CHAPTER 7A

ASSEMBLING A DIET FROM DIFFERENT PLACES

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Abstract. Resources are unequally distributed over the landscapes and it is only seldom that food of a herbivore at a given spot exactly matches its requirements. However, because non-sessile animals can move, they can assemble a diet from different patches that, in its total, does meet the intake requirements. Because herbivores of different sizes have different requirements for energy and nutrients, a linear-programming model that takes into account the different satisficing requirements of herbivores of a range of body masses (or of reproductive status) yields new insights into the causality of the differential way that these animals use the same landscape. Depending on landscape configuration and extent, and especially grain size of the distribution of resources, our model predicts that lactating females are much more constrained than other animals of the same species vis-à-vis the array of patches in the landscape. We also predict that small ruminants should be much rarer than large ruminants, and conclude that small ruminants can only survive under most circumstances if they are specialised feeders or if they live in a fine-grained landscape. We further conclude that natural selection favours ruminants with a large body mass to those with a small body mass if nutrient acquirement is the dominant selection force.

Keywords. landscape grain; resource distribution; diet selection; body mass; linear programming, pleistocene extinctions

INTRODUCTION

Resources are rarely homogeneously distributed so animals have to move in their search for food. This movement takes place at several scale levels: from steps between foraging stations, to daily movement in home ranges, to even seasonal migratory movements. For the better understanding of foraging in a spatial context, it is useful to introduce the concept of ‘patch’. Patches are defined as localities (areas) that are more or less homogeneous with respect to a measured variable. It is, indeed, only rarely that in a given patch with food, a foraging animal can satisfy all its nutrient and energy requirements. For example, a patch of vegetation often does not satisfy the nutrient and energy requirements of herbivores. Even if one ignores

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the issues of patch depletion or patch size, and if one assumes that the instantaneous intake rate can be maintained for a prolonged period, it is clear that the vegetative parts of plants are barely sufficient to meet the requirements of an animal simply because nutrients are encapsulated in a matrix of carbon-based fibre. This matrix can be mechanically broken up, so as to gain access to the protein-rich cell content; the cell wall then is no source of energy but only an impediment to the process of nutrient acquirement. This is the case for animals with a simple digestive system, such as geese. The matrix can also be degraded with the aid of microbes. This process of fermentation yields energy but this energy has to be shared by the host with the microbes, which extract a price in the form not only of energy lost but also in the form of amino acids that are degraded (see Van Soest 1982). Ruminants are typically animals that rely on fermentation of their food.

The ultimate aim of the foraging herbivore is to cover its energy requirements (for maintenance, locomotion, possibly for pregnancy and lactation too, and perhaps as buffer for lean periods), and to maintain its store of minerals and amino acids in the form of its body tissues and skeleton. Ideally, any quantity of vegetation thus has a perfectly balanced mineral composition; that is, the ratio between nitrogen, phosphorus, calcium and potassium or even iron, zinc, magnesium and cobalt in the plant material (after digestion) perfectly reflects that in the animal's body and its depletion rates. Simultaneously, that ideal quantity of vegetation also yields a positive energy balance for the herbivore, it has the right balance between energy and proteins (Prins and Beekman 1989), and it even has all the essential amino acids in the proper relative amounts. In other words, the ideal patch of vegetation contains plant material that has all characteristics of animal tissue, and a herbivore would be better off as carnivore! For example, the calorific value and nitrogen content of the bodies of herbivores and carnivores are roughly equal. The calorific value of the herbivore's body, however, is approximately 1.5 times higher than that of the plants it eats, while the nitrogen concentration is 2.5 times higher (Table 7.1) (Crawley 1983 p. 184). Plant material is, however, much more available and easier to find, especially leaves and twigs that form the bulk of a plant's mass (see the so-called fibre curves of Demment and Van Soest 1985) than meat.

In reality, the vegetative parts of the vegetation hardly ever reflect the herbivore's ideal diet, and most of the primary production (about 90% on average) is not eaten by herbivores, whether invertebrate or vertebrate (Crawley 1983, p. 14). Plant production is selected for a maximum plant growth rate under the given conditions of availability of light, water and soil nutrients. Maximum growth is necessary so as to outcompete the neighbouring individuals of the same or other plant species. For example, plants invest in the carbon-based matrix referred to above, namely in cellulose and lignin, so as to grow tall to intercept the light before a neighbouring plant can make use of it. In nutrient-rich systems plants can and should invest more in stems than in leaves or roots, but in nutrient-poor systems the optimum is to invest in roots and leaves (Tilman 1988, p. 107 *et seq.*; Gleeson and Tilman 1994; Grace 1995). Because plants cannot move, they have to make best use of the available soil nutrients, even if these do not perfectly reflect what the plant

Table 7.1. *Relative proportion of elements ($g\ g^{-1}$) in the crust of the Earth, the average in plants (Van Soest 1982), the marginal levels minimally needed for animals (Robbins 1993) and the average in animals (Robbins 1993). n.r = not reported.*

%w/w	Crust: Granite	Crust: Basalt	Average crust	Average plants	Marginal level for animals in food	Average animals
Si	51.90	41.68	46.79	0.03 - 20	n.r.	n.r.
Al	15.22	15.17	15.20	n.r.	n.r.	n.r.
Fe	9.38	15.89	12.63	n.r.	0.005	0.034
Mg	3.91	6.78	5.35	0.20	0.2	0.11
Ca	6.80	11.68	9.24	0.03 - 3.0	0.4	2.91
Na	5.34	4.21	4.78	0.01 - high	0.05 - 0.18	0.46
K	4.87	2.30	3.58	1.5 - 3.0	0.6	0.90
Mn	0.19	0.45	0.32	0.01	0.001	0.002
Zn	trace	trace	trace	0.003 - 0.01	0.002	0.010
Cu	trace	trace	trace	0.001	0.001	0.002
S	0.09	0.00	0.05	0.12 - 0.3	0.2 - 0.6	n.r.
P	0.24	0.36	0.30	n.r.	0.2	1.88
C	0.17	0.00	0.08	n.r.	n.r.	n.r.
N	0.00	0.00	0.00	4.00	n.r.	10.00
Rest	1.89	1.49	1.69	n.r.	n.r.	n.r.

needs. In other words, at any given locality, the production of plant material in a patch of vegetation is nearly always limited by some nutrient. In most terrestrial systems, nitrogen is the limiting factor for plant growth but quite often plant growth is limited by both N and P (DeAngelis 1992, p. 41, Table 3.2; Ludwig 2001). The basic cause is that neither micro-nutrients nor macro-nutrients are distributed homogeneously in space, nor do they occur in the ‘right’ balance.

If, thus, a herbivore aims at ingesting a perfectly balanced quantity of plant material from a given patch, the chances are high that it cannot do so: at this locality the plant material lacks in, for instance, phosphorus, and that locality lacks in, for example, calcium. The ratio between Ca and P ($g\ g^{-1}$) in a mammal is 2:1. In forage this can range from 6:1 (e.g., in red clover) to 1:8 (e.g., in peanuts) (Robbins 1993, p. 40, Table 5.2). The solution for the herbivore is threefold. The first is differential rates of absorption from plant tissue through the digestive tract into the animal’s body. The second is different rates of secretion. The third is by blending the intake from these ‘imperfect’ patches into a diet that satisfies the needs of the herbivore. The herbivore can blend its intake by moving from patch to patch whereby, ideally, ingested plant material low in, for instance, phosphorus from one patch is compensated by food high in phosphorus from another patch.

Plants and especially the vegetative parts of plants are rarely of sufficiently high quality to meet all requirements of animals

A herbivore thus has to assemble a diet from different plant species, from different patches, and sometimes from different seasonal ranges (e.g., dry and wet season ranges), and only the assembled diet can meet all of its requirements (Prins and Beekman 1989; Simpson et al. 2004). The aim of this chapter is to explore this problem of how the herbivore has to move between different patches that are imperfect from the herbivore's point of view, but that in combination can satisfy the herbivore's requirements.

Box 7.1. *Water consumption of large herbivores*

Ungulates, like all other organisms, need water for their survival. They have two sources of water, namely surface water and plant leaf water. The daily water needs of ungulates are about 4% of their body mass (du Toit 1996). These needs are not a function of body mass (see Table in this box; consumption data after Delany and Happold 1979, Table 11.3).

Table 11.3. *Water needs of ungulates*

	Body mass	Ambient T 22^0C	Ambient T $22\text{-}40^0$C	Average
	kg	litre/100 kg	litre/100 kg	
Dikdik	5	5.59	7.72	
Thompson's gazelle	25	2.20	2.74	
Impala	52	2.49	2.93	
Grant's gazelle	55	2.08	3.86	
Oryx	169	1.88	3.00	
Waterbuck	211	5.98	no data	
Blue wildebeest	276	2.99	4.81	
Hartebeest	465	2.98	4.04	
Eland antelope	476	3.74	5.49	
African buffalo	636	3.43	4.58	
Average		3.34	4.35	3.84

Measuring stable isotopes of oxygen in body tissues or bone enables establishing the proportions of plant leaf water and free-standing water in the total water intake of an animal (e.g., Johnson et al. 1998). Some ungulates can cover all their requirements from water in plants, Oryx for instance, but others need free-standing water if the dry-matter content falls below a certain threshold. Impala need surface water if the dry-matter concentration of their food plants is higher than 67% (du Toit 1996), and buffalo always need surface water (Prins 1996). Oryx are thus not restricted in their search for food by surface water, impala are restricted during the dry season, while buffalo are always found within a couple of hours walking distance from a river or a waterhole.

In contrast to many other investigations into the foraging ecology of herbivores, we not only look at the two usual properties of a resource, namely vegetation quantity and vegetation quality, but we take a third important property into account, namely the grain size of the landscape. Grain size is a relatively new concept that describes the spatial array of patches of vegetation in a landscape (e.g., Murwira 2003; Skidmore and Ferwerda, Chapter 4).

We first review existing knowledge on requirements of herbivores and how these requirements are allometrically scaled. We then develop a model to investigate diet and patch selection of herbivores in environments that differ in the grain size of the food, that is, the distances between patches of grassy vegetation differ from close together to large inter-patch distances. We look for conditions where herbivore species can meet their energy and nutrient requirements and therefore can exist (we assume that other resources such as water are not limited, and that predator or parasite avoidance does not play a role). These conditions may differ for herbivores with different body sizes. As the possibility to meet the energy and nutrient requirements determines the presence and absence of species of different body sizes, the heterogeneity in food may determine the structure of herbivore communities. We therefore explore the effect of inter-patch distance and diet assembly on community structure. Finally, we discuss several hypotheses derived from our modelling study that may explain dramatic changes in herbivore assemblages such as the Pleistocene extinctions.

Small herbivores need, proportionally to body mass, more energy and nutrients than large herbivores, but not more water

In our analysis of interpatch movements we ignore the water requirements of the animals. We do this on purpose because, first, water requirements scale to body mass with a factor 1 (Box 7.1). In other words, on average ungulates need water as a fixed proportion of their body mass (for further reading, see Wallis et al. 1997; Williams et al. 1997; Evans et al. 2003). This makes water less interesting a parameter to include in our model, which investigates the effects of body mass. The second reason is that interspecific variation is very large indeed (Box 7.1). This second reason defeats the purpose of our investigation because it does not facilitate finding general rules to predict movements of animals. We thus acknowledge the fact that searching for water may be more important, on the short term, than searching for food, but in the present analysis we ignore this.

REQUIREMENTS OF HERBIVORES AND SIZE CONSTRAINTS

Body tissues of herbivores are the same as those of other animals, so the ultimate needs of herbivores are similar to those of carnivores when minerals, amino acids and vitamins are considered. Herbivores that make extensive use of fermenting microbes, however, have much less stringent needs vis-à-vis vitamins or specific amino acids (Robbins 1993, p. 17; Van Soest 1982, p. 246). In this chapter, we thus concentrate on ruminants, because the dietary needs of large ruminants can adequately be described in terms of digestible fibre for energy and of macro-nutrients. Requirements are very well known for domestic ruminants and to a lesser extent for some wild herbivores.

Energy requirements

Both theoretical considerations and measurements point out that smaller animals need, proportionally to body mass, more energy. There has been a controversy about the scaling factor with which energy expenditure scales with body mass, but it is now generally assumed that energy scales with a factor 0.75 (Moen 1973, p. 116; Hudson 1985; Robbins 1993, p. 123 *et seq.*; Nagy et al. 1999; West et al. 2002, 2003).

Daily basal metabolic rate E_{BMR} [kJ d^{-1}] is taken as [1]:

$$E_{BMR} = 293 \times W^{0.75} \tag{1}$$

where W is body mass [kg]. Body mass is the single most important factor explaining variation between species within a taxonomic class (it explains between 93 and 95%) (Nagy et al. 1999). Body mass is also important because it is related to speed of locomotion, foraging radius and home range size. The energy expenditure for each kilometre of walking per unit mass, E_w, for ruminants [kJ kg^{-1} km^{-1}] is related to body mass (Robbins (1993, p. 133; see also Moen 1973, p. 349) as

$$E_w = 10.75 \times W^{-0.316} \tag{2}$$

For climbing, the energy expenditure for each kilometre per unit mass, E_c [kJ kg^{-1} km^{-1}], appears to be independent of body size. Moen (1973, p. 349) reports 27.36 kJ kg^{-1} km^{-1}, whereas Robbins (1993, p. 137) gives 25.10 kJ kg^{-1} km^{-1}. We take the mean value of these two as

$$E_c = 26.23 \tag{3}$$

The energy expenditure per day including moving over a certain distance, E_{BW} [kJ d^{-1}], is then

$$E_{BW} = E_{BMR} + (E_w + E_c \times H) \times D \times W \tag{4}$$

where H is the vertical height ascended expressed as percentage of km on level, D the distance travelled [km d^{-1}].

Energy expenditure for standing, E_s, may be taken as 20% above E_{BMR} (Fancy and White 1985; Robbins 1993, p. 129), while running, E_r, may be 8 times more expensive than E_{BMR}, foraging E_f can be taken as 54% above E_{BMR} and, finally, ruminating E_h as 24% above E_{BMR} [all kJ d^{-1}], thus

$$E_s = 0.2 \times E_{BMR} \tag{5}$$

$$E_h = 0.24 \times E_{BMR} \tag{6}$$

$$E_f = 0.54 \times E_{BMR} \tag{7}$$

$$E_r = 8.0 \times E_{BMR} \tag{8}$$

Energy expenditure is strongly influenced by pregnancy and by lactation. We do not follow Moen's (1973, p. 353) approach but take a simplified one. Hudson (1985) gives the gestation length, L_d [d], for artiodactyls and for ungulates in general as

$$L_d = 120.31 \times W^{0.16} \text{ (for artiodactyls)} \tag{9a}$$

$$L_d = 109.97 \times W^{0.19} \text{ (for ungulates)} \tag{9b}$$

Oftedal (1985) calculated the costs for peak lactation for ungulates with a single young, E_{PL} [kJ d^{-1}], and then for the whole period of lactation, E_L [MJ], as

$$E_{PL} = 669 \times W^{0.70} \tag{10a}$$

$$E_L = 38.6 \times W^{0.81} \tag{10b}$$

Also for ungulates with a single young, he determined the total costs for pregnancy, E_P, and lactation, E_L, so the costs for reproduction, E_R [all MJ]. He found these relationships to be different for animals lighter than about 450 kg, and animals heavier than that as

$$E_R = E_P + E_L = 7.64 \times W^{0.90} + 38.6 \times W^{0.81} \text{ (for 4 – 450 kg)} \tag{11a}$$

$$E_R = E_P + E_L = 23.5 \times W^{0.68} + 38.6 \times W^{0.81} \text{ (for > 450 kg)} \tag{11b}$$

Since we know the length of gestation (eqn 9), we can calculate the average energy expenditure per day for this period. We can do the same for the average cost of lactation, because the age at weaning, L_w [d] (given by Peters 1983, p. 282), is

$$L_w = 34 \times W^{0.15} \tag{12}$$

Much work has been done on measuring energy expenditure (field metabolic rate, FMR) of animals under field conditions. A good overview can be found in Nagy et al. (1999). Their review shows that desert mammals have lower energy expenditures than mammals under mesic conditions (see also Tieleman and Williams 2000).

Nutrient requirements

Just as energy expenditure scales with body mass, so do nutrient requirements. It should be realised that, although ruminants have a large store of macro-nutrients in body tissues and the skeleton (Table 7.2), loss rates do not adequately reflect the problem animals face when they forage for macro-nutrients. With a loss rate for Ca of 0.25 g kg^{-1} d^{-1}, it would take 3.2 years before the calcium store would be finished. Of course, the animal would have severe difficulties before that time, and that is why we concentrate on the amounts of nutrients the animal needs to maintain balance.

Table 7.2. *Proportion of minerals in whole animals (mg g^{-1} d.w.) (from Robbins 1993)*

Element	White-tailed deer	Short-tail shrew	Cotton mouse	Golden mouse	Old-field mouse	Fox squirrel	Blue tit	Coal tit	Gold crest	Meadow pipit	Rook	Average
Ca	3.09	3.44	4.05	3.74	1.6	2.56	3.28	3.31	2.84	2.04	2.04	2.91
P	2.26	1.72	1.67	1.92	1.86	1.80	2.04	2.08	1.88	1.65	1.75	1.88
K	0.95	n.r.	n.r.	n.r.	1.2	1.07	0.58	0.63	0.58	1.27	0.94	0.90
Na	0.39	0.42	0.24	0.36	0.43	0.84	0.37	0.39	0.40	0.83	0.45	0.46
Mg	0.09	0.14	0.12	0.14	0.06	0.13	0.10	0.11	0.11	0.13	0.09	0.11
Fe	0.016	0.050	0.020	0.024	0.038	n.r.	n.r.	n.r	n.r.	0.040	0.048	0.034
Zi	0.007	0.012	0.010	0.011	0.013	n.r.	n.r.	n.r	n.r.	0.011	0.010	0.010
Mn	0.003	n.r.	n.r.	n.r.	0.001	n.r.	n.r.	n.r	n.r.	0.001	0.003	0.002
Cu	0.003	n.r.	n.r.	n.r.	n.r.	n.r.	n.r.	n.r	n.r.	n.r	0.001	0.002

Deduction of a ruminant's nitrogen needs from its known energy expenditure

It can be assumed that there is a constant tissue turnover, and for nitrogen this can be expressed as the average nitrogen intake to achieve nitrogen balance, N_b [g d^{-1}] (see Moen 1973, p. 334; Robbins 1993, p. 180 *et seq.)*: $N_b = 0.650 \times W^{0.75}$, but this equation does not take into account that when an animal expends much energy, it also loses more nitrogen due to enzymatic turnover. However, because the ratio of endogenous urinary N in mg to kcal in the equation for basal metabolism is 2 (Moen 1973, p. 334), which thus equals $N_b = 0.140 \times W^{0.75}$ [g d^{-1}], we can deduct a relationship between energy expenditure and nitrogen needs. The energy expenditure for basal metabolism (eqn 1) is 293 $W^{-0.75}$ kJ d^{-1}, i.e., 70 $W^{-0.75}$ kcal d^{-1}, meaning that the constant for the N intake for an animal functioning at basal metabolic rate only is 0.140 = (70 × 2)/1000 g d^{-1}. As a matter of fact, for ruminants, the constant is 0.093 and for non-ruminants it is 0.160 (Robbins 1993, p. 180). Because the amount of energy an average animal spends is 2 × E_{BMR}, we have taken the nitrogen intake to achieve nitrogen balance,

N_b, to be proportional to this. We then assume that if the animal spends 4 × E_{BMR}, it needs twice the amount of nitrogen to stay in balance, hence N_b is per multiple of E_{BMR}

$$N_b = \gamma \times 0.325 \times W^{0.75} \tag{13a}$$

where γ is the coefficient to scale the required amount of nitrogen to achieve nitrogen balance, N_b, with the energy required for maintenance, E_{BMR}. The coefficient γ [-] is defined as

$$\gamma = \frac{E_{tot}}{2 \times E_{BMR}} \tag{13b}$$

where E_{tot} is the total daily energy expenditure, including energy needed for maintenance, walking, foraging, etc. (eqn 4). Equation (13a) includes nitrogen lost through abrasion of tissues in the gastrointestinal tract and appears to be a constant of 5 g N per kg dry-matter intake. For growth, the nitrogen retention has been estimated to vary between 2.4% and 3.5% of the body mass gain (see for further details on pregnancy and lactation Moen 1973, p. 343 *et seq.*; Robbins 1993, p. 177 *et seq.*).

Eqn 13a tallies well with the estimate for the digestible protein requirement at maintenance, DP [g d^{-1}], for ruminants (Lloyds et al. 1978, p. 425 *et seq.*) as $DP = 3.150 \times W^{0.75}$, taking into account the conversion factor of 6.25 with which N has to be multiplied to calculate protein. On the basis of this we calculate the amount of protein to achieve protein balance DP_b per multiple of E_{BMR} as

$$DP_b = \gamma \times 2.03 \times W^{0.75}; \tag{14}$$

for γ see equation (13b).

For calcium, not much is known about the daily quantities needed. Robbins (1993, p. 37) reports a loss of 22 to 28 mg Ca kg^{-1} d^{-1}, and maintenance of a Ca balance at an intake of 73 mg Ca kg^{-1} d^{-1} (with a net retention of 30-39%). The ARC (1980, p. 186), however, is sceptical about the use of net retention. A regression on advisory dietary requirements ARC (1980, Tables 5.3 and 5.6, columns with no growth) for cattle and sheep yields the amount of calcium needed to achieve calcium balance, Ca_b [g d^{-1}], as

$$Ca_b = 0.024 \times W^{1.00} \tag{15a}$$

$$Ca_b = 0.048 \times W^{1.00} \text{ (while pregnant)} \tag{15b}$$

$$Ca_b = 0.096 \times W^{1.00} \text{ (when lactating)} \tag{15c}$$

Dietary calcium to phosphorus ratios between 1:1 and 2:1 are best for proper absorption (Robbins 1993, p. 38; ARC 1980, p. 201). Daily requirements for phosphorus to achieve phosphorous balance, P_b [g d^{-1}], can be deduced from ARC (1980, Tables 5.14 and 5.17, columns with no growth). A regression on the sheep and cattle data yields

$$P_b = 0.020 \times W^{1.00} \quad (16a)$$

$$P_b = 0.040 \times W^{1.00} \text{ (while pregnant)} \quad (16b)$$

$$P_b = 0.080 \times W^{1.00} \text{ (when lactating)} \quad (16c)$$

The minimum intake necessary to balance sodium, Na_b, is 9 mg Na kg^{-1} d^{-1} (Robbins 1993, p. 44). This is approximately the same prediction as based on ARC (1980, Table 5.36)

$$Na_b = 0.009 \times W^{1.00} \quad (17a)$$

$$Na_b = 0.018 \times W^{1.00} \text{ (while pregnant)} \quad (17b)$$

$$Na_b = 0.036 \times W^{1.00} \text{ (when lactating)} \quad (17c)$$

For pregnant animals eqns (15-17) the requirements were doubled, and for lactating females they were quadrupled (see ARC 1980).

Foraging time and intake requirements

Finally, because nutrient turn over and energy expenditure is proportionally higher in smaller ruminants than in larger ones, the throughput rate of the food through the gut is lower while the stomach is larger in large ruminants as compared to small ones. This implies that large ruminants can acquire a blended diet more easily than smaller ones. Different relations are important to model food intake and food acquisition for differently sized herbivores. Foraging time, T_f, as proportion of a day and time for foraging and ruminating, T_{f+h} [both have no units] are body-mass-dependent (Hudson 1985)

$$T_f = 0.24 \times W^{0.08} \text{ (for ungulates)} \quad (18a)$$

$$T_{f+h} = 0.52 \times W^{0.09} \text{ (for ruminants)} \quad (18b)$$

Regarding daily food intake, I [kg d^{-1}], there has been some controversy in the literature, and sometimes it is taken to scale with body mass, e.g., for African herbivores intake has been reported to be $0.058 \times W^{0.80}$ (Hudson 1985) but it can better be taken as a constant proportion of body mass, so scaling with $W^{1.00}$ (Arnold 1985; Van Soest 1982; Prins 1996, p. 264) as

$$I = 0.025 \times W^{1.00} \text{ (for ruminants)} \qquad (19)$$

Because in ruminants the rumenoreticular volume [litre] relates to metabolic body mass, and not to body mass, and has been found to be equal to $-3.49 + 0.77 \times W^{0.75}$ (Bunnell and Gillingham 1985; Demment and Van Soest 1985), fermentation in the stomach of small ruminants has to be higher than in large ones. Indeed, the rumenoreticular volume of, for example, a 45-kg-small impala (*Aepyceros melampus*) in relation to its metabolic body mass is 0.57 litres per kg of metabolic mass (9.9 litre with a metabolic mass of 17.37 kg), while in a 620 kg large buffalo (*Syncerus caffer*) this is 0.74 litre per kg of metabolic mass (92 litre with a metabolic mass of 124.2 kg). Therefore, small ruminants thus need a higher-quality food to enable a higher rate of fermentation.

It is fundamentally easy to imagine why the spatial array of patches in a landscape is of importance for the survival of herbivores

For ruminants, the daily intake rates are often constrained by the rate of digestion and passage through the rumen (Voeten and Prins 1999). The digestibility rate of food is correlated with the cell wall content, measured in the vegetation type i as the percentage neutral detergent fibre NDF_i [g kg^{-1}]. Reid et al. (1988) calculated from a feeding trial of cattle on a C_4-grass diet that the maximum daily $NDFM$ intake [kg d^{-1}] can be calculated as

$$NDFM = 66.7 \times 10^{-3} \times W^{0.75} \qquad (20)$$

All these considerations enable us to predict that small ruminants are more constrained by patch differences and differences in grain size of the vegetation than larger ones. This can easily be imagined when one patch has, for instance, a deficit in phosphorus and an excess of nitrogen, while another patch has the opposite: assume that both patches would exactly compensate each other. If the distance between these two patches is 10 km, then it would take a buffalo (620 kg) approximately two hours to reach the second patch after visiting the first. Because the average throughput rate of buffalo food is approximately 36 hours, the forage from the two patches can be well blended. However, for a dikdik (*Madoqua spec.*) (5 kg) these two patches represent two 'different worlds' because the average home range of a dikdik is measured in hectares: the two patches are simply too widely separated for the dikdik to achieve a

The scaling of stomach size and the necessary associated rate of fermentation of food in the rumen explains why small ruminants need better-quality food blended diet, and it ends with food that does not meet all its requirements. Interpatch distance is thus of considerable interest to understand the possibilities the landscape offers for a herbivore to survive. In another context, Crawley (1983, p. 150) draws attention to the interaction between an animal's dispersive abilities and the plant pattern: if plants occur in a density with inter-plant distances shorter than the ranging distance of caterpillars, there will be a high herbivore survival. However, if this distance is too long, then plants will generally survive while the herbivore goes extinct.

MODELLING DIET AND PATCH SELECTION AS FUNCTION OF AMOUNT, QUALITY AND SPATIAL DISTRIBUTION OF FOOD

To simply model diet and patch selection in landscapes with different grain size, we consider a model with two patches that can contain food that differs in amount and quality. Also, the distance between the two patches is variable. To do this, we use an approach analogous to the linear-programming model introduced by Belovsky (1978). Central in this approach is that the selection of its diet (Belovsky 1978), the selection of patches (Ludwig et al. 2001) and the migratory movements (Voeten and Prins 1999) are all based on the constraints for herbivores to meet their requirements. Often such linear-programming models are used to determine the best diet possible where the animal meets all its requirements. Instead of looking at the maximum, we will use this approach to study whether herbivores can meet all their nutritional and energy requirements by selecting food from one of the two patches or a combination of both. Extension of the two-patch model is possible, but will increase the computational efforts. Our model is largely based on Voeten (1999) and Ludwig (2001).

We formulated minimum requirements for nutrient, protein and energy intake and a maximum value for fibre intake based on the requirements of herbivores and size constraints as formulated before. The energy intake necessary for maintenance, E_{BMR} (eqn 1), walking, E_w (eqn 2), foraging, E_f (eqn 7), and ruminating, E_h (eqn 6) [all kJ d^{-1}] is formulated as the constraint

$$E_{BW} + \left(E_f + E_h\right) \times T_{f+h} \leq \sum_{i=1}^{k} G_E \times \%DOM_i \times c_{GD} \times X_i \qquad (21)$$

where E_{BW} is given by eqn (4) (assuming a flat area where $H = 0$), T_{f+h} is the fraction of the time needed for foraging and ruminating (eqn 18b), G_E is the energy content of tropical grasses per mass unit dry weight [kJ kg^{-1}], $\%DOM$ the digestibility of organic matter of the vegetation type i, c_{GD} is the fraction of the digestible energy of grasses that is converted into metabolic energy [-], k is the number of vegetation types (in our model $k = 2$). The left-hand side of eqn (21) is the total daily energy expenditure of the animal, E_{tot}. The parameter X_i is the decision variable representing the intake of the animal in patch i. The sum of the intake per patch should be less than or equal to the daily intake (eqn 19):

$$\sum_{i=1}^{k} X_i \leq I \tag{22}$$

In Box 7.2, the model for wildebeest (*Connochaetes taurinus*) is given as an example.

The third constraint is the digestible-protein requirement at maintenance DP_b (eqn 14). This can be formulated as

$$DP_b \leq \sum_{i=1}^{k} aDP_i \times X_i \tag{23}$$

The available digestible protein aDP [mg g^{-1}] for tropical grasses of type i can be calculated from crude protein CP_i [mg g^{-1}] (Prins 1987a) as

$$aDP_i = 0.91 \times CP_i - 32.2 \tag{24}$$

The constraints for nutrient requirements of herbivores concern the amount required to achieve a balance for nitrogen N_b, phosphorus P_b, sodium Na_b and calcium Ca_b, see eqns 15-17. The constraint equations for maintenance level are (Murray 1995)

$$N_b \leq \sum_{i=1}^{k} aN_i \times X_i \tag{25a}$$

$$P_b \leq \sum_{i=1}^{k} aP_i \times X_i \tag{25b}$$

$$Na_b \leq \sum_{i=1}^{k} aNa_i \times X_i \tag{25c}$$

$$Ca_b \leq \sum_{i=1}^{k} aCa_i \times X_i \tag{25d}$$

where aN_i, aP_i, aNa_i and aCa_i [all mg kg^{-1}] are the concentrations of these nutrients measured in vegetation type i. Since often the Na concentration in the vegetation is not sufficient to meet the requirements of the animal (for example, see Voeten and Prins 1999; Ludwig 2001), we assume that the animals find alternative sources for Na and ignore the Na requirement in our model.

Based on the rate of digestion and passage through the rumen (eqn 20), the maximum daily intake rate for herbivores is

$$NDFM \geq \sum_{i=1}^{k} NDF_i \times X_i \tag{26}$$

For the values of the vegetation parameters in the two patches, we used data obtained by Ludwig et al. (2001). They measured the vegetation parameters for several grass species under tree canopy, just outside tree canopy and in open grassland. The parameter values are enumerated in Table 7.3.

Finally, to grasp the issue of getting the right time horizon into our model, we assume that a ruminant needs to keep the food mass in its rumen well within the constraints set by the requirements of the microbes. We thus assume that the herbivore allows a deviation of the allowable solution of the linear modelling of maximally 10%. We thus reasoned that its rumen contents can be emptied for maximally 10%, to be filled up again by 10% with food from a different patch, to maintain a well-blended food mass in its rumen from which it derives its needed energy and macro-nutrients. Because the retention time of particles can well be described with a Michaelis-Menten function, and because the retention time, T_R [hours], of particles is known (that is, the time after which 95% of the particles have left the rumen) through Demment and Van Soest (1985) as

$$T_{R,0.95} = 7.67 \times Dig \times W^{0.346} \text{ (95\% disappeared)} \tag{27a}$$

thus

$$T_{R,0.1} = 0.045 \times Dig \times W^{0.346} \text{ (10\% disappeared)} \tag{27b}$$

The latter provides the maximum time an animal can walk between patches of food. In this equation, *Dig* stands for digestibility of the food [ranging between 0 and 1, no units]. In the present analysis we have taken a disappearance of 10% only, but we can adopt other thresholds too, if necessary. We now calculate the maximum allowable inter-patch distance taking the time it maximally walks to be equal to $T_{R,0.1}$.

Table 7.3. *Digestibility of organic matter (%DOM), neutral detergent fibre (NDF) and nutrient concentrations of grass species growing under and just outside canopies of large Acacia tortilis trees and in open grassland patches (Ludwig et al. 2001). Variance of data was analysed with a GLM with grass species and location (open grassland and under and outside canopies) as fixed factors. Species with the same letter are not significantly different (Tukey HSD, P > 0.05) (* P < 0.05, *** P > 0.001)*

DATA Location	Species	*%DOM* (%)	*NDF* (%)	*CP* mg g^{-1}	*P* Mg g^{-1}	*K* mg g^{-1}	*Ca* mg g^{-1}	*Mg* mg g^{-1}	*Na* mg g^{-1}
Under tree canopy	*Panicum maximum*	65.65^{ab}	70.60^{ab}	141.1^{b}	1.77^{ab}	40.62^{a}	4.12^{c}	3.25^{b}	0.10^{a}
	Cynodon spp.	70.33^{a}	61.45^{a}	165.1^{a}	1.80^{ab}	38.41^{a}	6.91^{a}	2.44^{bcd}	0.12^{a}
	Cenchrus ciliaris	59.78^{ab}	70.12^{ab}	136.8^{b}	1.74^{ab}	44.83^{a}	4.34^{c}	1.95^{def}	0.21^{a}
Outside tree canopy	*Cynodon spp.*	65.07^{ab}	66.49^{ab}	126.8^{bc}	2.38^{bc}	36.07^{a}	6.70^{ab}	2.58^{bcd}	0.17^{a}
	Cenchrus ciliaris	57.96^{ab}	71.45^{ab}	105.5^{cd}	2.43^{bc}	41.89^{a}	3.30	1.87^{def}	0.14^{a}
	Digitaria macroblephera	62.64^{ab}	72.91^{ab}	74.5^{e}	2.85^{cd}	38.35^{a}	3.75	2.26^{cde}	0.20^{a}
	Chloris virgata	66.80^{ab}	70.40^{ab}	104.6^{cd}	2.59^{cd}	37.56^{a}	4.91	3.03^{bc}	0.87^{b}
	Urochloa mosambicencis	69.13^{a}	64.77^{ab}	104.0^{cd}	3.59^{e}	44.28^{a}	5.28^{ab}	4.00^{a}	0.13^{a}
	Heteropogon contortis	56.97^{ab}	70.15^{ab}	81.5^{e}	1.46^{a}	17.17^{b}	3.30^{c}	1.64^{def}	0.14^{a}
Open grassland	*Heteropogon contortis*	51.68^{b}	74.00^{b}	67.6^{e}	1.65^{ab}	15.08^{b}	3.31^{c}	1.22^{f}	0.13^{a}
	Sehima nervosum	54.66^{ab}	74.65^{b}	60.8^{e}	1.46^{a}	12.02^{b}	4.67^{c}	1.47^{ef}	0.14^{a}
STATISTICS									
Species	F	2.25^{*}	2.42^{*}	14.09^{***}	5.45^{**}	8.79^{***}	7.75^{***}	13.51^{***}	18.43^{***}
Location	F	1.19	1.53	6.91^{***}	9.07^{***}	0.57	0.72	0.91	0.02
Species × Location	F	0.26	0.60	0.29	0.09	0.01	0.66	0.27	1.15

Box 7.2. *Illustration of the diet and patch selection model for the wildebeest (Connochaetes taurinus) (Voeten 1999; Ludwig 2001; see also Murray and Brown 1993, Murray 1995)*

The energy intake necessary for maintenance, E_{BMR}, and walking, E_w, and foraging and ruminating, E_f and E_h, is formulated as the constraint (eqn 21). We use the equations 1, 2, 4, 6, 7, and 18b to obtain the following constraint ($H = 0$):

$$E_{BMR} + E_w \times W \times D + \left(E_f + E_h\right) \times T_{f+h} \le \sum_{i=1}^{k} G_E \times \%DOM_i \times c_{GD} \times X_i$$

that becomes

$$293 \times W^{0.75} + 10.75 \times W^{-0.316} \times W \times D + \left(0.54 + 0.24\right) \times 293 \times W^{0.75} \times 0.52 \times W^{0.09} \le \sum_{i=1}^{k} 19 \times 10^3 \times \%DOM_i \times 0.82 \times X_i$$

when G_E is 19×10^3 kJ kg^{-1} (Crampton and Harris 1969) and c_{GD} is 0.82 (Van Soest 1994). This equation can be re-arranged as

$$293 \times W^{0.75} + 10.75 \times W^{0.684} \times D + 118.8 \times W^{0.84} \le \sum_{i=1}^{k} 15.6 \times 10^3 \times \%DOM_i \times X_i$$

For wildebeest with the average weight of 143 kg, this means

$$19.8 \times 10^3 + 320.3 \times D \le \sum_{i=1}^{k} 15.6 \times 10^3 \times \%DOM_i \times X_i \ .$$

The second constraint is that the maximum distance D_{max} (eqns 23, 27b, 29) is limited by the time period needed for foraging as

$$D_{\max} \le V \times \left(1 - T_m\right) \times 24$$

that becomes

$$D_{\max} \le 1.188 \times W^{0.21} \times \min\left(1 - 0.52 \times W^{0.09}, 0.045 \times Dig \times W^{0.346}\right) \times 24 \ .$$

For wildebeest, the maximum distance [km] that can be covered with walking during 1 day is

$$D_{\max} \le 16 \ \text{(for } Dig = 0.8\text{)}.$$

Box 7.2 (cont.)

Box 7.2 (cont.)

The third constraint for the digestible-protein *DP* requirement for maintenance is (eqns 14, 23 and 24)

$$\frac{E_{tot}}{2\times E_{BMR}}\times 2.03\times W^{0.75}\leq\sum_{i=1}^{k}\left(0.91\times CP_i-32.2\right)\times X_i$$

where E_{tot} is the left-hand side of the first equation. For wildebeest, this constraint becomes

$$60.4+1.11\times D\leq\sum_{i=1}^{k}\left(0.91\times CP_i-32.2\right)\times X_i \quad .$$

The constraint equations for the requirements of nitrogen, phosphorus, sodium and calcium (eqns 15, 16, 17 and 25) are:

$$\gamma\times 0.325\times W^{0.75}\leq\sum_{i=1}^{k}aN_i\times X_i \quad \text{and} \quad 0.02\times W\leq\sum_{i=1}^{k}aP_i\times X_i$$

$$0.009\times W\leq\sum_{i=1}^{k}aNa_i\times X_i \quad \text{and} \quad 0.024\times W\leq\sum_{i=1}^{k}aCa_i\times X_i$$

For wildebeest, these equations become:

$$9.7+0.18\times D\leq\sum_{i=1}^{k}aN_i\times X_i \quad \text{and} \quad 2.86\leq\sum_{i=1}^{k}aP_i\times X_i$$

$$1.29\leq\sum_{i=1}^{k}aNa_i\times X_i \quad \text{and} \quad 3.43\leq\sum_{i=1}^{k}aCa_i\times X_i$$

The digestion constraint is (eqns 20, 26):

$$66.7\times 10^{-3}\times W^{0.75}\geq\sum_{i=1}^{k}NDF_i\times 0.025\times W \quad .$$

Box 7.2 (cont.)

Box 7.2 (cont.)

For wildebeest, this equation becomes:

$$2.76 \geq \sum_{i=1}^{k} NDF_i \times 3.6 .$$

Combining these constraints leads to the feasible region as depicted in Figure 7A.

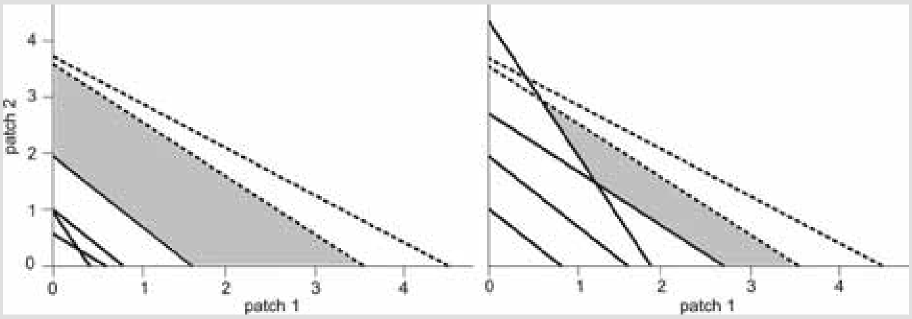

Figure 7A. *Graphical representation of the energy and nutrient constraints, predicting whether wildebeest can meet their daily requirements for energy, nutrients and protein by selecting forage from under tree canopies or in open grassland patches. Each line indicates the minimum food intake required to meet nutrient, energy or protein requirements (solid lines). The maximum daily intake and the intake to meet the maximum digestibility due to the fibre content are given as maximum constraints (dashed lines). The shaded part (the 'feasible region'; see Box 7.3) indicates all possible combinations of food sources that meet all nutrient, energy and protein requirements (left-hand figure with distance D = 0 km and figure a the right with distance D = 180 km)*

The maximum distance travelled per day, D_{max}, is the product of the speed of locomotion, V [km hr^{-1}], and the maximum number of hours an animal can move when not foraging and ruminating is then

$$D_{\max} = V \times T_m \times 24 \qquad (28)$$

where T_m is the fraction of the day that the animal is moving. We set $T_m = 1 - T_{f+h}$. If T_m is larger than $T_{R,0.1}$, the maximum fraction of the day that the animal is moving becomes $T_{R,0.1}$. Thus, $T_m = \min(1\text{-}T_{f+h}, T_{R,0.1})$. The speed V is important for understanding how animals can amalgamate their intake from different patches of vegetation. Hudson (1985) provides the formula for speed for mammals in general as $V = 5.5 \times W^{0.24}$, but this yields too high speeds for understanding the problem of normally walking animals. Peters (1983, p. 89) gives the optimal rate of moving, which formula we adopt, as:

$$V = 1.188 \times W^{0.21} \tag{29}$$

Model analysis and results

We analysed the diet and patch selection model in several ways. First, we calculated the extent of the feasible region. The feasible region is the set of combinations of food from different patches limited by the constraints as set by the animal's requirements (see Box 7.3). The extent of the feasible region is an indication of the tolerance of the animal to collect its food under the conditions of the vegetation amount and quality (such as nutrient concentration and fibre percentage) and the requirements of the animal. A larger extent implies that the combination of patches provides a larger tolerance. Second, we determined the contribution of each patch in the absence of the other patch. Therefore, we calculated for example the possible intake of vegetation in patch 1 [in kg] that can meet the requirements of the animal in the absence of patch 2, that is, the distance between the lowest maximum requirement and highest minimum requirement on the axis of patch 1. This indicates the relevance of each patch in the diet composition of the animal. In Box 7.3, the extent of the feasible region and the contribution of each patch in the absence of the other patch are illustrated.

First, we determined the effect of body size on the extent of the feasible region (see Figure 7.1). Here, we assumed that the 2 patches are close together. It appears that the extent of the feasible region increases with body size. For lactating animals, the extent of the feasible region is smaller, implying that lactating animals are more constrained by the possible combination of patches in the landscape. For lactating females it is thus much less easy to find an array of patches that serves their needs than for non-lactating individuals, and this differential increases with body mass. However, this differential handicap of demands for lactation is not fully set off by the benefits of increased body mass.

In Figure 7.2, the effect of body size on the contribution of one patch in the absence of the other patch is given. For small animals, patch y (in Box 7.3 named patch 2) does not meet all the requirements (in Box 7.3 this is C2), so they have to concentrate on patch x. This means that with decreasing body mass, it becomes rarer and rarer that a ruminant can make use of one patch only. However, simultaneously, it becomes rarer and rarer that an increasingly smaller ruminant can compensate for this by making use of another patch *and* satisfice the requirements. Thus the chances that an array of patches satisfices the requirements of a ruminant decrease with decreasing body mass. Hence it follows that ruminants become rarer with decreasing body mass. Figure 7.3 gives the extent of the feasible region as function of the distance between

Body mass is a critical parameter to understand the way ruminants can make use of a landscape

***Box 7.3.** The feasible region in a linear-programming problem*

Two of the most basic concepts associated with a linear-programming problem are feasible region and optimal solution. For defining these concepts, we use the term point to mean a specification of the value for each decision variable (Winston 1994). The feasible region for a linear-programming problem is the set of all points satisfying all the constraints. For a maximisation problem, an optimal solution to a linear-programming problem is a point in the feasible region with the largest objective function value. Similarly, for a minimisation problem, an optimal solution is a point in the feasible region with the smallest objective function value. The extent of the feasible region is illustrated in figure 7B.

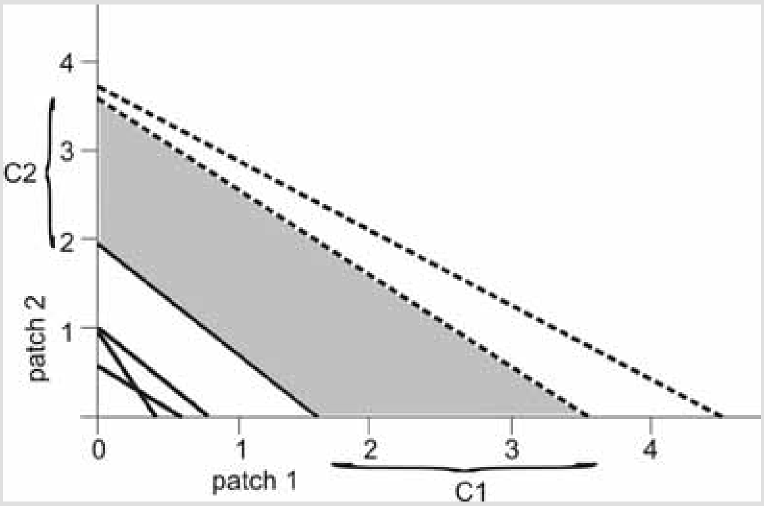

***Figure 7B.** The extent of the feasible region in a linear-programming problem is the shaded region bounded by the minimum (dashed lines) and the maximum (solid lines) requirements of the animal. The contributions of each patch in the absence of the other patch are C1 for patch 1 (in the absence of patch 2) and C2 for patch 2 (in the absence of patch 1)*

the patches for wildebeest solely based on the energy and nutrient requirements. Here, the time after which 10% of the particles has left the rumen, $T_{R,0.1}$ (eqn 27b), is not included. The point where the line meets the x-axis is the maximum distance that an animal can move between patches based on diet assembling over a range of body mass. When the maximum distance is also determined by $T_{R,0.1}$, then the maximum distance over which wildebeest (143 kg with *Dig* = 0.8) can move between patches is 16 km.

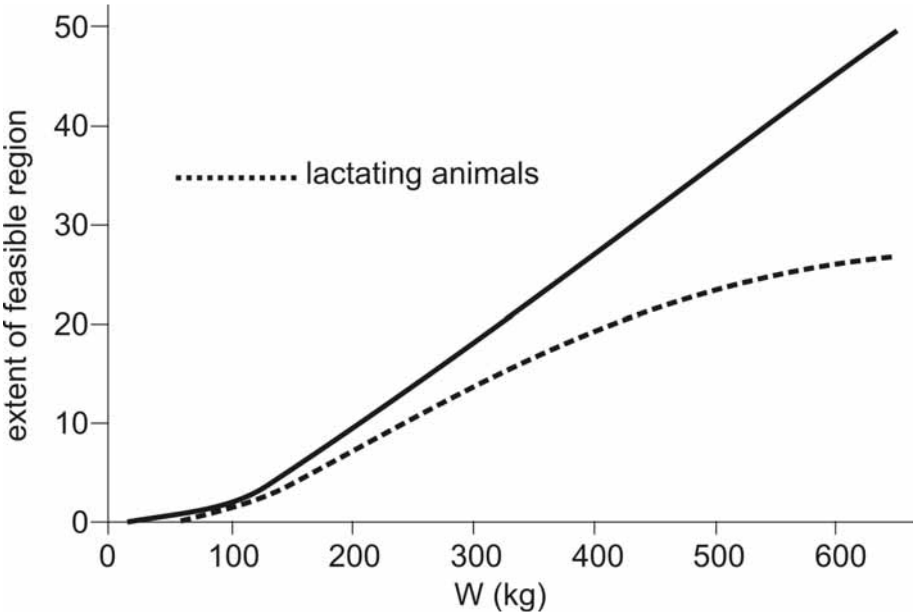

Figure 7.1. *Extent of the feasible region as function of body mass (dashed line is for lactating animals). Parameter values based on the vegetation measurements of patch 1 under trees and patch 2 in open grassland (see Table 7.3), the distance between the patches D =0 km*

Figure 7.4 shows the effect of the inter-patch distance on the extent of the feasible region with and without considering the time after which 10% of the particles has left the rumen, $T_{R,0.1}$ (eqn 27b). It appears that energy is not the limiting factor for animals because the maximum allowable inter-patch distance in Figure 7.4 is unrealistically high (top line in the figure); this implies that plants can provide more than sufficient energy. When including the throughput rate ($T_{R,0.1}$) in the constraints, the maximum allowable inter-patch distance becomes much smaller (bottom lines in Figure 7.4). Recall that rumen micro-organisms are not primarily limited by energy but by macro-nutrients (Van Soest 1982) for which we have included the parameter $T_{R,0.1}$. This parameter represents the necessity for the rumen micro-organism to have a well balanced food mass in the rumen. When including the constraints set by the lactating female's requirements for Ca and P, no feasible region could be found. This indicates that plants cannot satisfice these nutrient requirements. Lactating females thus have to find other sources for these nutrients during this time of their life cycle, or they have to mobilise them from their skeleton. This confirms that plant biomass, generally speaking, is only marginal from the animals' perspective.

Often in grass the amounts of calcium and phosphorus are too low to satisfy the needs of females when producing milk

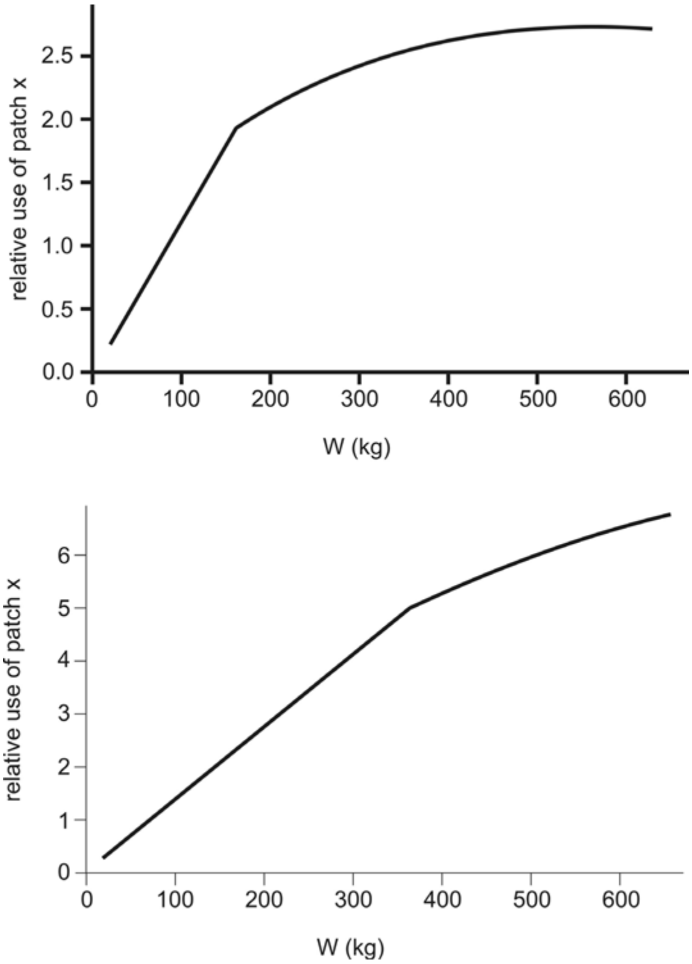

Figure 7.2. *The contribution of one patch in the absence of the other patch as function of body mass. Parameter values based on the vegetation measurements of patch x under trees and patch y in open grassland (see Table3), the distance between the patches D = 0 km*

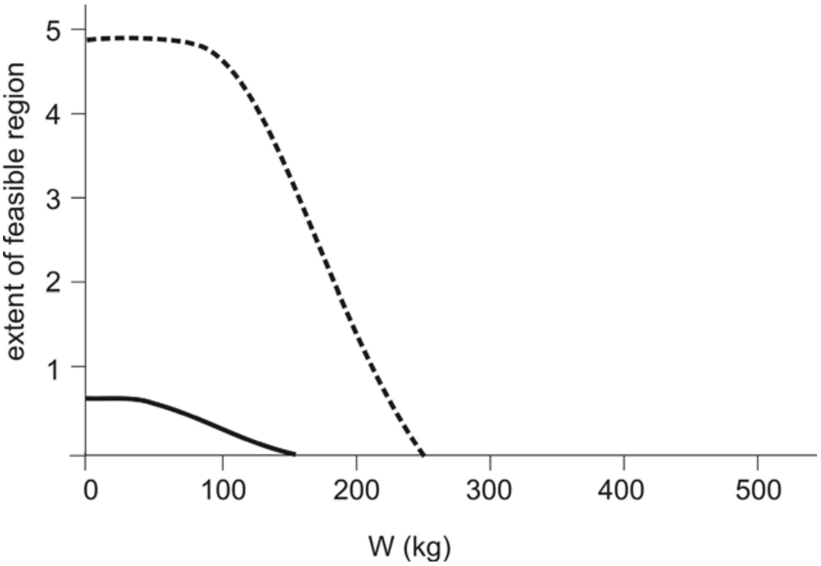

Figure 7.3. *Extent of the feasible region as function of the inter-patch distance. Parameter values based on the vegetation measurements of patch 1 under trees and patch 2 in open grassland (see Table3), the body mass is 50 kg (solid line) and 143 kg (dashed line). The maximum distance that a wildebeest of 143 kg can walk is 16 km when the time after which 10% of the particles have left the rumen,* $T_{R,0.1}$ *(eqn 27b), is included (Dig = 0.8)*

DISCUSSION

In this chapter, we present a modelling approach to explore the conditions for the presence or absence of foraging animals based on the energy and nutrient requirements that should be met. We did not only look at vegetation quantity and vegetation quality, but we took a third property into account, namely the grain size of the landscape. Grain size describes the spatial array of patches of vegetation in a landscape (e.g., Murwira 2003, Skidmore and Ferwerda Chapter 4). In our approach, the spatial distribution of patches with acceptable food and areas without, or with vegetation that is non-food from the herbivores' perspective, is of critical importance for understanding how herbivores can use the vegetation. This spatial distribution determines usage just as properties of the animals, such as body mass and digestion system. We explored this for herbivores since a lot of information on requirements is available, but it can also be applied to other forager types that make use of spatially dispersed food.

Spatial distribution of food and 'non-food' (just as, for instance, an animal's physiology) co-determines usage

We stress that the requirements of an animal often force it to forage from different patches with resources when the availability and quality of the resource is spatially heterogeneously distributed. Since we believe that food in the real terrestrial world is always heterogeneously distributed, movement and searching, and thus the selection of patches to obtain a well balanced diet, will always be necessary for a herbivore. A herbivore thus has to assemble a diet from different patches, and from different plant species, and only the assembled diet can meet all of its requirements. The herbivore has to move between different patches that are imperfect from the herbivore's point of view, but that in combination can satisfy the herbivore's requirement. We show that the requirements of the animal set limits to the amount and spatial distribution of the diet components. The model makes predictions when herbivore species can meet their requirements or not, and thus when it can be present or not.

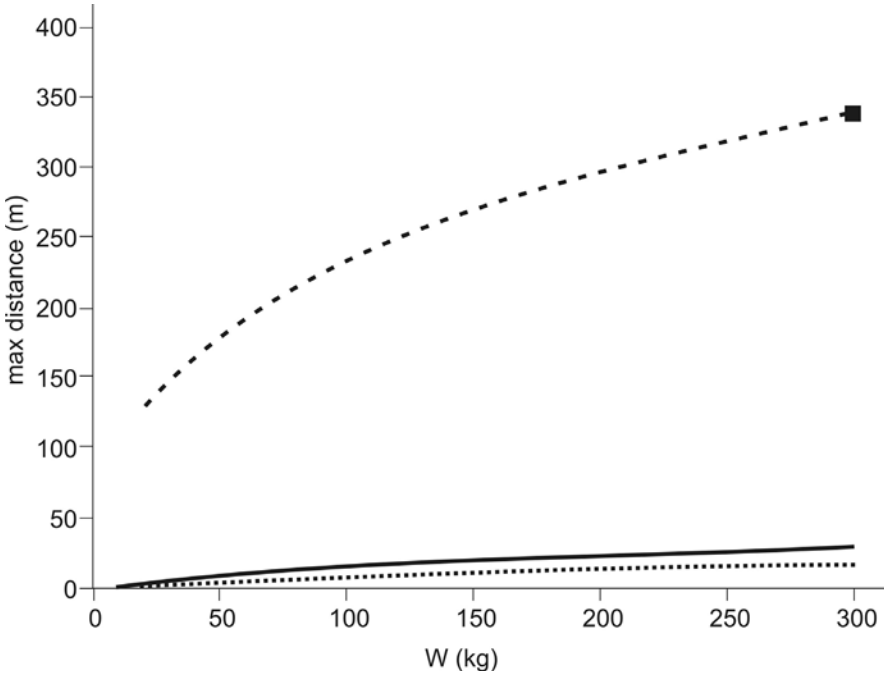

Figure 7.4. *The maximum distance based on diet assembling over a range of body mass: when the time after which 10% of the particles have left the rumen,* $T_{R,0.1}$ *(eqn 27b), is not included (dashed line); when* $T_{R,0.1}$ *is included for Dig = 0.8 (solid line); and Dig = 0.6 (dotted line)*

Since nutritional requirements and energy balance are allometrically scaled, we can express the conditions for presence or absence as a function of body size (Figures 7.1 and 7.4). Figure 7.1 shows that large ruminants have a much wider tolerance for assembling a diet from different patches than smaller ruminants. Alternatively stated, smaller ruminants have much less freedom in assembling a diet from patches with different quality than larger ones. Based on this finding, we predict that, firstly, smaller ruminants appear to be much more specialised than larger ones. We secondly predict that it is easier for large ruminants to assemble a satisficing diet from different patches than it is for smaller ones (see also Figure 7.2), and hence, thirdly, we predict that large herbivores are more common than small ones. The critical assumption behind this last prediction is that at a meta-scale ('landscape', 'ecosystem') the juxtaposition of patches of vegetation with different quality is more common than the concurrence of patches with the same quality that simultaneously are of sufficiently high quality to meet the requirements of the small ruminants. Based on the availability, quality and spatial distribution of different resource types, we can thus predict the number of species that can be present in a given situation and relate the number of species to minimum body size.

Our model predicts that large herbivores should be more common than small ones

If it is true that the steppe-tundra during the Pleistocene was more fine-grained than the succeeding steppes, tundras or boreal forests, as suggested by Guthrie (1990), due to increased temperature, and perhaps increased precipitation too, which led to a segregation of plant species that occurred together before, then we would predict the opposite from what has been observed. This steppe-tundra would namely have been a better place for smaller ruminants than the succeeding coarse-grained vegetation types. Indeed, we would then expect that large herbivores, and especially the megafauna, have survived better than the smaller ruminants. This is in contrast to what generally has been assumed.

Box 7.4. *Testable hypotheses for future research*

Hypothesis 1. Given equal conditions of disturbance and predation and equal body mass, individuals of ungulate species that are adapted to dry conditions and which are not dependent on surface water, can assemble an optimal diet on a shorter time horizon than individuals of species that need surface water.

Hypothesis 2. Given equal conditions of disturbance and predation and equal body mass, individuals of ungulate species that are adapted to dry conditions and which are not dependent on surface water, need smaller body reserves for nutrients and/or energy than individuals of species that need surface water.

Hypothesis 3. Given equal conditions of disturbance and predation, individuals of ungulate species that are not adapted to dry conditions and which are dependent on surface water during the dry season but not during the wet season, can assemble an optimal diet on a shorter time horizon during the wet season than during the dry period.

Hypothesis 4. Given equal conditions of disturbance and predation and need for surface water, individuals of large ungulate species can assemble an optimal diet much more easily than individuals of small species.

From our analysis, we can draw some other conclusions too. First, increasing inter-patch distance, measured in absolute terms, increases the difficulty for a herbivore to assemble a diet sufficiently able to cover its requirements (Figure 7.3). Larger herbivores, however, are less constrained than smaller ones (Figure 7.3). Increasing inter-patch distance puts a heavier constraint on acquiring sufficient energy and nitrogen from the food than on obtaining adequate amounts of other macro-nutrients. From this we can deduce that in coarse-grained landscape especially the N:P ratio is of importance: in such a coarse-grained landscape nitrogen is more limiting to the herbivore (and the N:P ratio should thus be high) than in a fine-grained landscape. Because smaller herbivores are more nitrogen-limited than larger ones and not *vice versa*, our analysis puts even more emphasis on the differential survival for large ruminants as compared to small ones. Our models would have predicted extinction of the *smaller* fauna at the end of the Pleistocene. Much attention has been devoted to the extinction of the megafauna. One should not forget, though, that numerous ‘ordinary’ (body mass mid-range) herbivores went extinct too. Cases in points are camelids, horses and pronghorn species in North America (e.g., Anderson 1984). Before we can draw a final conclusion, though, we have to explore how our conclusions hold for non-ruminant herbivores, and it may be that our model results do not hold for mammoths or woolly rhinoceroses. This we have not done yet. There is no convincing evidence for overkill of large herbivore populations by early Man (see Anderson 1984; Graham and Lundelius 1984; Murray 2002). Late Pleistocene extinction of large mammals is certainly real (Graham and Lundelius 1984; Table 3.6 in Prins 1998). Perhaps the unusually high mortality of the end of the Pleistocene is best regarded as a natural consequence of high faunal turn-over caused by major oscillations during the Pleistocene and the Holocene in climate and environmental heterogeneity (Gingerich 1984), together with our explanation about the increasing difficulty smaller ruminants would have faced to assemble a diet from an increasingly coarser-grained environment. This would have turned out to be even more difficult for lactating females (Figure 7.1). Added to this then was the increased leaching of the soil in the wetter parts of the temperate zone during the Holocene, which further exacerbated the difficulties of meeting a balanced and sufficient diet in a coarse-grained landscape.

In coarse-grained landscapes nitrogen is more limiting than in fine-grained landscapes; this affects smaller ruminants more than larger ones

We can thus deduce that is more difficult for a small herbivore to live in a coarse-grained environment than in a fine-grained one. This is enforced by the finding that for a lactating female this is even more difficult (Figure 7.1). In our equations, we have shown that the nutritional requirements of pregnant and, especially, lactating females are much higher than those of animals that are not reproducing. From our model it is clear that this has important implications for the fit of animals of different body masses in the landscape. Our fourth conclusion is then that, given the same body mass, non-reproducing individuals can cope with longer inter-patch distances than lactating females can cope with (Figure 7.1). We found that for lactating females it is much less easy to find an array of patches that serves their needs than for non-lactating individuals. We also found that this differential increases with body mass, but that this differential handicap of demands for lactation is not fully set off by the benefits of increased body mass. We can thus conclude that this must have led to a strong selection pressure favouring larger body masses in ruminants in the course of evolution. A larger size simply means that it is easier to satisfy the nutritional requirements in a landscape. Again, we have not investigated yet whether this holds also for non-ruminant herbivores, but we suspect this to be the case because generally speaking evolution shows an increase in body mass of, for example, equids and other hindgut fermenters.

Lactating females have difficulties finding landscape configurations that match their needs; natural selection favours high body mass

With our set of formulas and given the assumption underlying equation 27b we can construct a graph (Figure 7.4) that shows that the maximum interpatch distance beyond which a herbivore cannot assemble a balanced diet anymore is dependent on body mass. This has important implications if the dominant scale of the landscape (*sensu* Murwira and Skidmore 2004) changes. Indeed, Murwira (2003) have shown that due to man this dominant scale has changed in, for instance, the communal lands of Zimbabwe. The same has happened in many other landscapes where the impact of humans changed the scale of the landscape from fine-grained to coarse-grained; cases in point are the countries of the European Union, where agricultural policy caused these changes. We thus predict that small herbivores face increasing chances of extinction when the dominant scale of the landscape increases. In fragmented landscapes, animals may thus be constrained by the possibilities to assemble their diet from different places. This provides an alternative explanation for the effects of the fragmentation of habitat on survival, which is different from the explanation that dispersal is constrained as is often suggested, especially in the context of metapopulation theory (Hanski 1999, 2001). Concurrently, large herbivores are more extinction-prone in such a landscape because large herbivores are more easily exterminated by man than smaller ones. We suggest further research based on the hypotheses derived in this chapter; see Box 7.4.

NOTES

[1] In published sources many formulas are reported using the calorie as unit. Throughout this chapter we have recalculated these by converting to Joule, by using one cal as 4.184 J.