

MAXIMIZING ENERGY RETENTION IN GRAZING RUMINANTS

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SUMMARY

(1) Costs of locomotion are frequently ignored in models determining the optimal diet of free-ranging ungulates. In order to determine whether such omissions are justified, the relationship between bite size and distance travelled per day is investigated in several wild species of ruminant grazing natural pastures in the Serengeti National Park, Tanzania.

(2) The distance travelled to obtain a gram of food rises exponentially as bite size declines. Animals feeding on short swards have small bite sizes, but it is suggested that animals feeding selectively on coarse grasslands would also have small bite sizes. It is shown that the heat production in locomotion of selective animals can form a large fraction of the daily intake of metabolizable energy.

(3) A simple model of the energy exchange in free-ranging ruminants is developed incorporating parameters of diet quality and heat production. The model applies to pastures which do not set a limit to the daily intake of dry matter. The optimum level of selection for high quality constituents in the grass sward is found by determining the conditions in which energy retention (net energy) is at a maximum.

(4) For any particular pasture, the optimum level of selection is found to be strongly dependent on the cost of locomotion per day and on the difference between the metabolizable energy concentration of high and low quality constituents, weakly dependent on the average quality of forage, and independent of the ruminant's resting metabolic rate.

(5) The model predicts that the optimum level of selection by large grazing herbivores will be lower than that of smaller animals. This is because large herbivores gain more from digesting low quality constituents due to their ability to digest cell walls, and also because the foraging costs of large animals are higher.

INTRODUCTION

By selectively grazing, herbivorous animals can enhance the proportion of green leaf in their diets well above that found in the grass sward. In grazing trials with three plains antelope of East Africa (topi, *Damaliscus lunatus* (Burchell), wildebeest, *Connochaetes taurinus* (Burchell), and hartebeest, *Alcelaphus buselaphus* (Pallas)) the level of selection for green leaf was found to be highest on mature pasture that had not been grazed previously. On a proportional basis, the food ingested contained up to seven times as much green leaf as was found in the sward (Duncan 1975; pers. records). On low biomass pastures (including both senescent and immature swards) little or no enhancement of green leaf in the diet was observed. As an increased

proportion of green leaf in the diet raises the content of metabolizable energy in the food ingested relative to the average for the sward, there has been much speculation about the constraints acting on selective feeding. Intuitively, one might expect selectivity to be increased at the expense of a reduced short-term rate of food intake (Stobbs 1973a; Hodgson 1982), but some studies investigating the effect of fasting and lactation on cattle and sheep grazing behaviour, have failed to demonstrate such an effect (Hodgson & Jamieson 1981; Greenwood & Demment 1988). However, by manipulating the sheep's appetite in a different way (reducing the animal's hunger by providing highly digestible feed prior to the grazing trial), Jung & Koong (1985) observed an inverse relationship between the quality of food selected and the intake rate, as expected. Similar trials on well-differentiated, tropical pastures have not been reported, but indirect evidence indicates that intake can be compromised for selectivity. The diets of large-sized ruminants are usually of low quality (Hoppe 1977; Owen-Smith 1982; Demment & Van Soest 1985), and this is thought to arise in part from their higher energy requirements and restrictively small bite volumes when selecting high quality food (Bell 1970; Jarman & Sinclair 1979; Illius & Gordon 1987).

These ideas have carried over to mathematical models predicting the composition of the diet of free-ranging ruminants. Either the quality of a food item is traded off against its abundance, or the availability of one limiting nutrient in a food plant is traded off against the scarcity of another (Owen-Smith & Novellie 1982; Belovsky 1984, 1986; Owen-Smith 1985; Verlinden & Wiley 1989; Illius & Gordon 1990a). Typically, the fitness of the foraging animal is described by a function of the gross rate of energy intake, or by a net rate that nevertheless fails to deduct the energy costs of foraging. The latter, being considered insignificant in relation to the energy income from food, is largely ignored.

In this paper, it is hypothesized that the major constraint on diet selectivity of free-ranging ruminants is not a declining rate of intake but an increasing expenditure of energy in foraging. It is assumed that free-ranging ruminants usually compensate for reduced, short-term rates of intake by extending the duration of foraging periods, so maintaining daily intake on all but the shortest of pastures. Field observations lend support to this contention. The time allocated to foraging each day by reindeer (*Rangifer tarandus tarandus* (L.)) increased in association with a declining rate of food intake on low biomass tundra (Trudell & White 1981). Similar responses have been noted in sheep (*Ovis aries* L.) (Pierson & Scarneccia 1987), wapiti (*Cervus elaphus* L.) (Gates & Hudson 1983), North American bison (*Bison bison* (L.)) (Hudson & Frank 1987) and African buffalo (*Syncerus caffer* Sparrman) (Sinclair 1977). Topi and hartebeest were observed resting without ruminating for long periods in the dry season, suggesting that their foraging bouts could have been extended without prejudice to other necessary activities (pers. records).

On pastures with very low plant biomass, the ruminant may not be able to maintain daily intake despite prolonged foraging (Stobbs 1973b; Trudell & White 1981; Wickstrom *et al.* 1984). Daily intake of sheep and cattle declined on grass swards less than 6 cm and 10 cm in height, respectively (Penning 1986; J. Hodgson, pers. comm.). On short swards, scaling of incisor arcade breadth with body size can limit the maximum daily intake of large animals, and this factor could influence habitat selection and diet quality (Gordon & Illius 1988; Illius & Gordon 1990b). But, diet quality may be limited by energetic constraints even on short swards.

On heavily grazed pastures, cattle (with or without removal of rumen contents) reduced the time spent grazing per day, suggesting that the costs of selecting for the small quantity of green leaf in the pasture were prohibitive (Chacon & Stobbs 1976). In the wild, ruminants usually forage on pastures that do not limit daily intake. Selective feeding (involving both a reduced bite size and a reduced density of acceptable feeding stations) will lead to an increase in the time spent travelling and to longer day-range lengths. Consequently, the animal which feeds selectively will incur a higher energetic cost derived from the increased heat production in locomotion.

If energetic costs of foraging are an effective constraint on diet selectivity, they must represent a substantial fraction of the energy budget. Therefore in investigating the hypothesis, I will first quantify the energy budget of a ruminant grazing selectively on pasture containing grass at a mature growth stage, evaluating the contribution of locomotion costs in foraging. With this empirical background in mind, a simple mathematical model will then be developed which enables further investigation of diet selection in relation to the ruminant's fasting metabolic rate, energetic cost of locomotion, and metabolizable energy content of food.

METHODS

Daily energy exchange is reckoned for a grazing ruminant (bulk and roughage feeder, Hofmann 1989), with body mass of 100 kg, foraging on tropical pastures with coarse, well-differentiated grass swards. This description could apply to a young, adult female topi grazing in the Serengeti National Park, Tanzania during the dry season. Change in the energy content of the topi's body is determined as the difference between the rate of intake of metabolizable energy and the rate of heat production (Fig. 1).

Intake of metabolizable energy

Two of the more important forage plants in the Serengeti National Park are the grass species, *Digitaria macroblephara* (Hack.) and *Themeda triandra* Forssk (Duncan 1975; Sinclair 1977). Herbage samples from these species were sorted into plant parts, dried at 65 °C and flown to the U.K. for analysis by the Agricultural Development and Advisory Service (ADAS) of the Ministry of Agriculture, Fisheries and Food, using their methods (ADAS 1986). Neutral detergent cellulase digestibility (*NCD*) was determined using the method of Dowman & Collins (1982, method e). Gross and metabolizable energy concentrations (E_I and E_M) were estimated from the regression equations in Givens, Everington & Adamson (1990):

$$E_I(\text{MJ kg}^{-1}) = 0.0065CP(\text{g kg}^{-1} \text{ DM}) + 17.7 \quad (\text{S.E.} = 0.34 \text{ MJ kg}^{-1})$$

and,

$$E_M(\text{MJ kg}^{-1}) = 0.0111NCD(\text{g kg}^{-1} \text{ DM}) + 3.24 \quad (\text{S.E.} = 0.65 \text{ MJ kg}^{-1})$$

where CP is the crude protein content and DM is dry matter. Equations derived for E_I and E_M of tropical forages have not yet included measurements of digestibility based on cellulase methods. The relationship between CP and NCD in our samples ($CP = -71.8 + 0.308NCD$) was close to that determined from temperate forage

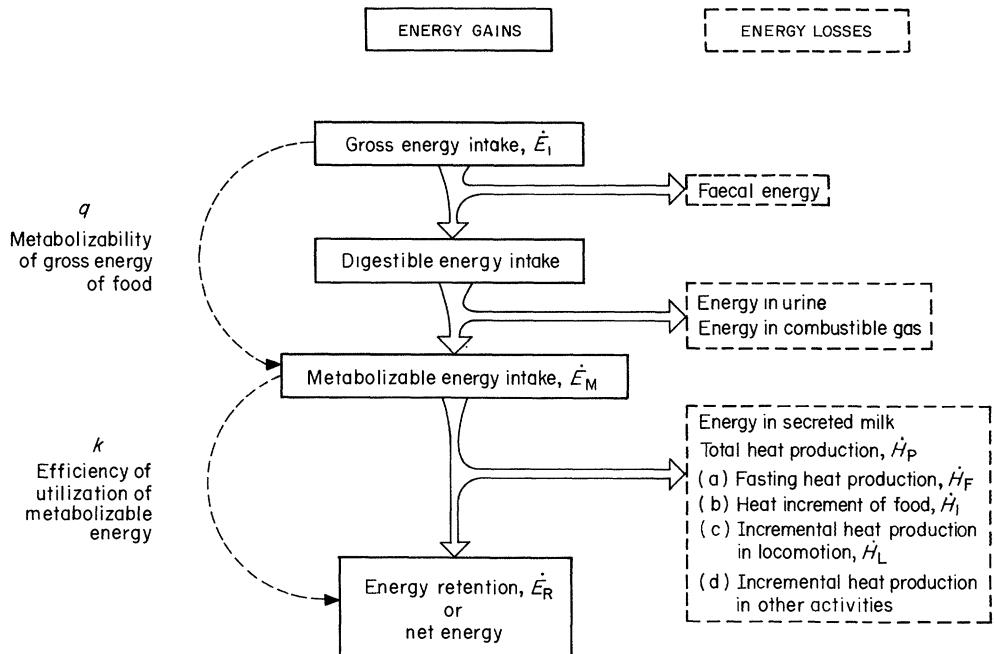


FIG. 1. Energy exchange in the free-ranging ruminant (adapted from ARC 1980)

($CP = -79.2 + 0.302NCD$) (D.I. Givens, pers. comm.). Metabolizability of gross energy (q) was determined as

$$q = E_M/E_I \quad (\text{ARC 1980}). \quad (1)$$

Two fractions of the topi's diet are considered: one with green leaf only, and the other with equal quantities by weight of brown leaf and live stem. Daily intake may be derived as a function of the proportion of green leaf in the diet, by calculating metabolizability (q) of the overall diet (i.e. by weighting q of green leaf and q of non-green leaf fractions according to their % contributions by weight), and substituting into the ARC (1980) equation for dry matter intake of cattle:

$$\dot{I}_D = 0.0241M^{0.75} + q(0.1065M^{0.75}), \quad (2)$$

where \dot{I}_D is the rate of dry matter intake (kg day^{-1}) and M is live mass (kg). Daily intake of metabolizable energy (\dot{E}_M) is then determined as the product of the metabolizable energy concentration of the overall diet (E_M) and \dot{I}_D . Equation (2) was derived largely from indoor trials with cattle fed long or chopped roughages, and can only serve as an approximation to the response expected from free-ranging, tropical ruminants. However, it has the advantage of being based on a large number of carefully controlled trials.

Heat production

Heat production in the free-ranging ruminant can be estimated by partitioning total daily heat production (\dot{H}_P) into several components (such as heat production in

the resting animal, the heat increment of food, and the increments of heat production for standing, ruminating, foraging, walking and for other muscular work) and summing the parts (Graham 1964; Osuji 1974; Tyler 1987; Blaxter 1989). For the purposes of constructing an energy budget for a topi, only three components of heat production will be considered: fasting metabolic rate; the heat increment of food; and the incremental cost of locomotion.

The fasting metabolic rate (\dot{H}_F) is usually measured over 24 h in animals that are fasted but free to move at will within the confines of a calorimeter or respiration chamber. Thus, \dot{H}_F is a measure of the heat production in the fasted animal when it is lying, with increments for standing and for vigilance. Summarizing values obtained from eighty-eight cattle*, ARC (1980) found:

$$\dot{H}_F = 0.53M^{0.67} \text{ MJ day}^{-1}.$$

The heat increment of food (\dot{H}_I) included components due to eating (prehending, masticating and swallowing), ruminating, fermentation and related biochemical events. It is determined as $\dot{H}_I = (1 - k_m)\dot{E}_M$, where k_m is the efficiency of utilization of metabolizable energy for maintenance (Blaxter 1989). Analysing the results of seventy calorimetric experiments in which cattle and sheep were fed natural diets, Blaxter & Boyne (1978) found that efficiency for maintenance could be predicted from nutritional properties of the diet:

$$k_m = 0.947 - 0.00010(CP/q) - 0.128/q,$$

where CP is the crude protein content of the organic matter of the diet (g kg^{-1}).

The energy cost of locomotion in sixty-five species of mammal, including nine species of ruminant and one suid, were investigated by Taylor, Heglund & Maloij (1982). They reported on the rate of oxygen consumption of animals trained to run on treadmills at different speeds. Combining results, they then formulated allometric equations for energy consumption in terms of speed and body mass. The regression equations have two components: the slope represents an incremental cost of locomotion, and the intercept represents an extrapolated cost at zero speed. The equation for the slope of all ten artiodactyls may be expressed as:

$$\dot{H}_L = V(15.82M^{0.589}),$$

where \dot{H}_L is the rate of heat production in locomotion (watts) and V is the speed (m s^{-1}). Confidence limits for the coefficient (15.82) are 11.09 and 17.91; those for the exponent (0.589) are 0.494 and 0.683. Assuming that the relationship between heat production and speed is linear (Taylor, Heglund & Maloij 1982), the net cost of moving 1 m is simply $15.82M^{0.589}(\text{J m}^{-1})$.

It was suggested above that the day-range length of a ruminant will increase with diet selectivity due to the decreasing size of bites and the increase in the distance between feeding stations. The distance travelled whilst foraging each day (L_D) can be determined as

$$L_D = \frac{N_s \dot{I}_D L_s}{2I_B},$$

* Equations relating resting metabolic rate to live mass of artiodactyls have been published in several comparative studies (e.g. Taylor, Heglund & Maloij 1982; Peters 1983; Hayssen & Lacy 1985; Blaxter 1989). The data are derived from different research groups and there is much variation in the predicted estimates.

where N_s is the average number of steps per bite, I_B is bite size (kg), and L_s is the stride length (consisting of two steps and estimated to be 1.24 m for topi, pers. records). The time required for foraging movements (T_L) will be L_D/V (s); V is estimated to be 0.98 m s⁻¹ (Pennycuick 1975; pers. records).

Intake and foraging behaviour

Bite and step sequences of wild ruminants (topi, hartebeest, wildebeest and waterbuck (*Kobus ellipsiprymnus* (Ogilby))) in the Serengeti were recorded with the aid of a computerized event recorder and 8 × 40 binoculars. The four species are of similar average body size and are classified by Hofmann (1973) as bulk and roughage feeders. Foraging groups were habituated to the observer's vehicle, and recording commenced after the focal animal had settled into a feeding bout. Feeding bouts of less than 200 s were discarded from the analysis (Underwood 1983). Immediately after making the behavioural recording, average grass biomass was measured along the foraging path with inclined point quadrats (Warren Wilson 1963).

Tame animals (three topi, two hartebeest and two wildebeest) were stabled at the Serengeti Wildlife Research Centre and walked to nearby pastures for feeding trials. The animals were 18–21 months of age at the start of feeding trials, with body mass ranging between 75 and 110 kg. Measurements of bite size were taken from one representative of each species: a female topi (80 kg); a male hartebeest (100 kg); and a male wildebeest (90 kg). The three species belong to the same subfamily (Alcelaphinae) and feed almost exclusively on grass. In feeding trials, animals were led onto 10 × 10 m plots each with a uniform grass sward. The halter was attached to a peg at the centre of the plot and the animal was left to graze undisturbed. The incentive to leave plots was reduced by cutting the grass short round the perimeter and, if necessary, by scraping the ground bare. Bite size was determined by weighing animals to the nearest 10 g before and after feeding trials in which bite number (approximately 1000 bites) and step number were recorded (Allden & Whittaker 1970; Penning & Hooper 1985). Allowance was made for insensible weight loss which was calibrated against radiant temperature for each animal. Grass biomass was measured by clipping four 25 × 25 cm quadrats inside each of the plots.

RESULTS

Topi energy budgets

The number of steps per bite of free-ranging and tame ruminants in the Serengeti National Park ranged from a minimum of 0.02 on moderate–heavy grass swards up to a maximum of 4.5 on light swards (Fig. 2). The smallest average bite size recorded in the tame animals was 0.01 g on a light sward (68 g m⁻²) rising to a peak of 0.5 g on a moderately heavy sward (614 g m⁻²) (Fig. 3). The two parameters are inversely related, with ruminants on light swards taking smaller bites and travelling further between bites (Fig. 4). A ruminant choosing to be selective for green leaf on a coarse pasture with little green leaf would also take smaller bites and travel further between bites. It is suggested that the relationship between bite size and number of steps per bite will be similar whether small bites are the consequence of grazing on low biomass swards, or the consequence of selective grazing on coarse swards.

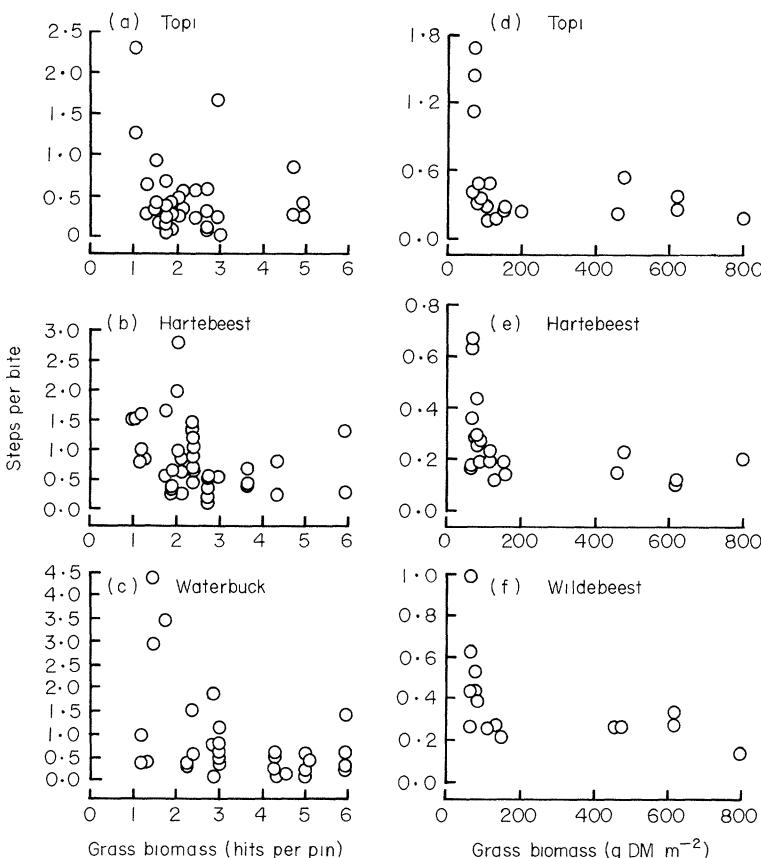


FIG. 2. Travel rates of grazing topi, hartebeest, wildebeest and waterbuck in relation to grass biomass: (a-c) free-ranging animals, (a) topi on dry grass swards, (b) hartebeest on green swards, (c) waterbuck on green swards; (d-f) tame animals on experimental swards.

Three levels of selectivity were chosen arbitrarily in constructing the energy budgets of topi: *highly selective* (100% green leaf in the diet) with a bite size of 0.05 g and 2 steps per bite; *moderately selective* (55% green leaf in the diet) with a bite size of 0.2 g and 0.3 steps per bite; and *not selective* (10% green leaf in the diet) with a bite size of 0.35 g and 0.1 steps per bite. The energy budgets of topi when feeding with these three different selectivities, on pastures composed of mature stands of either *Themeda triandra* or *Digitaria macroblephara*, are enumerated in Table 2.

Energy retention is found to be highest in the moderately selective animal but positive energy retention is only attained on a diet of *Digitaria macroblephara*. Negative retention of energy on a diet of *Themeda triandra*, with 55% green leaf, is surprising: it suggests that the estimate for fasting metabolic rate may be high, or that metabolizability of the diet has been underestimated (Table 1). The main points emerge clearly from a perusal of Table 2: the heat production in locomotion can be a large proportion (up to two-thirds) of the intake of metabolizable energy; the

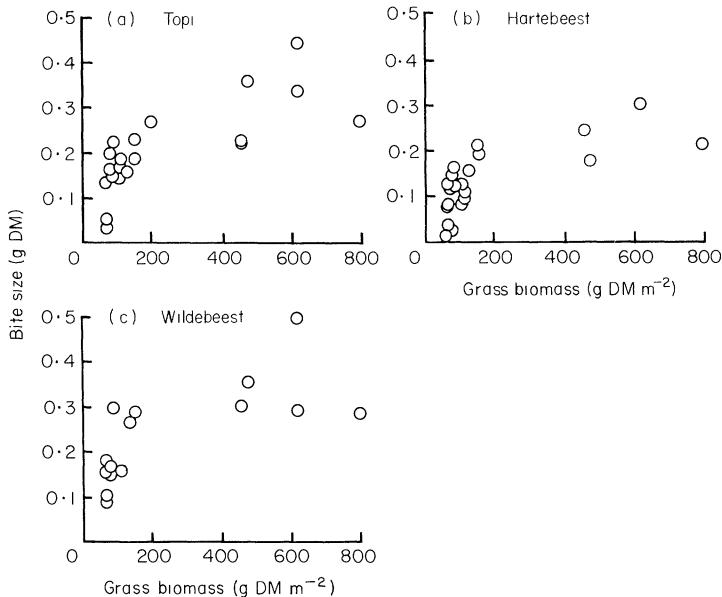


FIG. 3. Bite size in relation to grass biomass of tame ruminants on experimental swards.

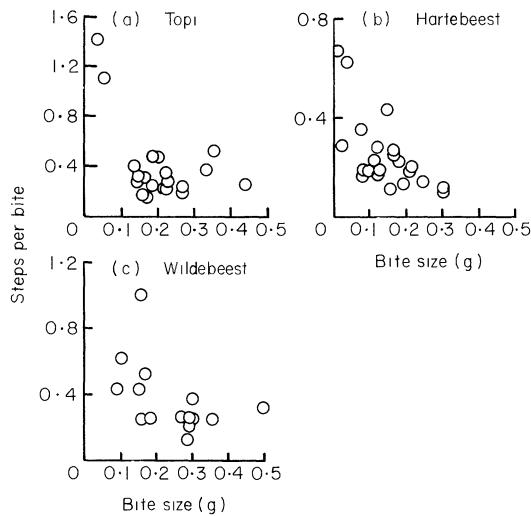


FIG. 4. Travel rate in relation to bite size of tame ruminants.

selectivity of topi can be strongly constrained by the energetic costs of locomotion; and energy retention is greatest when the time and energy investment in locomotion during foraging is modest.

TABLE 1. Nutritional properties* of two forage grasses in the Serengeti National Park

Plant part	<i>NCD</i> (g kg ⁻¹ DM)	<i>CP</i> (g kg ⁻¹ DM)	<i>E_L</i> (MJ kg ⁻¹ DM)	<i>E_M</i> (MJ kg ⁻¹ DM)	<i>q</i>
<i>Themeda triandra</i>					
Green leaf	510.4	80.5	18.22	8.91	0.489
Brown leaf	420.8	37.0	17.94	7.91	0.441
Live stem	261.3	15.6	17.80	6.14	0.345
<i>Digitaria macroblephara</i>					
Green leaf	536.0	103.6	18.37	9.19	0.500
Brown leaf	423.4	42.4	17.98	7.94	0.442
Live stem	398.7	32.8	17.91	7.67	0.428

* Values represent averages of 4–8 samples.

A model of diet selection in the free-ranging ruminant

Formulation

Suppose that a ruminant spends the day grazing on one particular pasture which offers sufficient food for the animal to keep its rumen full. The pasture contains both high quality constituents (e.g. green leaf) and low quality constituents (e.g. stem) with metabolizabilities q_H and q_L , respectively. On that pasture, the level of selection (s) is determined by the proportion of high-quality constituents in the diet. We will seek the optimum level of selection, i.e. that selection level at which energy retention, or net energy, is maximized.

Firstly, we require an expression for intake of metabolizable energy in terms of s , q_L and q_H . This is not quite straightforward as the daily intake of dry matter depends on diet quality, being lower when the concentration of metabolizable energy in the diet is low. An empirically derived expression relating intake to diet quality in cattle was stated earlier (eqn (2)). Dry matter intake (kg day⁻¹) may be converted to gross energy intake (MJ day⁻¹) by multiplying by 18.4 (ARC 1980; Givens *et al.* 1989a, b), allowing us to restate eqn (2) as

$$\dot{E}_I = k_1 + qk_2,$$

where q is the metabolizability of the diet as a whole, and k_1 and k_2 are mass-specific constants. By substitution into eqn (1), we then obtain

$$\dot{E}_M = qk_1 + q^2k_2. \quad (3)$$

In the case of a 100-kg ruminant, k_1 is 14.023 and k_2 is 61.968 (see eqn (2)) with \dot{E}_M measured in MJ day⁻¹. The metabolizability of the overall diet may be broken down into its component parts:

$$q = sq_H + (1 - s)q_L.$$

By substitution into eqn (3), we arrive at the desired formulation for the daily intake of metabolizable energy:

$$\dot{E}_M = [q_L + s(q_H - q_L)]k_1 + [q_L + s(q_H - q_L)]^2k_2. \quad (4)$$

Secondly, we required an equation for daily heat production in the ruminant.

TABLE 2. Daily energy budget of a 100-kg ruminant feeding on monospecific pastures of *Themeda triandra* (T.t.) or *Digitaria macroblephara* (D.m.)

(a) Energy intake		Selectivity of diet		
Grass species	Indices of diet	Not selective	Moderately selective	Highly selective
	% green leaf	10	55	100
T.t.	$\frac{q}{CP \text{ (g kg}^{-1})}$	0.40	0.45	0.49
	$\dot{I}_D \text{ (kg day}^{-1})$	31.7	56.1	80.5
	$\dot{E}_M \text{ (MJ day}^{-1})$	2.119	2.264	2.408
		15.29	18.25	21.44
D.m.	$\frac{q}{CP \text{ (g kg}^{-1})}$	0.44	0.47	0.50
	$\dot{I}_D \text{ (kg day}^{-1})$	44.2	73.9	103.6
	$\dot{E}_M \text{ (MJ day}^{-1})$	2.249	2.349	2.447
		17.86	20.12	22.48
(b) Heat production		Selectivity of diet		
Grass species	Components of heat production	Not selective	Moderately selective	Highly selective
	$\dot{H}_F \text{ (MJ day}^{-1})$	11.60	11.60	11.60
T.t.	$\dot{H}_I \text{ (MJ day}^{-1})$	5.79	6.43	7.12
	$L_D \text{ (km)}$	0.38	2.11	59.72
	$T_L \text{ (h)}$	0.11	0.60	16.93
	$\dot{H}_L \text{ (MJ day}^{-1})$	0.09	0.50	14.23
	$\dot{H}_P \text{ (MJ day}^{-1})$	17.47	18.53	32.94
D.m.	$\dot{H}_I \text{ (MJ day}^{-1})$	6.30	6.85	7.41
	$L_D \text{ (km)}$	0.40	2.18	60.68
	$T_L \text{ (h)}$	0.11	0.62	17.20
	$\dot{H}_L \text{ (MJ day}^{-1})$	0.09	0.52	14.46
	$\dot{H}_P \text{ (MJ day}^{-1})$	17.99	18.96	33.47
(c) Energy retention		Selectivity of diet		
		Not selective	Moderately selective	Highly selective
T.t.	$\dot{E}_R \text{ (MJ day}^{-1})$	-2.19	-0.28	-11.49
D.m.	$\dot{E}_R \text{ (MJ day}^{-1})$	-0.13	1.16	-10.98

Consider just two components: one incorporating those elements that are independent of change in the pattern of grazing activity (including resting metabolism); and the other with elements directly associated with grazing activity (including heat production in eating and walking). The heat production in these latter activities will be particularly influenced by the cost of locomotion, which increases exponentially with the degree of selectivity. An exponential rise is suggested by the observations of

ruminants grazing on natural pastures in the Serengeti and elsewhere, which show that small bite sizes are associated with a greater travel distance between bites (Fig. 4; Wickstrom *et al.* 1984). The exponential form is revealed when data in Fig. 4 are recast to show the relationship between number of steps taken per g of grass ingested and bite size (Fig. 5).

The function for heat production is formulated as:

$$\dot{H}_P = a + b^s, \quad (5)$$

where the first term (a) represents heat production that is independent of grazing activity, and the second term (b^s) is the heat production that increases exponentially with selectivity. The constant, b , may be thought of as the maximum daily heat production in locomotion.

An expression for daily energy retention can now be found by subtracting the expression for \dot{H}_P from that for \dot{E}_M :

$$\dot{E}_R = [q_L + s(q_H - q_L)]k_1 + [q_L + s(q_H - q_L)]^2k_2 - (a + b^s). \quad (6)$$

To find that level of selection (s^*) at which \dot{E}_R is maximized, we differentiate with respect to s :

$$\partial\dot{E}_R/\partial s = (q_H - q_L)k_1 + 2(q_H - q_L)[q_L + s(q_H - q_L)]k_2 - b^s \log_e b.$$

\dot{E}_R will be at a maximum (or minimum) when $\partial\dot{E}_R/\partial s = 0$, or

$$(q_H - q_L)k_1 + 2(q_H - q_L)[q_L + s(q_H - q_L)]k_2 = b^s \log_e b. \quad (7)$$

Equation (7) can be solved iteratively by the Newton-Raphson method (Harding & Quinney 1986). Note also that

$$\partial^2\dot{E}_R/\partial s^2 = 2(q_H - q_L)^2k_2 - b^s (\log_e b)^2,$$

which is negative with s and b large enough. By substituting values for s^* obtained from eqn (7) into eqn (6), it is possible to find the maximum energy retention, $\dot{E}_{R\max}$.

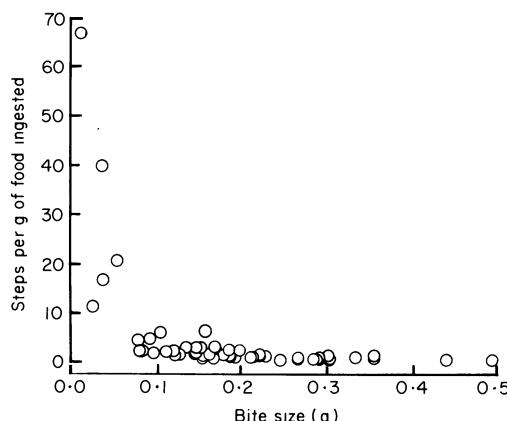


FIG. 5. Steps per unit of food ingested in relation to bite size of tame animals. Data for topi, hartebeest and wildebeest are combined.

Predictions

Curves describing energy intake and heat production, in relation to the level of selection for high-quality plant constituents, are illustrated in Fig. 6a for the case of a free-ranging ruminant of 100 kg body mass. The optimum level of selection (s^*) coincides with the maximum energy retention. From eqn (7) and Fig. 6b, it can be seen that s^* will be unaffected by the location of the y intercepts of these functions but will be determined by the slopes. This means that a reduction in the resting metabolic rate of a ruminant (parameter a in eqn (5)) will not change its optimum level of selectivity, although it will increase the maximum energy retention (Fig. 7). A reduction in the cost of locomotion (parameter b in eqn (5)) will raise the optimum level of selection (Fig. 8a) and maximum energy retention (Fig. 8b).

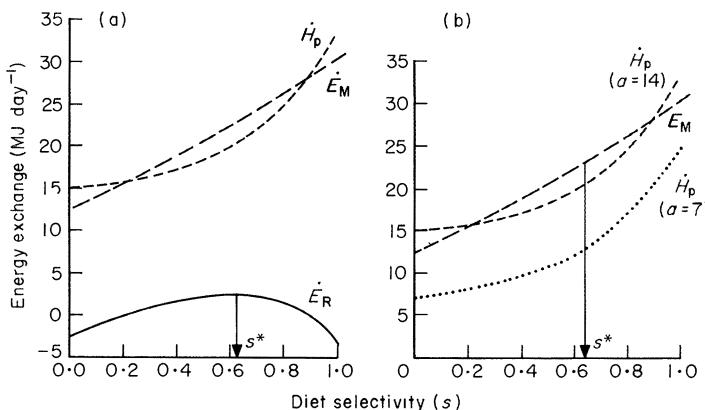


FIG. 6. Energy exchange in the model ruminant as a function of diet selectivity: (a) metabolizable energy intake, heat production and energy retention as functions of the level of selection (parameters in eqns (4) and (5) were set as follows: $q_L = 0.35$, $q_H = 0.60$, $a = 14$, $b = 20$; (b) \dot{E}_M and \dot{H}_P as functions of the level of selection, showing that s^* is independent of the size of parameter a .

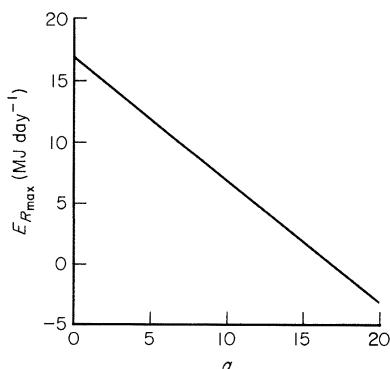


FIG. 7. Maximum energy retention of the model ruminant as a function of the resting metabolic rate (parameters were set as: $q_L = 0.4$, $q_H = 0.55$, $b = 15$).

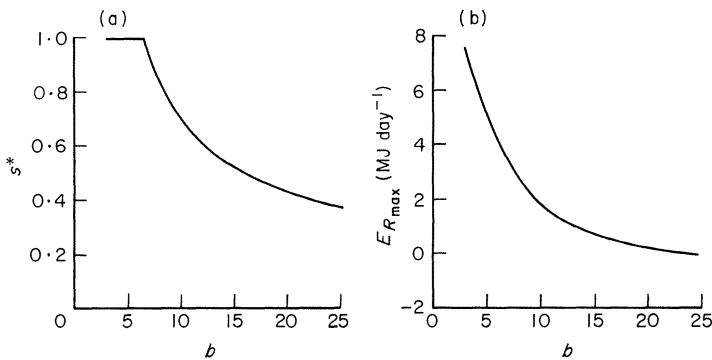


FIG. 8. Influence of the incremental cost of locomotion on (a) the optimum level of selection and (b) the maximum energy retention ($q_L = 0.4$, $q_H = 0.55$, $a = 16$).

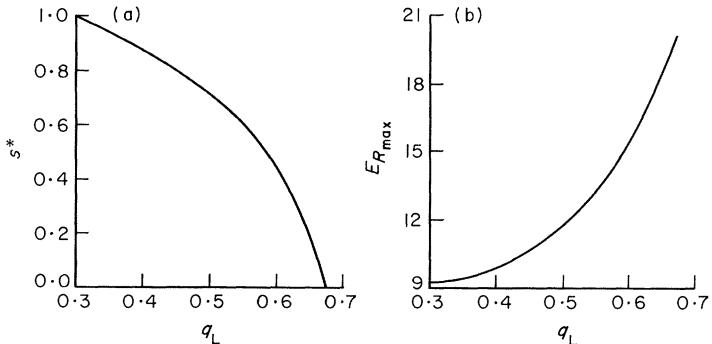


FIG. 9. Influence of metabolizability of the low-quality constituents of a pasture (note q_H was fixed at 0.7) upon (a) the optimum level of selection and (b) the maximum energy retention. Other parameters were $a = 16$, $b = 15$.

With reference to the intake function, the level of selection was positively but weakly related to the overall quality of food, reflecting the form of the relationship between daily intake and metabolizability of the overall diet. However, when the metabolizability of the low-quality constituents of the pasture declines relative to that of the high-quality constituents, s^* rises sharply (Fig. 9a) and the maximum energy retention drops exponentially (Fig. 9b). The added importance of selecting for leaf, when feeding from a grass sward with stem of low digestibility, can be gauged from a comparison of the topi's intake of metabolizable energy on grass swards containing *Digitaria macroblephara* and *Themeda triandra* (Table 2).

Body mass was not incorporated in the model as a variable, but it is still possible to consider some of the implications of a change in body mass with regard to the optimum level of selection. First, it is necessary to consider the relationship between bite size and body size at the same level of selection. On dense swards with a high proportion of green leaf, bite size will probably increase with body size without

prejudice to selection (Illius & Gordon 1987). Where green leaf is more scarce, larger bites are associated with lower levels of selection (pers. records). On such pastures, I assume that bite size is approximately constant across body sizes for the same level of selection. In that case a doubling of the daily intake of dry matter (I_D) will be associated with a doubling in the number of bites per day, this in turn will double the distance moved by the foraging animal per day. Now the incremental cost of locomotion is proportional to $M^{0.68}$ (Taylor, Heglund & Maloiy 1982), which is similar to the scaling for metabolic energy requirements (Hayssen & Lacy 1985). This means that a larger animal which has double the intake of a smaller one will have approximately twice the incremental heat production in locomotion per metre. Thus, the daily increment in heat production in locomotion (b^o) is approximately quadrupled. From Fig. 8a, it can be seen that the overall effect will be a reduction in the optimum level of selection. But this is not the only effect: large ruminants extract more metabolizable energy per unit of food ingested than do small ruminants, especially if the diet has a large fraction of cell wall that is potentially digestible (Van Soest *et al.* 1983). In general, this will be more true for lower-quality than for higher-quality constituents of the grass sward. Therefore, the difference between the metabolizable energy concentrations of high and low-quality constituents will be smaller for larger ruminants, further reducing the optimum level of selection (Fig. 9a). This analysis suggests that even on high-biomass grass swards, large ruminants will select lower-quality diets because their foraging costs are higher at any given level of selection, and their more efficient fibre digestion reduces the advantage to be gained by selective feeding. Conversely, small ruminants will be more selective as travel costs are cheap and their capacity to digest fibre is poor.

DISCUSSION

The main conclusion to emerge from this investigation of the ruminant's diet is that the incremental heat production in locomotion constitutes a major constraint on both the optimum level of diet selection and the maximum energy retention. The magnitude of the cost of locomotion will depend on the spatial distribution of food. Selection for green leaf would be very costly on senescent, grass swards that have been heavily grazed as they contain only occasional items of short green leaf. Yet, this is a common condition of dry season pastures in Africa.

In Table 2, it is suggested that a ruminant selecting strongly for green leaf on poor pasture would need to forage over 60 km to maintain daily intake. This is further than the maximum movement rates reported by field workers. For instance, mean daily movement of migratory caribou (*R. t. granti* Allen) reached 14–26 km in midsummer, with a maximum rate in excess of 40 km day⁻¹ in some circumstances (Fancy *et al.* 1989). During the spring migration of saiga antelope (*Saiga tatarica* (L.)), herds travelled an average of 21 km day⁻¹ with rates of 40–50 km day⁻¹ recorded in one year (Bannikov *et al.* 1967). Cattle, when pressed to their limit by Masai pastoralists, travelled up to 35 km every 2 days between pasture and water (Western 1975). Arabian oryx (*Oryx leucoryx* (Pallas)) walked 3–7 km day⁻¹ when resident within their temporary ranges, but daily distances of 25–40 km were common during forays into unused or formerly used areas (Stanley Price 1989). In dry conditions, topi range widely across the northern Serengeti: one group under observation travelled slowly but steadily covering 15 km in daylight hours. (P. Arcese, pers. comm.).

It is unlikely that ruminants would choose to travel 60 km day⁻¹, as a strategy to enhance the quality of food procured. Nevertheless, this figure indicates the magnitude of the energetic costs that *would* be incurred were an animal to select strongly for green leaf on senescent pasture. Heavily grazed and senescent pastures are commonplace in the Serengeti during dry conditions, but topi and wildebeest do not select for green leaf on this type of grassland (Duncan 1975; pers. records).

The cost of locomotion will also depend on the nature of the terrain (White & Yousef 1978; Fancy & White 1985a, 1987), and on the net efficiency of locomotion in the animal. The rate of use of metabolic energy varies with walking speed (Cavagna, Heglund & Taylor 1977; Hoyt & Taylor 1981; Fancy & White 1985b) and rises with increasing body size (Taylor 1980; see *Predictions* above). Significant differences between individuals may occur for other reasons (e.g. Fancy & White 1987) which have not been investigated.

Of course, in choosing to feed selectively, the ruminant can by-pass these considerations by following a simple rule of thumb that integrates all relevant processes: 'increase level of selection up to the point at which energy retention (net energy) begins to decline'. Contrast this rule with one that could apply to ruminants foraging according to models that consider nutritional constraints alone: 'increase selectivity up to the point at which the intake of metabolizable energy begins to decline'. A model based on 'maximizing energy retention' is applicable when herbivores are able to increase their intake of metabolizable energy through a process that increases the daily cost of foraging (measured in terms of time spent foraging and distance moved). Models that rely heavily on ingestive or digestive constraints may be sufficient when high-quality food is abundant (e.g. Owen-Smith & Novellie 1982; Belovsky 1984).

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