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Optimal diet selection by a generalist grazing herbivore

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Summary

1. We develop a stochastic dynamic programming model of grazing behaviour for a generalist mammalian herbivore. The model considers that behaviour depends upon three state variables: stored energy, digestible gut fill and indigestible gut fill. When the plant community comprises two alternative species, the animal must choose between five alternative behaviours: grazing species *i*, grazing species *j*, grazing whichever species it encounters, resting or ruminating.

2. We use the model to distinguish diet preference and diet selection. Diet preference is the diet selected by the animal when it is operating under a minimum of environmental constrains and diet selection refers to the way in which environmental constraints modify the animal's diet preference.

3. Although the model can be used for any mammal grazing in any plant community, we demonstrate solutions derived from parameter values relevant to sheep grazing a grass–clover plant community.

4. The model demonstrates that diet preference may depend on the relative intake rates of the two alternative plant species. Furthermore, preference may depend on the absolute intake rates at which the relative comparison is made. The model demonstrates that the optimal diet should have a temporal pattern across the day and that it may be sensitive to predation hazard. The model also predicts total daily intake.

5. We use the model to demonstrate that the complex patterns of diet preference are further modified when considering total abundance of species in the community (e.g. cover).

6. We explain how the model is heuristic in pointing out reasons why the literature on diet selection in this system, and in herbivores more generally, is equivocal on what is the basis of selection and preference.

Key-words: Clover sheep, ryegrass, stochastic dynamic programming

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Introduction

Herbivory is an important determinant of the plant community composition and stability in any ecosystem. In grassland systems, the equilibrium community composition that is achieved (if one is achieved) will depend to a great extent on the grazing behaviour of large generalist herbivores. These animals may exert their influence on the community in a variety of ways, for example through trampling, dung and urine deposition, spatial pattern of grazing and diet selection. Much research effort has been aimed at understanding the behaviour of grazing herbivores in order to understand the population dynamics of plant communities and their interactions with the population dynamics of the associated animal communities.

Perhaps the most direct influence that large grazing animals have on the plant community is through their grazing behaviour. Many researchers have taken the ability of grazing animals to obtain a diet composition that differs from the relative abundance of plant species in the community as evidence of selective grazing. When herbivores graze one plant species more frequently or more heavily than they graze its neighbours, then that species may be at a disadvantage in terms of plant–plant competition. Thus, constant dietary selection by large grazing mammals may lead to local extinction of preferred plant species. If, however, the grazing selection varies, then the com-

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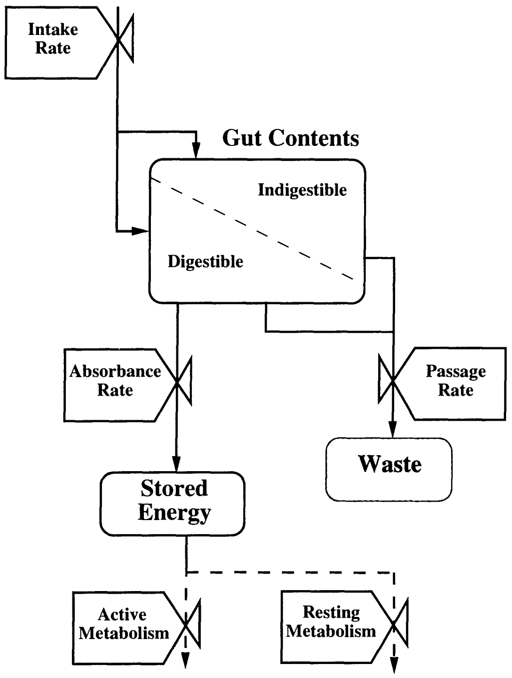

Fig. 1. Schematic diagram of state flows in the model. The three states considered by the model are stored energy (X_t), digestible gut fill (Y_t) and indigestible gut fill (Z_t).

munity may remain in a constant state of flux, it may reach some dynamic equilibrium, or it may be fixed through stochastic events.

The terms *diet preference* and *diet selection* have caused confusion in the literature. In this paper we follow Hodgson's (1979) definitions. *Preference* is 'the discrimination exerted by animals between sward or sward components'. *Selection* is '… the removal of some sward component(s) plants or plant parts rather than others. It is a function of preference … modified by the opportunity for selection, which is determined by the relative proportions of the preferred components in the sward, and their distribution within the canopy'.

That grazing herbivores exhibit dietary selection is hardly a point of contention. The basis upon which animals select their diets however is a point of considerable contention. Some experimenters have advocated diet selection based on intake rate (e.g. Kenney & Black 1984; Arnold 1960, 1987), some advocate a nutritional balance (e.g. Westoby 1974; Watkin & Clements 1978; see review in Provenza & Balph 1990), others suggest that density of vegetation is the basis of selection (Black & Kenney 1984), and others suggest that plant height and species mixture is the basis for discrimination (e.g. Illius, Clark & Hodgson 1992).

In this paper we model both diet preference and diet selection. Previous attempts to model grazing selection have been either simple teleonomic models (e.g. Owen-Smith & Novellie 1982; Thornley *et al.* 1994) or complex mechanistic models (e.g. Spalinger & Hobbs 1992; Parsons *et al.* 1994b). In this model we use stochastic dynamic programming (e.g. Bellman 1957; McNamara & Houston 1986; Mangel & Clark 1986) to combine the optimality approach with a simplistic mechanistic submodel in order to investigate factors affecting selection behaviour and total daily intake. This model is necessarily a simplification and we have no delusion that the model is predictive other than in its general behaviour. However, it points out possible reasons why the basis of diet selection in large generalist herbivores is equivocal. We demonstrate solutions derived for parameter values relevant to adult sheep grazing perennial ryegrass and white clover. However, the model can be applied to any large mammalian herbivore grazing in any plant community for which the relevant parameters can be estimated.

Model

We model behaviour as depending on physiological state. The choice of states is important and may differ between animal species. Without loss of generality, we assume that behaviour depends on three states: the amount of stored energy (energy available for growth, maintenance and reproduction), the amount of material in the animal's gut that is digestible and the amount of material in the gut that is indigestible. The gut contents are constrained such that their sum must never exceed the gut capacity. Mass flows through this system according to rate constants, which may differ depending on the species grazed. Figure 1 shows a schematic diagram of the states and flows in the model.

TERMINAL REWARD FUNCTION

In stochastic dynamic programming models, the animal's fitness (in the Darwinian sense) at the end of the modelled period is related to the values of the state variables at that time. The Darwinian fitness of an organism is defined by the number of offspring that survive to reproduce. As we will be concerned only with behaviour during the non-breeding season, the animal's Darwinian fitness will be proportional to the probability that it survives to reproduce (e.g. Houston & McNamara 1988). The animal must survive both predation hazard and starvation. We consider that the animal survives starvation according to a logistic function which relates energy at the final time to fitness. Specifically, we use the following function:

$$\psi(X_T, Y_T, Z_T) = \frac{1}{1 + a\, e^{b(c - X_T - \xi(Y_T, Z_T))}} \qquad \text{eqn 1}$$

where X_T is the amount of stored energy available to the animal at the final time T, Y_T is the amount of digestible material in the animal's gut at time T, Z_T is the amount of indigestible material in the gut at time

T, $\xi(Y_T, Z_T)$ is a function that describes the digestion of the gut contents during the non-grazing period (i.e. night), and *a, b* and *c* are shape parameters. The function $\psi(X,Y,Z)$ is a sigmoid function in $(X_T - \xi(Y_T, Z_T))$ reaching an upper asymptote at 1.

Biologically, equation1 represents the situation in which an animal that ends the day having ingested and stored more energy (i.e. it is in better *relative* physiological condition) will have a greater chance of surviving until the next grazing period and hence will have a higher relative fitness; that is, fitness is an increasing function of physiological condition. The specific form of the function indicates that a bite of food is more valuable to animals that are in relatively poor physiological condition (where the function increases in a convex manner) than that same bite would be to animals that are in very good physiological condition (where the function increases in a concave manner).

Appendix 1 shows the specific values used for the parameters in equation 1 and provides some justification for the choice of these values. Although the specific solutions to the model (see below) will depend on the choice of these parameters, the general form of the solution will not; that is, as long as the function is generally increasing, the general behaviours will be the same (for more information on the terminal reward function see Mangel & Clark 1986, 1988; Houston & McNamara 1988).

STATE VARIABLE DYNAMICS

Let X_t denote the level of stored energy at some time $t < T$ measured in joules. Let Y_t denote the level of digestible material in the gut and Z_t denote the amount of indigestible material in the gut, both measured in grams of dry matter (g DM). Let *i* and *j* denote two plant species. The intake rate derived from these species may depend on many factors including, but not limited to: the physical density of plant mass, the bite mass achieved by the animal, and the degree of mastication (for more information on determinants of intake rate see Spalinger & Hobbs 1992; Newman, Parsons & Penning 1995; Parsons *et al.* 1994b; G.R. Edwards, A.J. Parsons, P.D. Penning & J.A. Newman, manuscript in review). These factors are more appropriately considered using a mechanistic model such as that of Parsons *et al.* (1944b). In this model we simply denote the intake rate when eating species *i* as ϑ_i (with units g DM per unit time) without regard to how it is obtained.

Throughout, we suppose that the animal has five behavioural options (denoted b_k, $k = 1,\ldots,5$) available to it during any one discrete time period: rest (b_1), ruminate (b_2), graze species *i* (b_3), graze species *j* (b_4) or graze whichever species is encountered (i.e. graze indiscriminately, b_5). When the animal chooses to rest (b_1), the state variables change as follows:

$$\begin{aligned} X^{b_1}_{t+1} &= \begin{cases} X_{\max} & \text{if } X_{t+1} > X_{\max} \\ X_t + Y_t \tau_a \varepsilon - \alpha_{\mathrm{r}} & \text{if } 0 < X_{t+1} \le X_{\max} \\ 0 & \text{if } X_{t+1} \le 0 \end{cases} \\ Y^{b_1}_{t+1} &= Y_t(1 - \tau_a - \tau_p), \\ Z^{b_1}_{t+1} &= Z_t(1 - \tau_p), \end{aligned} \qquad \text{eqn 2}$$

where τ_a and τ_p are rate constants representing the rates of absorption and passage respectively, α_{r} is the metabolic cost of resting and $X_{\max}$ is the maximum amount of energy the animal is capable of storing, and ε is a factor that expresses the efficiency with which mass is converted to energy by the process of digestion and is measured in units of J g^{-1} DM.

When the animal chooses to ruminate (b_2), the state variables change as follows:

$$\begin{aligned} X^{b_2}_{t+1} &= \begin{cases} X_{\max} & \text{if } X_{t+1} > X_{\max} \\ X_t + (Y_t \tau_a + \delta(Z_t))\varepsilon - \alpha_r & \text{if } 0 < X_{t+1} \le X_{\max} \\ 0 & \text{if } X_{t+1} \le 0 \end{cases} \\ Y^{b_2}_{t+1} &= Y_t(1 - \omega(\tau_a - \tau_p)) \\ Z^{b_2}_{t+1} &= Z_t(1 - \omega(\tau_p)), \end{aligned} \qquad \text{eqn 3}$$

where $\delta(\cdot)$ is a function that describes the conversion of previously indigestible material into digestible material (e.g. the liberation of some material through the physical breakdown of the cell wall) that arises from rumination, and $\omega(\cdot)$ is a function that describes the increased rates of absorption and passage of material from the gut owing to the increased particulate breakdown that results from rumination (e.g. Poppi, Minson & Ternouth 1981; Poppi, Hendricksen & Minson 1985). The specific forms of both these functions are shown in Appendix 2.

When the animal chooses to graze species *i* only, then the state variables change according to:

$$\begin{aligned} X^{b_3}_{t+1} &= \begin{cases} X_{\max} & \text{if } X_{t+1} > X_{\max} \\ X_t + Y_t \tau_a \varepsilon - \alpha_a & \text{if } 0 < X_{t+1} \le X_{\max} \\ 0 & \text{if } X_{t+1} \le 0 \end{cases} \\ Y^{b_3}_{t+1} &= \begin{cases} Y_t(1 - \tau_a - \tau_p) + \kappa_i E[\gamma_i] & \text{if } Y_{t+1} + Z_{t+1} \le \eta \\ Y_t(1 - \tau_a - \tau_p) & \text{otherwise} \end{cases} \\ Z^{b_3}_{t+1} &= \begin{cases} Z_t(1 - \tau_p) + (1 - \kappa_i) E[\gamma_i] & \text{if } Y_{t+1} + Z_{t+1} \le \eta, \\ Z_t(1 - \tau_p) & \text{otherwise} \end{cases} \end{aligned} \qquad \text{eqn 4}$$

where α_a is the metabolic cost of activity, κ_i is the proportion of species *i* ingested that is digestible, η is the gut capacity and $E[\gamma_i]$ is the expected mass gained by grazing over one time period when searching only for species *i*. Let $\gamma_{i,\max}$ be the maximum amount of mass ingested if the animal found species *i* immediately at the start of the discrete time period. Then, $\gamma_{\mathrm{i,max}} = \vartheta_i$, recall that ϑ_i is the intake rate in g DM per time period. Now, consider that the animal must search for species *i*. Let the discrete time period *t* be divided into *l* discrete subunits. Then the expectation of γ_i is given by:

$$E[\gamma_i]=\sum_{l=1}^{l_{\max}}\rho_i(1-\rho_i)^{l-1}\gamma_{i,\max}.$$

In this expression, ρ_i is the probability of randomly encountering species *i* per time subunit *l*. This expression is the sum of the gains achieved over fixed time periods weighted by the probability that the animal would graze that long (determined by how quickly it finds species *i*, if at all).

The changes in the state variables given that the animal chooses to graze only from species *j* (b_4) are given by equation 4 with the appropriate substitution of subscripts *j* for *i* and b_4 for b_3.

If the animal chooses to graze whichever species it first encounters (i.e. graze indiscriminately) then the state variables change according to:

$$X_{t+1}^{b_5}=\begin{cases}X_{\max} & \text{if } X_{t+1}>X_{\max}\\ X_t+Y_t\tau_a\varepsilon-\alpha_a & \text{if } 0<X_{t+1}\le X_{\max}\\ 0 & \text{if } X_{t+1}<0\end{cases}$$

$$Y_{t+1}^{b_5}=\begin{cases}Y_t(1-\tau_a-\tau_p)+ \\ \quad(\rho_i\kappa_i\gamma_{i,\max}+\rho_j\kappa_j\gamma_{j,\max} & \text{if } Y_{t+1}+Z_{t+1}\le\eta\\ Y_t(1-\tau_a-\tau_p) & \text{otherwise}\end{cases}\qquad\text{eqn 5}$$

$$Z_{t+1}^{b_5}=\begin{cases}Z_t(1-\tau_p)+(\rho_i(1-\kappa_i)\gamma_{i,\max} \\ \quad+\rho_j(1-\kappa_j)\gamma_{j,\max}) & \text{if } Y_{t+1}+Z_{t+1}\le\eta\\ Z_t(1-\tau_p) & \text{otherwise}\end{cases}$$

For a two-species plant community with a closed canopy, $\rho_j=(1-\rho_i)$.

PREDATION HAZARD

In a general context, many researchers have considered how predation hazard should interact with foraging considerations, both experimentally (e.g. Newman & Caraco 1987; Newman *et al.* 1988; see Lima & Dill 1990 for review) and theoretically (e.g. Newman & Caraco 1989; Newman 1991; see Houston, McNamara & Hutchinson 1993 for review). Taken together these results suggest that predation strongly shapes the behaviour of most animals. As many grazing animals suffer from predation hazard we include this consideration for the sake of generality. Equations 2–5 show the energetic cost of each behaviour. However there is also a predation cost associated with each behaviour.

The predation cost does not manifest itself in terms of changes to the dynamics of the state variables. Rather, it plays the role of discounting the future (e.g. Kagal, Green & Caraco 1986). That is, the animal must weight the expected future values of its state variables, which result from adopting a particular behaviour, by the probability that it survives the predation hazard associated with that behaviour. This is accomplished, mathematically, by the inclusion of a parameter for the probability of death by predation per unit time, μ_{bk}. The subscript denotes that the predation hazard depends upon the behaviour adopted. Throughout, we assume that grazing is more hazardous than resting or ruminating (see Appendix 3) because the head is up (rather than down, looking at the pasture) while resting and hence the animal can be vigilant for predators (see the Discussion for more detail).

DYNAMIC PROGRAMMING EQUATION

Let

$$F(X_{T-1},Y_{T-1},Z_{T-1})=\max_{bk}(1-\mu_{bk})\psi(X_T^{bk},Y_T^{bk},Z_T^{bk})$$

be the maximal unconditional expectation of the terminal reward function, one step from the terminal time horizon. The term $(1-\mu_{bk})$ is the probability that the animal survives the single time step from $(T-1)\rightarrow T$ where μ_{bk} is the one step predation hazard and depends on the behaviour adopted. The states X_T^{bk}, Y_T^{bk} and Z_T^{bk} depend upon the behaviour adopted and are given by equations 2–5.

The stochastic dynamic programming equation can then be written, for any time $t<T$, as:

$$F(X_t,Y_t,Z_t)=\max_{bk}(1-\mu_{bk})F(X_{t+1}^{bk},Y_{t+1}^{bk},Z_{t+1}^{bk}).\qquad\text{eqn 6}$$

Note that this equation is recursive in *t*. Because this process is Markovian, the optimal policy (specification of optimal one-step decisions for all combinations of time and states) can be calculated by backward induction starting from time $t=T-1$ and going backwards until $t=0$.

MODEL SYNOPSIS

We model behaviour as depending on three physiological states of the animal: stored energy, digestible gut fill and indigestible gut fill. We model behaviour over the daylight portion of a day. At the end of the daylight portion, the terminal reward function describes the probability that the animal will survive the night (i.e. survive until the next morning when it begins to forage again) as a function of its physiological states at the end of the day. Behaviour occurs during discrete time periods (8 min) in the model. During any time period, the animal's objective is to maximize its chance of surviving (both starvation and predation) from that time until the start of the next day. This probability depends upon the time period and the combination of states that the animal is in currently, and on the behaviour it adopts during the next 8 min period. That is, the model's solution tells us the optimal behaviour (rest, ruminate, graze grass, graze clover or graze either grass or clover) to adopt during every 8 min period in every combination of the three states. There are 175 500 combinations of the three

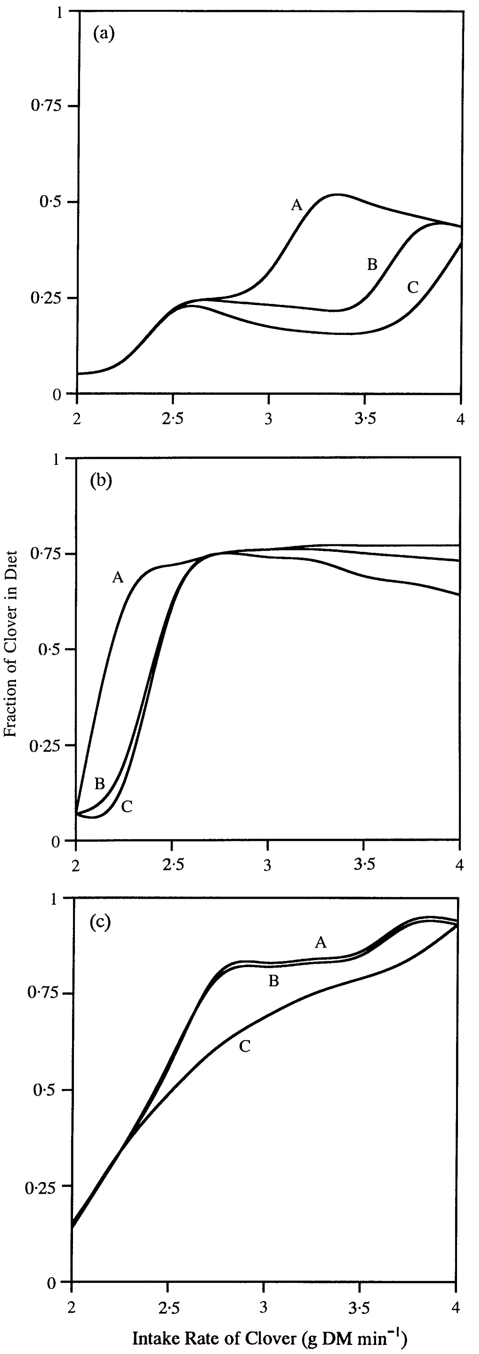

Fig. 2. The effects of intake rates of the two species on diet preference: (a) diet preference of a dry ewe grazing for up to 13·3 h day^{-1}; (b) diet preference of a dry ewe grazing for up to 10 h day^{-1}; (c) preference of a lactating ewe grazing for up to 13·3 h day^{-1}. The X-axis shows the intake rate for the animal when grazing clover and the three lines denote three different intake rates for grass. Line A denotes an intake rate of grass that is 0·05 g DM min^{-1} greater than clover (x-axis); line B denotes that the intake rate of grass is the same as that of clover; line C denotes a grass intake rate that is 0·05 g DM min^{-1} less than clover. In general, sheep should eat more clover as the intake rate of clover increases and more clover as the intake rate of grass increases relative to the intake rate of clover.

state variables and 100 time periods: the 'optimal policy' tells us the best behaviour to adopt for every one of these combinations. The model determines the best behaviour for every combination of states and time by calculating the *expectation* of the animal's probability of surviving the non-foraging period (i.e. expectation is the value of the terminal reward function weighted by the probability of suriving until the end of the day), for every possible behaviour. The behaviour which yields the highest expectation is the optimal behaviour for that combination of time and states.

Thus, the solution to the model, called the optimal policy, is the behaviour that should be adopted in each of the 175 500 combinations of time and states. The daylight day is then simulated with the decisions being specified by the optimal policy It is this stimulation that translates the specification of the optimal behaviour during an 8 min period into behaviours more recognizable by empiricists; e.g. daily grazing time, total daily intake and diet composition.

Results

Default parameter values and approximations are contained in Appendixes 2 and 3. Unless otherwise stated these values were used to generate all solutions. Appendix 3 contains details of solution generation.

DIET PREFERENCE

As stated earlier, 'diet preference' is what the animal would choose to eat if it were unconstrained by the environment. We use our model to consider this by setting $\rho_i = \rho_j = 1$ and eliminating behaviour b_5 as an option. That is, if the animal chooses to graze species i, then it can graze that species without having to search for it. This situation is analogous to that used by Newman *et al.* (1994; see also Parsons *et al.* 1994a) in which the two species are highly aggregated in space. In these two experiments whole fields comprised two monocultures side by side. No searching was necessary in order to locate either species. Unless otherwise stated, all results are for dry ewes grazing during a 13·3:10·7 h photoperiod.

PROPORTION OF CLOVER IN THE OPTIMAL DIET

Figure 2 shows the proportion of clover in the optimal diet assuming a range of values for the intake rate of clover (x-axis) for three cases: (1) the rate of intake for grass is 0·05 g DM min^{-1} greater than that for clover, (2) the rate of intake for grass is the same as the rate of intake for clover and (3) the rate of intake for grass is 0·05 g DM min^{-1} less than that for clover. Figure 2 (a) shows the proportion of clover in the optimal diet for dry ewes grazing for up to 13·3 h day^{-1}, (b) shows the diet for dry ewes grazing for up

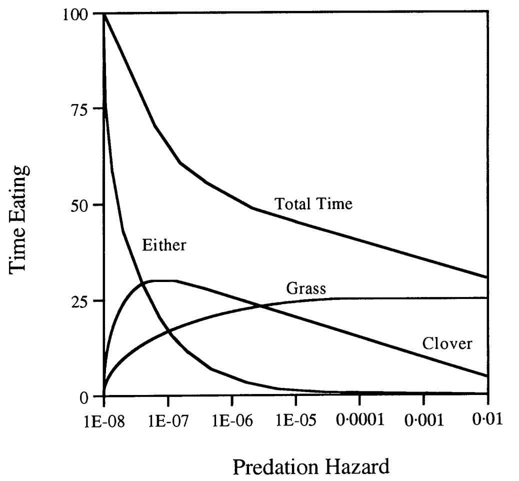

Fig. 3. Time spent grazing either indiscriminately, grazing grass or grazing clover as a function of predation hazard. The solutions are for dry ewes grazing grass and clover at 3·75 g DM min^{-1}. As predation hazard increases, the time spent grazing decreases and the animal should rapidly move from grazing indiscriminately to a preference for clover and eventually to a preference for grass.

to 10 h day^{-1} and (c) shows the optimal diet composition for lactating ewes grazing for up to 13·3 h day^{-1}. The figure shows that in all cases a mixed diet should be selected. The mixture results from a trade-off between intake rates, rates of absorption and rates of passage (Appendix 2). Notice that the mixture is not constant; it varies both between cases and with the absolute intake rates (x-axis). That is, animals should eat a greater proportion of clover when the intake rate for grass is higher (curve $A \geq B \geq C$ for all three combinations of animal state and day length). They should also eat a greater proportion of clover when the absolute intake rates of herbage increases (i.e. moving along the x-axis in Fig. 2) such as may arise because both species are more abundant.

Figure 3 shows the optimal time a dry ewe should spend grazing grass, clover or indiscriminately. These values are shown as a function of predation hazard. Two responses to predation are demonstrated. First, the total time spent grazing decreases as predation hazard increases because the optimal policy is a trade-off between eating to avoid death by starvation and not eating (so being vigilant) to avoid death by predation. As predation hazard increases, the optimal solution is therefore to graze for less time and so, in Fig. 3 the curve showing the total time spent grazing decreases as predation hazard increases. The second response to predation hazard is that the proportion of clover in the optimal diet changes as a function of predation hazard. Notice how the curves for grass and clover in Fig. 3 change relative to each other and in fact cross over. That is, animals should, in this case, eat more clover (intake rate = 3·75 g DM min^{-1}) when predation hazard is low and gradually switch to grass (intake rate = 3·75g DM min^{-1}) as predation hazard increases. The increase of grass in the diet is accompanied by an increase in rumination time (not shown in Fig. 3). In this case the optimal strategy is to change to a diet that includes a larger proportion of material with a longer digestion time (grass) and spend more time ruminating that material. The increased rumination functions both to reduce exposure of the animal to predation (as it can be vigilant and ruminate simultaneously) and to enhance the digestion of the grass (see Appendix 2 for more on the effects of rumination).

Another important result from this model concerns the temporal pattern to diet preference. Figure 4 shows an example of the accumulation of intake across the day for a lactating ewe. In this case there is a period of approximately 40 min in the morning when the optimal diet is pure clover followed by a rather longer period when the diet comprises grass only; this is then followed by a period towards the end of the day where both species are grazed, and the day ends with a bout of 80 min grazing grass. It is important to emphasize that this is an example and many other types of patterns occur in the results. However, this example does show that, depending upon when estimates are taken, it is possible to conclude that ewes have a preference for grass, clover, neither or both species, depending upon the duration and timing of the observation.

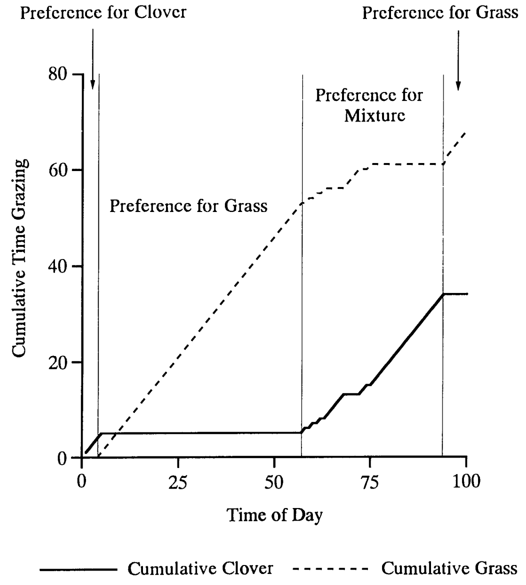

Fig. 4. An example of a temporal pattern that the model predicts. The prediction of a temporal pattern has important implications for conducting experiments. Many grazing selection experiments are conducted with fistulated animals which can only graze for about 30 min at a time. The implication of this Figure is that the conclusion reached regarding diet preference would depend upon when the measurement is made and for how long the measurement is made.

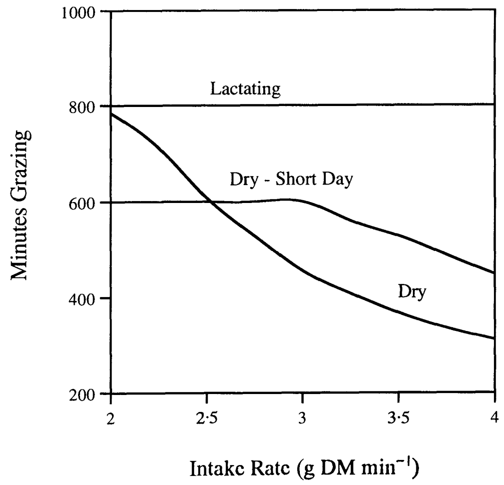

Fig. 5. The optimal time spent grazing by sheep for two different physiological conditions (dry *vs* lactating) and two different day lengths (13·3 *vs* 10 h). The grazing time of lactating ewes should be fairly insensitive to intake rates, but that the grazing time for dry ewes should decrease with increasing intake rate.

TOTAL DAILY INTAKE

Figure 5 shows the time spent grazing (which is proportional to total daily intake) for the same three situations shown in Fig. 2: dry ewes grazing up to 13·3 h, dry ewes grazing up to 10 h and lactating ewes grazing up to 13·3 h. The figure shows that lactating ewes have such an increased demand for energy that they must graze most of the day (800 min) and even when the intake rates of grass and clover are each around 4 g DM min^{-1} lactating ewes may still not be able to meet their daily energy requirement. In the cases of dry ewes, as the intake rates increase (cf. total availability of herbage increases), the time spent grazing decreases. This result follows from the interaction between the hazard of predation and the shape of the terminal reward function (described earlier).

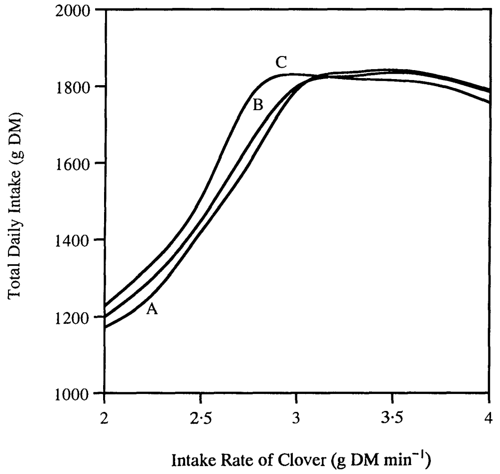

Fig. 6. The predicted total daily intake for a dry ewe grazing for up to 10 h day^{-1} Although the optimal time spent grazing by these animals diminishes after about 3 g DM min^{-1}, the total intake does not fall off as rapidly, if at all. Lines A, B and C are as defined in Fig. 2.

Spending less time grazing as the environment improves (in terms of total herbage availability) does not necessarily mean that animals should eat less. Figure 6 shows an example of total daily intake for a dry ewe grazing for up to 10 h day^{-1}. The figure shows that the animal increases its grazing time and total intake as intake rates increase up to about 3 g DM min^{-1}. After this point the animal's total daily intake remains approximately constant while it decreases the time spent grazing (see Fig. 5).

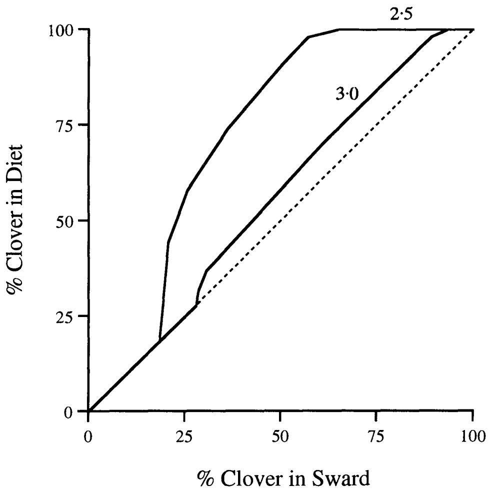

Fig. 7. The effects of encounter rates on diet selection. The results are for dry ewes grazing up to 13·3 h per day^{-1} when the intake rate for clover is 3·5 g DM min^{-1}. The two curves shown are for intake rates of grass of 2·5 and 3·0 g DM min^{-1}. In both cases, the diet preference for these two comparisons should be 100% clover in the diet. The environment (in the form of encounter rates) modifies the diet preference and produces the diet selection shown by the solid lines (the dashed line shows indifference).

DIET SELECTION

To demonstrate the effects of the environment on diet preference (i.e. diet selection) we vary the parameters that describe the encounter probability for clover and grass, ρ_i and ρ_j. We envisage a closed canopy pasture such that $\rho_i = (1-\rho_j)$. In the model, if the optimal decision is that the animal should seek one particular species, then the animal foregoes the opportunity to graze the alternative species if it is found. This effectively adds a second 'cost of selection/preference' (the first being the predation hazard discussed above).

The impact of the additional time and energy costs needed to find the preferred species can be seen in Fig. 7, which shows the effects of varying the relative abundance of each species on the optimal proportion of clover in the diet. When the model is run to consider diet preference in these circumstances, the optimal diet is 100% clover when the intake rates for grass are 2·5 and 3·0 g DM min^{-1}. When the animal must find the food, then encounter rates (i.e. ρ_i and ρ_j) alter the optimal decisions, and in these cases the proportion of clover in the diet declines.

Discussion

As mentioned earlier, the choice of state variables is crucial to the predictions and may differ from one animal species to another, or indeed may differ within the same animal species but between environments or plant communities. For example, in the case of sheep grazing ryegrass and clover, it has been suggested that the mixed diets observed by these animals may have more to do with sulphur–nitrogen ratios or levels of crude protein than they do with intake, absorption and passage rates (e.g. Parsons *et al.* 1994b). On the other hand, to many grazers balancing energy content and bulk content may be of paramount importance. Our point in this modelling exercise is to emphasize the state-dependent approach. Animals should make decisions that depend upon their physical stages, the states that are most important may vary depending on the environment (e.g. improve temperate grassland, natural C4 pasture, etc.) and the details of the animal's nutritional requirements (e.g. sodium in Belovsky's moose; Belovsky 1981). However, we believe that there is much to be gained by thinking about the problems of diet selection and diet preference from a state-dependent and dynamic framework.

BASIS OF DIET SELECTION AND DIET PREFERENCE

Grazed grass/clover pastures provide a valuable model in which to study diet preference and selection in grazing herbivores (reviewed by Newman, Parsons & Harvey 1992). There is a large body of knowledge on the physiology, morphology and ecology of both plant species (owing partly to their economic importance). Moreover, in cool–temperate grassland systems, it is difficult to imagine two plant species more dissimilar: one is a leguminous, stoloniferous dicot, the other is a non-leguminous, non-stoloniferous, monocot. Although morphologically and physiologically dissimilar, these two species have surprisingly similar nutritional values. They both have approximately the same gross energy content (*c.* 18 MJ kg^{-1} DM) and ultimate digestibility (*c.* 75%). There appears to be no nutritional obligation for the animals to graze a mixed diet (i.e. there is no known nutrient or mineral that is available in one species but not the other, although the quantities of these nutrients and minerals may differ between plant species). Unlike cattle, pure clover diets do not appear to cause bloat in sheep. In all these different 'currencies', there seems to be little to distinguish the two species except in the intake rates achievable from differently structured pastures (e.g. differences in leaf area index, cover, plant height, specific leaf area, bite masses, bite volumes, etc.). However, in many experiments of diet preference, animals eat a mixed diet (e.g. Newman *et al.* 1994; Parsons *et al.* 1994a). The model produces solutions in which the optimal diet is often a mixture of grass and clover. The model suggests this is an optimal trade-off between relative intake rates and absorption rates (and to a lesser extent passage rates). Whether this is the major explanation of mixed diets in reality (in the case of grass and clover) is less important than pointing out that mixtures may be preferred for reasons that have nothing to do with nutrients.

Although the model presented will not end the debate regarding the basis of diet selection and diet preference, either specifically for sheep or generally for herbivores, it does have some heuristic value in pointing out whŷ the literature might be equivocal on these topics. Figure 2 demonstrates that diet preference is likely to be sensitive to both the relative differences between species (e.g. *relative* vertical abundances, cf. relative heights of each species) and the absolute variability of herbage (e.g. *total* vertical abundances). In addition, Fig. 7 shows that diet selection may also be modified by the relative horizontal availability of each species (e.g. their fractional cover). Controlling these three variables in grazing experiments is very difficult and constructing replicate fields is even harder. Often experimental results that report preference or selection are not directly comparable because they will almost certainly differ between these three variables. More importantly, perhaps, is that because these effects have not been appreciated previously, this information has sometimes not been reported at all.

Even when experimenters have controlled the relative vertical and horizontal abundances and total availability, the resulting estimates of preference and/or selection often differ. Figure 4 demonstrates that the time of day during which experiments are conducted may have important effects on the subsequent conclusions. The existence of daily patterns in diet preference has been demonstrated experimentally by Parsons *et al.* (1994a) and Newman *et al.* (1994). Most previous experiments have been of short duration (0·5–1 h) owing to the techniques used (i.e. fistulation). These 'snap-shots' of grazing behaviour are not able to capture the dynamics of the grazing process. It is very difficult to deduce the behaviour of a dynamic system from a collection of snap-shots. As the experiments reported in the literature tend to be of short duration and were conducted at different times of day, it is not surprising that there is disagreement in the literature.

The model also suggests that diet preference and selection should be sensitive to predation hazard (see

Fig. 3). In an ecological context predation hazard can often be equated with group size. Penning *et al.* (1993) have previously shown that total daily intake depends on group size (see below), but to date no one has investigated whether diet preference depends on group size. However, as experiments in the literature are often conducted with groups of different size, it is possible that differences between studies may also be attributable to these group sizes (and hence predation hazard).

In an ecological context, diet selection may be more relevant than diet preference. Diet preference is often the subject of experimental work because the results are easier to interpret and because it is thought that insight into diet preference will help us to understand diet selection. In the literature, diet selection has often been assessed by comparing the percentage of some diet component (e.g. clover) with the percentage of that component in the environment. The difficulty with this method is in deciding the appropriate measure for assessing the composition of the environment. That is, a 10% clover pasture might mean that clover comprises 10% of the standing biomass, 10% of the standing dry matter, or 10% of the surface area. The model suggests that these measures will produce different results.

TOTAL DAILY INTAKE

Total daily intake has been an important area of research in agricultural studies for many years. For many animals grazing improved (e.g. sown, fertilized, etc.) temperate pastures, mechanistic models (e.g. Illius & Gordon 1991) suggest that these animals are physiologically and morphologically capable of increasing their daily intake. That is, there is currently no known physiological mechanism that adequately explains grazing time (and hence daily intake). Large research programmes are aimed at assessing the 'palatability' (loosely translated as how good something tastes) of various forages. It is hoped that a forage can be identified that the animals find particularly tasty, and that they will graze for longer and hence eat more (thus living up to their physiological potential).

The model that we present here provides a *non-mechanistic* hypothesis for a limit to daily intake. In cases where the animal is not physiologically limited in its intake, it may stop grazing in order to engage in other fitness-enhancing activities. In the model, total daily intake is a prediction that results from two assumptions in the model: the shape of the terminal reward function (see Appendix 1) and the predation hazard. These two parameters trade-off such that eventually the added benefit to continued grazing is outweighed by the costs. However the costs are not simply energetic [see Illius & Fitzgibbon (1994) for more on the costs of vigilance in foraging ungulates]. The exact prediction of daily intake depends on how the terminal reward function approaches its maximum (and we think we have chosen the most biologically reasonable form, see Appendix 1) and how different, in terms of hazard of predation, grazing is than resting or ruminating.

Because total daily intake (via grazing time) is a prediction of the model, it is important to point out that some of the results we present here may be incomplete in terms of understanding behaviour. Most of the results of diet selection and preference are prescribed as percentages, to be comparable to other experimental and theoretical studies. However, we must emphasize that the prediction of optimal diets is a total quantity of intake that comprises a certain mixture of the two species, and often changes in mixture are accompanied by changes in daily intake.

PREDATION HAZARD

As predation hazard plays an important role, both in terms of diet preference and total daily intake, it is worth mentioning some justification for this assumption. For many wild herbivores, there is no doubt that these animals suffer from predation (e.g. Gluesing & Balph 1980; Skogland 1991; Heard 1992; Scheel 1993). Indeed, some herbivore populations may be more strongly limited by predation hazard than by food availability (e.g. Sinclair 1989). Some behavioural studies have shown that grazing animals spend less time being vigilant and more time grazing when they are in larger groups (e.g. Lipetz & Bekoff 1982; Underwood 1982; Lagory 1986; Scheel 1993; Bednekoff & Ritter 1995), and the generality of this result extends to many social animals [see Lima & Dill (1990) for review]. There is, however, great debate about whether domestic grazing animals are under any serious threat of predation (see Gluesing & Balph 1980) or even whether they retain any evolved anti-predator behaviours. Pulliam & Caraco (1984) have enumerated reasons why animals should live in groups (i.e. herding behaviour). However, outside the mating season, the most reasonable explanation for grazers is that group living affords protection from predators (either through 'dilution' or 'many eyes' effects, see Pulliam & Caraco 1984). Most researchers who study domestic animals fail to consider anti-predator behaviour as they know that their animals are not under any threat of predation. However, Penning *et al.* (1993) have shown that sheep grazing in southern Britain (where there is no serious threat of predation) graze for longer when they are in larger groups. This is exactly the same type of response that has been evident in more 'natural systems' and has previously been interpreted as an anti-predator behaviour (e.g. Scheel 1993). Moreover, some breeds of sheep have been bred to flock together (in groups), to ease their management, in the presence of domestic dogs. It is possible that this breeding has been successful in exploiting the 'natural' anti-predator behaviour of these animals.

Whether or not animals are under real threat of predation may be irrelevant to their subsequent behaviour, only a 'perception' of hazard is necessary to produce results like those demonstrated in this paper. Furthermore, the model suggests that behaviour should be fairly sensitive to this 'perception'. If this is true, then researchers should take care to ensure that group sizes used in experiments are realistic compared to groups found in more natural grazing circumstances.

Conclusions

We have presented a general model of grazing behaviour that is state dependent and dynamic. The model combines a teleonomic approach with a simplified mechanistic submodel of the digestion process. We have solved the model for parameters relevant to sheep grazing from a perennial ryegrass–white clover pasture. In a variety of circumstances the model predicts an optimal diet that is a mixture of the two species. This mixture occurs for reasons that have nothing to do with nutrition but rather reflect a trade-off in the dynamics of the digestive processes between intake rates, passage rates and absorption rates. The model points out several reasons why the literature on preference and selection in grazing animals may be equivocal. Among these reasons are that preference should depend on the relative and absolute intake rates and may be modified by the relative horizontal abundances of each species. Both of these behaviours may show temporal patterns, and they should be sensitive to the predation hazard that the animal suffers or perceives itself to suffer. Finally the model makes predictions regarding total daily intake. This has been an area in which totally mechanistic models have failed to provide predictions. A teleonomic model such as this can provide a non-mechanistic prediction based on an evaluation of the fitness consequences of alternative behaviours.

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Appendix 1. Terminal reward function

This appendix describes the terminal reward functions used for the numerical solutions contained in this paper

THE $\xi(Y_T,Z_T)$ FUNCTION

In equation 1, the terminal reward function, the function $\xi(Y_T,Z_T)$ describes digestion, during the non-grazing period, of material still contained in the gut at the terminal time horizon, T. For all numerical examples contained in this paper $\xi(Y_T,Z_T)$ takes the following form:

$$\xi(Y_T,Z_T)=(Y_T+\delta(Z_T))\varepsilon.$$

The function $\delta(Z_T)$ is described in detail in Appendix 2; it is a function that reflects the physical breakdown of material in the gut through rumination. One function of rumination is to break down the otherwise indigestible cell wall and hence liberate a small fraction of material for digestion. ε is a measure of the efficiency with which mass is converted to energy through digestion. It reflects the efficiency of conversion from digestible energy into metabolizable energy (0·81) and metabolizable energy into net energy (0·75, i.e. $0{\cdot}81\times0{\cdot}75=0{\cdot}6075$; Alderman 1984). Both grass and clover have a gross energy content of approximately 18 MJ kg^{-1} DM (Alderman 1984). Each unit of gut fill (Y and Z) is 80 g DM, so each unit of gut fill is equivalent to 1·44 MJ. Each unit of stored energy (X) is equivalent to 352 kJ, so each unit of gut fill has an equivalent gross energy content of 4·1 units of stored energy. So, $\varepsilon=0{\cdot}81\times0{\cdot}75\times4{\cdot}1=2{\cdot}49$ is the conversion of digestible mass in the gut into stored energy. For more details on the scaling of the state variables, see Appendices 2 and 3.

SHAPE PARAMETERS OF THE TERMINAL REWARD FUNCTION

In equation1 there are three shape parameters denoted a, b and c. These parameters have no biological meaning but

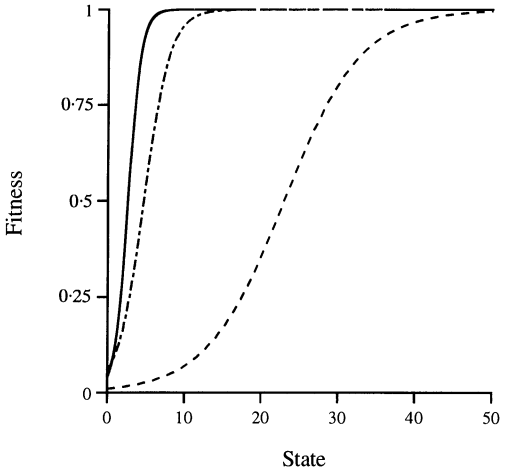

Fig. A1. The three principal terminal reward functions used throughout the paper: (——) the terminal reward function, $\psi(X_TY_T,Z_T)$ (see equation 1) as a function of $\theta = (X_T + \xi(Y_t,Z_T))$ for a dry ewe grazing for up to 13·3 h day^{-1}; (- ·· ·-) the terminal reward function for a dry ewe grazing up to 10 h day^{-1}; (---) the function for a lactating ewe grazing for up to 13·3 h day^{-1}.

control the shape of the function. The function is convex–concave in $\theta = (X_T + \xi(Y_T,Z_T))$, with the inflection point given by $\theta(\text{inflection}) = (\ln a)/b + c$ and an upper asymptote of 1. The upper boundary is only important when the animals are near that boundary (which they are not in the results presented in this paper). Otherwise the general behaviour will be similar (see Mangel & Clark 1986). A dry ewe requires approximately 6 MJ net energy day^{-1} (ARC 1980). During summer days in northern latitudes, there are approximately 13–14 h of daylight. For an animal to meet its daily energetic requirements, it must end the daylight portion of the day with a store of 2·67 MJ (i.e. sufficient quantity to survive the non-grazing hours of darkness). This quantity is equivalent to 7·6 units of X (see Appendix 2). We set the parameters a, b and c so that equation 1 is approximately 0 when $\theta = 0$ and approximately 0·95 when $\theta = 7{\cdot}6$. One set of numbers that achieves this is {7,1·2,1}. We use this set as our default parameters (see Appendix 3).

This function can easily be scaled to consider variable day length (i.e. number of daylight hours) or physiological state (e.g. lactating). Consider a day that has only 10 h of daylight. To meet its daily energy requirement, the animal must survive the daylight portion of the day with an energy store of 3·5 MJ or 9·96 units of X. A set of parameters that satisfy the conditions that equation 1 is approximately 0 when $\theta = 0$ and approximately 0·95 when $\theta = 9{\cdot}96$ is {5,0·6,2}. These values are used in the numerical examples of the effects of day length on the grazing behaviour of dry ewes. A lactating ewe requires approximately 17·5 MJ net energy day^{-1} to meet its energetic requirements. To do this in 13·3 h of daylight, the animal must survive the daylight day with 14·17 MJ or stored energy of 40·31 units of X. A set of parameters that satisfy the conditions that equation 1 is approximately 0 when $\theta = 0$ and approximately 0·95 when $\theta = 40{\cdot}31$ is {1,0·2,23}. These values are used in the numerical examples of lactating ewes. Other combinations of physiological states and day lengths are easily calculated.

Gladstein, Carlin & Austad (1991; see also Houston, McNamara & Thompson 1992) have pointed out that the solutions are sensitive to the form of the terminal reward function and that sensitivity analyses should be performed. The three terminal reward functions used to generate the results in this paper are shown in Fig. A1. Changing the shape parameters has the effect of changing the inflection point and changing how rapidly the function reaches its asymptote. We have equated these changes with changes in the animals' environment (e.g. day length) or physiological condition (e.g. lactating). We have tried other parameter values, and they cause the optimal policy to change in obvious directions, as illustrated in the Results.

Appendix 2. State variable dynamics

This appendix dicusses specific forms of the functions and equations used to calculate the state variable dynamics in the numerical examples contained in this paper.

THE $\delta(\cdot)$ AND $\omega(\cdot)$ FUNCTIONS

Rumination assists in the physical breakdown of herbage particles in the gut. It is sometimes referred to as delayed handling, in that animals may defer some mastication during eating by swallowing relatively large particles and then masticating this material at some later time via the process of rumination. The physical breakdown of particles increases the speed with which material is digested and the speed with which it flows through the gut. This breakdown may also liberate a small fraction of material that would otherwise have been indigestible (e.g. through the breakdown of the cell wall). The function $\delta(\cdot)$ serves the latter purpose and the function $\omega(\cdot)$ serves the former purpose.

In the numerical examples contained in this paper, $\delta(\cdot)$ takes the following form:

$$\delta(Z_t) = 0{\cdot}02Z_t. \qquad \text{eqn A1}$$

That is, we assume that the additional mastication makes 2% of the material that would otherwise have been indigestible, digestible.

We assume the following form of the $\omega(\cdot)$ function in all numerical examples:

$$\omega(\cdot) = 2(\cdot). \qquad \text{eqn A2}$$

That is, we assume that for the period of rumination, the relevant rate constant (see equation 3) is increased by a factor of 2. In reality there is likely to be a lag before the increase in flow rates occurs but this is omitted for the sake of simplicity. These two parameters have their most significant effects in determining optimal rumination durations. However, they also play a role in determining the optimal diet composition.

DIFFERENTIAL FLOW RATES

For the numerical examples used in this paper we approximate parameters for sheep grazing perennial ryegrass and

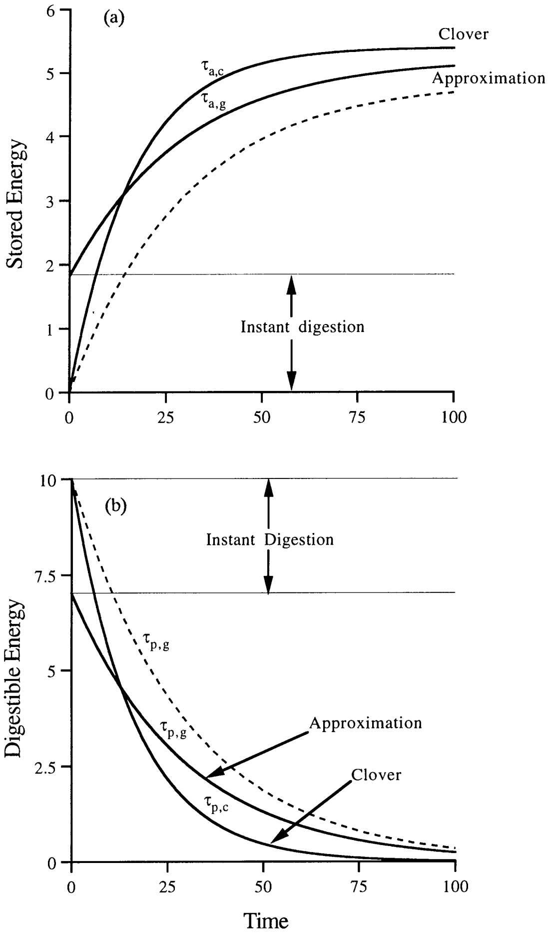

Fig. A2. The approximation method used for absorption rates in this model: (a) the accumulation of stored energy through digestion for clover (——) and grass (---) and the approximation which is used to approximate the clover line; (b) shows the same information except that it represents the disappearance of digestible material from the gut.

white clover (see Appendix 3). Two differences between these species are rate of absorption and rate of flow through the gut. Although both species have a similar overall digestibility, the sparse evidence available suggests that clover is absorbed and passed at about twice the rate of grass (Losada 1983). The state variables that describe the gut fill do not distinguish species composition. Furthermore, it is computationally intractable to do so (the number of computations increases exponentially with increasing dimensions, this is known as 'the curse of dimensionality'). However, we can take account of this difference in rates by using the following approximation.

Assume that all material in the gut is absorbed or passed at the rates associated with grass (i.e. $\tau_p=\tau_{p,g}$ and $\tau_a=\tau_{a,g}$). In the model, when grass is ingested, it is partitioned into two components: the fraction of digestible material (κ_i from equation 4) and the fraction of indigestible material ($1-\kappa_i$ from equation 4). In order to approximate the absorption and passage rates of clover, we assume that when clover is ingested it is first partitioned into the same two components. However, these two components are each partitioned into a further two components. In the case of the digestible material, this is partitioned into a quantity that is digested instantly and a quantity that is digested normally following the rate constant used for grass. For the indigestible material a similar partition is constructed: a quantity that is passed instantly and a quantity that is passed normally according to the rate constant for grass.

First, consider the digestible material. The state dynamics for digesting a diet of pure clover would be:

$$X^c_{t+1}=X^c_t+2Y^c_t\tau_{a,g}\varepsilon-\alpha$$

$$Y^c_{t+1}=Y^c_t(1-2(\tau_{a,g}-\tau_{p,g})).$$

We wish to approximate this over a period of 13·3 h (which is used as the standard day length throughout the numerical examples). To do this, suppose that $Y^a_0=\lambda_y Y^c_0$ is the *approximated* amount of digestible material that will be digested normally, The term $0\leq\lambda_y\leq 1$ represents the fraction of the total digestible material at the start of the approximated period (i.e. time 0), Y^c_0. Also, let $X^a_0=(1-\lambda_y)Y^c_0\varepsilon$ be the amount of energy that is absorbed instantly into the stored energy state variable. Then, the dynamics of the approximated variables are:

$$X^a_{t+1}=X^a_t+Y^a_t\tau_{a,g}\varepsilon$$

$$Y^a_{t+1}=Y^a_t(1-\tau_{a,g}-\tau_{p,g}).$$

The object is then to choose λ_y such that:

$$\min_{\lambda_y}\left(\sum_{t=0}^{100}((X^a_t-X^c_t)^2+(Y^a_t-Y^c_t)^2)\right).$$

That is, we chose λ_y such the the sum of the squared differences between the actual state variable dynamics and the approximated state variable dynamics is minimized over 100 discrete time periods. We solved for this approximation numerically to the nearest 0·005 and found $\lambda_y=0{\cdot}700$ to be the best fit. This approximation is illustrated in Fig. A2. The areas between the lines representing the dynamics of clover and the approximation are being minimized. The dynamics of grass is shown as a dashed line for illustrative purposes and is not considered in the approximation.

The approximation for passage rates can be solved in a similar way, but as it depends only on the dynamics of Z, it is reasonably approximated by $\lambda_z=0{\cdot}5$. For grass and clover, sensitivity analyses suggest that the solutions are relatively insensitive to the value of this parameter.

The above approximation is only one way in which to approach this problem. Obviously the approximation will be critical to the quantitative predictions of the model. Any approximation, however crude, which reflects a difference between the absorption and passage rates between grass and clover, will tend to produce similar general solutions. We have tried other approximations and other values of this approximation and it seems to make little difference to the general form of the solutions.

Thus, throughout the numerical examples presented in this paper, equation 4 is true for grass, and for clover we used:

$$X^{b_3}_{t+1}=\begin{cases}\max X & \text{if } X_{t+1}>\max X\\ X_t+Y_t\tau_a\varepsilon+(1-\lambda_y)\kappa_i E[\gamma_i]\varepsilon-\alpha_a & \text{if } 0<X_{t+1}\leq\max X\\ 0 & \text{if } X_{t+1}\leq 0\end{cases}$$

$$Y^{b_3}_{t+1}=\begin{cases}Y_t(1-\tau_a-\tau_p)+\lambda_y\kappa_i E[\gamma_i] & \text{if } Y_{t+1}+Z_{t+1}\leq\eta\\ Y_t(1-\tau_a-\tau_p) & \text{otherwise}\end{cases}\qquad\text{eqn A3}$$

$$Z^{b_3}_{t+1}=\begin{cases}Z_t(1-\tau_p)+\lambda_z(1-\kappa_i)E[\gamma_i] & \text{if } Y_{t+1}+Z_{t+1}\leq\eta\\ Z_t(1-\tau_p) & \text{otherwise}\end{cases}$$

which reflects the above approximation.

Table A1. Default parameter values, meanings and references

Parameter	Meaning	Value	Scaled value	Reference and notes
a,b,c	Shape parameters			Appendix 1
ϑ_i	Intake rate species i	0·5–4·5	0·05–0·45	Penning, Rook & Orr 1991
τ_a	Absorption rate	0·264	0·0264	Losada 1983
τ_p	Passage rate	0·666 g DM min^{-1}	0·0066 Y units t^{-1}	Losada 1983
α_a	Metabolic cost of activity	12898·9 J min^{-1}	0·29 X units t^{-1}	ARC 1980
α_r	Metabolic cost of resting or ruminating	6103·38 J min^{-1}	0·139 X units t^{-1}	ARC 1980
κ_i,κ_j	Proportion of herbage that is digestible	$i=j\approx 0{\cdot}8$		Alderman 1984
max X	Maximum amount of energy the animal is capable of storing	17·578 MJ	50 X units	
η	Gut capacity	2 kg DM	25 Y or Z units	
l	Subunits of time	1 min	1/8 t	
$\mu^{b}_{1,2}$	Predation hazard when resting or ruminating	0/2000 death day^{-1}	0·00000 deaths t^{-1}	Default value
$\mu^{b}_{3,4,5}$	Predation hazard when active	≈1/2000 death day^{-1}	0·00001 deaths t^{-1}	Default value
t	Discrete time unit	8 min	1 t	$100t = 13{\cdot}33$ h
X	Stored energy		max = 50 min = 0	351 560 J = 1 unit X
Y	Digestible gut fill		max = 25 min = 0	80 g DM = 1 unit Y
Z	Indigestible gut fill		max = 25 min = 0	80 g DM = 1 unit Z
ε	Energy conversion efficiency	0·6057	$2{\cdot}48(Y) = X$	Alderman 1984
ρ_i,ρ_j	Probability of finding plant species in one subunit of time			
λ_y	Approximation of absorption rate		0·7	Appendix 2
λ_z	Approximation of passage rate		0·5	Appendix 2

Appendix 3. Parameter values and solution generation

The stochastic dynamic programming equation is solved using backward induction. This yields an exact solution for the optimal behaviour in every combination of time and state. The optimal policy, as it is known, is then simulated forward in time for 10 'animals' with the initial states of $X_0 = 2$, $Y_0 = 0$, $Z_0 = 0$, and the results are expressed as means. Linear interpolation was used to evaluate the expectation of the terminal reward function when state variable dynamics resulted in non-integer changes of state. Table A1 shows the default parameter values used unless otherwise stated.