The challenge is not only to determine the nutrient requirements of wild animals but also to understand how animals compile their own diets.

From studies in biochemistry and physiology, we know that some macro minerals such as, sodium (Na), phosphorous (P), nitrogen (N), potassium (K), magnesium (Mg), calcium (Ca) and carbon (C) are essential to animals (McDonald et al. 1995). Phosphorous, Mg and Ca can readily be stored in bone, whereas K and Na are not stored to a great extent in animal tissue. Although K is generally readily available from plants (Robbins 1993), Na, P and N, are often found at low levels in plants in southern Africa (du Toit et al. 1940, Weir 1969, Snyman 2002). Carbon based energy rich compounds can be stored as fat, but energy constantly needs to be replenished to sustain metabolic demands (Brown et al. 2004). Nitrogen forms the building blocks of muscle, it has a high turnover rate leading to endogenous losses that need to be replenished on a daily basis and it can also serve as a less efficient source of energy (McDonald et al. 1995). Adding to the complexity of the multiple nutrients that need to be selected for in the wild is the presence of chemical

deterrents in plants, such as condensed tannins that negatively affect the ability of an animal to digest nutrients (Robbins 1987).

In this paper, we aim to provide a mechanistic framework for plant selection by a wild animal based on plant availability, nutrient and deterrent content. Nutrients are assumed to be selected for based on their availability in the environment in relation to the animal's nutrient requirements (Hengeveld et al. 2009). To emphasize the tradeoffs between plant quality and quantity we chose to study the largest terrestrial mammalian herbivore, the African elephant *Loxodonta africana*. Some experimental studies on elephant nutrition have been conducted in zoos (Clauss et al. 2003, 2005b). However, most conventional studies in the wild are descriptive and case sensitive as nutrient selection is determined using consumption rates of plant species high in a specific nutrient in relation to its availability in the environment. From these studies, elephant have been shown to select for Ca (Greyling 2004, Stokke 1999), Na and N (Jachmann and Bell 1985). Because plant quality and quantity show large temporal variation and no clear evidence exists for the selection of only one currency by elephant over time, we will test several postulated hypotheses to see which nutrient selection strategies best fit the observed diets over time.

Due to the enormous size of an elephant, its absolute forage requirements are very high. Since the Pleistocene, the morphological and behavioural forage adaptations of the elephant's ancestors have closely followed changes in the abundance of forage on earth (Hofmann and Stewart 1972, Ehleringer et al. 1997, Cerling et al. 1998). As elephant are sometimes classified as non-selective bulk feeders (van Soest 1981) and have the largest daily intake of all terrestrial herbivores, the best null model would be to expect that modern day elephant randomly include plant species in their diet according to availability. Alternatively, we can argue that an elephants' high absolute energy requirements will hamper the animal from consuming too many rare plants that will cost more energy to find. Moreover, high absolute energy requirements will also force the animal to select plants of higher quality and digestibility so that energy intake can be maximized. If this is the case, we can expect elephant to maximize energy intake by including the plant species that are both most abundant and have the highest metabolizable energy value in their diet.

Besides energy maximization being used as the ultimate model for explaining plant selection, there is growing support for models satisfying requirements of multiple nutrients (Yearsley et al. 2001). Raubenheimer and Simpson (Simpson and Raubenheimer 1993, Raubenheimer and Simpson 1997, 1999) found that insects could adjust the amounts of food ingested from different food sources in order to keep the balance between different nutrients, and consistently reach the same target, i.e. their daily nutrient requirements. In the wild, animals also need to aim to reach targets of nutrient requirements for maintenance, growth, mobility and reproduction. As an alternative foraging strategy, we expect elephant to select the combination of plants in the diet that will yield nutrients that is as close to the minimum requirement for each macronutrient as possible.

Recently, Ludwig et al. (2008) and Treydte et al. (2009) demonstrated, using linear programming models, how grazing ungulates can meet their daily nutrient requirements by consuming the right combinations of grass from under tree canopies and in open grasslands before reaching their maximum intake as determined by grass fibre concentrations. Even though these studies took a multi-nutrient objective approach to understand how an animal satisfies its requirements, they did not consider temporal variation in availability of different plant species. Although linear programming models have been used in foraging ecology for a long time (Westoby 1974, Belovsky 1978), they stand under criticism because of the sensitivity of the model's parameters (Huggard 1994, Yearsley et al. 2001). In calculating diets for the current study, we not only specified dietary constraints but also included goal functions to define foraging strategies. These foraging studies described decision rules with regard to foraging and diet composition, such as maximization of N, P, Ca and Na intake, and minimization of condensed tannin intake. The deviation between the nutrient content of observed and predicted diets, calculated from linear programming models, is used as a relative measurement to test the hypotheses on diet choices.

Methods

The study was conducted in the northern parts of the Timbavati- and the Umbabat Private Nature Reserves, South Africa (24°14'11.760"S, 31°22'32.184"E) between December 2005 and 2007. A homogeneous layer of *Colophospermum mopane* shrubveld on granite soils dominates the area. The rainfall season normally extends from October to March and during the wet season of 2005/2006 it rained 427 mm and of 2006/2007, 390 mm.

At the beginning of the study, 13 plant species were selected and their leaf biomass and chemical composition measured at monthly intervals over a period of two years. These species represented forage available for elephant to choose a daily diet from and their selection was based on their abundance within the study area, on preliminary forage observations on herbivores in the field and from literature (Stokke 1999, Greyling 2004). Tree species selected for measurement consisted of the six most common and frequently utilized browse species including *Colophospermum mopane*, *Grewia monticola*, *Acacia nigrescens*, *Combretum apiculatum*, *Lannea schweinfurthii* and *Dichrostachys cinerea* and the rare but well utilized browse species *Maerua parvifolia*. Herbaceous species selected for measurement consisted of the three most common and frequently utilized grass species *Panicum maximum*, *Digitaria eriantha* and *Urochloa mosambicensis*, the rare but well utilized annual grass species *Brachiaria deflexa*, a common herb (*Indigofera* spp.) and a rare and frequently utilized herb (*Cyperaceae* spp.). The study was divided into five periods at three-month intervals stretching over a wet-, late wet/early dry- and dry season and two late dry/early wet seasons. The total nutrient content of observed and predicted diets, compiled from the available thirteen plant species, were calculated for each period using the following variables.

Plant structural characteristics

Nine monitoring sites were randomly selected throughout the study area in vegetation typically representative of the dominant *Colophospermum mopane* shrubveld. At each site, the area used for sampling was about 10 ha in size. Leaf cover and biomass measurements of the thirteen selected plant species were conducted every month at all nine sites and the data pooled at three-month intervals. For trees, intra-plant species distance, height, canopy height, maximum canopy diameter and perpendicular canopy diameter of each species were determined at the beginning of the study using the point centre quadrat (PCQ) method (Mueller-Dombois and Ellenberg 1974). This entailed recording the distance to the closest species and to the selected tree species in each of the four quadrates at 20 m intervals along a 100 m transect at each of the nine study sites. For each of the seven selected tree species at these PCQ transects, we calculated available browse volume per tree according to the biomass estimates from canopy volume (BECVOL) method (Smit 1996). To determine the intra-plant species distance and ground biomass of herbaceous species the dry-weight-rank (Dekker et al. 2001) and comparative yield methods (Haydock and Shaw 1975) were used and repeated at monthly intervals along the transects at each of the nine study sites.

Along with herbaceous biomass estimations in $0.5 \times 0.5 \times 0.5$ m metal frames at each site each month, a representative sample of each selected browse, herb and grass species was cut in the same size frame resulting in nine frame cut samples per species per month. These samples were dried at 70°C for 24 h, the leaf material separated from the stem and weighed. For each grass and herb species, the average leaf mass per frame for each period was weighted. For each browse species, the average leaf mass determined for each species per frame was used along with the available browse volume estimates from BECVOL to calculate the total available leaf mass per tree per period.

Leaf nutrient and deterrent content of plant species

The dried leaf samples collected each month per frame for each of the thirteen plant species were pooled per species at a three monthly interval and milled through a 1 mm sieve. Quality of the leaf samples were determined at the laboratory through analysis of the major elements N, P, Ca, Na, K, Mg and deterrents including acid detergent fibre (ADF), acid detergent lignin (ADL) and condensed tannins. Dry matter content was determined by drying the samples for 8 h at 70°C. Total N, Ca, Mg, Na, K and P content were measured with an auto analyzer, after destruction with a mixture of H_2SO_4 , selenium and salicylic acid (Novozamsky et al. 1983). Condensed tannins content were measured using the proanthocyanidin method (Waterman and Mole 1994) and ADF content by using a fibre analyzer followed by treatment with 72% H_2SO_4 and ignition at 525°C for 3 h to determine ADL.

Metabolizable energy content of forage

Intake of elephant on a dry matter basis has been estimated by Owen-Smith (1988) to be between 1 and 2% of body weight. We assumed 1.5% daily intake of body mass for a 3500 kg elephant, which equates to 53 kg dry matter per day. Metabolizable energy values of plant species were calculated from gross energy values from literature, taking into account forage digestibility and estimated methane and urine energy loss. Digestibility of food measured in zoos range from 22% to 36% (Rees 1982, Pendlebury et al. 2005) and in the wild from 30% to 45% (Owen-Smith 1988, Meissner et al. 1990). To determine digestible energy values of individual plant species from their ADF content, a regression equation was calculated for digestibility of ADF from the ADF content of food (digested ADF = $6.665e^{0.0246(ADF \text{ diet})}$, $R^2 = 0.87$, $n = 8$) and of digestible energy from digested ADF (digested energy = $64.850 \times \text{digested ADF}^{-0.205}$, $R^2 = 0.60$, $n = 8$) only using data from feeding trials of elephant in zoos where both the digestibility of ADF and gross energy contents were measured (Ullrey et al. 1979, Foose 1982, Tomat et al. 1999, Clauss et al. 2003).

Gross energy values for plants do not vary much and generally range between 16.8 kJ g^{-1} and 21 kJ g^{-1} (Robbins 1993). Values for *Panicum* and *Brachiaria* species, for example, have been estimated at 16.8 kJ g^{-1} in (Adu and Adamu 1982, Tiemann et al. 2008) and for *Colosphermum mopane* between 18.5 kJ g^{-1} to 20.4 kJ g^{-1} (Styles and Skinner 1997, 2000). We used an 18 kJ g^{-1} gross energy content for grass species and 20 kJ g^{-1} for browse and herb species. Dry matter digestibility was calculated from digested energy values as explained above (digested energy = $0.984 \times \text{DM digestibility} + 1.991$, $R^2 = 0.92$, $n = 8$). These dry matter digestibility values for each plant species were then compared with values presented by Meissner et al. (1990) to estimate urine and methane energy loss. Metabolizable energy content of each plant species (ME) was calculated as follows:

$$ME \text{ (MJ kg}^{-1}\text{)} = \frac{\text{gross energy (MJ kg}^{-1}\text{)} \times \text{energy digestibility/100 (\%)} - \text{methane and urinary energy loss (MJ kg}^{-1}\text{)}}{100 (\%)}$$

Nutrient requirement estimation

Most research on animal's nutritional requirements has been undertaken using animals in the agriculture industry such as cattle and pigs. Consequently, extrapolated values from feeding trials on these livestock species under controlled environments were applied to wild species. The problem with this method is that little is known about the scaling of requirements for different nutrients in relation to body size. For example, a linear extrapolation of a drug like lysergic acid diethylamide at a level of tolerance for humans led to a fatality in an elephant (Rucker 2007). We used a combination of extrapolations from values stipulated by the Agriculture Research Council (ARC 1989) for horses, zoo studies and studies in the wild on elephant to compile a set of minimum and average daily nutrient requirements for an adult elephant (Table 1).

Table 1. Large herbivore nutrition related data from literature and assumed minimum and average nutrient requirements for adult elephants used in this study.

| Species | Source | Body mass (kg) | Intake % of body mass | Dmd% | N% | p% | Ca% | Na% | K% | Mg% | ADF% | Reference |
|-----------------|----------------|----------------|-----------------------|-------|------------|-------------|------------|------------|------------|------------|-----------|---|
| Elephant | Zoo | 3500 | | 22–35 | 1.6–1.9 | 0.3 | 0.5–1.5 | 0.1–0.2 | 0.5–0.6 | 0.1 | 30–48 | Ulrey et al. 1997, Stevenson and Walter 2006 |
| Elephant | Zoo/Field | 3300–3700 | 1–2 | 30–45 | | 0.3 | 0.4 | | | | 35–48 | Meissner 1982, Owen-Smith 1988 |
| Elephant | Field | | | | 1.3–2.9 | 0.15–0.3 | 0.4–2.5 | 0.13–0.75 | 1.2 | 0.3 | 32.4–37 | Bax and Sheldrick 1963, Dougall 1964, McCullagh 1969, Williamson 1975, Jachman 1989, Greyling 2004, Rode 2006 |
| Horse | ARC | 500 | 1.2–1.9 | | 1.3–2.1 | 0.2–0.3 | 0.4–0.5 | 0.1–0.15 | 0.3–0.6 | 0.3–0.4 | | ARC 1989 |
| Elephant | Minimum | 3500 | 1.5 | | 1.3 | 0.15 | 0.4 | 0.1 | 0.5 | 0.1 | 30 | Assumed for current study |
| Elephant | Average | 3500 | 1.5 | | 2.1 | 0.2 | 0.6 | 0.2 | 0.7 | 0.3 | 48 | Assumed for current study |
| Cow | ARC | 300 | 1.3 | 64–76 | 1.4–2.2 | 0.15–0.3 | 0.2–0.7 | 0.08–0.27 | 0.9 | 0.07–0.1 | | ARC 1989 |
| Sumatran rhino | Zoo | 698 | 1.4–2.5 | 50 | 1.4 | 0.25 | 2.4 | 0.15 | 1.35 | 0.3 | 36 | Dierenfeld et al. 2000 |
| Black rhino | Zoo/Field | 1000 | 1–2.5 | 60 | 1–2.2 | 0.05–0.26 | 1.8 | 0.1 | 0.3–2 | 0.1–0.9 | 40–45 | Dierenfeld et al. 1995, Clauss et al. 1995 |

DMD - dry matter digestibility, ADF - detergent fibre.

It is generally accepted that metabolic energy scales with a factor of 0.75 to body mass (Kleiber 1961). Daily energy requirements were calculated from equations obtained from Prins and van Langevelde (2008) so that daily basal metabolic energy requirements (E_{bm}) equals:

$$E_{bm} \text{ (kJ day}^{-1}\text{)} = 293 \times BW^{0.75}$$

For a 3500 kg elephant this would be 133 327 kJ day⁻¹. Energy expenditure for foraging (E_f) is:

$$E_f \text{ (kJ day}^{-1}\text{)} = 0.54 \times E_{bm}$$

which for an elephant equals 72 000 kJ. Energy for standing (E_s) is:

$$E_s \text{ (kJ day}^{-1}\text{)} = 0.2 \times E_{bm}$$

which for an elephant equals 26 665 kJ. Thus requirements for basal metabolic rate, standing and foraging for a 3500 kg elephant equal 232 MJ day⁻¹. This amount excludes energy required for walking to find food, which will vary depending on the availability of food. The energy expenditure per km of walking per unit mass (E_w) is:

$$E_w = 10.75 \times BW^{-0.316}$$

The energy expenditure per day (E_{bw}) including moving over a certain distance (D) and feeding is:

$$E_{bw} = E_{bm} + (E_w \times D \times BW) + E_f + E_s$$

Where D is the distance travelled in km (adjusted from Prins and van Langevelde 2008). The average distance walked per day over a two-year period for 30 different collared elephants at our study area was 8.3 km (Pretorius unpubl.). Therefore, the energy expenditure for an elephant of 3500 kg per day for walking, standing and feeding is estimated at 258 MJ. However, this value excludes energy required for digestion and assumes that the elephant is moving across a flat landscape. Alternatively Robbins (1993) suggests that free-ranging terrestrial eutherians that are not actively breeding have daily energy expenditures of 2.3 times basal metabolic rate, which amounts to 307 MJ for the elephant. From field studies on elephant, Meissner (1982) calculated the metabolizable energy requirements of a fifty year old bull of 3700 kg to be 310 MJ, close to our calculated value, while Owen-Smith (1988) estimated energy requirements of a female elephant at 259 MJ. As energy requirements estimated for elephant vary in literature, we replicated calculation of predicted diets three times using the following energy values: 258 MJ, 280 MJ and 307 MJ.

Plant species composition of observed diets

Leaves from the thirteen measured plant species were sampled for an epidermis reference collection. Plant parts were cleared in household bleach for 24 h and washed out in water. Leaf epidermis fragments were stripped off and mounted in glycerol on slides. Photographs of these slides were used to identify the epidermis and cuticle fragments present in the faeces (De Jong et al. 2004).

Every month ten fresh (less than 12 h old) adult elephant faecal samples, the size of a golf ball, were collected throughout the study area. A teaspoon of each of these samples

was pooled together at three-month intervals. Each pooled sample was analysed and represented the diet of the adult elephant population for a particular three-month period. In order to separate inner tissue from epidermis and cuticle, a 5 g subsample was washed in a blender and strained first over a 1.5 mm sieve to eliminate coarse fibre, then over a plankton sieve (0.01 mm) (De Jong et al. 2004). The subsample was transferred into a petri dish and allowed to settle after which ten random grab samples of the residue were taken and each droplet put on a glass slide. On each slide, ten epidermis fragments were identified using the reference material and their surface areas measured through a grid of 0.01 mm² squares in the microscopic eyepiece (De Jong et al. 2004).

The results of the ten grab samples were pooled for every faecal sample. Plant epidermal fragments that could not be identified down to species, genus or family level were categorized as either 'monocotyledon – unidentified' or 'dicotyledon – unidentified'. The abundance of each forage type and species was represented as a percentage of the total measured fragment area (De Jong et al. 2004). The proportion of each plant species in the observed elephant diets was assumed to be equal to the proportion of fragments of each plant species in the faeces (Stewart 1967). Because > 50% of fragments consisted of the thirteen plant species selected, the percentage of fragments for each of these selected species were extrapolated to calculate a total observed daily diet of 53 kg for each period.

Diet calculations

For comparison with the observed diets, seven possible foraging strategies were used to calculate predicted diets in MATLAB (ver. 6, The MathWorks, Inc.) using linear programming. These strategies included random foraging, energy maximization, nutrient satisficing, N-maximization, P-maximization, Ca-maximization, Na-maximization and condensed tannin-minimization. The proportions of each plant species that needed to be included in the random diet were equal to the relative abundance of each plant species in the study area. The maximum energy diet was calculated as a 100% consumption of the most abundant plant species in the environment with the highest metabolizable energy value, which would therefore require the least amount of energy to find. Each of the remaining strategies was defined as the goal function in the linear models and the diets calculated under the constraints that minimum energy and P, K, Mg, N, Ca and Na requirements, or only minimum energy requirements had to be satisfied.

For each diet the nutrient content for each food type (plant species) was multiplied by the proportion of the food type in the diet and summed over all species to yield the total content for each nutrient in the whole diet.

The energy gain of each diet was calculated by subtracting the energy spent walking to find each of the plant species in the diet with the metabolizable energy content of each species at the proportions that they occurred in the diet. The energy expenditure for locating each plant species (Ewd) was calculated as:

$Ewd = 10.75 \times BW^{-0.316} \times \text{Distance to find plant species (km)} \times BW$ (adapted from Taylor and Heglund 1982).

After preliminary tests of the model we realised that predicted diets for the wet season deviated greatly from the observed diets for most nutrients, possibly because animals replenish stores of many of the nutrients during these times of abundance. Because the model calculated only one optimal solution, small changes in some of the specified constraints resulted in completely different diets. We used the deviation of species composition of predicted diets from observed diets to indicate which nutrient constraints were most sensitive. For example, if *Colophospermum mopane* had high levels of Ca but low levels of P, and Ca levels were lower in most of the other species, a small increase in the constraints specified for P would not only increase the chances of mopane being excluded from a diet but also decrease the total Ca gained in a diet. Through sensitivity analysis we determined changes in energy constraints to be the most sensitive. As the exact nutrient requirements of an adult elephant were unknown and to avoid the pitfall of generating constraints from the data, all seven theoretical diets, excluding the random diet, were calculated six times using three different energy values (257 MJ, 280 MJ, 307 MJ) and one of two sets of dietary requirements that were in agreement with literature (Table 1: minimum and average). This resulted in 43 predicted diets in total for each of the observed diets in each of the five periods. Because elephant are known to satisfy their Na requirements from other sources such as soil and water (Holdø et al. 2002), constraints for Na were set to zero.

The linear programming technique only allowed one goal function to be specified at any run. As phosphorous was deficient in the area (Treydte et al. 2008), requirements for P, as specified in the constraints, could not be reached for most of the diets. Therefore, we assumed maximization of P first by setting the constraints to the maximum value of P that could be reached in the study area for a specific period. This value was determined by removing all other nutrient constraints, except minimum energy requirements, and then calculating a diet that maximized P intake.

Data analysis

Plant species and nutrient composition of each predicted diet were viewed as co-ordinates in a species or nutrient space respectively. Therefore, the differences between each predicted diet and the observed diets were calculated as distances relative to the requirement, as follows:

Diet X_i where $i = 1, 2, 3, \dots, 37$

Nutrients N_j where $j = 1, 2, 3, \dots, 7$

$$N_j = \begin{bmatrix} N \\ P \\ Ca \\ Na \\ K \\ Mg \\ Energy \end{bmatrix} \quad N_j \text{ Requirement} = \begin{bmatrix} 0.68 \\ 0.05 \\ 0.132 \\ 0.005 \\ 0.16 \\ 0.05 \\ 257 \end{bmatrix} \quad \text{for a 53 kg DM diet}$$

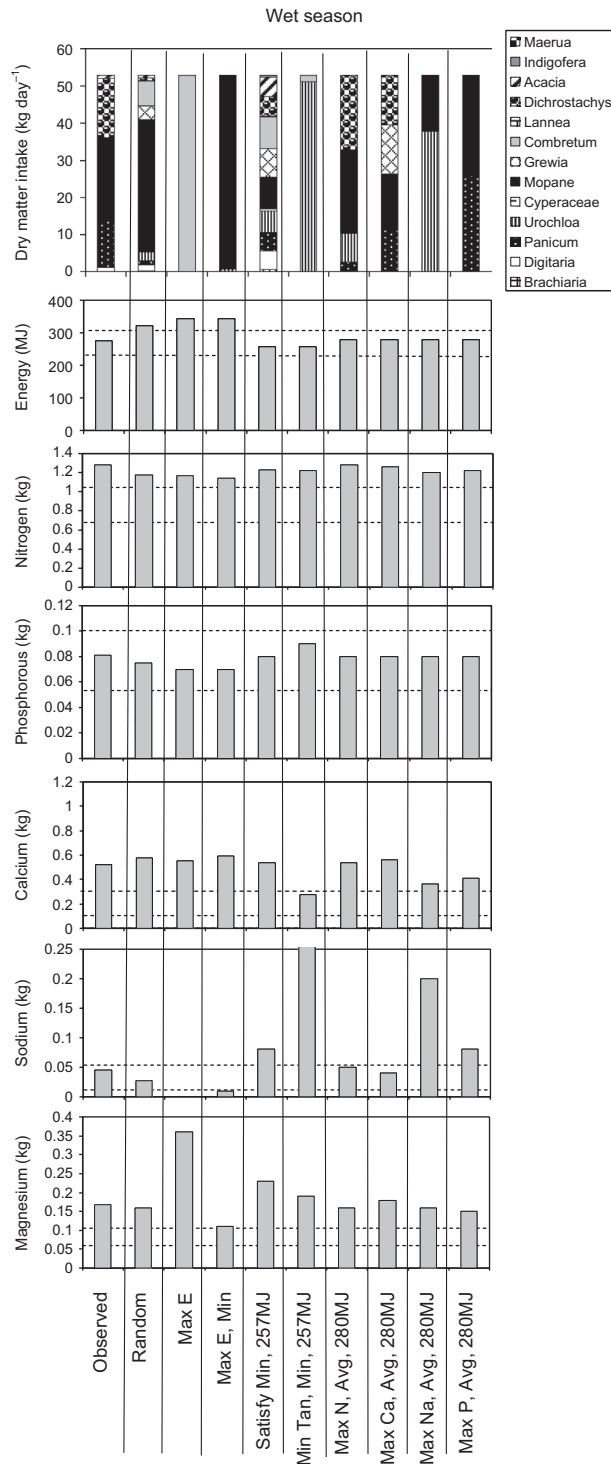


Figure 1. Plant species (top graph) and nutrient composition, expressed as part of a 53 kg daily dry matter intake, for observed (left most column) and each of nine predicted diets of elephant during the wet season: random food selection, energy maximization, energy maximization with minimum nutrient requirement constraints, satisficing of minimum nutrient requirements under energy constraints of at least 257 MJ, minimization of condensed tannin with constraints satisfying minimum nutrient requirements and at least 257 MJ energy, maximization of N with constraints satisfying average nutrient requirements and at least 280 MJ energy, maximization of Ca with constraints satisfying average nutrient requirements and at least 280 MJ energy, maximization of Na with

But $X_i = [N_j]$

$$Dev(X_i) = \sum_{j=1}^7 \sqrt{\left(\frac{N_j \text{ Predicted}^2 - N_j \text{ Observed}^2}{N_j \text{ Requirement}^2} \right)}$$

The predicted diet with the smallest nutrient deviation from the observed diet was considered to be the strategy followed by the elephant. The same approach was used to determine deviation between species composition of predicted and observed diets by replacing nutrients in the above equation with plant species.

Diet X_i where $i = 1, 2, 3, \dots, 37$

Plant species S_j where $j = 1, 2, 3, \dots, 13$

$$S_j = \begin{bmatrix} \textit{Colophospermum} \\ \textit{Combretum} \\ \textit{Grewia} \\ \textit{Acacia} \\ \textit{Lannea} \\ \textit{Dichrostachys} \\ \textit{Maerua} \\ \textit{Urochloa} \\ \textit{Panicum} \\ \textit{Digitalia} \\ \textit{Brachiaria} \\ \textit{Indigofera} \\ \textit{Cyperaceae} \end{bmatrix}$$

But $X_i = [S_j]$

$$Dev(X_i) = \sum_{j=1}^{13} \sqrt{(S_j \text{ Predicted}^2 - S_j \text{ Observed}^2)}$$

Results

Predicted diets for the elephant show that at the beginning of the wet season, a diet aimed at maximizing energy intake would force an elephant to only feed on *Combretum apiculatum*, thereby leading to a deficiency in Na. However, a diet minimizing condensed tannin would mainly consist of grass species like *Urochloa mosambicensis*, resulting in a very high Na content but Ca levels below the average requirements (Fig. 1). For this period, the predicted diet with the smallest deviation in nutrient composition from the observed diet had a composition where maximum P could be gained under a 280 MJ energy constraint, N was maximized, and average requirements for Mg, K, Na and Ca were satisfied. Towards

constraints satisfying average nutrient requirements and at least 280 MJ energy, and maximization of P with constraints satisfying average nutrient requirements and at least 280 MJ energy. Lower and upper dotted lines represent minimum and average nutrient requirements for elephant respectively, as derived from literature (Table 1).

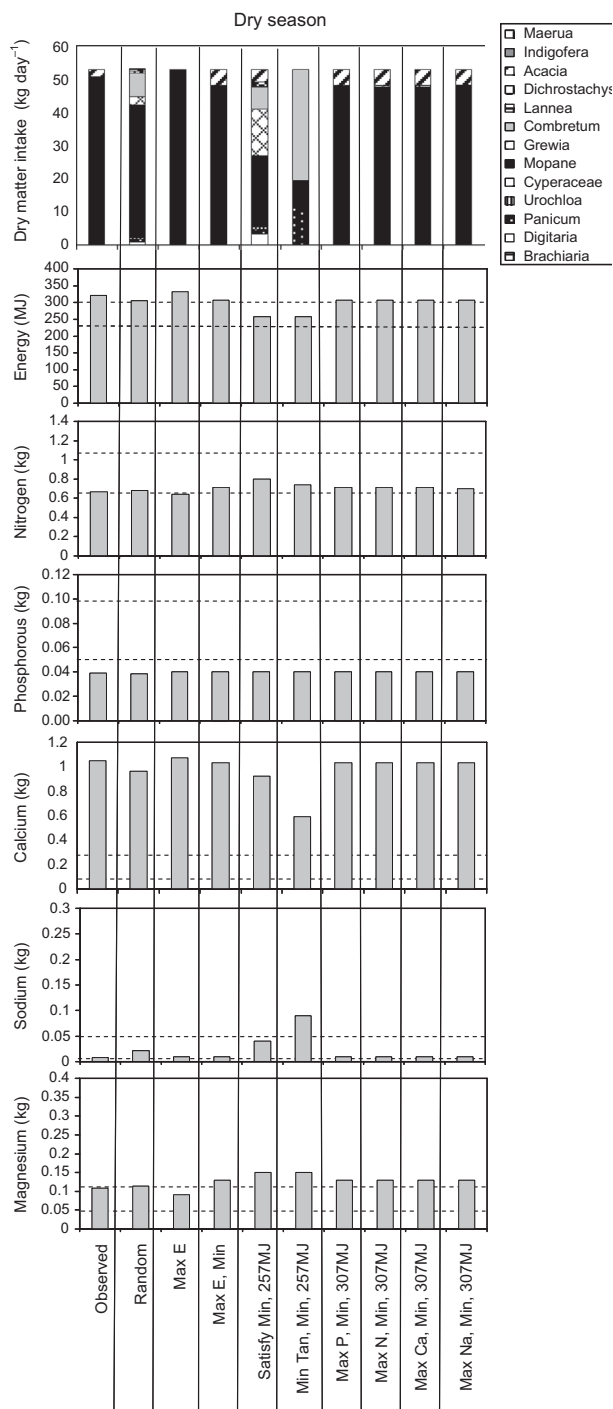


Figure 2. Plant species (top graph) and nutrient composition, expressed as part of a 53 kg daily dry matter intake, for observed and each of nine predicted diets of elephant during the dry season: random, energy maximization, energy maximization with minimum nutrient requirement constraints, satisfying of minimum nutrient requirements under energy constraints of at least 257 MJ, minimization of condensed tannin with constraints satisfying minimum nutrient requirements and at least 257 MJ energy, maximization of P with constraints satisfying minimum nutrient requirements and at least 307 MJ energy, maximization of N with constraints satisfying minimum nutrient requirements and at least 307 MJ energy, maximization of Ca with constraints satisfying minimum nutrient requirements and at least 307 MJ energy and maximization

the end of the wet season the best fit with the observed diet was the same as for the beginning of the wet season but at a lower energy constraint of 257 MJ.

During the dry season, most of the predicted diets that best fitted the observed diet included more than 75% *Colophospermum mopane*. The predicted diet with the smallest deviation included 100% *Colophospermum mopane* and maximized energy intake. However, the N content of this diet was below the minimum requirement. The second closest diet maximized energy and P under a 307 MJ energy constraint whilst satisfying minimum requirements for N, Ca, Na, Mg and K (Fig. 2).

The strategy followed by elephant at the switch between the dry and wet season appeared to be affected by the quantity of the first rains. Between September and October 2006, it had only rained 50 mm whereas 120 mm of rain was recorded for the same period in 2007. For the drier period during 2006, elephant appeared to maximize P intake at high energy constraints (307 MJ) whilst satisfying minimum requirements of N, Mg, Na, K and Ca. However, in 2007 during the same period elephant followed a similar strategy as they did for the early wet season by maximizing N intake at energy constraints of 280 MJ.

For each period, predicted diets with the smallest deviation from observed diets in terms of nutrient composition also had the smallest deviation in species composition (Fig. 3).

Discussion

In this study, we aim to understand the strategy by which elephant compile their daily diets. Our approach contributes to the emerging theory on understanding foraging for multiple resources over time as we considered both the satisfying of multiple nutrients as well as the possibility of maximization of particular nutrients and avoidance of deterrents. We found that elephant at our study area did not feed at random or exclusively maximized intake of a single nutrient. Instead, elephant used a combination of satisfying requirements of some nutrients whilst maximizing intake of others depending on the availability of resources in the environment. As nutrient availability changed over the seasons, the foraging strategy of the elephant also changed to maintain their metabolic requirements.

Metabolic rate in heterotrophs equals the rate of respiration, which is the main process that sources energy (Brown et al. 2004). Therefore, when determining the value of a plant species to an animal, not only does the energy content of the plant need to be considered but also the increased respiration and energy cost to find it. This becomes especially important for a large animal with high absolute energy demands, like the elephant. During the dry season, both surface water availability and plant water content decrease. Buffalo have been found to obtain all their water requirements from the

of Na with constraints satisfying minimum nutrient requirements and 307 MJ energy. Lower and upper dotted lines represent minimum and average nutrient requirements for elephant respectively, as derived from literature (Table 1).

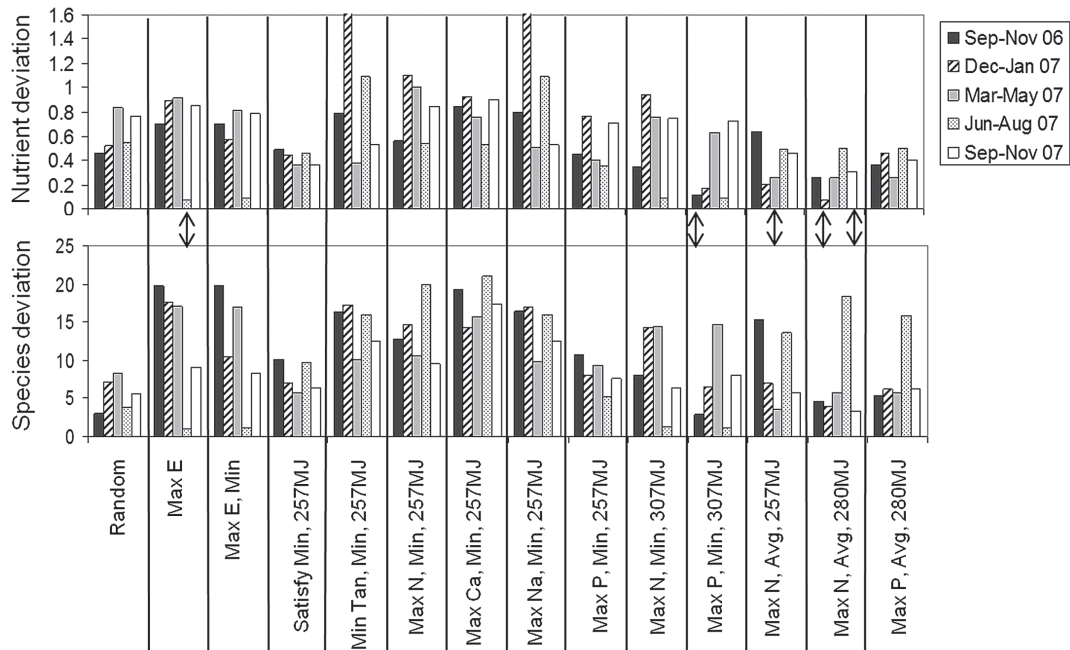


Figure 3. Deviation in nutrient (top graph) and species (lower graph) composition between observed and predicted diets (random, energy maximization, energy maximization with minimum nutrient requirement constraints, satisfying of minimum nutrient requirements at energy constraints of at least 257 MJ, minimization of condensed tannin with constraints satisfying minimum nutrient requirements and at least 257 MJ energy, maximization of N with constraints satisfying minimum nutrient requirements and at least 257 MJ energy, maximization of Ca with constraints satisfying minimum nutrient requirements and at least 257 MJ energy, maximization of Na with constraints satisfying minimum nutrient requirements and at least 257 MJ energy, maximization of P with constraints satisfying minimum nutrient requirements and at least 257 MJ energy, maximization of N with constraints satisfying minimum nutrient requirements and at least 307 MJ energy, maximization of P with constraints satisfying minimum nutrient requirements and at least 307 MJ energy, maximization of N with constraints satisfying average nutrient requirements and at least 257 MJ energy, maximization of N with constraints satisfying average nutrient requirements and at least 280 MJ energy, maximization of P with constraints satisfying average nutrient requirements and at least 280 MJ energy). Arrows indicate predicted diet with the smallest deviation from the observed diets.

plants they eat in the wet season whereas they become more dependent on surface water in the dry season as the water content in plants decrease (Prins 1987). Therefore, during the dry season, the elephant does not only need to reduce searching costs for food that is rich in nutrients other than energy so that its net energy gain is still positive, but the animal also has to increase energy intake to compensate for the cost to find water. This was clearly illustrated at our study site when elephant increased their energy intake in the dry season by consuming more of the most abundant food species *Colophospermum mopane*.

Using surface water demands as an explanation for higher energy demands in the dry season can further be supported by the sodium content of the diet during this time. Elephant have been known to select soils and water sources with high sodium content (Weir 1969, Holdø et al. 2002). As the elephant becomes more dependent on surface water sources to fulfil its water requirements its sodium requirements can simultaneously be satisfied in the same way. In Kruger National Park sodium levels in water averages 280 ppm (Leyland and Witthüser 2008). If an elephant consumes 160 litres of water a day (Guy 1975) it will gain 4.5% Na from the water, which is much higher than the estimated average requirement of 0.2%. Therefore, the sodium obtained through foraging does not have to be high, which is reflected in our results of the dry season diet.

In the wet season, as surface water availability and plant water content and abundance increase, energy restrictions and demands of elephant also decrease. During this period, nutrient reserves are replenished causing demands for all nutrients to be higher (Parker et al. 2009). Throughout the wet season elephant maximized their nitrogen intake. Nitrogen is the building blocks for structural proteins in an animal's body whereas plants consist more of carbohydrates (Mattson 1980). For this reason, herbivores need to spend a great deal of time eating and processing food to correct for the low ratio of nitrogen to fibre and carbohydrate in their food (White 1978, Mattson 1980).

The metabolic rate of an animal is determined by the accumulation rate of nutrients required for the biochemical reactions that drives metabolism (Brown et al. 2004). These nutrients are required in fixed amounts and ratios, and according to Elser et al. (2000) the growth of herbivore populations can be limited directly by minerals such as P, Ca and N. Nitrogen and P have also been shown to colimit vegetation productivity on nutrient poor bushland sites (Augustine et al. 2003). Therefore, a deficiency in one of the essential nutrients will necessitate selection for that nutrient. When investigating nutrient selection of herbivores in a particular area, the nutrient contents of plants in the area are seldomly placed in context of nutrient availability at larger scales. Phosphorous can be regarded as deficient in our study

area as can be seen from comparisons of P levels of plant species at our study site with minimum P requirements of large herbivores and similar plant species elsewhere in Africa (Fig. 4; Treydte et al. 2008). Responding to this deficiency, the elephant at our study area maximized phosphorous intake for all observed diets throughout the year. We suggest that a general deficiency in a particular nutrient, like P, can be used as a predictor of what plant species elephant are most likely to consume.

Condensed tannin content of the elephant's diet in our study area were always much higher than predicted from the theoretical diet where minimization of tannin content was used as a foraging strategy. Tannin binds to protein and renders it unavailable for digestion. Thus, in a pre-gastric fermenter the N from protein cannot be incorporated into microbial protein, which negatively effects digestion. However, in monogastric animals, food first enters the stomach where extreme acidic conditions and enzymes cause for the tannin-protein complexes to dissociate and the protein to become available for digestion (McArthur et al. 1991).

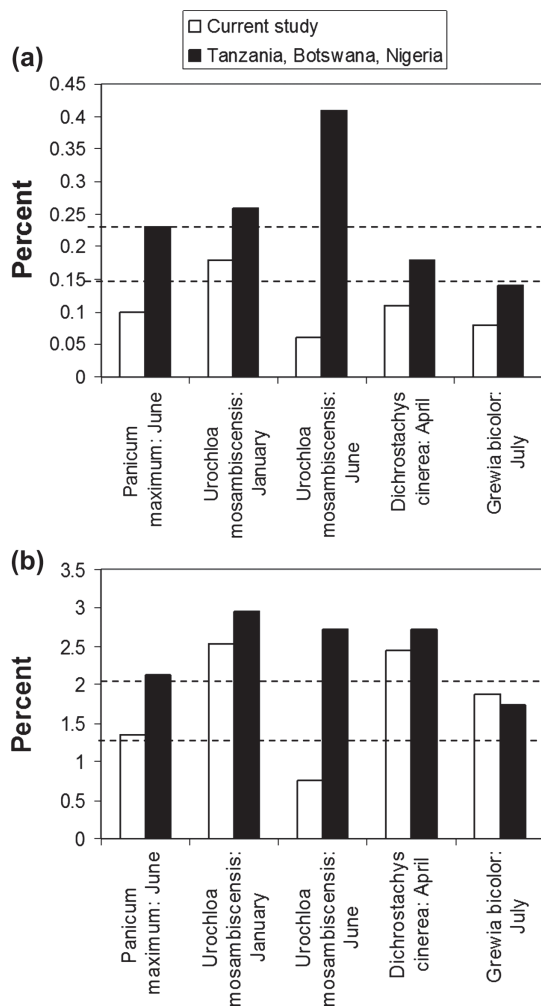


Figure 4. A comparison of (a) phosphorous and (b) nitrogen content of plant species in the current study with the same species in other parts of Africa (from the database of the Resource Ecology Group, Wageningen University, the Netherlands). Dotted lines represent minimum and average nutrient requirements for elephant as derived from literature.

Moreover, salivary tannin-binding proteins also exist in monogastric species (Clauss et al. 2005a). Therefore, monogastric animals could be less sensitive to high tannins levels in their diet, and as such explain the large deviation between predicted diets with low tannin contents and the observed diets with unexpected high tannin concentrations.

During the last decade there has been growing support in nutritional ecology to not only consider single nutrients or deterrents as the determining forces behind forage selection but to look at the satisficing of multiple nutrients (Raubenheimer and Simpson 1999, Raubenheimer et al. 2007, Ludwig et al. 2008, Prins and van Langevelde 2008). Developments using a geometric framework by Simpson and Raubenheimer (1999) have proved to be very useful in understanding foraging of insects and more recently primates (Felton et al. 2009). However, the limitation of this approach is that a foraging strategy aimed towards reaching a target intake is assumed, limiting the ability to explore selection of specific nutrients beyond this target when restrictions on daily food intake is also taken into consideration. Linear programming resembles the geometric framework approach in that it too considers selection of food types based on the content of multiple nutrients. However, the big advantage of linear programming is that on top of satisficing requirements of multiple nutrients, different strategies of maximization of specific nutrients can also be explored.

In this study, by using linear programming models we have identified possible mechanisms by which elephant compile their daily diets over time. We showed that elephant satisfied requirements of some nutrients whilst maximizing intake of others, in relation to the availability of resources. Elephants did randomly feed or maximized intake of a single nutrient. We recognize that linear programming should be used with caution as each outcome is highly dependent on the specified constraints. Moreover, the time scale over which nutrient intake is maximized or satisfied deserves further attention. As the exact nutrient requirements of an elephant are unknown, we reason that the constraints can be fine-tuned as long as the nutrient requirements used as constraints can be justified from literature and are not derived from field data.

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References

- Adu, E. F. and Adamu, A. M. 1982. The nutritive value and utilization of three tropical grass hays by sheep. – *Trop. Grasslands* 16: 29–33.
- Agricultural Research Council (ARC) 1989. The nutrient requirements of Ruminant Livestock. – Commonwealth Agricultural Bureaux, Farnham Royal, UK.
- Augustine, D. J. et al. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. – *Ecol. Appl.* 13: 1325–1337.

- Bax, P. N. and Sheldrick, D. L. W. 1963. Some preliminary observations on the food of elephant in the Tsavo Royal National Park (east) of Kenya. – *Afr. J. Ecol.* 1: 40–51.
- Belovsky, G. F. 1978. Diet optimization in a generalist herbivore: the moose. – *Theor. Popul. Biol.* 14: 105–134.
- Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. – *Ecology* 85: 1771–1789.
- Cerling, T. E. et al. 1998. Carbon dioxide starvation, the development of C₄ ecosystems, and mammalian evolution. – *Phil. Trans. Biol. Sci.* 353: 159–171.
- Clauss, M. et al. 2003. Studies on feed digestibilities in captive Asian elephants (*Elephas maximus*). – *J. Anim. Physiol. Anim. Nutr.* 87: 160–173.
- Clauss, M. et al. 2005a. Tannin-binding salivary proteins in three captive rhinoceros species. – *Compar. Biochem. Physiol. A* 140: 67–72.
- Clauss, M. et al. 2005b. Testing predictions on body mass and gut contents: dissection of an African elephant *Loxodonta Africana* Blumenbach 1797. – *Eur. J. Wildlife Res.* 51: 291–294.
- De Jong, C. B. et al. 2004. Relationships between diet and liver carcinomas in roe deer in Kielder forest and Galloway forest. – *Vet. Record* 155: 197–200.
- Dekker, B. et al. 2001. Use of the dry-weight-rank method of botanical analysis in semi-arid savanna communities. – *Afr. J. Range For. Sci.* 18: 63–66.
- du Toit, P. J. et al. 1940. A study of the mineral content and feeding value of natural pastures in the Union of South Africa. – *Onderstepoort J. Vet. Sci. Anim. Ind.* 14: 123–127.
- Ehleringer, J. R. et al. 1997. C₄ photosynthesis, atmospheric CO₂ and climate. – *Oecologia* 112: 285–299.
- Elser, J. J. et al. 2000. Nutritional constraints in terrestrial and freshwater food webs. – *Nature* 408: 578–580.
- Felton, A. M. et al. 2009. Protein content of diets dictates the daily energy intake of a free-ranging primate. – *Behav. Ecol.* 20: 685–690.
- Foose, T. J. 1982. Trophic strategies of ruminant versus nonruminant ungulates. – PhD thesis, Univ. of Chicago.
- Greyling, M. D. 2004. Sex and age related feeding distinctions in the feeding ecology of the African elephant, *Loxodonta africana*. – PhD thesis, Univ. of Witwatersrand.
- Guy, P. R. 1975. The daily food intake of the African elephant *Loxodonta africana* Blumenbach, in Rhodesia. – *Arnoldia* 26: 1–6.
- Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (*Cervidae*). – *Oikos* 79: 209–218.
- Haydock, K. P. and Shaw, N. H. 1975. The comparative yield method. – *Aust. J. Exp. Agric. Anim. Husbandry* 15: 663–670.
- Hengeveld, G.-M. et al. 2009. Optimal foraging for multiple resources in several food species. – *Am. Nat.* 174: 102–110.
- Hofmann, R. R. and Stewart, D. R. M. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. – *Mammalia* 36: 226–240.
- Holdø, R. M. et al. 2002. Geophagy in the African elephant in relation to availability of dietary sodium. – *J. Mammal.* 83: 652–664.
- Huggard, D. J. 1994. A linear programming model of herbivore foraging: imprecise, yet successful? – *Oecologia* 100: 470–474.
- Jachmann, H. and Bell, R. H. V. 1985. Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. – *Afr. J. Ecol.* 23: 245–258.
- Kleiber, M. 1961. *The fire of life*. – Wiley.
- Leyland, R. C. and Witthüser, K. T. 2008. Regional description of the groundwater chemistry of the Kruger National Park. – Report to the Water Research Commission by Dept of Geology, Univ. of Pretoria, South Africa.
- Ludwig, F. et al. 2008. Impacts of savanna trees on forage quality for a large African herbivore. – *Oecologia* 155: 487–496.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. – *Annu. Rev. Ecol. Syst.* 11: 119–161.
- McArthur, C. et al. 1991. Physiological strategies of mammalian herbivores against plant defenses. – In: Palo, R. T. and Robbins, C. T. (eds), *Plant defences against mammalian herbivore*. CRC Press, pp. 103–114.
- McDonald, P. et al. 1995. *Animal nutrition*, 5 edn. – Longman.
- Meissner, H. H. 1982. Theory and application of a method to calculate intake of wild southern African ungulates for purposes of estimating carrying capacity. – *S. Afr. J. Wildlife Res.* 12: 41–47.
- Meissner, H. H. et al. 1990. Quality of food and ad libitum intake by elephant as measured by lignin index. – *S. Afr. J. Wildlife Res.* 20: 104–110.
- Mueller-Dombois, D. and Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. – Wiley.
- Novozamsky, I. et al. 1983. A novel digestion technique for multi-element plant analysis. – *Comm. Soil Sci. Plant Anal.* 14: 239–248.
- Owen-Smith, N. 1988. *Megaherbivores: the influence of very large body size on ecology*. – Cambridge Univ. Press.
- Parker, K. L. et al. 2009. Nutrition integrates environmental responses of ungulates. – *Funct. Ecol.* 23: 57–69.
- Pendlebury, C. et al. 2005. Acid-insoluble ash as a measure of dry matter digestibility in captive African elephants (*Loxodonta africana*). – *Zoo Biol.* 24: 261–265.
- Prins, H. H. T. 1987. The buffalo of Manyara: the individual in the context of herd life in a seasonal environment of East Africa. – PhD thesis, Univ. of Groningen.
- Prins, H. H. T. and van Langevelde, F. 2008. Assembling a diet from different places. – In: Prins, H. H. T. and van Langevelde, F. (eds), *Resource ecology: spatial and temporal dynamics of foraging*. Springer, pp. 129–155.
- Raubenheimer, D. and Simpson, S. J. 1997. Integrative models of nutrient balancing: application to insects and vertebrates. – *Nutr. Res. Rev.* 10: 151–179.
- Raubenheimer, D. and Simpson, S. J. 1999. Integrating nutrition: a geometrical approach. – *Entomol. Exp. Appl.* 91: 67–82.
- Raubenheimer, D. et al. 2007. Nutrition, ecology and nutritional ecology: toward an integrated framework. – *Funct. Ecol.* 23: 4–16.
- Rees, P. A. 1982. Gross assimilation efficiency and food passage time in the African elephant. – *Afr. J. Ecol.* 20: 193–198.
- Robbins, C. T. 1987. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? – *Ecology* 68: 1606–1615.
- Robbins, C. T. 1993. *Wildlife feeding and nutrition*, 2nd edn. – Academic Press.
- Rucker, R. B. 2007. Allometric scaling, metabolic size and interspecies comparisons of basal nutritional requirements. – *J. Anim. Physiol. Anim. Nutr.* 91: 148–156.
- Shipley, L. A. et al. 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. – *Oikos* 84: 55–68.
- Simpson, S. J. and Raubenheimer, D. 1993. A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. – *Phil. Trans. R. Soc.* 342: 381–402.
- Simpson, S. J. and Raubenheimer, D. 1999. Assuaging nutritional complexity: a geometrical approach. – *Proc. Nutrition Soc.* 58: 779–789.
- Smit, G. N. 1996. *Becvol: biomass estimates from canopy/volume (ver. 2). Users guide (unpublished manual)*. – Univ. of Orange Free State, Bloemfontein, South Africa.
- Snyman, H. A. 2002. Short-term response of rangeland botanical composition and productivity to fertilization (N and P) in

- a semi-arid climate of South Africa. – *J. Arid Environ.* 50: 167–183.
- Stewart, D. R. M. 1967. Analysis of plant epidermis in faeces: a technique for studying the food preference of grazing herbivores. – *J. Appl. Ecol.* 4: 83–111.
- Stokke, S. 1999. Sex differences in feeding-patch choice in a mega-herbivore: elephants in Chobe National Park, Botswana. – *Can. J. Zool.* 77: 1723–1732.
- Styles, C. V. and Skinner, J. D. 1997. Seasonal variations in the quality of mopane leaves as a source of browse for mammalian herbivores. – *Afr. J. Ecol.* 35: 254–265.
- Styles, C. V. and Skinner, J. D. 2000. The influence of large mammalian herbivores on growth form and utilization of mopane trees, *Colospermum mopane*, in Botswana's northern Tuli game reserve. – *Afr. J. Ecol.* 38: 95–101.
- Taylor, C. R. and Heglund, N. C. 1982. Energetics and mechanics of terrestrial locomotion. – *Annu. Rev. Physiol.* 44: 97–107.
- Tiemann, T. T. et al. 2008. Effect of the tropical tannin-rich shrub legumes *Calliandra calothyrsus* and *Flemingia macrophylla* on methane emission. – *Animal* 2: 790–799.
- Tomat, L. et al. 1999. Digestibility studies with captive African elephants (*Loxodonta africana*). – First European Zoo Nutrition Meeting, Rotterdam Zoo Veterinary Faculty of Utrecht, Rotterdam, the Netherlands.
- Treydte, A. C. et al. 2008. Improved quality of beneath-canopy grass in South African savannas: local and seasonal variation. – *J. Veg. Sci.* 19: 663–670.
- Treydte, A. C. et al. 2009. Modelling ungulate dependence on higher quality forage under large trees in African savannas. – *Basic Appl. Ecol.* 10: 161–169.
- Ullrey, D. E. et al. 1979. Comparative digestibility studies with zoo herbivores. – *Am. Ass. Zoo Vet. Ann. Proc.*, pp. 120–121.
- van Soest, P. J. 1981. Impact of feeding behaviour and digestive capacity on nutritional response. Animal genetic resources and management. Proc. FAO/UNEP Tech. consultation. – FAO UN.
- Waterman, P. G. and Mole, S. 1994. Analysis of phenolic plant metabolites. – Blackwell.
- Weir, J. S. 1969. Chemical properties and occurrence on Kalahari sand of salt licks created by elephants. – *J. Zool.* 158: 293–310.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. – *Am. Nat.* 108: 290–304.
- White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. – *Oecologia* 33: 71–86.
- Yearsley, J. et al. 2001. Theoretical developments in the study and prediction of food intake. – *Proc. Nutr. Soc.* 60: 145–156.