Martyn G. Murray and David R. Baird. 2008. Resource-ratio theory applied to large herbivores. *Ecology* **89:1445-1456.**

Appendix C. The body size competition model.

The model has three components: food intake, digestion and energy balance (see Appendix D for a diagrammatic representation of the model).

Intake Component of BSC Model

The intake model described here differs in two main respects from the Fryxell / Wilmshurst models. Firstly, the Fryxell / Wilmshurst models incorporate an implicit description of the environment by assuming that daily gut capacity falls with increasing vegetation standing biomass. This is because digestibility is negatively correlated to vegetation biomass, and retention times increase to cope with poorer quality food. The current model explicitly models the increase in retention times caused by poorer quality food intake, removing the direct relationship between forage abundance and gut retention time. This is necessary because the aim of the model is to predict competitive outcomes under a variety of resource supply scenarios, including variation in abundance that is independent of quality, and *vice versa*. The model does not assume that cell wall and cell content are directly correlated.

The second difference is that the Fryxell / Wilmshurst models convert dry matter intake directly into metabolizable energy intake by applying a conversion factor. The model presented here uses an explicit model of digestion that partitions food intake into cell wall and cell content fractions.

The first intake constraint models daily intake as a function of gut capacity and food retention time. Gut capacity limits daily intake according to the species' gut size divided by the mean retention time of food in the gut:

$$FILL_d[g\ DM.day^{-1}] = 24 \frac{GC}{RT} \qquad (C.1)$$

Gut capacity is a linear function of body size:

$$GC[g\ DM] = 21W[kg] \qquad (C.2)$$

($R^2_{adj} = 0.98$, $n = 18$, Illius and Gordon 1991).

Whole-gut retention time is modelled as a modification of:

$$RT[hrs] = 14.1W^{0.27} \qquad (C.3a)$$

Illius and Gordon (1991) derived this relationship as a simplification of

$\ln(RT[hrs]) = 2.725 + 0.251\ln(W)$, $R^2_{adj} = 0.76$, $n = 26$.

As retention time however is expected to vary with diet quality as well as body size, we use an empirical adjustment to increase or decrease RT according to the proportion of indigestible food ($INDF$):

$$RT_{adj} = \left(\frac{W}{500}\right)^{0.5} \times 0.15 \tanh\left(\frac{INDF}{125} - 3\right) \qquad (C.3b)$$

$$RT = \left(1 + RT_{adj}\right) \times 14.1W^{0.27} \qquad (C.3c)$$

The second intake constraint models the functional response, i.e., the eating rate of ungulates as a function of vegetation standing biomass and body size. Vegetation

standing biomass is the sum of cell wall biomass (kg.ha^{-1}) and cell contents biomass (kg.ha^{-1}). Fryxell (1991), Wilmshurst, Fryxell and Colucci (1999), and Wilmshurst, Fryxell and Bergman (2000) used the Michaelis-Menten equation to model the functional response:

$$CROP_d[g\ DM.day^{-1}] = \frac{R_{max} \times 0.1V}{b + 0.1V}.t_{max} \qquad (C.4)$$

Although the maximum daily feeding time, t_{max}, may be expected to vary with body size, in fact there is little evidence of a systematic relationship. Data from Demment and Van Soest (1983, in Van Soest 1994, Table 4.7) show only a weak correlation of time spent feeding to body size ($r = 0.31$, $n = 23$, n.s.), and this disappears when male and female elephant are excluded ($r = 0.024$, $n = 21$, n.s.).

The parameters b and R_{max} were derived from data in Wilmshurst, Fryxell and Bergman (2000). They collated estimates of b and R_{max} for a variety of species from the literature. Regressing their data against body size gave significant relationships which were used to predict b and R_{max} in the present model:

$$R_{max} = 1.977 + 0.162W \qquad (C.5)$$

$$r = 0.97,\ n = 15,\ P \ll 0.001$$

$$b = -34.99 + 0.663W \qquad (C.6a)$$

$$r = 0.79,\ n = 15,\ P = 0.00045$$

Equation C.6a predicts negative half-maximum intake for animals smaller than 52.78 kg. In fact the intercept is not significantly different from zero ($P = 0.37$), and the relationship was recalculated through the origin to give:

$$b = 0.577W \tag{C.6b}$$

$$r = 0.77, R^2_{adj} = 0.60, n = 15, P = 0.00052.$$

Daily intake is the minimum of the two constraints:

$$C_d[g\ DM.day^{-1}] = \min[CROP_d, FILL_d] \tag{C.7a}$$

Intake of CC and CW are modelled in two ways. In the basic model, the proportion of CC and CW in the diet is the same as in the sward. The animals are completely unselective (Eqs. C.7b and C.7c). In Eqs. C.7d – C.7f, selectivity is introduced by analogy to the selectivity observations of Murray and Illius (2000), with an arbitrary modification to make smaller ungulates more selective of CC than larger ungulates. As all forage contains some cell wall, selectivity is constrained to a maximum of 45 per cent CC in the diet.

$$CC_i[g\ DM.day^{-1}] = C_d\frac{CC_S}{V} \tag{C.7b}$$

$$CW_i[g\ DM.day^{-1}] = C_d\frac{CW_S}{V} \tag{C.7c}$$

$$pCCi = \frac{0.45 * \exp(x)}{1 + \exp(x)}, \quad 0 \le pCCs \le 0.45 \tag{C.7d}$$

$$\text{where,} \quad x = -\left(2 + \frac{\ln(W)}{2}\right) + 45 \times pCCs \tag{C.7e}$$

$$CC_i[g\ DM.day^{-1}] = C_d \times pCCi; \quad CW_i = C_d \times (1 - pCCi) \tag{C.7f}$$

Digestion Component of BSC Model

Daily dry matter intake (from the intake model) is divided into cell contents and cell wall by the selectivity model if implemented, or else according to their proportions in the sward. Cell contents are assumed to be completely digestible. Givens, Everington and Adamson (1990*b*) measured the energy content of ether extract from British commercial forages to be 41 MJ.kg^{-1}, and this figure is used for the energy content of cell contents:

$$E_{CC}[MJ.day^{-1}] = \varepsilon_{CC}.CC_a \qquad (C.8)$$

Cell wall digestion depends upon the composition of the cell wall, particularly its lignin content (Van Soest 1994). Cell wall is mainly composed of cellulose, hemicellulose, and lignin, with additional proteins, pectin and waxes. The latter three are relatively easily extracted, whereas the cellulose and hemicellulose are insoluble and require specialised fermentation before they can be reduced to soluble compounds. Lignin cannot be broken down by digestion, and in fact inhibits digestion of the other cell wall components. The cell wall therefore cannot be completely digested. Assimilated cell wall is calculated as the product of the ingested DM of potentially digestible cell wall and the actual proportional extent of digestion. Potentially digestible cell wall intake is:

$$PDCW_d[g\ DM.day^{-1}] = 0.001CW_i \times PED \qquad (C.9)$$

$$PED[g.kg^{-1}] = \frac{920.48}{[1 + 6.309.\exp(-0.007173DOM)]} \qquad (C.10)$$

$$r = 0.85, R^2_{adj} = 0.72, n = 40, P \ll 0.001$$

Equation C.10 is derived from data in Prins et al. (1983) obtained from ungulates fed diets of varying digestibility (further detalis in Baird, 2001). *PED* is the in vitro digestibility of the forage when digested for a long time. *DOM* is the proportion of digestible organic matter calculated from in vivo trials.

DOM is calculated from:

$$DOM\ [g.kg^{-1}] = 1210 - 0.769NDF \qquad (C.11)$$

$R^2_{adj} = 0.529$, $n = 170$ (Givens, Everington and Adamson 1990*a*)

The actual proportional extent of digestion is $\left[1 - \left(1 - k_2\right)^{RT}\right]$, and assimilated cell wall is:

$$CW_a[g.day^{-1}] = PDCW_d\left[1 - \left(1 - k_2\right)^{RT}\right] \qquad (C.12)$$

RT is calculated as described in the intake model.

The assimilated cell wall, CW_a, is affected by body size solely through retention time. The calculation of *RT* should ideally incorporate a term relating *RT* to the proportion of indigestible cell wall in the diet. This adaptive variation in *RT* (and hence *in vivo* cell wall digestibility) would explain why *DOM* is independent of *W* (Baird 2001). From data in Illius and Gordon (1991 Table 2), k_2 can be related to the indigestible fraction (*INDF* [g.kg^{-1}]) by:

$$k_2 [\text{fraction } PDCW_d.hr^{-1}] = 0.0891 - 0.000106INDF \qquad \text{(C.13)}$$

$$r = 0.396, R^2_{adj} = 0.117, n = 23, P = 0.061$$

$$INDF[g.kg^{-1}] = (1000 - DOM)\frac{CW_S}{V} \qquad \text{(C.14)}$$

This relationship is however weak, and dependent on two data points. We elected to use a constant for k_2 ($k_2 = 0.02\ h^{-1}$).

Givens, Everington and Adamson (1990*b*) measured the energy content of organic matter minus crude protein and ether extract from British commercial forages to be 18.5 MJ.kg^{-1}, and this figure is used for the energy content of cell wall:

$$E_{CW}[MJ.day^{-1}] = \varepsilon_{CW}.CW_a \qquad \text{(C.15)}$$

Energy Balance Component of BSC Model

Some of the gross digested energy intake (GE_d) is lost from the ruminant by various pathways. Faeces contain undigested food, microbial matter and endogenous material that have a total energy content (FE_d) that is lost to metabolism (Van Soest 1994). Givens, Everington and Adamson (1990*a*) report a figure of 26% of GE_d for sheep. The largest component is undigested food, which has already been excluded from energy intake in the digestion model. We have no data on the other energetic components in the faeces, but assume they are small and can be neglected (FE_d is set to zero).

As well as energy lost in faeces, there is a small amount of energy lost in urine (UE_d) and methane (PE_d). Urinary energy is positively related to the protein content of the food:

$$UE_d = 0.0121 + 0.000259CP \qquad \text{(C.16)}$$

$$\text{mean } UE_d = 0.055GE_d$$

$R^2_{adj} = 0.541$, $P < 0.001$ (Givens, Everington and Adamson 1990a)

Energy lost as methane is a negative function of GE_d (Blaxter 1969). Givens, Everington and Adamson (1989) used an equation from Blaxter and Clapperton (1965) to predict methane losses (in sheep), with:

$$\text{mean } PE_d = 0.083GE_d \qquad \text{(C.17)}$$

With these losses, metabolizable energy intake is:

$$
\begin{aligned}
ME_d [MJ.day^{-1}] &= GE_d - \left(FE_d + UE_d + PE_d\right) \\
&= \left[1 - \left(0 + 0.055 + 0.083\right)\right]GE_d \\
&= 0.862GE_d
\end{aligned}
\qquad \text{(C.18)}
$$

Fermentation and digestion of the food are important energetic processes. The total energy cost of digesting the food is termed the heat increment. It is made up of the heat of fermentation, the heat of digestion, the work of rumination, and a term for radiative losses. The heat increment is particularly high in ruminants, and is strongly influenced by the fibre content of the diet (Van Soest 1994).

The work of rumination is proportional to fibre content (Van Soest 1994). Heat production of sheep increases by 40–80% during, and for up to two hours after, feeding and is a function of time spent feeding rather than intake (Webster 1978, in

Van Soest 1994). These observations suggest a structure to account for the heat increment:

$$E_r [MJ.day^{-1}] = r.CW_i \qquad\qquad (C.19)$$

$$E_h [MJ.day^{-1}] = 0.25 E_{ma\,int} \frac{(t_{max} + 2)}{24} \qquad\qquad (C.20)$$

$$HE_d [MJ.day^{-1}] = E_r + E_h \qquad\qquad (C.21)$$

Webster (1978, in Van Soest 1994) estimated that cattle (with body mass of 400 kg) expend about 21.15 MJ per day ruminating. From Eq. C.1, and using the body size regression (Eq. C.3a) to calculate RT, daily fill for a 400-kg animal is 2836 g.day^{-1}. Assuming a 50 % fibre content (NDF = 500 g.kg^{-1}) and non-selective feeding, CW_i = 1418 g.day^{-1} and Eq. C.19 gives:

$$r = 14.92 \; MJ.kg^{-1}$$

Subtracting the heat increment from the metabolizable energy intake gives the net energy available for maintenance and growth: $NE_d [MJ.day^{-1}] = ME_d - HE_d$.

Maintenance energy is the sum of basal heat production at maintenance levels of energy intake, plus an allowance for activity. The activity allowance ranges from one to two times the basal heat production (Peters and Wassenberg 1983). Maintenance requirements are given as 0.4W$^{.73}$ by Illius and Gordon (1991) and 0.2975W$^{.73}$ by Demment and Van Soest (1985). We have set maintenance requirement to

$$E_{main} [MJ.day^{-1}] = 0.35 W^{0.73}$$

The resulting profit or loss is called G_d, the energy available for growth, and is expressed as multiples of maintenance requirements:

$$G_d = \frac{NE_d - E_{main\ t}}{E_{main\ t}} \qquad\qquad (C.22)$$

To generate the ZNGI, the model is solved for $G_d = 0$. In practice, the model is too complex to solve analytically, but the numerical estimation graphing capabilities of Maple were used to plot the ZNGIs.