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HERBAGE INTAKE IN RELATION TO AVAILABILITY AND SWARD STRUCTURE: GRAZING PROCESSES AND OPTIMAL FORAGING

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SUMMARY

(1) The relation between grazing intake, herbage availability and sward structure is investigated using grazing process models. The general model expresses the instantaneous intake rate (IIR) while grazing as the ratio of bite weight to the sum of searching and handling time per selected bite.

(2) The general model is modified to make it applicable to three different descriptions of the sward. Model A analyses the effects of vegetation cover, height, bulk density, and herbage mass on IIR, assuming uniform distribution of herbage mass within food items. Model B explores the effect of spatial heterogeneity on IIR, using a theoretical normal function to describe the availability of bite weights. It is assumed that the animal selects a range of bite weights so as to maximize IIR. Model C proposes a method of characterizing sward heterogeneity from empirical data. The model is applied to field data.

(3) Model A shows that the mechanism and magnitude of intake response to increasing herbage mass depends upon the combination of sward structural attributes that led to that increase. Similarly, intake rate at a given herbage mass depends strongly upon the spatial organization of the herbage.

(4) Models B and C show that the greater the variance of bite weight in the sward at a given mean herbage mass, the greater the maximum IIR, and the narrower the range of bite weights selected. At constant bite weight variance, IIR increases asymptotically with mean herbage mass.

(5) These models may explain the considerable variation in functional response to herbage availability reported in the literature. It appears that heterogeneity in potential bite weight needs to be accounted for if realistic predictions of intake rate and sward dynamics are required.

INTRODUCTION

The rate at which a grazing animal ingests herbage is a central variable in any livestock–pasture system. Herbage intake rate is a major determinant of animal nutrition and hence of liveweight change, lactation, and reproductive performance. The consumption process has a direct effect on leaf area and herbage mass, pasture growth rate, canopy structure, and, in the longer term, on botanical composition (Vickery 1981).

The factors affecting intake can be grouped as features of the environment, the animal and the pasture. Pasture-dependent features can be divided into aspects of 'availability' and 'quality'. Availability refers to the quantity and distribution of herbage mass in space, and affects intake rate through the mechanics of food-gathering. Quality refers to all physical and chemical attributes of the herbage material. Quality affects intake rate directly via selective grazing (Heady 1964), and indirectly via the rate of food processing in the gut (Bines 1971).

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The function relating intake rate to vegetation availability (the 'functional response', after Solomon 1949 and Holling 1959a) has long been a focus of study in grazing systems research. Empirical studies have generally found that intake rate initially increases with increasing herbage availability, becoming insensitive to it beyond a certain level (Willoughby 1959; Arnold & Dudzinski 1967a; Arnold 1975; Mulholland *et al.* 1976). This shape of the functional response has qualitative consequences for the dynamics and stability of grazed swards (Noy-Meir 1975, 1978a, 1978b). Less clear is the most appropriate definition of availability. Biomass per unit area (to be termed herbage mass; Hodgson 1979) has been the most commonly used measure (Willoughby 1959; Arnold & Dudzinski 1967a; Mulholland *et al.* 1976; Birrell 1981; Milne, Maxwell & Souter 1981). Leaf length or sward height has often been found to be an adequate index of availability and, in some cases, a better predictor of intake than herbage mass (Arnold & Dudzinski 1967b; Allden & Whittaker 1970; Arnold 1975; Baker, Alvarez & Le Du 1981). Allden & Whittaker (1970) clearly demonstrated that herbage mass *per se* is not a reliable guide to the intrinsic availability of herbage to the grazing animal. The high variability in functional response obtained under seemingly similar sward conditions (e.g. Arnold & Dudzinski 1967a) supports this claim.

A better understanding of the factors affecting intake has come from more detailed studies of the grazing process. Spedding, Large & Kydd (1966) defined daily intake as the product of the time spent grazing, the number of bites per unit time, and the average weight of each bite. Many grazing process studies have measured one or more of these components (Arnold & Dudzinski 1967a; Allden & Whittaker 1970; Donnelly, Davidson & Freer 1974; Arnold 1975; Arnold & Birrell 1977; Stobbs 1977; Jamieson & Hodgson 1979; Le Du *et al.* 1979; Birrell 1981; Hodgson & Jamieson 1981). Since one might expect there to be some degree of relation between bite weight and the distribution of herbage in space, a number of studies have measured the herbage mass per unit volume (to be termed bulk density) in the sward profile (Stobbs 1973a, b, 1975). Correlations have been found between bite weight, biting rate, grazing time and various herbage availability attributes. Nevertheless, a theoretical framework relating the empirically determined functional response and the mechanics of the grazing process has not been explicitly formulated.

In this paper, current knowledge and hypotheses about some of the basic processes of grazing are formalized into a general mathematical model. This general model is then developed further to make it applicable to three different descriptions of the sward as part of a theoretical exploratory study (Ungar 1984; Ungar & Noy-Meir 1986). The models refer to intake rate during periods of active grazing on a time scale of seconds and minutes, termed the instantaneous intake rate (IIR). The models are used to predict the functions relating IIR to characteristics of the pasture sward, in particular various measures of availability. We are interested in the individual bite; its weight, the time taken to search for and select a bite, and the time taken to handle (bite, chew, swallow) a bite. Each of these components of the grazing process is expressed in terms of basic anatomical and behavioural parameters of the animal and structural parameters of the sward. The approach is similar in some respects to that taken in an earlier unpublished study (Arnold, Noy-Meir & Galbraith 1982).

Attention is thus focused on conditions where intake is limited primarily by the rate at which green herbage, of generally good quality but low availability, can be found and prehended. Effects of low or variable quality on digestion rates, and selection for quality are not included in the models. Such conditions of availability-limited intake prevail during the first part of each growing season in semi-arid and mediterranean grasslands

(Heady 1961; Tadmor, Eyal & Benjamin 1974; Gutman & Seligman 1979; Breman & de Wit 1983) and probably also in many temperate grasslands with cold winters (Eadie & Maxwell 1975).

The first model (A) attempts to analyse the effects of the various components of pasture availability and sward structure (plant cover, height, bulk density, and herbage mass) on the ingestion rate.

The two subsequent models (B, C) explore the effects on intake rate of horizontal heterogeneity within the sward in availability, expressed now in terms of the weight of herbage that can be ingested in one bite. This requires specification in the models of rules by which animals select in such a sward. The assumption is made here that selection is optimal, in the sense of maximizing IIR. This is consistent with the principles of the theory of optimal foraging (Schoener 1971; Pyke, Pulliam & Charnov 1977; Krebs & McCleery 1984). In most of the optimal foraging models in the ecological literature, including that dealing with herbivores, these principles are applied to selection for food quality and to discrete feed categories (Westoby 1974; Belovsky 1978; Owen-Smith & Novellie 1982). Here, the same principles are applied to selection for availability (bite weight), the variation in which is described by continuous distributions. In model B a theoretical normal distribution is used.

Model C proposes a simple method of characterizing sward heterogeneity from empirical data which does not require the use of standard mathematical functions.

GENERAL MODEL

The grazing process consists of 'searching' (scanning, recognition, decision) and 'handling' (biting, chewing, swallowing). The model deals with periods of 'active grazing' during which the whole time is spent either searching or handling. It is assumed that these processes occur sequentially without overlapping in time, and that rumination occurs in separate, non-grazing periods. The sward is divided into 'food items', perceptual units of the animal, each containing n ($n \geqslant 1$) bite-size units.

No distinction is made between selecting clumps or patches of food and selecting food items from those available within a patch. A patch selection model might be appropriate for certain systems in which the available grazing area divides into patches of differing vegetation types, and the animal incurs a time cost travelling between patches. Such a model may also apply to shrub grazing. The simpler situation of a single, more or less continuous sward is considered here, and hence the concept of patch selection is not relevant. See Table 1 for definitions and standard parameter values.

The intake rate during active grazing, I, is defined as:

$$I = \frac{w}{t_s/n + t_h} \tag{1}$$

where w is the mean herbage weight per bite ingested, t_s is the mean searching time per food item selected for consumption, and t_h is the mean handling time per bite ingested. Since quality is uniform, the value of food items is defined in units of mass. The general model is of the form of Holling's 'disc equation' (Holling 1959b).

TABLE 1. Definition of symbols and standard parameter values

		Model		
		A	B	C
a	Surface area of a bite (cm^2)	10	30	30
B	Mean biting rate during active grazing (min^{-1})			
c	Cover of food items encountered (—)			
c'	Cover of food items selected (—)			
d	Mean number of food items per unit area in the horizontal plane (cm^{-2})			
d'	Mean number of selected food items per unit area in the horizontal plane (cm^{-2})			
f_h	Fraction of canopy depth grazed from the top (—)			
f_v	Fraction of herbage mass in vertical profile that is grazed (—)			
h	Sward height at the food item site (cm)		12	12
h'	Bite depth (cm)			
h_r	Ungrazable residual plant height (cm)	0·5	0·5	0·5
h_x	Maximum bite depth (cm)	5	6	6
I	Intake rate during active grazing (g h^{-1})			
M_i	Cumulative mean ranked biomass of ith biomass estimate (g m^{-2})			
n	Number of bite-size units per food item (—)	1		
r	Radius of a food item (cm)			
s	Standard deviation of herbage mass (g m^{-2})		50	
t_b	Constant representing biting time per bite ingested (s)	0·7	0·736	0·736
t_c	Constant representing chewing time per unit bite weight (s g^{-1})	2·5	5·66	5·66
t_h	Mean handling time per bite ingested (s)			
t_s	Mean searching time per food item selected for consumption (s)			
U	Mean walking speed during the search phase (cm s^{-1})	50	50	50
U'	Mean walking speed during active grazing (cm s^{-1})			
V	Mean herbage mass (g m^{-2})		50	
V_n	Mean selected herbage mass in standard units (—)			
V_s	Mean selected herbage mass (g m^{-2})			
w	Mean herbage weight per bite ingested (g)			
Z	Selectivity level in standard deviations from the mean (—)			
Z^*	Optimal selectivity level in standard deviations from the mean (—)			
δ	Bulk density in the bite volume (g cm^{-3})			

Bite weight

A bite has an effective equivalent pasture volume which is assumed to be cylindrical in shape, though this shape is not an essential feature of the model. Bite volume is therefore the product of bite surface area, a, and bite depth, h'. Bite depth is defined as:

$$h' = \min (\max[0, h - h_r], h_x) \qquad (2)$$

where h is the sward height at the food item site, h_r is the ungrazable residual pasture height, and h_x is the maximum bite depth.

If δ is the mean bulk density in the bite volume, bite weight is defined as:

$$w = a\, h'\, \delta \qquad (3)$$

Searching time

The animal is assumed to be searching for food while walking at random. Food items are randomly distributed in the horizontal plane with mean number of food items per unit area d. The selected food items have a mean number of food items per unit area d', where $d' \leqslant d$. The ratio d'/d represents the proportion of food items encountered that are selected, which is our definition of selectivity. Perception of a food item is via one or more of the special senses (Arnold 1981), and there is an effective searching band width within which all food items are perceived. It is convenient to assume that food items present a

circular surface of radius r. Thus, the narrowest effective search band width is $2r$, since any food item whose centre lies within one food item radius either side of the search line will be perceived. This value of $2r$ is taken here. The animal travels with a mean speed U during the search phase of the grazing process. Recognition and decision do not incur an additional time cost since these processes are assumed to occur whilst the animal moves along its search path. Thus:

$$t_s = 1/(2rd'U) \tag{4}$$

Handling time

t_h is assumed to be linearly related to bite weight:

$$t_h = t_b + t_c\, w \tag{5}$$

t_b and t_c are constants. Parameter t_b may represent time requirements for biting, which can be assumed to show relatively little variation with w, and t_c may represent the chewing time requirement per unit bite weight. A linear relationship between t_h and w implies that an increase in bite weight will always increase intake rate, i.e. the effects of increasing bite weight and handling time on intake rate cannot cancel. This can be shown by differentiating I with respect to w, which yields an expression which is always positive.

By introducing eqns (3), (4) and (5), eqn (1) expands to:

$$I = \frac{a\,h'\,\delta}{1/(2rd'\,Un) + t_b + t_c\,a\,h'\,\delta} \tag{6}$$

The cover of food items encountered, c, is given by:

$$c = \pi r^2 d = n\,a\,d \qquad (c \leqslant 1) \tag{7}$$

The cover of food items selected, c', is given by:

$$c' = \pi r^2 d' = n\,a\,d' \qquad (c' \leqslant 1) \tag{8}$$

MODEL A

Model A uses the simplest possible description of sward structure. The sward consists of identical food items (e.g. plants) with areas of zero biomass in between. Herbage is distributed uniformly between food items in both the horizontal and vertical plane. Herbage mass, V, can be defined as:

$$V = h\,c\,\delta = h\,a\,n\,d\,\delta \tag{9}$$

Thus, eqn (6) re-arranges to:

$$I = \frac{2rUV(h'/h)(d'/d)}{1 + 2rU[d'nt_b + t_cV(h'/h)(d'/d)]} \tag{10}$$

In the absence of heterogeneity of biomass distribution between food items, the question of optimal selectivity is trivial, since intake rate is maximized when the animal takes all food items it encounters. Nevertheless, model A can be used to examine the importance of sward structure, given that the grazing animal selects some fraction of food items it encounters. Sward parameters h, c and δ define how herbage mass is spatially organized. In fact, any three of the parameters V, c, h and δ define the fourth. Thus, δ does not appear in eqn (10) but is determined by V, c and h.

TABLE 2. Behaviour of model A with two sward characteristics held constant

Case	Sward characteristics*				t_s	Effect on w	I
	Varied†		Held constant				
Spread and dilute	↑c	↓δ	h	V	↓	↓	↓
Thickening growth	↑V	↑δ	h	c	↔	↑	↑
Shorten and spread	↑c	↓h	V	δ	↓	↔$h' \geqslant h_x$	↑
						↓$h' < h_x$	↓
Shorten and compress	↑δ	↓h	V	c	↔	↑$h' \geqslant h_x$	↑
						↓$h' < h_x$	↓
Horizontal growth	↑c	↑V	δ	h	↓	↔	↑
Vertical growth	↑h	↑V	δ	c	↔	↔$h' \geqslant h_x$	↔
						↑$h' < h_x$	↑

* Herbage mass V is defined as the product of sward height h, the cover of food items encountered c, and bulk density δ. Of the two sward characteristics varied, one is forced to increase or decrease, whilst the other changes such that the equality $V = h\,c\,\delta$ is maintained. Intake rate I is defined as the ratio of bite weight w to the sum of searching time t_s and handling time t_h (not shown). h' is the bite depth, h_x is the maximum bite depth.

† ↑ = increase, ↓ = decrease, ↔ = constant.

Results

Table 2 shows the direction of effect on intake where two sward parameters are varied and the remaining two are constant. The pasture height that corresponds to the maximum bite depth of the animal (h_x) is a critical threshold in determining the direction of effect of a change in certain sward structural parameters on intake rate. Above h_x, an increase in bulk density always increases intake. For cover, height, and herbage mass, the intake response is variable, depending on which second sward characteristic the change is coupled to. Intake declines with increasing cover when coupled with a decrease in bulk density, and intake declines with increasing height when coupled with a decrease in either bulk density or cover. Below h_x, an increase in height always increases intake.

Figure 1 shows the effect of holding one parameter constant. A positive, zero, or negative intake response can result from a change in any pair of sward parameters. For example, under conditions of constant height, intake rate can remain constant while both cover and herbage mass increase (Fig. 1a). Such a scenario would involve a decline in bulk density (Fig. 1b). At constant height, the intake response to increasing herbage mass is positive, and greater at low levels of cover. At constant herbage mass, the intake response to increasing bulk density is positive, and lessens at low levels of cover (Fig. 1c). At constant bulk density, intake rises asymptotically with increasing cover (Fig. 1e). There is a single functional response at all levels of height above h_x. Below h_x, the asymptote declines with declining height.

Model A demonstrates that intake rate at a given herbage mass depends strongly on the spatial organization of the herbage. The model suggests that, for a given growth curve of herbage mass, the priority in structural characteristics to maximize intake rate in the short term would be: (a) increasing height (until $h' = h_x$), (b) increasing bulk density within food items, and (c) increasing cover.

MODEL B

Model B increases the realism with which sward structure is described by introducing heterogeneity of bite weight between food items. A continuous distribution function
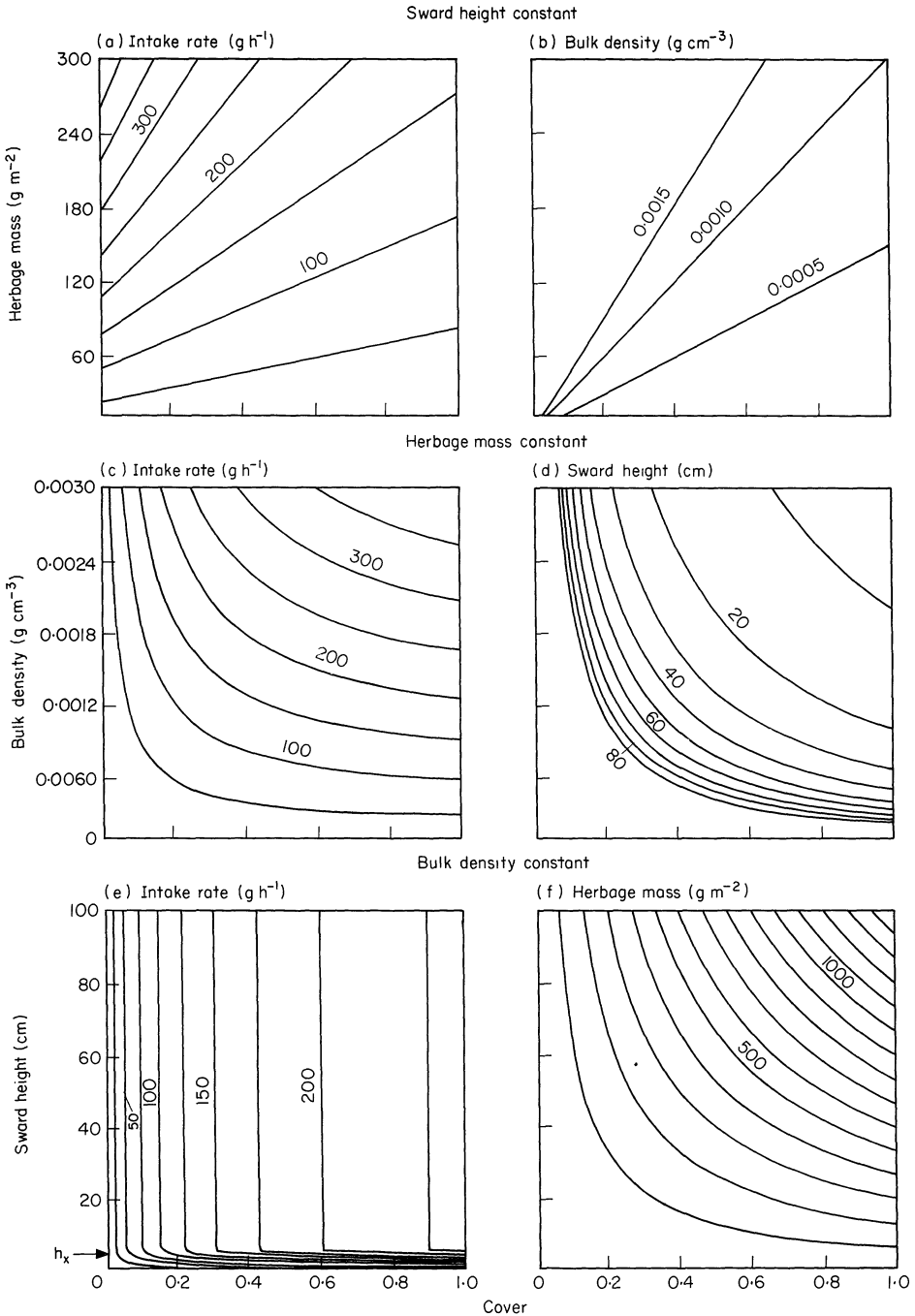
FIG. 1. Behaviour of model A with one sward characteristic held constant. Contour diagrams (a), (c) and (e) show intake rate isolines as a function of (a) cover and herbage mass, at a constant sward height of 30 cm, (c) cover and bulk density, at a constant herbage mass of 200 g m^{-2}, (e) cover and sward height, at a constant bulk density of 0·0015 g cm^{-3}. The x and y axes and the sward characteristic held constant define three of the variables in the equality $V = h\,c\,\delta$ (symbols defined in Table 1). Contour diagrams (b), (d) and (f) show the fourth variable such that this equality is maintained.
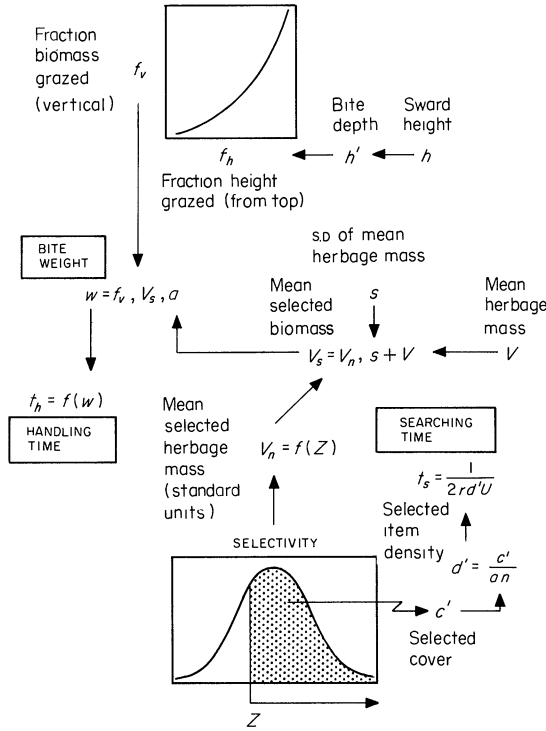
FIG. 2. Outline of model B showing the derivation of searching time, handling time, and bite weight. Herbage mass at the food item level is normally distributed. Z is the selectivity threshold, in standard deviations from the mean, above which all food items encountered are selected. The area under the normal curve above Z defines the cover of selected food items (given in tables), and the mean selected herbage mass in standard units (eqn (16)). Symbols are defined in Table 1.

describes the distribution of herbage mass in the horizontal plane. Sward height is constant and there is complete cover. The distribution function of herbage mass is therefore equivalent to the distribution function of bulk density of food items. This is in turn equivalent to the distribution function of available bite weights in the sward, since bite surface area and bite depth are constant.

Distribution of biomass in the vertical plane is not generally uniform but shows a higher concentration of biomass closer to the ground (Milne *et al.* 1982). This can be expressed in a relationship giving the fraction of herbage mass grazed, f_v, as a function of fraction canopy depth grazed, f_h (from the top). Assumed parameter values are $h = 12$ cm, $h_x = 6$ cm and $h_r = 0.5$ cm. Thus, from eqn (2), $h' = 6$ cm, and therefore $f_h = 0.5$. This contains approximately 20% of herbage mass, on the basis of data from Milne *et al.* (1982).

The model assumes that the animal selects food items with large bite weights and that there is a threshold 'selectivity level' above which all bite weights are selected. Food items with bite weight less than this threshold value are passed over. We examine the implications of taking the normal (Gaussian) distribution function. This function, defined by the mean herbage mass, V, and the standard deviation, s, provides a convenient
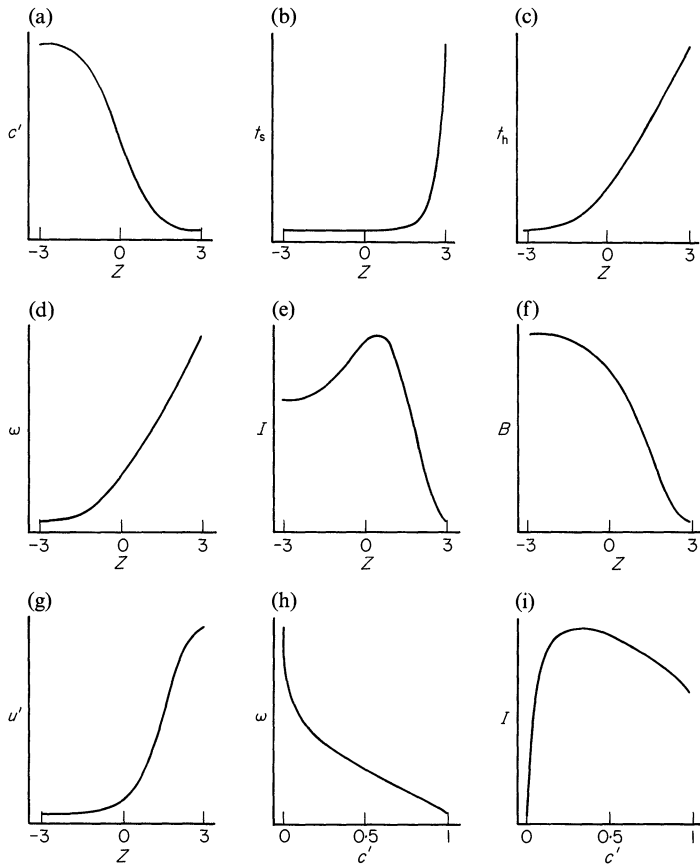
FIG. 3. Qualitative behaviour of model B. Z is the selectivity threshold, in standard deviations from the mean, above which all food items encountered are selected. c' is the cover of food items selected. The response to Z and c' is not equivalent since these are not linearly related, as shown in (a). Symbols are defined in Table 1.

TABLE 3. The effect of coefficient of variation of herbage mass on grazing behaviour in model B. Symbols and parameter values as defined in Table 1. The mean herbage mass is 50 g m^{-2} throughout

C.V. (%)	Z^* —	V_s (g m^{-2})	w (g 10^{-3})	t_h (s)	t_s (s)	I (g h^{-1})	B (min^{-1})	U' (cm s^{-1})	c' —
25	−0·2	58	35	0·93	0·17	115	54	7·6	0·58
50	0·2	73	44	0·98	0·23	130	49	9·5	0·42
75	0·4	90	54	1·04	0·28	147	45	10·6	0·34
100	0·5	107	64	1·10	0·31	164	42	11·1	0·31
125	0·6	126	75	1·16	0·35	179	40	11·7	0·27
150	0·6	141	85	1·22	0·35	194	38	11·3	0·27
175	0·6	156	94	1·27	0·35	208	37	10·9	0·27
200	0·7	179	107	1·34	0·40	222	34	11·5	0·24

TABLE 4. *The effect of herbage mass on grazing behaviour in model B. Symbols and parameter values as defined in Table 1. The coefficient of variation of herbage mass is 100% throughout. Z^*, t_s and c' are constant at 0·5, 0·31 s, and 0·31, respectively*

V (g m^{-2})	V_s (g m^{-2})	w (g 10^{-3})	t_h (s)	I (g h^{-1})	B (min^{-1})	U' (cm s^{-1})
20	43	26	0·88	77	50	13·2
30	64	39	0·95	109	47	12·4
40	86	51	1·03	138	45	11·7
50	107	64	1·10	164	42	11·1
60	128	77	1·17	187	40	10·6
70	147	88	1·23	205	39	10·2
80	168	101	1·31	224	37	9·7
90	189	113	1·38	241	35	9·3
100	210	126	1·45	257	34	8·9

way of introducing selectivity. The selectivity threshold, Z, is expressed in standard deviations from the mean. A value of -3 approximates zero selectivity and a mean selected herbage mass equal to the field mean.

Intake rate is computed from eqn (1). The cover of food items selected, c', required in the computation of t_s, is defined by the area under the normal distribution function above Z. We define this as $1 - \phi(Z)$, where:

$$g(t) = 1/\sqrt{(2\pi)} \exp(-t^2/2) \tag{11}$$

$$\phi(t) = \int_{-\infty}^{t} g(t)\, dt \tag{12}$$

A numerical approximation of this integral is provided in tables.

Bite weight is defined as the product of the fraction of herbage mass in the vertical profile that is grazed (f_v), the surface area of a bite (a), and the mean selected herbage mass (V_s). This expression is equivalent to eqn (3). Since the selectivity threshold is expressed in standard deviations from the mean, V_s is computed from the normalized deviation of the mean selected herbage mass, V_n, as follows:

$$V_s = V_n s + V \tag{13}$$

V_n is computed over the interval Z to ∞. Thus, we require:

$$V_n = \frac{\int_{Z}^{\infty} t\, g(t)\, dt}{\int_{Z}^{\infty} g(t)\, dt} = \frac{\int_{Z}^{\infty} t\, g(t)\, dt}{1 - \phi(Z)} \tag{14}$$

The integral in the numerator is solved as follows:

$$\int_{Z}^{\infty} t\, g(t)\, dt = \frac{1}{\sqrt{(2\pi)}} \int_{Z}^{\infty} t \exp(-t^2/2)\, dt = \frac{1}{\sqrt{(2\pi)}} [-\exp(-t^2/2)|_{Z}^{\infty}] = \frac{\exp(-t^2/2)}{\sqrt{(2\pi)}} \tag{15}$$

Therefore:

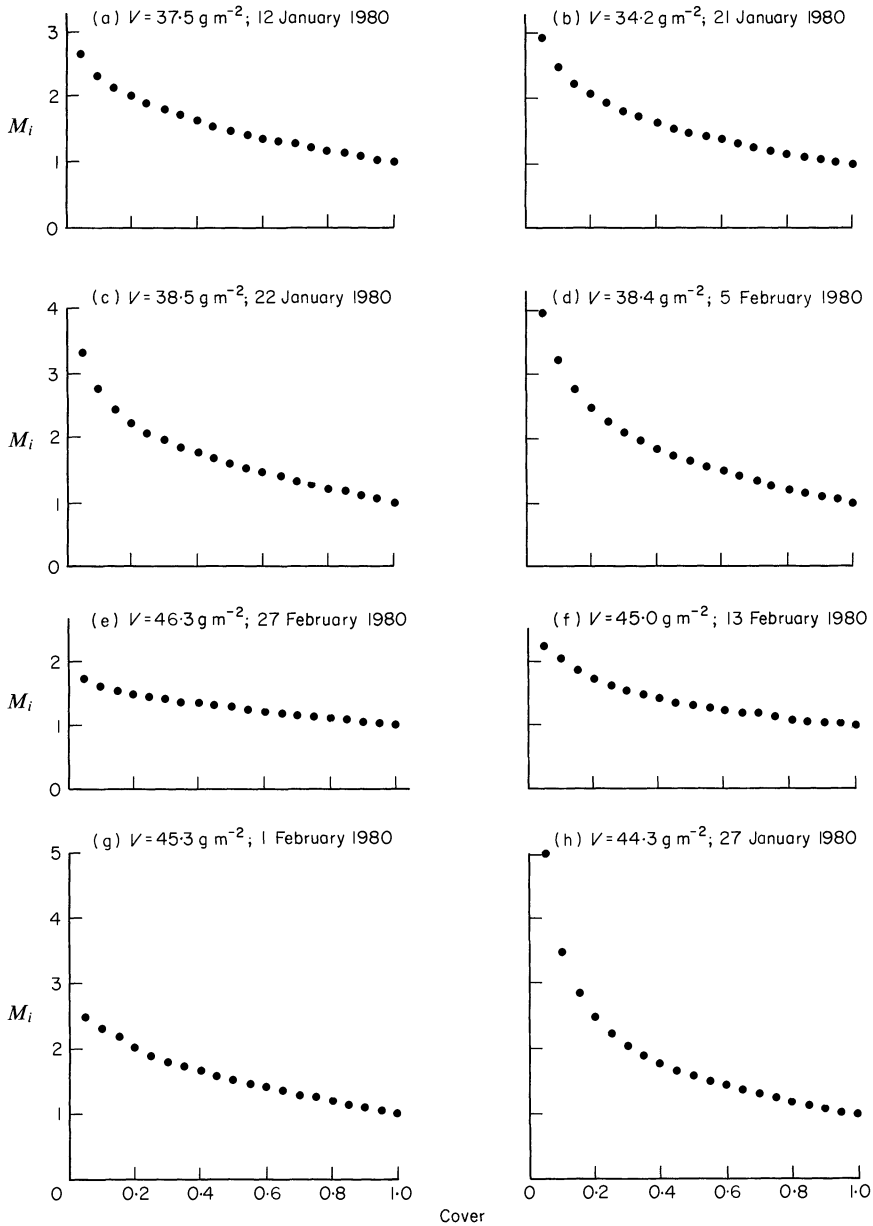$$V_n = \frac{\exp(-Z^2/2)}{\sqrt{(2\pi)} [1 - \phi(Z)]} \tag{16}$$

Fig. 4. The cumulative mean ranked normalized biomass function for a selection of eight biomass estimate data sets from various fields, of different grazing histories, at the Migda experimental farm. Each data set comprised 100 biomass estimates. The cumulative mean ranked normalized biomass M_i is plotted at an interval of five percentile units. V is the mean herbage mass.

The optimal selectivity threshold, Z^*, is located numerically by extending the range of selected bite weights from the largest down, until intake rate reaches a maximum. According to optimal foraging theory, the optimal diet is determined by adding food types to the diet in their rank order of w/t_h. This process is continued so long as w/t_h for
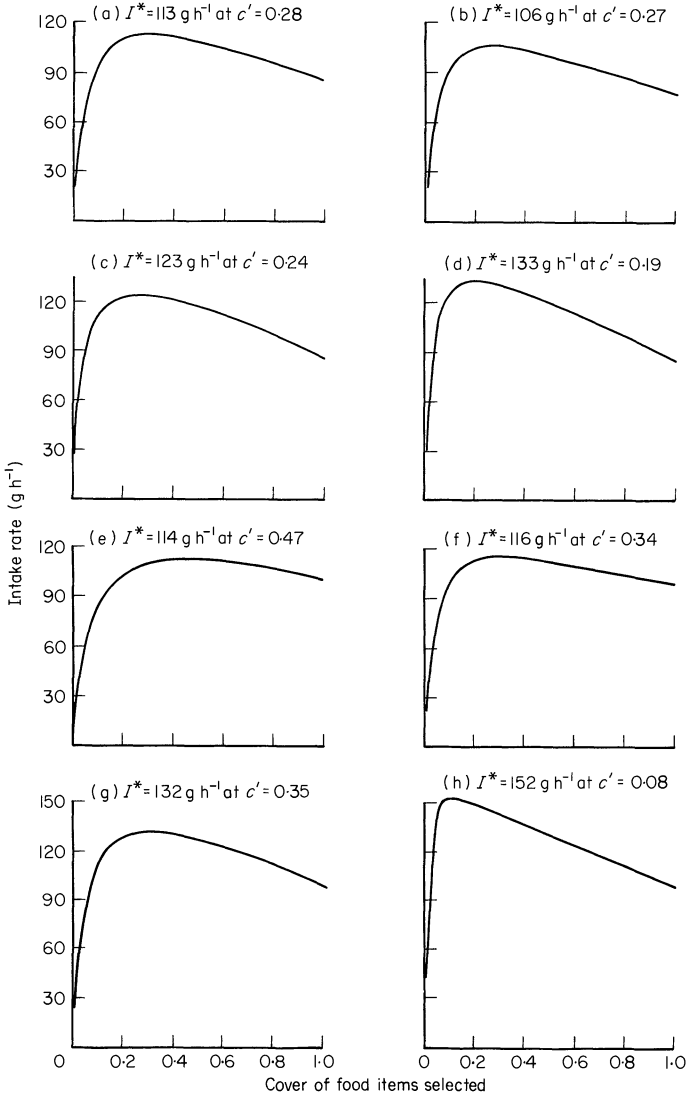
FIG. 5. The relationship between intake rate (I) and selectivity level expressed as the cover of food items selected (c') corresponding to the eight functions of the cumulative mean ranked normalized biomass presented in Fig. 4. I^* is the maximum intake rate attained.

each addition to the diet is greater than the intake rate for the diet without the addition. When this inequality reverses, the optimal diet has been obtained (Pyke, Pulliam & Charnov 1977). However, as long as $t_b > 0$, i.e. a non-zero biting time, then w/t_h increases with bite weight. Thus, ranking by this ratio or by bite weight are equivalent.

The mean biting rate, B, and mean walking speed during active grazing, U', can be derived as follows:

$$B = 1/(t_s + t_h) \qquad (17)$$

$$U' = U[1 - t_h/(t_s + t_h)] \qquad (18)$$

Model B is summarized in Fig. 2.

Results

Intake rates were computed for Z values from -3 to $+3$, using the standard parameter values given in Table 1. A number of relationships with Z and c' are shown in Fig. 3 (Z and c' are not linearly related; Fig. 3a). As selectivity declines (decreasing Z) the rapid decline in t_s (Fig. 3b) has a much greater effect on intake than the gradual reduction in w (Fig. 3d), and intake rate increases sharply (Fig. 3e). Below $Z \approx 1 \cdot 2$, t_s declines relatively little whilst w continues to fall at almost the same rate, hence the effect on intake rate is reduced. At $Z = 0 \cdot 5$, the opposing effects on intake rate exactly cancel and the function is at a maximum. Further reduction in selectivity reduces intake rate because there is insufficient saving in t_s to offset the decline in w. The relationship between I and Z indicates that the cost to the animal of over-selectivity is greater than that of under-selectivity.

Under the standard parameter set, Z^* corresponds to a field cover of selected items of 31% and mean selected herbage mass $2 \cdot 1$ times the mean herbage mass of the field. t_s, t_h and w are $0 \cdot 31$ s, $1 \cdot 1$ s, and 64×10^{-3} g, respectively. I, B and U' are 164 g h^{-1}, 42 bites min^{-1} and $0 \cdot 11$ m s^{-1}, respectively.

The effect of heterogeneity at constant herbage mass is shown in Table 3. Z^* and the corresponding intake rate increase with heterogeneity. At constant heterogeneity, Z^* is independent of mean field herbage mass, V (Table 4). Since t_s is a function of selectivity, it also remains constant with V. Bite weight increases with V and therefore intake rate at Z^* increases. The relationship between intake rate (at Z^*) and V is that of a saturation functional form. Increasing sward heterogeneity steepens the initial ascending section of the function and raises the asymptote (or satiation intake rate). The sensitivity of intake rate (at Z^*) to coefficient of variation of biomass is greater at lower V.

MODEL C

It seems reasonable to assume that the frequency distribution of herbage mass at the food item level can take a wide range of shapes. Any single functional form is unlikely to encompass the range of possibilities, and problems of fitting and manipulating the function become serious with increasing complexity of functional form. To overcome these problems, a conceptually and mathematically simple method of characterizing the distribution function is used. In this preliminary analysis, statistical problems of estimation are ignored and we assume that a representative sample of herbage mass can be obtained.

Let $V_1, V_2, \ldots, V_k$ represent a set of herbage mass estimates, based on k quadrats of approximately food item area, ordered by descending rank. We define the cumulative mean ranked normalized biomass of the ith estimate, M_i:

$$M_i = \frac{1}{iV} \sum_{j=1}^{i} V_j, \qquad V_1 \geqslant V_2 \geqslant \ldots \geqslant V_k \qquad (19)$$

The biomass estimates are normalized by dividing through by the mean, V, in order to facilitate comparison between different sets of field estimates. Since each field measurement is an estimate of the herbage mass for $1/k$ of the field area, M_i represents the mean normalized biomass of the top i/k fraction of the field area. Thus, M_k is exactly 1. The relationship between M_i and i/k is necessarily monotonic descending (assuming variance of V to be > 0), though the concavity or convexity of the function over any section is data-dependent.

The relationship between M_i and i/k is of interest because i/k comprises food items with the highest available herbage mass. Thus, i/k can represent the level of grazing selectivity, and is equivalent to the cover of selected food items, c'. The mean selected herbage mass is provided directly by M_iV. In all other respects, models B and C are identical.

Results

As a preliminary examination of the cumulative mean ranked biomass function, and its implementation in model C, data from the Migda experimental farm in the northern Negev region of Israel were taken (unpublished data). Over 100 sets of biomass estimates for natural pasture swards were gathered in the 1979–80 growing season. A double sampling technique, of 100 visual weight estimates calibrated by harvesting, was employed in each set of measurements (Tadmor *et al.* 1975). The quadrat size was 100 cm^2, which is somewhat larger than the ideal for present purposes, though this should not affect the essential qualitative behaviour of the model. Analysis of these data sets showed that the frequency distribution of herbage mass is highly skewed early in the season, with a high proportion of low biomass cover in the field. The distribution becomes less skewed as the season progresses, becoming approximately symmetric 6–8 weeks after emergence.

Figure 4 shows the cumulative mean ranked normalized biomass function for a selection of eight data sets. Calculated M_i values are plotted at an interval of five percentile units. Figure 4(i)–(iv) and Fig. 4(v)–(viii) are for a mean herbage mass of approximately 35 g m^{-2} and 45 g m^{-2}, respectively, with each group covering a wide range of frequency distribution shape. A high intercept indicates highly skewed distributions. Normally distributed data would yield an intercept in the range 3·3–3·6 (based on randomly generated data sets). Lower intercepts indicate more uniform frequency distributions.

Each of the functions shown in Fig. 4 was incorporated in model C as a look-up table, and the relationship between selectivity level and the mean intake rate was computed. The results are shown in Fig. 5. As the distribution function becomes less uniform, selectivity increases, the intake response to selectivity becomes more sharply peaked, and the intake rate at the optimum selectivity level, $c'*$, increases. In the region of the optimum, the cost of under-selectivity is always less than the cost of over-selectivity. At the extremes, differences of over 30% in intake rate at $c'*$ can be obtained. Optimal selectivity $c'*$ itself can range from about 8% to almost 50% cover, though in most cases it is 20–40%.

DISCUSSION

The results of model A (Table 2) highlight the respective roles of three attributes of sward structure and availability. When herbage mass increases by an increase in just one of these components, a higher intake rate results in each case, though by different mechanisms. Increased cover asymptotically decreases search time; increased sward height (over a limited range) or bulk density increases bite weight. When only sward structure varies, at a given herbage mass, the effect of bulk density overrides that of cover, while the effect of sward height overrides both cover and bulk density as long as height limits bite depth. Beyond that, increasing height at the expense of bulk density or cover reduces intake. These predictions of the model can explain the apparent contradictions in the evidence on whether intake is higher in short, dense or in tall, sparse swards (at constant total mass) (Stobbs 1973b; Hodgson 1981; McNaughton 1984; Westoby 1985). Increase in bite weight and intake rate up to a certain height and decrease beyond it is indicated in the

results of Black & Kenney (1984). Their evidence that, at given low total mass, a sward with sparsely spaced bunches of long tillers allowed greater intake than one with closely spaced short ones due to the greater bite weight, is also consistent with the prediction of the model that height overrides cover. The very close linear relation they found over a wide range between bite weight and herbage mass per bite area provides some justification for the assumption made in eqn (3) of our model.

The assumption in the model (eqn (2)) was that bite weight is related to sward height by a 'ramp function' which is linear between a lower threshold h_r and an upper limit h_x. This simplification probably captures the general shape of the relationship well enough. However, some of the results reported by Hodgson (1981) and Black & Kenney (1984) indicate the need for a more mechanistic derivation of this function.

In model A, horizontal heterogeneity in the sward was only crudely represented by 'cover'. The results of models B and C show that in general, the greater the horizontal variance at a given average herbage mass and potential bite weight, the greater the IIR that a grazing animal can potentially achieve. The increase in intake rate due to sward patchiness can be substantial, but it is realized only to the extent that grazing animals select for large bites in such a way as to maximize IIR. From evolutionary considerations, animals should tend to behave that way when intake is limited by availability. Experimental results of Kenney & Black (1984) as well as field observations (unpublished) indicate that they do.

The wide scatter of points usually seen in experimental data on intake versus average herbage mass may often result from differences in sward patchiness. The results from our models, and our unpublished experimental data from Migda, suggest that, unless the sward is known to be always uniform, horizontal heterogeneity in potential bite weight needs to be accounted for and quantitatively characterized if realistic predictions of intake rate and sward dynamics under grazing are required.

Our models were deliberately limited to the prediction of IIR from pasture availability, in conditions where these are the factors limiting animal nutrition (e.g. in the first part of the growing season). Daily intake is the product of IIR and daily grazing time, which is also a variable controlled by animal behaviour. Animals tend to compensate for lower IIR by extending daily grazing time (Allden & Whittaker 1970; Chacon & Stobbs 1976); thus, in general, daily intake will be less sensitive to availability than IIR is. However, this mechanism is limited, or at least counteracted, by environmental stresses imposed by grazing at certain times of the day, and by the need to spend time on other activities, in particular rumination. Interactions with digestion rates and diet quality may then appear. It has been found that fasted steers increased daily grazing time at the expense of rumination time, and simultaneously increased biting rate while decreasing chewing time per unit weight (parameter t_c in our model) (G. B. Greenwood & M. W. Demment, unpublished). These are indications that grazing behaviour responds also to rumen fill, in ways which may affect both daily intake and IIR. Our restricted model would have to be expanded to account for these mechanisms. The optimality principle would still be invoked in such a model, but the rate to be maximized would be the daily rate of digestion of nutrients.

In situations where digestion rate, and not only ingestion rate, may be limiting daily intake, selection for diet quality (digestibility, nutrient content or passage rate) as well as for availability (bite size) is likely to become important. Here again, the optimal foraging principle may be applied, as has indeed often been done, also for ruminants (Westoby 1974; Belovsky 1978, 1981; Owen-Smith & Novellie 1982). Of particular interest is a model which describes the grazing process in terms very similar to those of the present

model, and then optimizes selection for bite quality (defined as digestibility and continuously distributed) so as to maximize digestible dry matter intake rate (E. A. Laca & M. W. Demment, unpublished). Though that model did not consider the distribution and selection of bite sizes as in models B and C here, it confirmed the predictions of model A that intake was higher when the same herbage mass was available as patches of tall or dense material than when it formed a uniform short or sparse sward. To be more generally useful for predicting ruminant intake the grazing process model will need to be developed to consider the joint distribution of bite size and quality and to maximize nutrient intake over it.

The model presented here, as well as that of Laca & Demment (unpublished), differs from previous applications of the optimal foraging principle in the ecological literature in two respects. Our models attempt to use this principle not only to predict qualitative patterns of selective behaviour in ruminants (though such predictions are the first, and very useful results) but also to improve the quantitative prediction of intake rates in relation to sward attributes in real grazing systems. Secondly, optimization here is over a continuously distributed attribute of the food, while conventionally food has been described as consisting of discrete types (usually species) with uniform 'food value' (energy per unit handling time) within each type. As pointed out by Lacher, Willig & Mares (1982), failure of the classical optimal foraging model may result when animals are able to select food value within type, and when the distributions of value overlap between types. The approach suggested here may thus be developed to produce more realistic optimal foraging models in ecological systems in general, not only in the specific context of domestic ruminants grazing pastures.

Optimal foraging theory predicts that animals should rank and select food items by the ratio of nutrient content (usually energy) to handling time, e/t_h. However, most studies have concentrated on optimal selection for food quality e, while ignoring differences in t_h. In this study, differences in quality have been ignored, and only optimal selection for $1/t_h$ (bite weight) has been considered. This may be justified only in certain conditions. However, selection for bite size by large herbivores is likely, in general, to be no less important than selection for quality.

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