CHAPTER 8A

EFFECTS OF TEMPORAL VARIABILITY
IN RESOURCES ON FORAGING BEHAVIOUR

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Abstract. Trait plasticity in physiology, behaviour, morphology and life history enables organisms to survive and populations to persist despite temporal variability in environmental conditions and resource availability. Through non-linear responses, the effect of adverse periods outweighs that of benign conditions, following Jensen's inequality. This chapter considers how large mammalian herbivores adjust broader aspects of their foraging behaviour to cope with variability over different temporal frames: within a day, day versus night, between days, over seasonal cycles and between years. It outlines the conceptual foundation for 'adaptive resource ecology', covering changes in diet composition, daily time allocation, foraging movements, metabolic rate, digestive capacity and fat stores. The functional response relating food intake rate to food availability changes its form depending on the temporal scale. To link resource variability in time and space to population dynamics, the intake response needs to be transformed into a biomass or energy gain response over a seasonal time frame. Foraging models based on rate averaging can be misleading, while challenges in applying dynamic optimisation models need to be surmounted. Models assuming equilibrium relationships between resource supplies and population growth are inappropriate for coupling resource gains to population dynamics.

Keywords. adaptive responses; diet selection; digestion processes; functional response; time budgets; trait plasticity

INTRODUCTION

Environments change in fundamental ways affecting resource availability for consumers over daily, seasonal and multi-annual time frames. To cope with such temporal variability, animals and plants must adapt phenotypically in physiology, behaviour, morphology and life history or, in other words, show 'trait plasticity' (Abrams 1995). For populations to persist, the individual organisms constituting these populations must be able to sustain their resource gains, relative to the expenditures involved in acquiring them, despite the ups and downs, troughs and pitfalls encountered while traversing a continually shifting fitness landscape

(Figure 8.1). Models dealing only with average, normal or equilibrium conditions fail to capture what most crucially governs ecological success or failure in growing, surviving, reproducing and ultimately in transmitting genes over evolutionary time frames. Large mammalian herbivores in particular face wide seasonal contrasts in food quality, and substantial differences between years in the timing of vegetation growth and dormancy and amount of available forage produced. In the summer or wet season, there is a vast superabundance of relatively nutritious forage. During the winter or dry season, vegetation becomes largely a non-renewing resource, of much-reduced nutritional value. In this chapter, I consider how large mammalian herbivores respond to temporal variability in an adaptive way, at various temporal scales, and also how such consumers depend on spatial heterogeneity to cope with it. I outline the consequences for the functional response linking food intake to resource availability over different temporal scales, and evaluate the applicability of alternative foraging models. Finally I note the inappropriateness of equilibrium concepts in models linking population dynamics to resource supplies.

Large herbivores respond to temporal variability, at various scales, and depend on spatial heterogeneity to cope with it

Behavioural ecology considers specifically how organisms respond to spatio-temporal variability in their interactions with resources, physical conditions, conspecifics, predators, parasites and competitors (Sibly and Smith 1985; Krebs and Davies 1997; Houston and McNamara 1999). Recently the importance of environmental heterogeneity has become more widely recognised in ecological literature (e.g., Kolasa and Pickett 1991; Tilman and Kareiva 1997; Turchin 2003). The conceptual foundations for an 'adaptive resource ecology', linking foraging behaviour with its consequences for population and community ecology in spatio-temporally variable environments, was developed in Owen-Smith (2002a), with large herbivores specifically in mind. Crossing hierarchical levels, both temporal and spatial scales expand to encompass additional environmental influences affecting resource gains (Table 2.1).
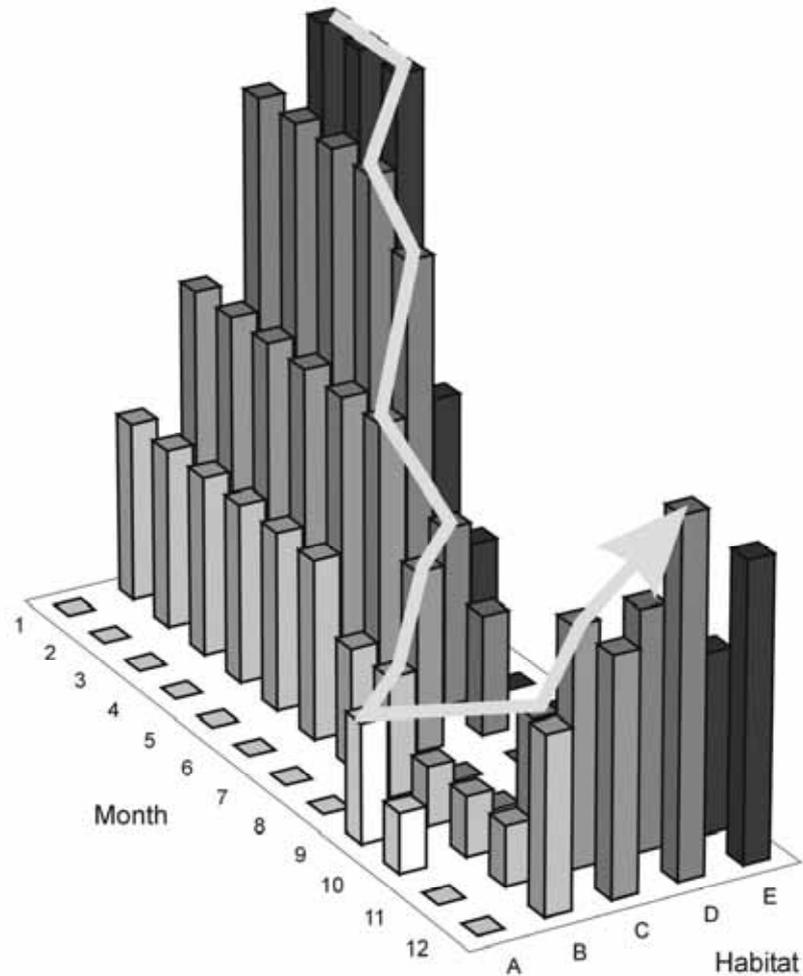
Figure 8.1. *The broken fitness landscape, with regular troughs and irregular pitfalls that organisms must traverse over time in order to survive and reproduce (from Owen-Smith 2002a)*

Short-term aspects of foraging behaviour including diet choice, intake rate and patch use are covered in earlier chapters (see Laca, Chapter 5, and Fryxell, Chapter 6). Subsequent chapters cover large-scale movements with landscapes and the consequences for population dynamics. My role in this chapter is to bridge between these realms, including not only changes in diet composition but also foraging-time allocation, searching movements, and associated physiological and morphological adjustments. The temporal scope extends from foraging spells of a few hours

through daily and seasonal cycles to between-year differences in conditions. Specific questions addressed are:

- How do animals choose what to eat, when what is available to them is uncertain and changes over time?
- How do animals adjust their foraging behaviour at night when food is less visible and perhaps less nutritious, and the risk of predation and hypothermia higher than during the day?
- How do animals balance their foraging behaviour between days when conditions are favourable and other days when conditions are adverse because of extreme weather?
- How do animals cope with the adverse season when food availability as well as its nutritional quality is greatly reduced?
- How do animals counteract the extreme conditions that arise in some years, in food availability or weather?
- How does the functional response change its form across temporal scales?
- How well do alternative foraging models accommodate spatio-temporal variability?
- Are equilibrium conditions between consumers and their resource supplies ever reached?

VARIABILITY AMONG FORAGING SPELLS

Foraging spells of large mammalian herbivores typically extend over one or more hours, and encompass a sequence of feeding bouts interrupted by movements

Food availability and thermal conditions differ between foraging spells, and animals adjust their diet choice accordingly

between food patches and other activities. They are separated by resting spells, or on occasions by extended travel to new foraging areas, water sources or other places (see also Bailey and Provenza, Chapter 2). Foraging spells take place within a foraging site defined by the speed of searching movements and the tortuousness of the foraging pathway. Successive foraging spells may take place within the same general area, or in different localities.

Diet selection models are concerned with how an animal selects what to eat given information about the range of food types (plant species and parts) available within some loosely defined area (Box 8.1). For herbivores the list of available plant species can be large, especially in or near the tropics. However, during foraging spells animals encounter only a limited sub-set of these food types. Rarer plant species, and more nutritious parts like new leaves or fruits, may not be contacted. How then should a hungry herbivore adjust its diets? Should animals keep searching for the best food types, expecting that these will eventually be found (even if only in a later foraging spell)? Or should they broaden their diet composition to encompass lower-value food types in the meanwhile?

Box 8.1. *Diet-breadth model*

The classical diet-breadth (or contingency) model of optimal-foraging theory addresses food selection by a consumer confronted with a set of potential food items intermingled in the same region. The solution depends on ranking the food types from best to worst, based on their effective nutritional yield, determined by the ingestion rate (or the inverse, handling time) and digestible energy or nutrient content obtained. The optimal solution is given by the dietary combination maximising the rate of gain of the target nutrient. Food types are added to the diet in order of their effective value; hence the model indicates the optimal diet in terms of the range or breadth of food types included. Whether a food type should be incorporated in the diet is assessed by comparing the value that it would yield if eaten against the rate of nutrient gain obtained from the set of food types currently included in the diet, i.e., whether $E/T_h > \check{E}/(\check{T}_h + \check{T}_s)$, where E is energy or nutrient yield, T_h handling time, T_s search time and $\check{}$ indicates values averaged over the food types in the diet. Hence a particular food type should be included in or excluded from the diet on an all-or-nothing basis (i.e., 1/0 acceptance). However, the model is idealised in only considering average nutrient yields, rates and times, and not their variability. Variation in nutrient contents, bite size or eating time within a food type, and in encounter rates with different foods indexed by the search time, could lead to departures from 1/0 acceptance, or so-called 'partial preferences'. Another problem arises when different factors affect the nutrient yields at different times, e.g., digestive processing time for herbivores often overrides the effects of handling time involved in food ingestion. For further reading, see Stephens and Krebs (1986), and for an application to large mammalian herbivores, see Owen-Smith and Novellie (1982).

The problem of dietary adjustments to stochastic variation in encounter rates with different food types has not been formally considered in the literature, at least not for large mammalian herbivores, so far as I am aware. Confronting it helps explain discrepancies between the predictions of simple rate-averaging models and observed diet choices. Herbivores generally select a broader diet than would seem optimal, and show partial rather than all-or-nothing acceptances of many food types (Westoby 1978; McNamara and Houston 1987a). A 'partial preference' means that animals eat certain food types on some encounters but not on others (Box 8.1).

The solution can be conceptualised using an elementary graphical model, incorporating a fundamental principle of environmental variability. Figure 8.2 illustrates a typical resource gain function for herbivores, and also many other consumers: a pattern of diminishing rate of gain towards higher resource levels. Accordingly, when by chance an animal finds itself in a foraging area richer than average in resources, it gains only a little more than it would at the mean resource level. When in a poorer-than-average area, it loses a lot more. The principle has become known as 'Jensen's inequality' (Ruel and Ayres 1999), and applies whenever gains are a saturating or decelerating function (convex upwards) of resource availability. The consequence of Jensen's inequality is that the overall gain over a sequence of foraging spells is enhanced if animals expand their dietary acceptance range to reduce deficits in poor localities. Hence partial acceptances should be shown for some less rewarding food types, eaten only when better food types are not encountered over some time period. The dietary range is consequently broader than predicted by a model treating diet choice only on the basis of average availability. This expectation has two underlying assumptions: (1) food types occur in patches containing limited sub-sets of the full range of food types available, rather than being dispersed in a fine-grained mix; and (2) foraging spells have a finite,

relatively short time horizon, in relation to the resource area potentially available. Other hypotheses have been advanced to explain partial preferences (McNamara and Houston1987a; Prins and Van Langevelde, Chapter 7), but stochastic variability in encounter rates seems most fundamental.
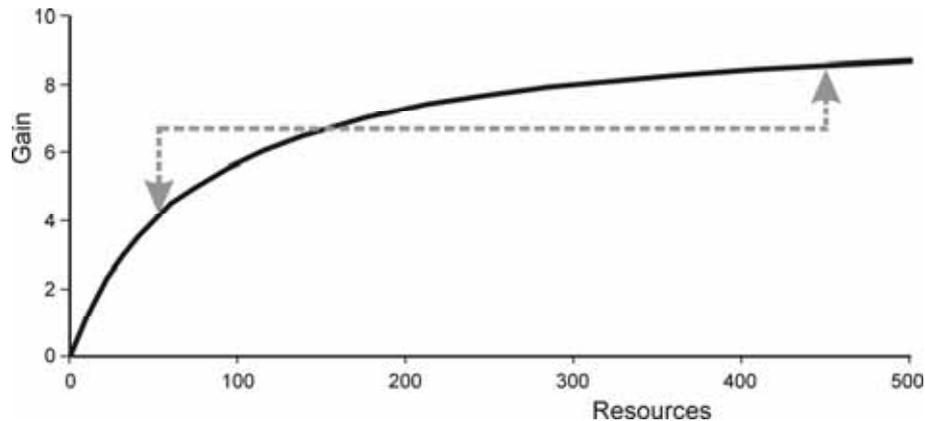
Figure 8.2. *Resource gain function illustrating Jensen's inequality (from Owen-Smith 2002a)*

Foraging spells are curtailed most basically because of heat build-up from muscular activity, with the heat load affected additionally by diurnal variation in ambient temperature, wind and solar radiation. I have in mind warm tropical environments, or summer conditions in higher latitudes, with activity levels of herbivores depressed by elevated midday temperatures. During winter, or even on relatively cold, windy days in the tropics, heat loss from exposure while foraging can restrict foraging activity (Parker 1988). Hence variation in thermal conditions over the diel cycle affects the duration of foraging spells, hence the time available to top up the rumen, and potentially also the diet composition within these spells. For most African ungulates, morning foraging spells are ended by rising heat towards midday, an exception being the African buffalo (Beekman and Prins 1989), while afternoon foraging spells can be prolonged into the cool of the evening. Buffalo in equatorial Tanzania even forage during the night (Prins and Iason 1989). Attenuated foraging periods should shift selection towards more rapidly ingested, less digestible food types. Over longer spells, animals have more time to seek out better-quality food types, even if these give reduced intake rates. For kudus, I observed such a pattern, with morning diets including relatively more woody browse, and afternoon diets more forbs (Owen-Smith 1993). A similar pattern has been reported for goats, in this case with more grass consumed in the morning and more woody browse in the afternoon (Solanki 1994).

DAY–NIGHT VARIATION

Over the 24-hour cycle, conditions differ between day and night not only in illumination and ambient temperature, but also in risk of mortality from predators relying on concealment. In Africa, the primarily nocturnal hunters for large herbivores include not only lions and leopards, but also spotted hyenas. The diurnal predators are cheetahs and African wild dogs, plus eagles for small antelope. Forage quality differs over the 24-hour cycle. Leaves are potentially less nutritious in soluble carbohydrates at night when they are respiring than during the day when they are actively photosynthesising.

A contrast between strategies of energy maximisation versus time minimisation was drawn early in the development of foraging theory (Schoener 1971; Fryxell, Chapter 6). The outcome is expressed through differences in the time allocated to

Contrasts in illumination, temperature and risk of predation between day-time and night-time affect foraging-time allocation and food selection

foraging relative to other activities, because in either case the net food gain should be maximised during foraging activity. For energy maximisers, fitness increases monotonically with additional food, supporting enhanced survival and reproduction, hence foraging time should be the maximum permitted by environmental conditions. Time minimisation is expected when animals incur substantial predation risks or other fitness costs while foraging, compared with periods of immobility, so that as a consequence foraging should not be prolonged much longer than the time required to secure the maintenance metabolic requirement. For herbivores, a complication arises because the long-term food intake is usually constrained by digestive capacity rather than by the food intake rate while foraging (Owen-Smith and Novellie 1982). The trade-off between predation risk and foraging behaviour may also restrict the habitats selected for foraging at times when predation risk is high (Brown et al. 1988), but lead to risk-prone foraging when food is in short supply (Hik 1995; Sinclair and Arcese 1995b). McNamara and Houston (1987b) explicitly modelled such fitness tradeoffs.

Most African ungulates of medium-large size devote relatively more time to foraging during daylight than at night (Owen-Smith 1988). Warthog, which are highly vulnerable to predation, restrict their foraging entirely to daylight hours, while certain solitary antelope of medium-small size forage more at night than in the day, probably because they depend on concealment to escape predation (Novellie et al. 1984; Roberts and Dunbar 1991). Buffalo, which rely upon herd protection rather than concealment, and mega-herbivores like elephants and rhinos, with low vulnerability to predation as adults, forage equally day and night (Owen-Smith 1988; Beekman and Prins 1989; Prins and Iason 1989; Prins 1996; Winterbach and Bothma 1997). The habitat areas used for foraging may differ between day and night (Waser 1975), and animals may move much less while foraging at night than during the day (Jarman and Jarman 1973).

As a consequence of contrasts in foraging time and habitat use, differences in food selection might be expected between day-time and night-time. Animals could function effectively as energy maximisers during the day (subject to thermal limitations), and as time minimisers at night (see also Beekman and Prins 1989). However, because of the impracticality of observing feeding at night, no relevant data seem to exist.

The day–night contrast in conditions can have ramifying effects ultimately affecting population dynamics. In arid environments, ungulates such as oryx may shift their foraging activity into the cool of the night at times when surface water is not readily available, lessening evaporative water losses (Taylor 1969). This exposes animals to greater predation risks in places where nocturnally hunting predators are common, and hence to their exclusion from such habitats. The vulnerability of roan antelope to predation, which has evidently led to their population collapse in northern Kruger (after a zebra influx, promoted by augmented water supplies and followed by a lion increase; Harrington et al. 1999), could possibly be related to their need to do more foraging at night under hot conditions on account of their large size. A small number of roans placed in a fenced enclosure keeping out lions has thrived and expanded, despite the effects of drought conditions on the vegetation.

DAY-TO-DAY VARIABILITY

While foraging, herbivores can potentially ingest food much faster than they can digest it (Owen-Smith and Novellie 1982). Over the course of a day, food intake is limited more by digestive processing capacity than by the food intake rate obtained while foraging. In such circumstances, the food intake rate should be held below its potential maximum so as to keep the gut filled close to its capacity, within the available foraging time, as discussed above in relation to foraging spells. However, available foraging time also varies from day to day, dependent on daily differences in temperature and other ambient conditions. On hot days, animals must restrict foraging time to avoid over-heating. On cold or windy days, they may need to seek seclusion, also restricting the time available for foraging and the food types encountered.

Thermal conditions vary between days with consequent differences in foraging activity and dietary intake

For kudus, the proportion of time spent active (mainly foraging) showed wide day-to-day variability, ranging between 50 and 80% of daylight hours (Owen-Smith 1998). Only when the maximum daily temperature exceeded 36°C during the summer wet season, activity was restricted below the mean level of 66%, because kudus compensated partly for high midday temperature by foraging longer in the afternoon. In the winter dry season the temperature threshold appeared lower, about 30°C, probably because of the thicker hair coat animals possessed then. Weather records showed that 15% of days exceeded these temperature limits in both seasons, suggesting that the foraging activity of kudus was restricted by high temperature levels on only about one day in seven. As a consequence of their tolerance for high
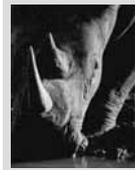
temperature levels, kudus are sensitive to mortality during extreme cold spells (defined by a midday temperature $\leq 14^oC$) that occur in the late dry season when their body reserves are depleted (Owen-Smith 2000). Observations on other African antelope species indicate that activity levels were reduced when midday temperatures exceeded about 32^oC (Lewis 1977; Leuthold and Leuthold 1978; Klein and Fairall 1986). Northern ungulates are much less tolerant of high-temperature conditions, because of their greater insulation to cope with cold. Summer activity levels of elk and deer in North America decreased from 70% of the 24-hour day at a mean temperature of 10^oC to about 40% at a mean temperature of 20^oC (Belovsky and Slade 1986). During winter, deer showed reduced activity when the ambient temperature rose above -1^oC (Schmitz 1991).

Herbivores may adjust their foraging behaviour, and potentially also their diet composition, in response to such weather variability. Under cold and wet conditions, hungry sheep increased bite size and biting rate to achieve almost double the rate of intake recorded a day later under more normal weather (O'Reagain et al. 1996). Sheep that were fasted overnight also showed a higher food intake rate than non-fasted animals, largely through taking large bites, and additionally foraged for longer during the day (Iason et al. 1999). Day-to-day variation in foraging time, and also perhaps in diet composition (such as observed for kudus, Owen-Smith 1993), suggests that dietary optimisation by herbivores takes place over periods somewhat longer than a day.

SEASONAL VARIATION AFFECTING FORAGING BEHAVIOUR

Environmental conditions vary seasonally in temperature and in precipitation, whether in the form of rain or snow. Close to the equator, annual temperature variation is slight. Beyond about 20° N or S, the summer – winter alternation becomes meaningful. In the tropics and subtropics, rainfall exerts a seasonal control on plant growth, and hence on food availability for herbivores. In high latitudes, precipitation commonly accumulates as snow during winter, making herbage somewhat inaccessible especially when a temporary melt leads to crusting of the snow. In northern regions, the spring growth of vegetation is supported largely by snowmelt, with the growth rate and duration of the growing season dependent on temperature conditions.

For kudus, the foliage biomass available within mouth reach on trees, shrubs and forbs declines, mostly due to leaf loss from deciduous species, to a minimum of around 8 g m^{-2} by the late dry season, amounting to about 10% of the wet-season peak (Owen-Smith and Cooper 1989; Owen-Smith 1994). For grazing ungulates, the seasonal change in available grass biomass is generally less marked, unless removed by fire or locally heavy grazing, but the proportion constituted by green leaves can be quite minute by the late dry season (e.g., Prins 1988; Prins and Beekman 1989). Hence grazers face a limitation in quality rather than quantity, because crude protein levels in dry grass commonly fall below 5% of dry mass, representing the minimum maintenance level for livestock (Owen-Smith 1982; Prins and Beekman 1989). I am not aware of comparable measurements of seasonal fluctuations in forage biomass for northern ungulates, but expect that it would be more extreme. The dependence on rainfall means that seasonal variation in food quantity and quality is somewhat more erratic in tropical and subtropical Africa and Australia than in northern latitudes where temperature is a more dependable influence.

During the adverse season, food availability and quality are reduced; herbivores alter their food selection, foraging activity and range use accordingly

During the summer or wet-season months, when there is a superabundance of food, herbivores can afford to be narrowly selective for the best-quality plant species and plant parts. During the winter or dry season, when food resources become progressively depleted through dieback and decay as well as consumption, herbivores must expand their diets to include lower-quality food types in order to maintain an adequate intake of food (Owen-Smith and Novellie 1982; Prins and Beekman 1989; Owen-Smith 2002a). Supporting adjustments also take place in daily foraging time, in the proportion of foraging time spent feeding, and in feeding durations in food patches (Beekman and Prins 1989; Owen-Smith 1994).

Figure 8.3 depicts how kudus expanded their diet over the course of the seasonal progression, from the mid-wet season through the dry season back into the early wet season, in terms of broad plant categories. The contribution of the staple deciduous trees and shrubs and favoured forb types declined progressively as these became less available during the dry season. Consumption of woody plant species with evergreen foliage was restricted mostly to the dry season. Less palatable deciduous species made their contribution during the early spring growing season from September on. Peaks in the consumption of fruits and flowers were evident when these plant parts became available. The daily food intake was elevated through most of the dry season, to compensate for the reduced nutritional quality of the food types included in the expanded diet. Only in September, when little green foliage remained, did daily food intake drop markedly.

The dietary expansion of the kudus was underlaid by seasonal changes in the frequency with which plants of particular types were eaten when encountered during foraging spells (Owen-Smith and Cooper 1987). The most favoured woody species remained highly acceptable throughout the year, as long as they retained leaves. These plant species were classed as palatable, i.e., whatever secondary chemicals they contained did not deter kudus from feeding on them. Relatively palatable

evergreens showed a sharp increase in their acceptability when they became incorporated into the diet in the early dry season, after the favoured deciduous species had started shedding their leaves. Unpalatable deciduous species also showed marked changes in acceptance when they were added to the diet, either in the late dry season when they still retained some leaves, or when they flushed new leaves in spring. Finally, even the most unpalatable among the evergreens became eaten at the end of the dry season when little other food remained, but were consumed in restricted amounts.
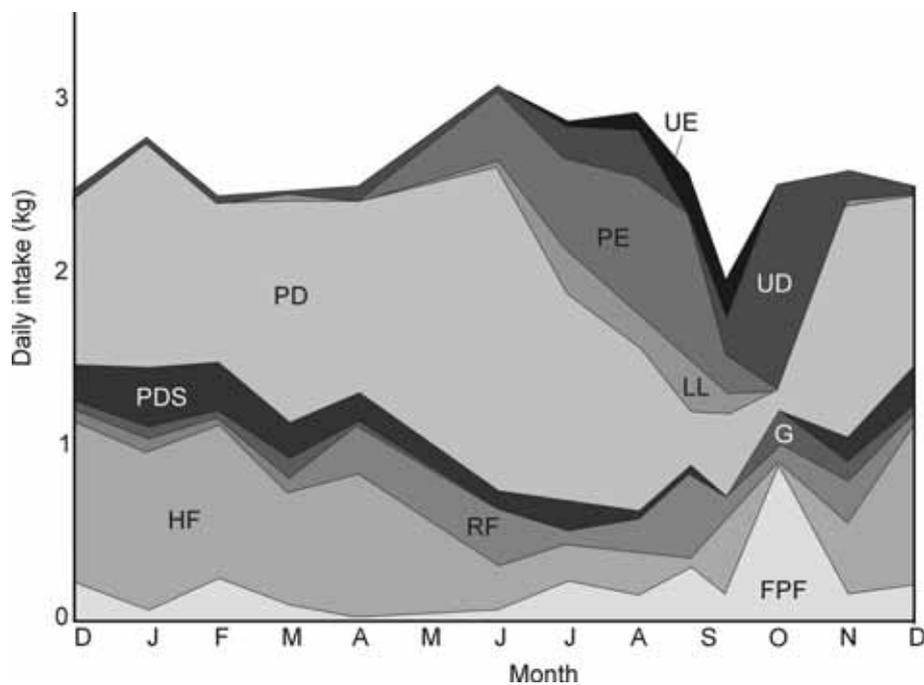

Figure 8.3. *Changing diet composition of kudus over the seasonal cycle, in terms of broad plant types: FPF = fruits, pods and flowers, HF = herbaceous forbs, RF = robust forbs, G = grass, PDS = palatable deciduous spinescent browse, PD = palatable deciduous unarmed browse, LL = leaf litter, PE = palatable evergreen browse, UD = unpalatable deciduous browse, UE = unpalatable evergreen browse (from Owen-Smith and Cooper 1989)*

Comparable shifts in the use of different grass species were recorded for free-ranging African buffalo through the dry season (Macandza et al. 2004). However, grasses favoured during the wet season can show decreased acceptability during the dry season, depending on phenological changes in green-leaf retention and in leaf:stem ratio (O'Reagain et al. 1996).

Dietary shifts make the measurement of food availability for herbivores problematic. During the wet season, kudus consumed only 3-6% of the potentially edible foliage biomass that they encountered within neck reach along their foraging pathway (excluding grass). By the late dry season, the fraction of plant biomass removed along the foraging pathway had increased to over 25% (Owen-Smith 1994). Although almost all plant species retaining foliage were accepted for feeding, animals still consumed only a portion of the potential forage offered by individual plants before moving on.

Herbivore species or feeding types differ in how they adjust their daily foraging time in response to seasonally changing food availability (Beekman and Prins 1989). Browsing kudus progressively increased the proportion of the daylight hours spent foraging as the dry season advanced, thereby partially compensating for reduced forage quality (Figure 8.4). A similar pattern was shown by impala and springbok, which although mixed feeders concentrated increasingly upon woody plants during the dry season (Jarman and Jarman 1973; Davies and Skinner 1986). Among grazers, blesbok, buffalo and white rhinos all showed reduced feeding time in the dry season, probably because of the lengthened digestion time required by the mature dry grass (Novellie 1978; Winterbach and Bothma 1997; Owen-Smith 1998). Nevertheless, all three of these grazers increased their daily foraging time in the transition period when green grass started reappearing in restricted amounts, especially in previously burnt grassland. In contrast, horses, which are also grazers but non-ruminants, expanded their daily foraging time from summer through winter in the Camargue region of France (Duncan 1985). Muskoxen, which are mixed feeders, showed a reduction in daily foraging time in mid-winter, apparently as an energy-conserving strategy, and a peak in spring (Forschhammer 1995). Browsing moose in Alberta, Canada, showed no change in daily foraging time between summer and winter, but a peak in spring (Renecker and Hudson 1989), while in Alaska the foraging time of moose was extremely low in mid-winter (Risenhoover 1986). This indicates responses to seasonally changing food quantity and quality. Temperature and day length can be subtler than a naive contrast between time minimisation and energy maximisation suggests, but a theoretical synthesis is still lacking.

Herbivores may also show contrasting responses in their foraging range to seasonal changes in food resources. Black rhinos and kudus, both of which are browsers, showed a contraction in their home-range extent during the dry season (Goddard 1967 and personal observations), whereas white rhinos, which are grazers, expanded the area they covered during the dry season (Owen-Smith 1975). This makes sense, because the woody plant species retaining leaves which the browsers depend on are localised in their occurrence and dependable in their phenology, while grazers could find areas where chance rain-showers or other local variability had promoted some green grass growth.
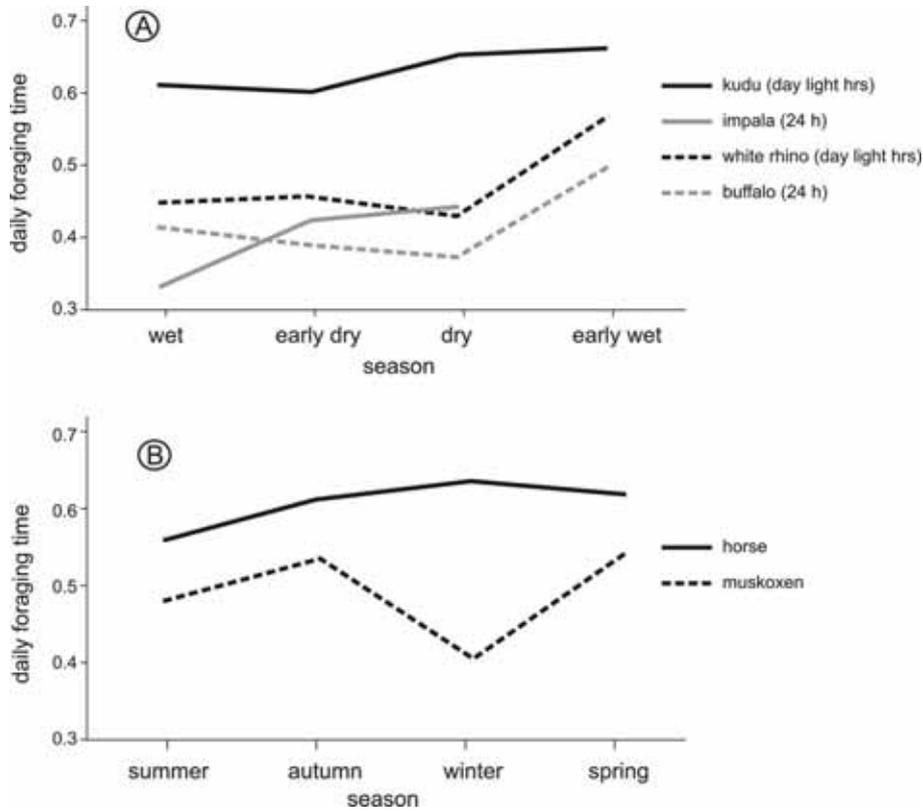
Figure 8.4. Seasonal changes in the proportion of the day spent foraging by representative grazers and browsers; (a) tropical or subtropical species, (b) northern species

SEASONAL VARIATION AND PHYSIOLOGICAL AND MORPHOLOGICAL ADAPTATIONS

Additional physiological and morphological adaptations may aid herbivores in meeting their nutritional requirements through the adverse season. Northern deer may show substantial fluctuations in metabolic rate between summer and winter (Silver et al. 1969; Weiner 1977; Regelin et al. 1985), although partly as a consequence of differences in food intake or activity (Mautz et al. 1992). Red deer exhibit a dramatic reduction in heart rate indicative of reduced metabolism during winter nights, associated with peripheral body cooling (Arnold et al. 2004). Many ungulates show changes in pelage between summer and winter. Digestive capacity can be expanded above the fill levels

Herbivores seasonally adjust their metabolic rate, gut capacity, fat stores and allocation to maintenance, growth or reproduction

apparent in summer (Baker and Hobbs 1987; Boomker 1987, cited by Owen-Smith 1994), and the internal morphology of the rumen controlling the surface area for absorption of digestive products may alter seasonally (Hofmann 1973).

Fat stores help animals survive through periods when food gains are inadequate to meet requirements. However, storing such reserves is costly, not only from the extra foraging time required to build them and the energetics of carrying the extra mass, but also potentially from the heightened predation risk associated with diminished mobility. Fat stores carried by tropical or subtropical ungulates amount to no more than 5-10% of body mass (Ledger 1968; Smith 1970), compared with 15-30% for many northern ungulates (Tyler 1987; Parker et al. 1993). Moreover, the fat carried by African antelope is associated internally with the kidneys and mesenteries, rather than being subcutaneous. This suggests that tropical ungulates avoid thermoregulatory problems, while ungulates living in high latitudes benefit from the insulation provided by surface fat. Because of the costs of carrying fat stores, fat is generally laid down towards the end of the benign season, and should theoretically amount to little more than is needed to carry animals through to when foraging conditions improve again (Owen-Smith 2002a).

The additional demands of reproduction raise the daily energy requirements of mothers almost twofold, and that for protein more than twofold, through late pregnancy and early lactation (Oftedal 1984; Prins and Beekman 1989; Chan-McLeod et al. 1994; Prins and Van Langevelde, Chapter 7). Free-ranging cattle in the Netherlands increased their daily food intake by almost 60% relative to the expected mean for the food quality, when they were supporting newborn calves in autumn (Van Wieren 1992). Dairy cattle can increase their effective rumen capacity by up to 40% in response to such demands (Campling 1970). The daily food intake may nevertheless be insufficient to support reproductive demands, forcing mothers to draw upon stored reserves of fat and body protein (for buffalo see, e.g., Prins 1989a). Accordingly, births generally occur at the time of the year when nutritional conditions are most favourable, most narrowly at high latitudes where the seasonal fluctuation in resources is greatest.

For young, growing kudus, foraging gains as indicated by daily energy intake exceeded estimated metabolic expenditures for tissue maintenance and activity for most of the year, and fell below the maintenance requirement by less than 10% even at the end of the dry season in September (Figure 8.5). Young black-tailed deer in Alaska showed somewhat greater seasonal variation, with the daily energy intake dropping to about one third of the summer maximum by late winter, well below the maintenance requirement (Parker et al. 1999). This was because the deep snow cover made food largely inaccessible, and movement costly, so that the deer showed no compensatory adjustment in daily foraging time (restricted also by the brief period of daylight). These deer used stored body reserves to carry them through the period of deficits. Young growing cattle in Colorado showed a more than twofold decline in daily energy intake seasonally, but compensated during late winter by reducing daily energy expenditures (Senft et al. 1987b).
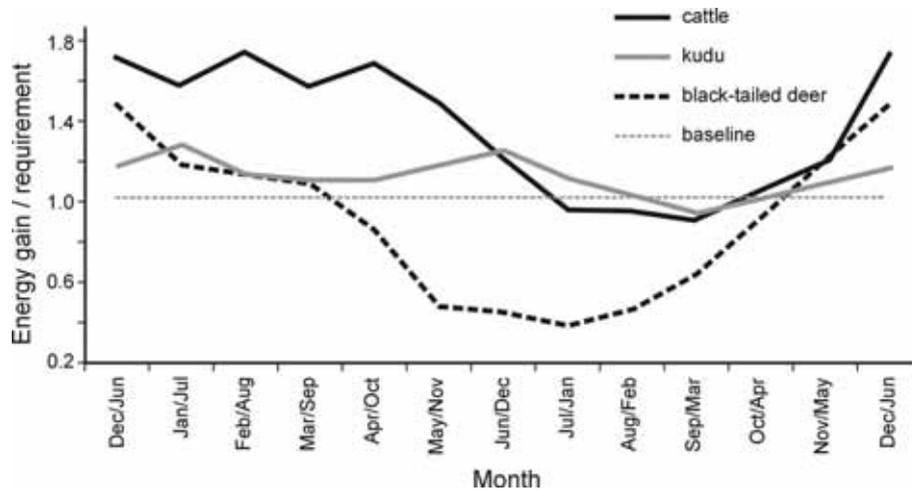
Figure 8.5. Seasonal changes in daily energy intake relative to maintenance requirements for kudus in South Africa (from Owen-Smith and Cooper 1989), black-tailed deer in southern Alaska (from Parker et al. 1999), and beef cattle in Colorado (from Senft et al. 1987b). Alternative months represent corresponding seasonal stages in the northern and southern hemispheres

Food resources differ in their contribution towards supporting the nutritional requirements of herbivores at different stages in the seasonal cycle (Owen-Smith and Cooper 1987; Owen-Smith 2002a). The following functional categories can be distinguished: (1) high-quality food types supporting peak reproductive outputs, (2) staple food types providing the bulk of the diet for much of the year, (3) reserve food types consumed when staple foods become depleted, (4) buffer food types consumed during critical periods, slowing the rate of starvation (Owen-Smith 2002a; see also Prins and Beekman 1989). Some food types can also serve as bridging resources during periods when little else is available, e.g., the deciduous trees with generally unpalatable foliage that leafed out ahead of the rains in early spring for kudus (Figure 8.3). Food types that are high in quality, but ingested at restricted rates, can be another functionally distinct category. They contribute towards enhanced diet quality, but need to be complemented by other food types that can be consumed more rapidly for animals to achieve an adequate daily food intake. Thorny acacia species fell into this category for kudus.

Food resources can be subdivided among functional categories in terms of their dietary contributions in different seasons

BETWEEN-YEAR VARIABILITY

While the basic seasonal cycle is fairly predictable in many regions, much variation can still occur between years in the specific conditions encountered at different times. Body reserves get progressively depleted through the adverse season, and whether the starvation threshold is reached depends on how prolonged the period of sub-maintenance diets lasts. Hence in tropical savannas, the timing of the early rains can be more important than how severe the food deficit was during late dry season. Kudus in Kruger Park died of hypothermia when cold spells occurred in September or October, in the transition period between winter and spring, although they tolerated colder temperatures during mid-winter (Owen-Smith 2000). On windy days, both kudus and white rhinos retreated to localities where dense bush provided some shield against the wind. In high northern latitudes, there is annual variation in the occurrence of extreme weather in the form of blizzards, snow depth and formation of ice crusts. Animals may survive through a few days of a blizzard by sacrificing feeding time to seek shelter, but if the bad weather is prolonged too long they die of hypothermia (Schaller and Junrang 1988). This may lead to episodic severe mortality, e.g., in Soay sheep associated with March gales (Grenfell et al. 1998).

Refuge resources or habitats are needed to cope with the extreme conditions that can arise in some years

Whether a population of a particular species persists in a region may depend crucially on how well animals are adapted to cope with the extreme conditions that occur infrequently, but in the long term inevitably. A population may thrive through nine years out of ten, but when the crunch conditions occur survival depends on having refuge resources or habitats available. No ungulate hibernates. The closest to hibernation is the congregation of white-tailed deer in 'deer yards' for a few weeks at the end of winter, while feeding little (Schmitz 1991). Stored body reserves can probably support animals for at most a month without food. Plant types not normally eaten can become crucial to bridge emergency periods. Fallen tree leaves may perform this role even for grazers like buffalo after virtually all grass has been consumed during severe droughts, although not for long.

TRANSFORMING THE FUNCTIONAL RESPONSE ACROSS TIME FRAMES

The relationship between the food intake rate obtained by a consumer and food abundance, commonly called the 'functional response', is of fundamental importance in theoretical ecology. For herbivores it is conventionally measured over short time periods while animals graze down available forage within an experimental enclosure. The classical 'Holling Type II' was originally conceptualised as an outcome of the trade-off between search time and handling time, but for large herbivores search time largely overlaps with handling time, so that changes in bite size exert the main control over short-term intake rates

(Spalinger and Hobbs 1992; Drescher 2003). Furthermore, over the daily cycle digestive handling time becomes the overriding constraint (except for domestic herbivores fed high-quality food) with bite sizes reduced below the maximum possible, leading to a truncated intake response (Figure 8.6a; Owen-Smith 2002a). If more abundant food is also less digestible, the daily intake response to changing food availability may become humped rather than asymptotically saturating in form (Figure 8.6b).

Functional response changes its form across time frames and should be transformed into biomass/energy gain for linking with population dynamics

The factors constraining daily food intake change over the seasonal cycle. When food is most abundant, digestive capacity may be limiting, but towards the end of winter or the dry season so little foliage may remain that the food intake rate becomes the main limitation. When forage quality is highest in spring, metabolic satiation may restrict the daily intake, i.e., animals eat as much as they need for maintenance and activity needs, and gain no further benefit from storing more fat than they already have. Metabolic satiation would not be a factor for females supporting growing foetuses or nursing offspring (see Prins and Van Langevelde, Chapter 7).

Adaptive changes in diet breadth also affect the form of the daily-intake response. Diet expansion plus additional behavioural compensation may result in the daily food intake remaining fairly constant, or even increasing, with seasonally diminishing food abundance, e.g., the daily food intake obtained by sub-adult kudus declined precipitously only when less than 2-3 g m^{-2} of accessible foliage remained on trees and shrubs (Figure 8.6c). Grazing ungulates may show a decline in daily food intake at somewhat higher levels of standing forage biomass than browsers, because forage biomass is determined largely by grass height, which also restricts bite sizes below some threshold height (Distel et al. 1995). Furthermore, diminishing grass quality lowers digestive processing capacity.

For linking with population dynamics, the gross food intake must be transformed into the consequent gain in consumer biomass or its energetic equivalent. Moreover, it is the seasonally changing food abundance that is most relevant. Net energy or nutrient gains generally decline over the adverse season, because the added food types do not replace the nutritional yields of the preferred but depleting foods. Hence the effective consumer gain response deviates from the food intake over the course of the seasonal cycle. For kudus, although daily food intake peaked at intermediate levels of food abundance in the early dry season, the daily energy intake declined progressively from the wet season through the dry season (Figure 8.6c). Small proportional differences in daily energy gains transform into huge differences when integrated over the annual cycle, e.g., a 1% increase daily results in a 38-fold compounded gain over the course of a year.
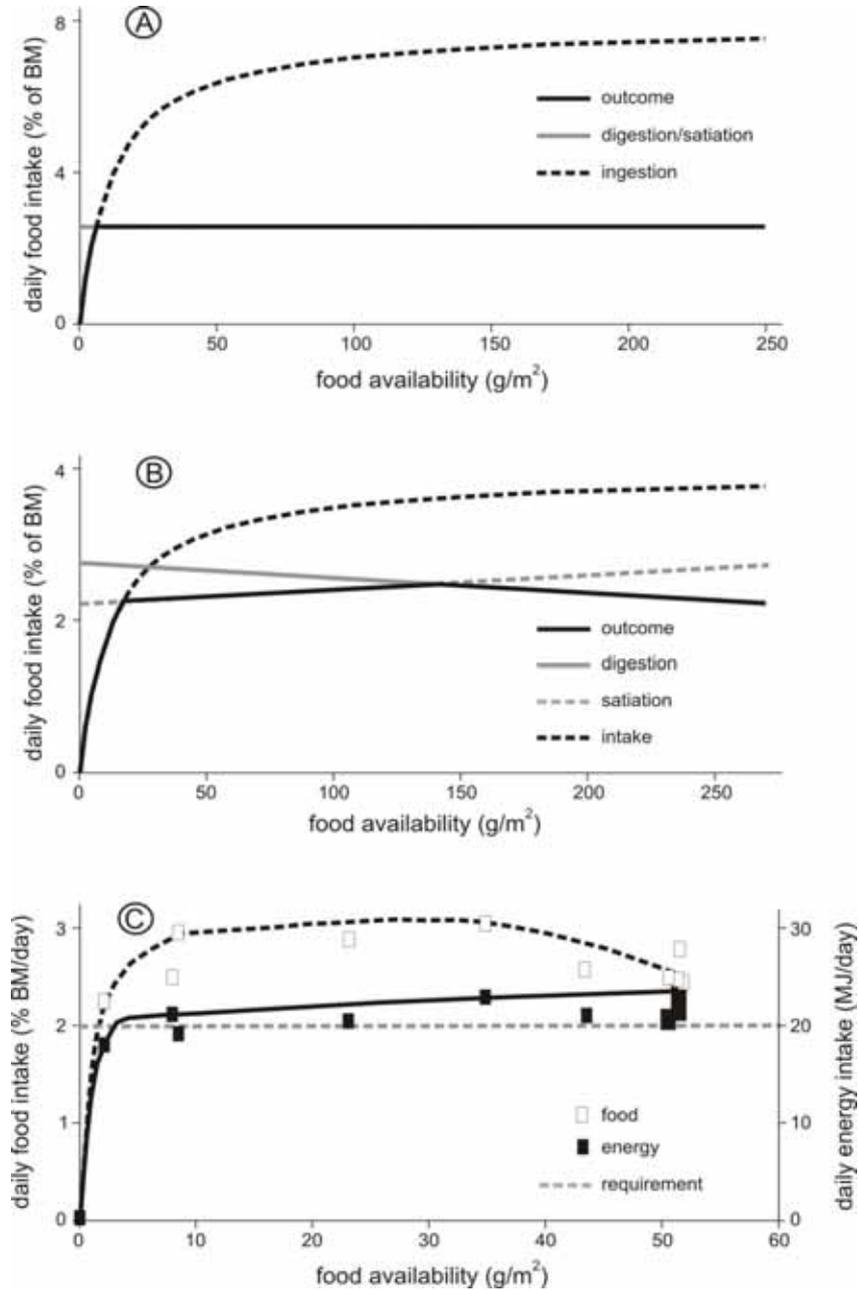
Figure 8.6. *Food intake and energy-gain responses of kudus to seasonally changing food availability, both in terms of gross food intake and rate of gain of digestible energy (from Owen-Smith 2002a)*

ACCOMMODATING ENVIRONMENTAL VARIABILITY IN FORAGING MODELS

Simple foraging models aimed at predicting average diets from average measurements on vegetation and other factors can be misleading. A good example is presented by the linear programming model (LPM, Belovksy 1986), which seemed amazingly accurate in predicting the broad diet composition, in terms of plant types

Rate-averaging models fail to accommodate environmental variability while dynamic state-variable models remain to be overcome

like grass versus browse, for almost all herbivore species to which it was applied. This model proposes that herbivores trade the nutritional benefits of abundant food offering high intake rates but restricted digestibility against those of more nutritious foods available in lower quantities, given the constraints of daily foraging time and digestive capacity. The underlying assumptions are reasonable and well supported, as documented above. Yet, given the practical difficulties in measuring all of the relevant factors influencing food gains, it seemed surprising that the predictions of LPM should repeatedly be so close to reality (Hobbs 1990; Huggard 1994). I was initially surprised to find a close match between predicted and observed diets when applying LPM to the data that I had collected for kudus (Owen-Smith 1993). I doubted that kudus made such a crude distinction between broad plant categories (woody browse versus forbs), given the wide variability in nutritional quality within these classes.

Hence I investigated further whether kudus actually responded to variation in the parameters determining the optimal diet in LPM between foraging sessions and days. They did not adjust their diet composition as predicted. This meant that the putative constraints of digestive capacity and daily foraging time were not actually effective. The apparent predictive success arose from a logical circularity in the way the model was being applied. Assuming that digestive capacity and foraging time were constraining, their upper limits were assessed from average observed values of digestive contents and daily foraging time. These values were then used to make predictions, which of course confirmed the model. Even if the potential digestive capacity (or foraging time) was actually greater than measured, the intersection of the average observed settings of the supposed constraints must correspond with the average observed diet, if measurements are accurate (Owen-Smith 1993, 1996).

Box 8.2. *Dynamic state-variable models*

Dynamic optimisation models differ from rate-averaging models by assessing optimality in terms of the state (of the gut, or body condition, or whatever) achieved as a result of decisions made over some extended time period. This state has an expected fitness associated with it, e.g., an animal that has ample fat stores is more likely to survive and reproduce than one lacking body reserves at the end of the summer season. However, animals that are too fat could have reduced fitness, through being more likely to be predated. While it might be quite easy to define the optimal state to aim at, how to get there is more problematic. The trick in solving a dynamic optimisation problem is to work backwards from the end time to the start time. The optimal solution depends on being in the optimal state for future fitness at each stage, and hence is evaluated using a state-dependent fitness function. Solving a dynamic optimisation problem analytically constitutes a huge challenge, but it can be made more tractable by dividing time into discrete steps. Such models can also take into account uncertainty in the situation confronted at each time step, e.g., a predator may or may not be encountered, and the food type sought may or may not be found at that time. This leads into a procedure called 'stochastic dynamic programming'. The limitation for such models is that each additional choice doubles the number of computations that must be performed at each time step, to consider all the options and their consequences for fitness, an obstacle known as the 'curse of dimensionality'.

Another approach to optimal decision-making in complex and changing environments uses concepts from neural networks to establish the weights to be given to various factors influencing the decision through intensive computation to explore the outcomes. This can be taken further using genetic algorithms to compute which sets of behavioural responses are more likely to persist in a population than others.

Mangel and Clark (1988) introduced the concept of stochastic dynamic programming to behavioural ecologists, while Clark and Mangel (2000) and Houston and McNamara (1999) present more comprehensive treatments. Anderson (1995) gives an introduction to neural networks, while Goldberg (1989) describes how genetic algorithms can be used.

More fundamentally, in variable environments one would expect animals to have some reserve capacity to cope with the extreme conditions that they have to face at times. Hence, under average or benign conditions they should appear somewhat

Models projecting equilibrium outcomes are inappropriate for representing effects of resource variability on population growth

slack in their foraging behaviour. How much reserve capacity should animals have, in digestive space, temperature tolerance or any of the other factors affecting foraging efficiency? I noted above that the daily foraging time of kudus was limited by high midday temperatures on about one day in seven. Over what period of the year is the maximum digestive capacity actually filled at the end of a foraging session, allowing for possible seasonal adjustments in the physical capacity?

Dynamic state-variable models projecting the trade-offs between current decisions and future states seem to offer the most appropriate framework for accommodating environmental variability (Box 8.2). However, the obstacle to be overcome is the 'curse of dimensionality'. Each additional choice doubles the number of computations, and once the number of options exceeds three or four, computer memory and computing time begin to become a restriction. At a plant species level, the number of food types available to kudus was well over 100. Nevertheless, most of these plant species are rare, and for the diet breadth model I

reduced the effective number of food types to around seven (Owen-Smith 1993). At any point in time, the alternate decisions are simply either widening the diet by one food type, or eliminating a food type from the diet. Hence I believe that a dynamic diet-choice model is feasible, if structured around a restricted set of choices at each time step. Neural network models (Anderson 1995) offer an alternative approach towards establishing the optimal choice in complex environments. They have been applied to habitat selection of, for example, panda bears (Liu 2001; Liu et al. 2002), but have yet to be applied to foraging behaviour.

The challenges of dynamic optimisation are more readily overcome considering the allocation decisions that herbivores must make for the surplus resources they have acquired: to grow bigger, to grow fatter, or to grow babies (Owen-Smith 2002a). If storing fat is costly for survival, animals should store fat as late as possible, and just enough for their needs to survive the adverse season, plus whatever additional amount is needed to ensure successful reproduction in spring. Hence during times of the year when fat reserves are adequate, animals may appear somewhat slack in their foraging behaviour.

For most models in ecology, equilibrium solutions are sought and identified analytically. For example, the environmental 'carrying capacity' is designated as the equilibrium population that can be maintained by the balance between density-dependent birth and death rates, dependent in some undefined way on resource availability. This zero-growth density may be asymptotically stable despite environmental perturbations to its level, and the disruption of lagged density feedbacks (Turchin 2003). An alternative approach links the population dynamics interactively to the growth potential enabled by resources consumed, less background mortality losses (Caughley 1976). It can generate either an asymptotic approach to an equilibrium density, or oscillations generated by the delayed effects of consumption on resource production. Both approaches overlook the enormous fluctuation in the vegetation resources supporting herbivore populations during the course of a year (e.g., Sinclair 1977; Prins and Beekman 1989; Prins 1996). Any equilibrium between population growth and resource supplies is no more than transient. In the benign summer or wet season, there is more food available than herbivores can possibly use, while during the adverse winter or dry season remaining resources do little more than alleviate starvation. The population level sustained is the emergent outcome of the counterbalancing of the changing gains and losses at different stages of the seasonal cycle. Storage buffers like body-fat reserves help dampen the seasonal fluctuations that might otherwise occur, but when thresholds are surpassed herbivore populations can crash (Walker et al. 1987).

To have predictive value, population models must incorporate the adaptive responses of consumers to the changing conditions that they face daily, seasonally and between years. The foundations for such a modelling approach, integrating foraging behaviour into population and community dynamics, are laid in Owen-Smith (2002a). Consumer-resource models incorporating functional heterogeneity in resources coupled with adaptive responses by consumers generate radically different dynamics to those assuming uniform, unchanging environments (Owen-Smith 2002b, 2002c).

SYNTHESIS

The foundations for theoretical resource ecology are taking shape, below the ecological sterility of classical population dynamics, which links consumers with resources through a nebulous 'carrying capacity', and the mechanistic vagueness of food-web analysis at the community level. Animal ecology needs to look upwards towards higher-level processes taking place beyond the time frame of bites and steps, and encompass phenotypic adaptation in physiology, morphology and life-history events as well as behaviour. Population ecology needs to explore the mechanisms linking the survival and reproductive rates of consumer to resource variability. The impacts of parasites and predators on populations operate to a large extent within the context of the resource status affecting the vulnerability of consumers to such amplifying influences on mortality (Hik 1995; Sinclair and Arcese 1995b; Prins 1996).

Box 8.3. *Testable hypotheses for future research*

Hypothesis 1. Changes in foraging behaviour are adapted more to reduce losses during adverse periods than to maximise gains during good times.
Hypothesis 2. Consumers have surplus capacity or tolerance to cope with adverse extremes that occur no more frequently than once in seven days, or other appropriate period of environmental variation.

This chapter has explored some of those links, moving upwards across temporal scales from periods within days through the diel and seasonal cycles to variability between years. It has encompassed not merely the direct consequences of foraging behaviour in terms of diet composition, but also the additional behavioural responses involved in food procurement, i.e., daily time allocation, searching movements, plus the phenotypic adjustments associated with processing and allocating the food gains. In the light of these responses, simplistic notions of the 'functional response' need to be modified, and alternative optimisation approaches accommodating environmental variability explored. Some hypotheses for future research are formulated in Box 8.3. Wide seasonal fluctuations in food availability expose the non-linearities inherent in functional relationships, and emphasise how the adverse extremes override the more prevalent benign conditions. Population models incorporating equilibrium 'carrying capacities' or average conditions are inappropriate and mechanistically misleading.

In a previous exploration of foraging theory, a 'dumb' ungulate, with inflexible food selection, was contrasted against a 'clever' ungulate, adjusting its diet selection to maximise its immediate rate of nutrient gain (Owen-Smith and Novellie 1982). The more far-sighted strategies of a 'wise' ungulate remain to be defined. The need to recognise 'individual trait plasticity' in both population and community ecology has become increasingly widely recognised (Schmitz et al. 2003). The importance of the key resources supporting animals during crucial periods of the year and in crunch years was emphasised by Illius and O'Connor (1999). Landscapes retaining functional heterogeneity in the resources supporting herbivore populations could avert the roller-coaster dynamics to which these species are prone (Owen-Smith

2004). The chapters of the book contribute substantially towards expanding the foundations for rigorous resource ecology, addressing consequences of the spatial and temporal variability that is a basic feature of the real-world environments that large herbivores, and indeed most other organisms, occupy.