

Control of energy balance by a wild ungulate, the kudu (*Tragelaphus strepsiceros*) through adaptive foraging behaviour

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Optimal foraging models are commonly based on the principle that animals maximize their net energy gains while foraging, subject to various constraints (Belovsky, 1978, 1986; Owen-Smith & Novellie, 1982; Stephens & Krebs, 1986). Energy maximization is contrasted with the alternative of obtaining minimal energy needs within the least time. Both of these objectives are naive, and fail to take into account the multiple costs and constraints that animals must contend with in obtaining their nutritional needs in variable environments. The basic physiological constraints considered in models developed for large mammalian herbivores include thermal tolerance, digestive-processing capacity, predation risk, and requirements for specific nutrients. In practice, these constraints are not rigid limits, but represent non-linearly rising costs with increasing departures from physiological and environmental norms. For example, animals can operate out of their thermoneutral zone, but at the cost of expenditures (e.g. fat mobilization) to maintain body temperature. Extreme conditions (e.g. severe cold) may be reached only intermittently. Animals must retain the ability to cope with these extremes, but for most of the time they operate within a comfort zone where they experience little stress (Owen-Smith, 1994).

Our studies conducted on an African browsing antelope, the greater kudu (*Tragelaphus strepsiceros*), reveal how individuals of this species cope with widely fluctuating environmental conditions over the seasonal progression, by adjusting their foraging behaviour appropriately. I will review these findings in relation to foraging theory, the operation of physiological constraints, and more generally in relation to the maintenance of energy balance by wild herbivores (for further details on the feeding behaviour, diet selection and nutritional intake of kudus, see Owen-Smith & Cooper, 1987, 1989; Cooper *et al.* 1988; Owen-Smith, 1993, 1994).

Our observations were made on free-ranging animals under semi-natural conditions. This brought problems of precision in measurements, but avoided the artifacts that may arise when animals are studied under unnatural conditions. Animals cannot be expected to perform close to optimally when confronted with novel situations differing radically from their previous individual experience, or from the evolutionary contexts that shaped the species. I have not had the opportunity to follow up the observational study with experimental manipulations. Hence the findings must be regarded as preliminary, and subject to confirmation by further investigations.

In a previous paper written for ecologists, I expressed the need for 'a genuinely interactive research program . . . involving physiologists and modellers in a collaborative endeavor' (Owen-Smith, 1994). I hope that this contribution will help draw physiologists into such a joint enterprise.

STUDY AREA AND PROCEDURES

The study area was the Nylsvley Nature Reserve in Northern Province of South Africa. Our subjects were four subadult kudus, aged 1.5–3 years, which had been habituated since a young age to close human presence. These animals were allowed to range freely within a

213 ha fenced enclosure containing natural savanna vegetation. We augmented the food that they obtained from the vegetation with small amounts of commercial antelope cubes during the late dry season. This was done to restrict weight loss by the animals under the confined conditions. Antelope cubes were not provided on days of observation. In addition, the kudu had access to salt blocks containing added minerals. The animals had been in the enclosure for more than 1 year before my observations commenced, and so were familiar with the food resources available to them. Rainfall in the study region was strongly seasonal, with over 80 % falling during the summer months October–March.

A pre-selected kudu was observed continuously from dawn to dusk. Changes in activity and plant species and parts eaten were recorded using a computer-compatible keyboard. Observations were conducted on three of four successive days each month, with a different individual forming the focal animal on sequential days. The study spanned a complete seasonal cycle, extended to 16 months to fill in missing days in certain months. No observations were made in May.

The diet of the kudu consisted mainly of the leaves and stems of trees, shrubs and forbs, supported by small amounts of fruits, flowers and grasses (Owen-Smith & Cooper, 1989). Food preferences were estimated by the frequency with which a species was eaten, when encountered while the kudu were foraging. Eating rates were estimated by recording bite sizes and biting rates for selected plant species. Leaves of fourteen woody species and eight forb species were analysed quantitatively for crude protein ($N \times 6.25$), minerals, neutral- and acid-detergent-fibre components, total polyphenols and condensed tannins, and qualitatively for alkaloids, terpenoids (diethyl ether extract) and saponins (foam production; for details of methods see Cooper *et al.* 1988).

The maintenance energy requirement of the kudu was estimated from studies done on related wild species, with standard increments for activity costs and growth (Table 1). Protein requirements were estimated as the sum of metabolic faecal protein, endogenous urinary protein, and protein required for growth (Table 1). Chemical components in leaves were used to estimate digestibility and energy and protein yields for selected plant species (Table 2). Tannins and other polyphenols were assumed to be unmetabolizable to energy, but no allowance was made for any effects that they might exert on cellulose digestibility. 'Available protein' was calculated by subtracting half the condensed tannin content from the crude protein content, for reasons justified in Owen-Smith & Cooper (1989). P needs were estimated from standard tables for domestic ungulates.

RESULTS

Seasonal variation in food availability

The trees and shrubs in the study area were predominantly deciduous, so that food abundance declined as the dry season progressed (Fig. 1). By September, the standing biomass of the foliage remaining amounted to only 4–5 % of the peak reached in the wet season. Food quality also declined markedly, because most of the leaves left by the late dry season were on evergreen or unpalatable deciduous species, offering low protein and high tannin and/or fibre contents (Table 2).

Energy and nutrient balance

Despite the extreme variation in food availability, the estimated energy intake of the kudu remained close to their daily requirements for maintenance, activity and growth (Fig. 1).

Table 1. *Estimates of energy and protein requirements for a 100 kg subadult kudu (Tragelaphus strepsiceros) (From Owen-Smith & Cooper, 1989)*

Component requirement	Formula	Daily requirement per animal
Energy		
Resting metabolism (MJ/d)	$0.44 \times M^{0.75}$	14 MJ
Activity costs (as multiples of resting metabolism):		
Standing resting	1.15	
Standing active	1.25	
Feeding	1.5	
Walking	2.5	
Integrated total for activity (seasonal variation)		5–7 MJ
Growth (kJ/kg live mass per d)	10.5	1 MJ
Total		20–22 MJ
Protein		
Metabolic faecal protein (g/kg DM eaten)	35	79–107 g
Endogenous urinary protein (g/d)	$1 \times M^{0.75}$	31 g
Growth (g/kg live mass per d)	0.4	40 g

$M^{0.75}$, kg live mass^{0.75}.

Table 2. *Estimates of energy and protein yields from food plants eaten by kudus (Tragelaphus strepsiceros) (From Owen-Smith & Cooper, 1989)*

Component	Formula	Range among species analysed (green season)	Monthly variation in diet
Crude protein content (CP)	$N \times 6.25$	0.095–0.20	0.09–0.145
Total polyphenol content (TPP)		0–0.27	0.03–0.065
Condensed-tannin content (CT)		0–0.12	0.02–0.035
Available protein	$CP - CT/2$	0.04–0.20	0.08–0.135
Digestibility of cell-wall cellulose	$1 - 1.75(L/(L + C))$	0–0.53	
Cell solubles*(CS)	$1 - \text{NDF}$	0.48–0.76	0.50–0.67
Metabolizable DM content	$CS + \text{DigCW} - \text{TPP}$	0.41–0.80	0.43–0.61
Energy yield from metabolizable organic matter	18 kJ/g		
Efficiency of utilization of metabolizable organic matter	0.83		

L, lignin + pectin; C, cellulose; NDF, neutral-detergent fibre; DigCW, digestible cell wall.

*Including soluble polyphenols.

Even in September, the mean daily energy intake (excluding supplements) fell to only 8 % below requirements. Surplus gains, exceeding requirements by more than 10 %, were recorded during the mid wet season, and at the start of the dry season. Although not statistically supported, this pattern appears biologically meaningful. In the wet season the kudus were recovering condition lost during the dry season, while in June they were preparing for dry-season deficits, probably by laying fat stores.

Daily protein intake greatly exceeded estimated requirements throughout the year, even allowing for the possible effect of tannins on protein availability (Fig. 1). There was an apparent deficit in P intake relative to needs over much of the year. However, the shortfall could have been met from the bone meal in the salt lick available to the kudus.

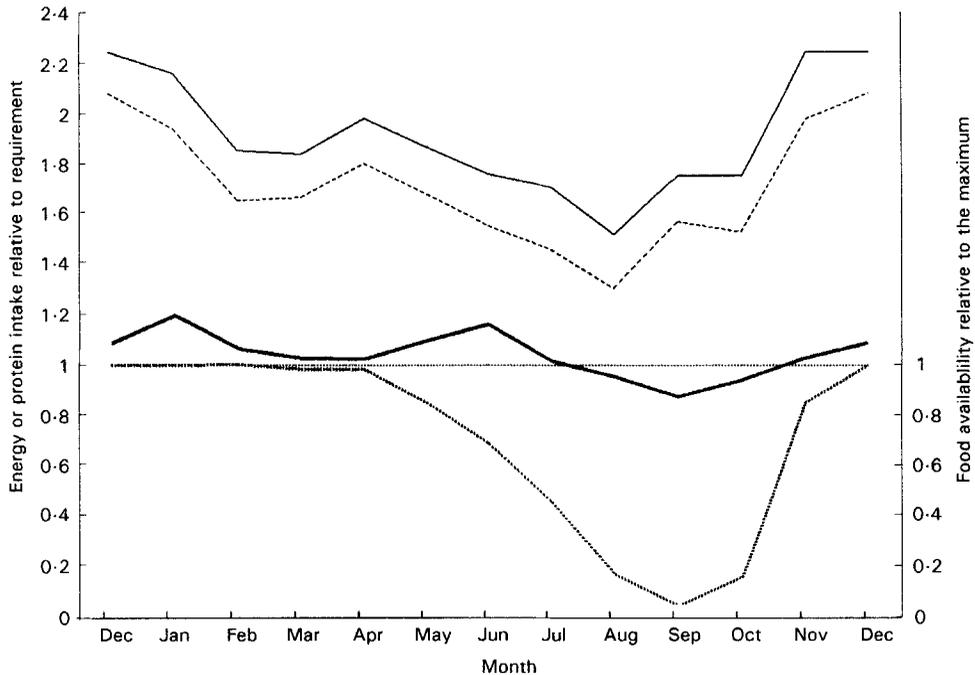


Fig. 1. Relative energy and protein balance of the kudu (*Tragelaphus strepsiceros*) through the seasonal cycle, in relation to changes in food abundance. (—), Protein intake relative to requirement; (---), available protein intake relative to requirement; (—), energy intake relative to requirement; (.....), food availability relative to the maximum.

Adaptive behaviour

The kudus increased their daily activity level to compensate for reduced food availability during the late dry-season and early wet-season periods, which correspondingly increased their daily energy needs (Fig. 2). Daily food intake was increased partly by including less nutritious plant species offering a higher eating rate in the diet, and partly by the increased foraging time. Notably, monthly variability in daily food intake (CV 0.095) exceeded that in relative energy gain (CV 0.087), but was less than that of the protein gain (CV 0.130). Nevertheless, energy balance was less precisely controlled on a daily basis. On some days the kudus foraged much less than usual, but then compensated by foraging for longer the next day.

Additionally the kudus concentrated their foraging where palatable foliage remained, and extended their feeding durations at evergreen trees and shrubs retaining leaves. Resting time was reduced to only 20% of the daylight hours in October, and less time was diverted to non-foraging activity during foraging spells than during the wet season (Owen-Smith, 1994).

Ecology texts (for example, Begon *et al.* 1990) suggest that food intake generally rises asymptotically with increasing food abundance, following a 'Type II' functional response. This is based on mechanistic relationships between search time and handling time. However, the daily food intake of the kudu tended to rise while food availability declined with the seasonal progression (Fig. 3). This was because the animals compensated for reduced food quality by eating more per d. The daily energy intake, relative to

requirements, remained effectively constant until little food remained, excluding the months when surplus consumption occurred.

While maximum daily food intake was recorded in June, in the early dry season, the limit to digestive capacity was probably reached only in August, when food quality was poorest. With the commencement of the new leaf flush on certain species in late September, food quantity rather than quality became the limitation. It was during this period that the animals foraged for longest, with thermal tolerance becoming a limitation on active time on hot days.

Factors governing food preferences

Acceptance frequencies showed no relationship with the rate of energy or nutrient ingestion that a plant species yielded. This was because the species that offered the highest eating rates were commonly unpalatable, with high condensed-tannin contents. Year-round mean acceptability was significantly correlated with mean leaf concentrations of both available protein and metabolizable dry mass (i.e. energy yield; Fig. 4). However, the latter relationship was not very convincing. The species with highest metabolizable dry-mass content were intermediate in acceptability, while those with highest acceptability gave moderate energy yields. The former species included thorny acacias, which offered low eating rates because of the coupling of the thorns with small leaf sizes. Because of high protein and low fibre contents in their leaves, these species were also outliers in the plot relating available protein to acceptability.

For mammalian herbivores, effective intake rate is generally limited by digestion rate, but for the acacia species ingestion rate was more restrictive. A highly significant correlation was obtained between acceptability and the effective intake rate of available protein, with only one outlier (Fig. 5). The latter was a moderately palatable evergreen shrub, which may have had an unidentified secondary metabolite counteracting its high nutrient levels. In contrast, the effective intake rate of metabolizable DM was not significantly correlated with acceptability. This was largely because the acacia species were not sufficiently high in energy yield to compensate for their low eating rate.

DISCUSSION

The observed foraging behaviour of the kudu fulfilled many of the predictions of foraging theory (Stephens & Krebs, 1986). The animals expanded their diet to include other food types as food availability from favoured species declined over the seasonal cycle. They extended their feeding durations in patches of food plants, and adjusted foraging paths, also as predicted. There was a close relationship between the acceptability of a food type and effective value, as assessed by rate of intake of nutrients (indexed by protein) relative to anti-nutrients (represented by condensed tannin). A less-good relationship was obtained with the index of energy yield. This may seem surprising, because energy appeared consistently more limiting than protein for the study animals.

This anomaly may have arisen because the metabolizable DM index was a misleading indicator of effective energy availability. An empirical finding of the study was that condensed tannin had a much stronger influence on palatability, and hence acceptability, than total polyphenol content (Cooper & Owen-Smith, 1985). The metabolizable DM index weighed all polyphenols equally. This raises the first physiological issue: exactly how do tannins and other phenolics influence nutritional value?

Illius & Jessop (1995) suggest that the metabolic costs of allelochemicals are incurred not so much through diminution of energy yield, but rather through catabolism of protein,

to maintain acid–base status through conjugation of absorbed compounds with glucuronic acid. This is unlikely to apply to condensed tannins, which are generally large molecules not easily degraded or absorbed from the gut. Nevertheless, a high protein concentration in the diet may have facilitated the detoxification of other phenolics, such as hydrolysable tannins, to which the kudu appeared more tolerant. Alternatively, leaf-protein concentrations may be a correlate of soluble carbohydrate levels and, hence, of effective energy availability, because most of the protein is associated with photosynthetic enzymes.

Contrary to the assumptions of naive foraging models, the kudu did not maximize their daily energy gains, neither did they minimize the time spent foraging. Rather they

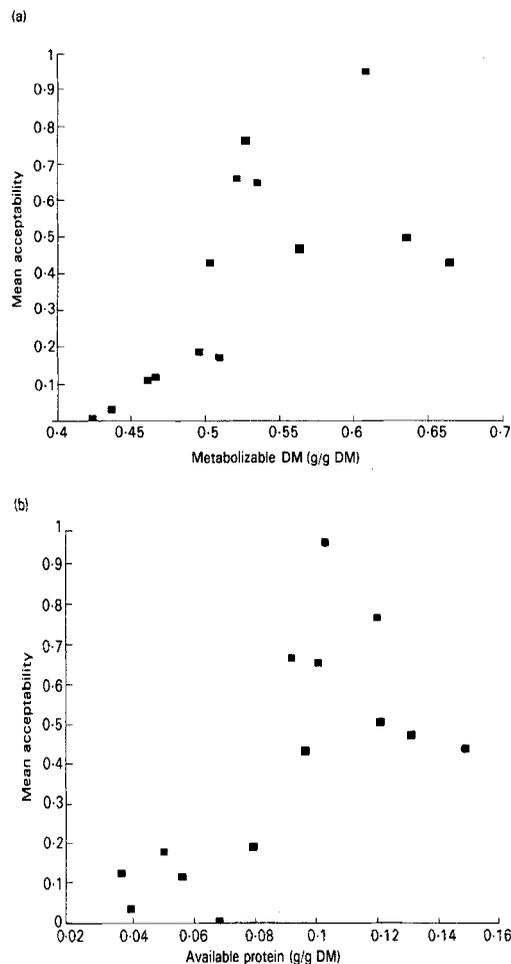


Fig. 4. Relationships between mean year-round acceptability of woody plant species eaten by kudu (*Tragelaphus strepsiceros*), and mean leaf concentrations of (a) metabolizable DM (g/g DM) and (b) available protein (g/g DM). Metabolizable DM indexes energy availability as total DM minus indigestible cell-wall components minus unmetabolizable polyphenols and ash. Available protein is indexed as crude protein ($N \times 6.25$) minus half condensed-tannin content, based on the canonical axis discriminating palatable from unpalatable woody plant species (Cooper *et al.* 1988). Coefficients of determination are: (a) metabolizable DM r^2 0.439 (NS), (b) available protein r^2 0.472 (n 14, 12 df, $P = 0.01$).

targeted closely on their energy requirements for maintenance, activity and growth. Energy gains in excess of these needs could only have been diverted to fat stores. It would seem advantageous to store fat in times of plenty, to buffer animals against the energy shortfalls incurred towards the end of the dry season. However, African ungulates store only limited amounts of fat, and build up their fat reserves late in the benign (e.g. wet) season (Ledger, 1968; Smith, 1970; Dunham & Murray, 1982). This suggests that there are costs to carrying excess fat. What are these costs?

Subcutaneous fat stores may reduce heat tolerance. Fat animals may also be less agile at evading predators. However, Tolkamp & Ketelaars (1992) proposed another potential cost associated with processing more food than immediately needed: that of tissue wear from O_2 metabolism. They suggest that the fitness benefits of short-term gains, e.g. in fat reserves for survival, are traded against long-term survival potential. Another possible cost

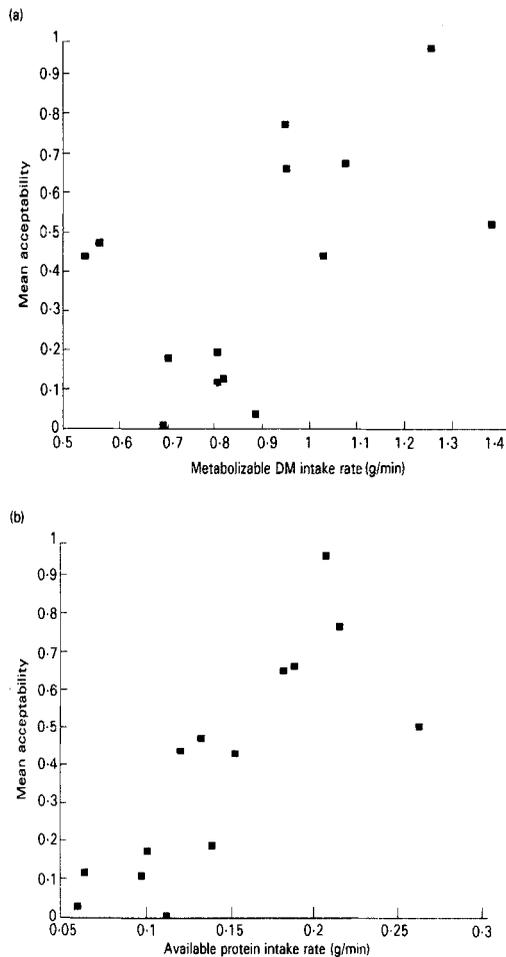


Fig. 5. Relationships between the mean year-round acceptability of woody plant species eaten by kudus (*Tragelaphus strepsiceros*) and the effective intake rate of (a) metabolizable DM (g/g DM) and (b) available protein (g/g DM). The effective intake rate is the lesser of the digestion rate or the ingestion rate. Coefficients of determination are: (a) metabolizable DM r^2 0.250 (NS), (b) available protein r^2 0.650 (n 14, 12 df $P = 0.001$).

is dental wear, which also influences longevity. How influential are such food-processing costs on ultimate fitness?

The kudu seemingly selected food types in order to meet their energy needs with the minimal food intake. For example, they favoured thorny species, which offered high nutrient concentrations despite low ingestion rates. Nevertheless, daily intake was the first compensatory adjustment the animals made early in the dry season, before foraging time was increased and before condensed-tannin-rich food types were eaten.

Foraging models formulated for herbivores have extended the simple models originally developed for predators by including multiple constraints, specifically those of maximum eating rate, thermal influences on foraging time, and digestive-processing limitations (Belovsky, 1978, 1986; Owen-Smith & Novellie, 1982; Verlinden & Wiley, 1989). However, they have not incorporated constraints arising from metabolic-processing capacity. Kudus could have taken advantage of the surplus food available during the wet season by growing faster. What limited their potential growth rate? Is growth limited by the uptake rate of digestive products across the gut wall, or by the rates of circulation and metabolism of these products? Or are all these rates co-adjusted?

Animals living in variable environments only experience physiological limitations periodically. Heat tolerance is needed only towards midday on exceptionally hot days in summer. Cold tolerance is needed only on cold, windy and perhaps wet days, especially late in the lean season when fat reserves are depleted. Gut space becomes a limitation only when food quality is poor, and foraging time is unrestricted by heat build-up. How much reserve capacity should animals retain to cope with these extremes? Should animals be able to tolerate once weekly, once per season, or once per lifetime, extreme events? Observations on the activity patterns of kudus, comparing the tame study animals with wild kudus, suggest that daily activity is restricted by extreme high temperatures on only about one day in seven, with the animals changing their temperature tolerance between summer and winter (N. Owen-Smith, unpublished results).

Our study incorporated simplifying assumptions, limited samples, lack of replication and uncertainty about how to assess key processes of conversion. It was perhaps fortuitous that estimates of mean monthly energy gain showed such a close correspondence with the estimated requirements. I believe that this striking finding was promoted by the natural environments in which we observed our subjects, and by allowing these animals adequate time to familiarize themselves with the habitats and food resources available to them. Different results may be obtained in short-term trials, or in experiments with artificially constructed environments, however precise the measurements.

The implications of our findings are limited by the fact that we studied growing subadult animals, which did not experience the additional nutritional costs of reproduction (the two females calved 2–3 months after the conclusion of the study). Because minerals were supplemented, we were not able to evaluate how animals might balance energy and protein needs with those of other nutrients. Wider changes in habitat selection to overcome the nutritional bottleneck of the late dry season were prevented by the fence around the enclosure. The energy supplementation that thereby became necessary during the critical period may have changed the use by the study animals of remaining food resources.

Despite its limitations, I believe that the findings of our study provide strong support for optimality principles in foraging behaviour, not in the static sense of average diets matching average conditions, but rather through the dynamic, adaptive responses to compensate for the changes in food availability and other environmental conditions. The potential for such adaptive behaviour is limited by the physiological processes governing thermal tolerance, digestive-processing capacity, effects of allelochemicals, food-

processing costs, and body growth potential. The mechanisms, costs and plasticity in responses associated with these constraining factors need further investigation.

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