

CHAPTER 6A

PREDICTIVE MODELLING OF PATCH USE BY TERRESTRIAL HERBIVORES

JOHN M. FRYXELL

Department of Zoology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada
E-mail: jfryxell@uoguelph.ca

Abstract. All animals are faced with substantial variation in resource abundance over time and space. Patch-use theory, often based on optimality principles, can be useful in gaining insight into possible evolutionary solutions to this puzzle. A key consideration in applying patch-use theory to large terrestrial herbivores is that local variation in the nutritional quality of food is often inversely related to local resource abundance. Trade-offs between resource quality and abundance can change traditional models of patch use in important ways, some of which are explored in this chapter. I consider two aspects of patch-use decisions: which patches to visit and how long to stay in a patch, once visited? Empirical data for large herbivores often suggest that optimality principles are useful in explaining which patches are used in a landscape, but are less successful at explaining how long herbivores choose to stay in a particular patch. I end the chapter by exploring emerging challenges in applying patch-use principles to landscape ecology of large herbivores.

Keywords. patch selection; giving up; patch departure; short-term versus long-term intake; constraints on foraging rates; functional response

INTRODUCTION

Trophic interactions by definition involve fluxes over time in the abundance of both resources and consumers. While general ecological theory was largely founded on the notion of well-mixed, homogeneous resources, this abstraction is at odds with ecological reality. For example, the foods required by all large herbivores are patchily distributed, regardless of whether those herbivores are grazers that feed predominantly on graminoids and sedges, or browsers that feed on forbs, shrubs or the lower branches of trees. An indiscriminate forager would almost always prove to be less efficient in acquiring vital nutrients or energy than one that is more selective, simply because the indiscriminate forager would be just as likely to feed in patches with low rates of gain as in more rapidly-yielding patches.

While it is debatable whether the fitness consequences of foraging indiscretion are inevitably serious, it nonetheless remains incontestable that appropriate decision-



Patch-use models can be used as a cornerstone for a new approach to trophic interactions

making should have selective advantages, at least sometimes. In this chapter, I consider the underlying nature of spatial variability in plant resources available to large terrestrial herbivores, review the potential constraints that may guide appropriate decision-making, apply optimal and sub-optimal models of decision-making in the face of such spatial variability,

and evaluate the empirical evidence for such decision-making. My objective in this chapter is to explore the use of patch-use models as a cornerstone for a new approach to trophic interactions, one that considers fluxes in resource and consumer abundance over space as well as time.

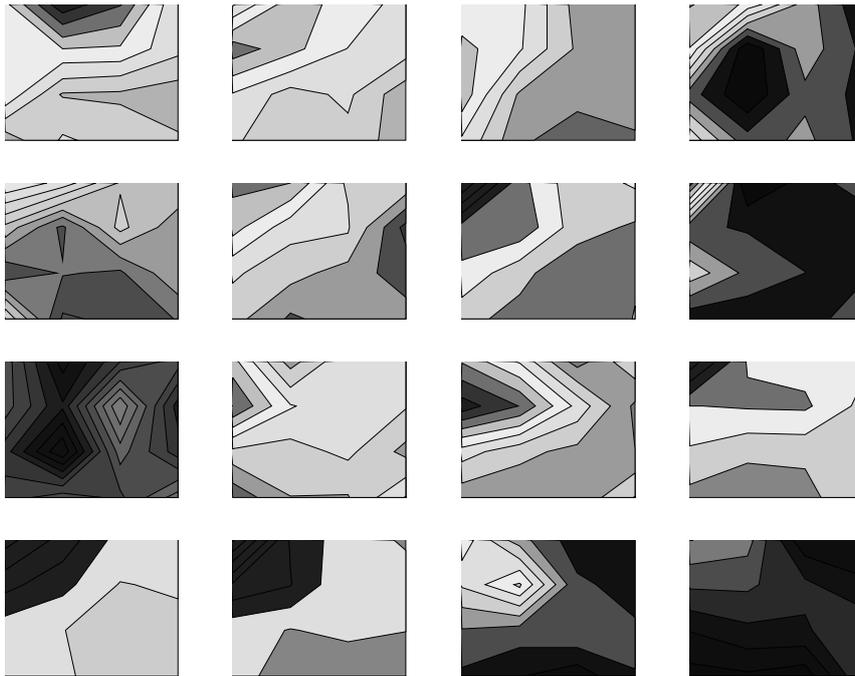


Figure 6.1. Spatial variation in grass biomass on the Serengeti Plains over the course of 2 growing seasons (1995 and 1996), based on 220 measurements per census of grass and cover taken every km during transects driven within a 40×40 -km grid (Fryxell et al. 2004)

RESOURCE VARIABILITY IN SPACE

At almost any spatial scale imaginable, there is pronounced variation in plant abundance and quality, even in rather featureless systems. Consider, for example, the Serengeti Plains of Tanzania. Growing conditions on the plains are tilted in favour of grasses in a variety of ways. There is a calcareous pan several feet below the surface that is too shallow to permit deep root penetration by tall trees, but deep enough to permit unrestricted rooting by graminoids. Rainfall is relatively low, sporadic, and temporally restricted to a short growing season of 4 or 5 months (McNaughton 1985). The net result is a sward of low-growing grasses and sedges mixed in with low-lying forbs and shrubs, and only a thin scattering of trees, particularly near watercourses. If there is a uniform resource base anywhere in the world, this should be it. Nonetheless, sampling of graminoid abundance over a 1600-km² study area clearly demonstrates considerable spatial variability at both fine and coarse spatial scales (Figure 6.1). Nor does the situation get better if one looks at ultra-fine scale, because there is obvious variation in biomass density and quality among grass tufts and even as one progresses from the soil surface to the growing point. If one repeats the exercise throughout the growing season, the patterns of graminoid abundance shimmer and shift in space from one census to the next (Figure 6.1). From a grazing herbivore's point of view, plant resources are highly variable in both time and space (Skidmore and Ferwerda, Chapter 4; Owen-Smith, Chapter 8).

Resource availability is perhaps slightly more consistent from the point of view of a browser, particularly those that feed on low branches of emergent woody plants,



There is no spatial scale at which resources are uniform for large herbivores

because growth rates are less pronounced and the spatial distribution of stems changes over a decadal, rather than annual, time frame. Even browsers, however, face considerable variation in the ratio of rich versus nutritionally-poor plant tissue within and among plant ramets. In seasonal environments, of course, usable tissue availability of woody plants varies considerably

over time (Owen-Smith, Chapter 8).

In sum, there is no spatial scale at which resources are uniform for large herbivores. Meaningful patch choices are possible at the scale of the feeding station, the foraging bout, daily home range, and seasonal home ranges.

ALTERNATE MODELS OF MASS, ENERGY, AND NUTRIENT INTAKE

Short-term intake of food or energy

Before one can consider patch-use decisions, further consideration of constraints on foraging rates is needed. The functional response is the cornerstone principle of all foraging models (Holling 1959; Spalinger and Hobbs 1992; Laca, Chapter 5). It specifies the pattern of food intake with respect to food abundance. The precise

manner in which this occurs depends, not surprisingly, on the mode of feeding and the distribution of food items in the environment.

The simplest (and oldest) way to represent this process is to imagine that food occurs in discrete chunks (bites) that are distributed randomly across the environment. We furthermore imagine that each forager wanders aimlessly across a featureless landscape, feeding continuously, with no other distractions or needs for shelter, social interaction, mating, or predator avoidance. These assumptions may seem ludicrous at first glance, but they may not be far off the mark for large herbivores that are commonly faced with sparse resource abundance. Indeed, it is not uncommon to find conditions under which large herbivores forage for 10-12 hours per day.

Spalinger and Hobbs (1992) started from the basic recognition that terrestrial herbivores differ from most other heterotrophs in being able to move from one prey 'encounter' to the next while they are processing the results of the last successful 'attack'. In other words, herbivores can walk while they chew. This subtle fact can have a surprisingly large impact on foraging because of its consequences for the rate at which a foraging herbivore encounters food. In conventional predators, once a prey item has been found, the predator must invest a further period of time in 'handling' the item before search can be renewed. In contrast, larger herbivores can move onward as soon as they have made a bite, processing the bite as they move on to the next feeding station. This shortens the intervals between bites considerably, particularly when the forager can see the next bite as it departs from the last one. Nonetheless, foraging reduces the velocity with which individuals move across the landscape.

If an animal is foraging in a desert-like landscape, then there can be an appreciable distance between bites. As before, the rate of encounter with bites (λ)



In contrast to other consumers, herbivores can walk while they chew, which has a large impact on the rate of encountering food

equals the velocity (v) multiplied by the foraging radius (w) and the density of bites per unit area (D). For the reasons mentioned above, velocity is compromised to a certain degree by each bite taken, so that effective velocity equals the maximum possible velocity (v_{max}) minus the bite frequency ($v w D$) multiplied by the velocity reduction per bite (δ).

Experimental work by Shipley et al. (1996) nicely illustrates that there are profound changes in movement velocity between feeding stations for terrestrial mammals faced with experimental swards. After rearranging the terms to solve for v , Spalinger and Hobbs (1992) would predict that a forager would have an average velocity of $v = v_{max} / (1 + \delta w D)$. It therefore follows that $\lambda = v w D = v_{max} w D / (1 + \delta w D)$. Hence, the food intake rate would equal bite size (S) multiplied by the encounter rate with bites (λ)

$$X(S) = \frac{v_{max} w D S}{1 + \delta w D} \quad (1)$$

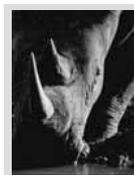
Note that there is no explicit handling time *per se* as the herbivore makes each bite. The successful forager loses velocity with each bite, but other than that there is no direct time investment in processing bites. The Spalinger-Hobbs equation predicts that intake will be linearly related to bite (i.e. stem) size, but the relationship to stem density will be curvilinear, with decelerating shape.

One troublesome element in the Spalinger and Hobbs (1992) functional response is that one cannot actually measure bite size without explicit reference to the animal. If one is prepared to assume that bites are synonymous with ramets, then one can make *a priori* predictions about bite rates and intake rates in relation to measurable ecological variables, ramet density and ramet size, which when multiplied together simply yield plant biomass ($V = SD$). It readily follows that cropping rates are a linear function of plant biomass under these conditions (by substituting V for SD in the equation for $X[S]$)

$$X(V) = \frac{v_{\max} w V}{1 + \delta w D} \quad (2)$$

The scenario in which bites are widely spaced was termed process-1 foraging by Spalinger and Hobbs (1992). It is directly comparable to process-2 foraging, in which the herbivore can actually detect each bite at some distance away, making a beeline between bites rather than searching blindly. This has rather an obvious, but minor, effect on feeding rates: encounter rates are increased relative to that of comparable process-1 foragers. A more important distinction can be drawn with situations in which bites are densely distributed across the landscape. This kind of ecological circumstance, termed process-3 foraging by Spalinger and Hobbs, implies that herbivores have insufficient travel time between bites to process the bite obtained at the preceding station. Under extreme bite densities, the rate of intake would therefore be completely dictated by the rate of clearance of bites from the mouth before a new bite could be taken, because the animal takes no time to move between bites. Hence, in process-3 foraging, intake is completely constrained by handling time rather than bite encounter.

What ecological factors might influence the all-important handling-time constraint? Bite size clearly must play a predominant role (Black and Kenney 1984;



Food intake can be constrained by searching and ingestion

Illius and Gordon 1987; Spalinger et al. 1988; Ungar et al. 1991; Shipley and Spalinger 1992; Gross et al. 1993; Bradbury et al. 1996; Wilmshurst et al. 1995; 1999b). Other factors that also influence the handling time are plant toughness or the amount of protection afforded by spines and thorns (Cooper and Owen-Smith 1986). Spalinger and Hobbs suggest that

handling time can be usefully decomposed into cropping of bites versus chewing those bites. These are mutually exclusive activities, so the time-budgeting logic that underlies other functional response behaviours can be applied to process-3 foragers.

One might predict that cropping rates would tend to decline with bite size because chewing of larger bites tends to lengthen the interval between bites, for the simple reason that the rate of input to the mouth cannot exceed the rate of output. Assume that there is a maximum rate of chewing (R_{max}) that decreases by each bite taken. It then follows that intake rate $X = R_{max} - \beta B$, where β is the effect of each bite on the rate of chewing and B is the bites per unit time. If we presume that intake rate can be estimated by multiplying together bite rate (B) and bite size (S), then substitution of $B = X/S$ for B in the expression $X = R_{max} - \beta B$ and rearranging terms to solve for intake as a function of size $X(S)$ yields the following functional response equation for process 3 herbivores (Spalinger and Hobbs 1992)

$$X(S) = \frac{R_{max} S}{\beta + S} \quad (3)$$

It may be useful once again to derive an equivalent expression for intake in relation to a measurable ecological variable such as biomass V , by converting $S = V/D$

$$X(V) = \frac{R_{max} V}{\beta D + V} \quad (4)$$

One interesting feature of this line of reasoning is that the same pasture could change from process-1 to process-3 conditions through simple growth processes. When ramets are small, chewing time is so short that there is no conflict with cropping. Hence, the functional response is linear, increasing proportionately with each unit increase in plant abundance. At ramet sizes above this threshold, the situation reverts to a process 3, and intake is curvilinearly related to plant abundance. The net effect of changing mechanistic constraints on intake is a discontinuous functional response, with the discontinuity at the point of transition between process-1 and process-3 foraging (Figure 6.2a). Similar conclusions have emerged from alternate mathematical formulations in which herbivore search can overlap with processing (Parsons et al. 1994; Farnsworth and Illius 1996). Mathematically, this switch in mechanistic constraints can be represented by the following piecewise function for food intake

$$X(V) = \min \left[\frac{v_{max} w V}{1 + \delta w D}, \frac{R_{max} V}{\beta D + V} \right] \quad (5)$$

A substantial body of experimental work corroborates the key predictions of the Spalinger-Hobbs model. Grazers presented with sward conditions likely to produce process-3 conditions usually show a smoothly decelerating functional response, as predicted (Wickstrom et al. 1984; Short 1985; Hudson and Frank 1987; Wilmshurst

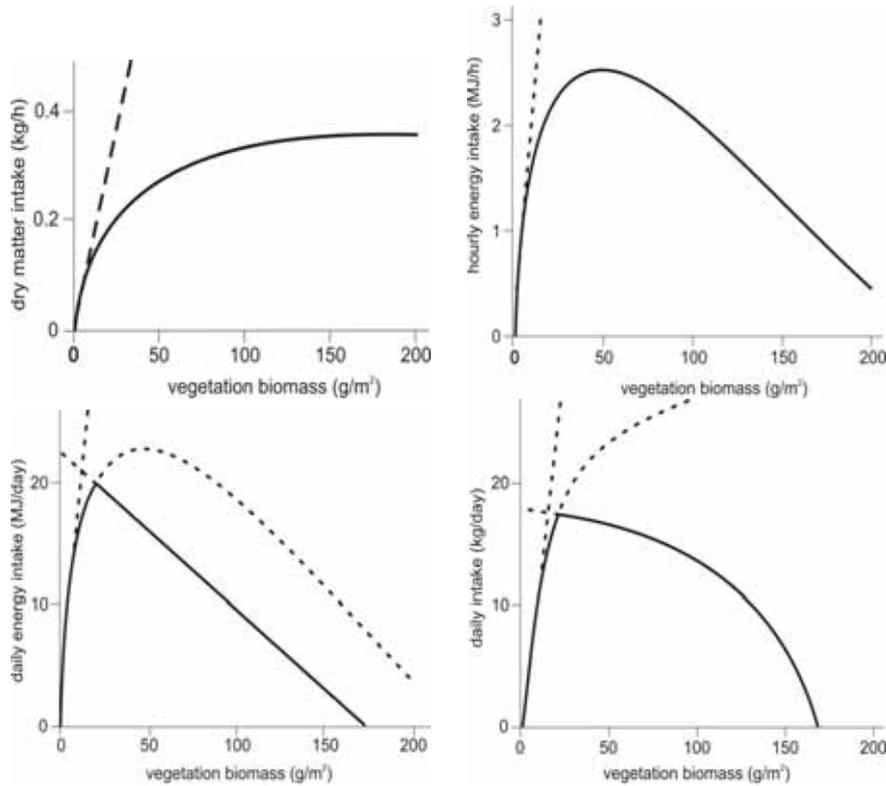


Figure 6.2. Estimated rates of intake of dry matter per hour (a), digestible energy per hour (b), digestible energy per day (c), and dry matter per day (d) for Thomson's gazelles, based on the experimental results of Wilmshurst et al. (1999)

et al. 1995; 1999a; Bergman et al. 2000). On the other hand, browsers often show very poor or no relationship to biomass per se (Trudell and White 1981; Spalinger et al. 1988), but do show positive relationships to bite size (Wickstrom et al. 1984; Spalinger et al. 1988). More tightly controlled comparisons have been enabled in recent years by the use of experimental swards mounted on plywood boards at different ramet spacing, ramet height, and biomass levels. Such experiments provide strong support for the prediction that intake should be positively related to plant size (Shipley and Spalinger 1992; Gross et al. 1993a, 1993b; Drescher 2003; Hobbs et al. 2003). Gross et al.'s (1993a) paper is particularly instructive, in that they experimentally controlled for the effects of plant size, plant spacing and plant biomass, which co-vary in most natural systems.

Based on a large set of these observational and experimental data, Shipley et al. (1994) calculated allometric coefficients for the key parameters in the Spalinger-Hobbs (1992) model, most of which were predicted with a remarkably high degree of precision. Key parameters relate of course to maximum rates of chewing and bite

dimensions. These characteristics are strongly affected by the shape and dimension of the dental arcade, which themselves scale allometrically with body size (Illius and Gordon 1987; Gordon et al. 1996). Controlled studies in experimental swards clearly demonstrate that bite dimensions depend strongly on the spatial distribution of plant tissues and sward height (Laca et al. 1992, 1994b), with profound impact on rates of depletion of swards (Laca et al. 1994a).

More recently, Hobbs and co-workers set up experimental trials to test directly the predictive ability of the Spalinger-Hobbs equations relative to other mathematical formulas for the functional response (Hobbs et al. 2003). Results from these experiments indicate that the mechanistic models of Spalinger and Hobbs (1992) were the best predictors of short-term food intake.

It is a relatively simple matter to expand the functional response to model short-term intake of specific nutrients or energy $Y(V)$, by simply multiplying the functional response by quality of the ingested forage $Q(V)$

$$Y(V) = \min \left[\frac{v_{\max} w V Q(V)}{1 + \delta w D}, \frac{R_{\max} V Q(V)}{\beta D + V} \right] \quad (6)$$

Because digestible energy or nutrient concentration usually declines with plant biomass, primarily due to maturational changes in tissue as plants increase in size, $Y(V)$ will often be a dome-shaped function of plant biomass (Figure 6.2b).

Digestive constraints and long-term intake of energy or mass

Over a longer time frame, such as a day, the rate of intake can be limited by digestion rather than ingestion (Belovsky 1978; Demment and Van Soest 1985; Fryxell 1991; Illius and Gordon 1992; Newman et al. 1995; Laca and Demment 1996; Hodgson et al. 1997). This is an important topic of continuing physiological



Over a longer time frame, the rate of intake can be limited by digestion rather than ingestion

research, and detailed discussion of the digestive kinetics is well beyond our review. Suffice it to say that clearance of digesta from the tract can be a rate-limiting step: more food cannot be ingested than gets cleared from the digestive tract. The time it takes to process material in the digestive tract tends to be inversely related to the nutritional quality.

Forage that is high in lignin and cellulose but low in cell contents tends to digest more slowly than material of higher nutritional quality. As a consequence, the potential for digestive constraints to limit daily intake is more pronounced in poorer forages than in better forages. That is not to say that there is no potential for physiological adjustment to poor nutritional quality. Indeed, there is some evidence that both small (Gross et al. 1985) and large (Owen-Smith 1994) herbivores can adjust digestive capacity or passage rate to some degree in response to declines in food quality, but perfect compensation seems to be rare or impossible. Otherwise, farmers would raise their livestock on sawdust.

In an ecological setting, this has interesting consequences. A herbivore feeding in patches of poor forage might have daily intake that is constrained by quality of food, whereas the same animal feeding in patches of high quality might have daily intake that is constrained by food abundance. Hence, it is plausible to postulate that daily intake could be regulated by either ingestive or digestive constraints (Belovsky 1978; Fryxell 1991; Newman et al. 1995), depending on the ecological circumstances.

Such trade-offs often come into play in comparing the energetic gain obtainable from grass patches of different maturational stage. As graminoids mature, the proportion of poorly digestible tissue increases in order to meet the structural needs of an erect versus prostrate growth form. Hence it is common, although by no means ubiquitous, for nutritional quality to decline with ramet height or biomass of the sward (assuming similar plant spacing). These maturational changes in quality suggest that daily energy gain in herbivores might be limited by ingestive constraints when plants are small, but by digestive constraints when plants are taller.

Wilmschurst et al. (1999a) tested this prediction for Thomson's gazelles in the Serengeti ecosystem of Tanzania. Digestibility of leaf and sheath tissue sampled from areas occupied by territorial gazelles declined by half with a fourfold increase in grass abundance. Feeding trials on captive animals presented with forage of



Daily energy gain in herbivores might be limited by ingestive constraints when plants are small, but by digestive constraints when plants are taller

varying maturational stage suggested that *ad libitum* daily intake of energy increased sharply with digestible energy content. Functional-response trials using experimentally controlled grass swards on plywood boards clearly demonstrated a positive relationship between instantaneous intake and plant abundance. As predicted by the Spalinger-Hobbs model,

instantaneous intake was significantly related to stem density per unit area for small ramets, but constant for large ramets. Daily energy gain potentially obtainable from the instantaneous functional response was then compared to the energy gain dictated by the *ad libitum* feeding trials. This comparison showed that ingestive processes regulate intake for only the shortest of swards commonly encountered on the Serengeti Plains. Similar patterns have been corroborated for two other wild herbivores: elk (Wilmschurst et al. 1995) and woodland bison (Bergman et al. 2000, 2001). The logical conclusion is that daily rates of energy gain in mammalian herbivores can be controlled by constraints on digestion, rather than ingestion.

Our conceptual understanding of the processes involved in digestion by wild ungulates lags far behind our conceptual understanding of ingestion, no doubt because it demands physiological experimentation that is intrinsically costly and logistically challenging for large, wild organisms. Fortunately, there is a substantial amount of information available on domesticated ungulates that can be taken advantage of to formulate predictive models of digestive limitation (Illius and Gordon 1992; Meissner and Paulsmeier 1995). This work suggests that daily intake of energy is proportionate to the digestible energy content of forage, which scales with plant biomass. We can accordingly combine the ingestive and digestive

constraints into the following piecewise formula, after scaling up the short-term functional response to a daily time scale, by multiplying by the maximum daily feeding time ($t_{max} = 9\text{h}$ in the case of Thompson's gazelles):

$$Z(V) = \min \left[\frac{v_{max} w V t_{max} Q(V)}{1 + \delta w D}, \frac{R_{max} V t_{max} Q(V)}{\beta D + V}, \alpha - \psi V \right], \quad (7)$$

where α is the maximum daily rate of energy consumption, and ψ is the rate of decline in the daily rate of energy consumption with each unit change in digestible energy content of the ingested forage. Note that we have presumed a linear function for the digestive constraint in relation to plant biomass V , based on the experimental data on Thomson's gazelles gathered by Wilmshurst et al. (1999a). This pattern is shown in Figure 6.2c. Note that we are now postulating a multiple piecewise formula, with the leftmost piece constrained by stem density, the middle piece constrained by bite processing, and the right-hand piece by digestion.

We can extend these results to consider a fourth alternative gain function: daily intake of dry matter (Figure 6.2d). This is simply obtained by dividing the formula for daily energy gain by energy content of the ingested forage

$$W(V) = \min \left[\frac{v_{max} w V t_{max}}{1 + \delta w D}, \frac{R_{max} V t_{max}}{\beta D + V}, \frac{\alpha - \psi V}{Q(V)} \right] \quad (8)$$

We now have 4 different foraging objectives that might conceivably influence patterns of patch use by large herbivores. They might prefer resource patches producing high rates of short-term intake of dry matter ($X[V]$), short-term intake of energy or nutrients ($Y[V]$), daily intake of dry matter ($W[V]$), or daily intake of energy or nutrients ($Z[V]$). To be honest, we have no *a priori* reason to expect one objective to dominate above all others, for all species, under all circumstances. For example, short-term intake of dry matter or energy might dominate behaviour of an animal faced with minor energetic stress or faced with other important needs, such as mating, predator avoidance or social needs. On the other hand, we might expect long-term energy or nutrient intake to dominate behaviour of animals facing significant energy shortfall. One could argue these circumstances, no doubt, long into the night. A more useful approach is to go back to nature, to see which objective (model) is most consistent with observed patterns of herbivore behaviour.

The actual pattern of patch use by herbivores depends, of course, on the degree to which herbivores select particular patches and time that herbivores tend to spend in each patch, at probably any spatial and temporal scale. In principle, it should be possible to consider each of these decision variables in isolation, but this is rarely done, particularly for free-ranging animals. Rather, most researchers score overall patch use, and interpret patterns with respect to one or the other decision variable.

PATCH PREFERENCES

Now that we are armed with some understanding about the constraints affecting the rates of dry-matter, nutrient or energy intake, we can consider patterns of patch preference. One common approach to testing such problems is to generate an experimental arena of patches of different resource levels.



Different foraging objectives might influence patterns of patch use by large herbivores

We have performed this kind of experiment twice, on wapiti (*Cervus elaphus* L.) and wood bison (*Bison bison athabascae*), making predictions about expected patterns of patch use on the basis of direct estimates of key

foraging parameters relating to both the ingestive and digestive constraints.

Parameter estimates for wapiti had indicated that net energy gain should be maximized when feeding on grass swards of 100-110 g m⁻² (Wilmshurst et al. 1995). We constructed large experimental mosaics of grasses ranging in biomass from 80 to 300 g m⁻². The patches that fell closest to the long-term rate-maximizing value were selectively used most heavily, with degree of use proportionate with net energy gain (Wilmshurst et al. 1995). By coincidence, an identical experiment was conducted simultaneously by another research team on red deer in Norway (Langvatn and Hanley 1993), with results also indicative of long-term nutrient or energy maximisation. These independent studies suggest that the behaviour of wapiti conformed to a matching rule. In other words, patches yielding twice as high a rate of energy gain were used twice as often as patches of lesser gain.

In a second study, we constructed similar mosaics of sedges ranging in biomass from 107 to 419 g m⁻². Prior experimental work (Bergman et al. 2000, 2001) had indicated that daily energy gains should be maximised at a sward biomass of 10 g m⁻², hence the shortest swards in our mosaic should have yielded the highest daily energy gain. Our results were totally inconsistent with the energy-maximising model: bison preferentially grazed in patches with a biomass of 217 g m⁻², well above the predicted value (Bergman et al. 2001). Why might this happen? Our interpretation was that instead of maximising daily energy gain, bison were maximising the short-term rate of energy gain, i.e. acting as though ingestive constraints were the sole determinant of fitness (Figure 6.2). This suggests that animals were basing their decision on a different time frame than we were, valuing instantaneous rates of energy gain more than daily rates of gain.

We have no idea why bison might differ from wapiti in their evaluation of short-term versus long-term gains. Maximising short-term gains allows foragers to minimise the time required to meet an arbitrary energetic target, while reserving time for other activities that might enhance fitness, such as social behaviour, grooming or avoidance of potential competitors or predators. Bison may be more sensitive than wapiti to foregoing such activities, perhaps because social interactions are so important to future fitness or because of feeding competition that can accompany life in large herds (Manseau 1996). In any case, the key point is that the predicted outcome of this particular optimal-foraging model depends on the time frame under consideration – i.e. it is scale-dependent.

There is similar ambiguity in patch preference studies reported in the literature. In tightly controlled experimental trials, Laca et al. (1993) and Distel et al. (1991, 1995) showed that patch use by cattle was strongly linked to instantaneous rate of



Some herbivore species prefer patches with highest nutritional quality but low abundance, whereas others have reversed preferences

energy gain, but the experimental design in this case probably generated similar levels of plant quality despite contrasting levels of plant abundance. Wallis de Vries (1996) performed detailed calculations of daily and instantaneous energy gain for wild cattle. Opportunistic field data showed that long-term energy gain was a better predictor of patch use by cattle than

short-term gain (Wallis de Vries and Daleboudt 1994). In later trials with a mosaic of patches with high ($>600 \text{ g m}^{-2}$) and moderate ($>300 \text{ g m}^{-2}$) biomass, cattle showed a strong preference for the patches of lower biomass, with correspondingly lower rates of hourly energy intake but high rates of daily energy intake. In small-scale trials on manipulated vegetation patches, wild Svalbard reindeer preferred the patches with highest plant abundance, but lowest plant quality (Van der Wal et al. 2000), early in the growing season. Later in the summer, reindeer showed no preference among patches.

The bottom line is that some species prefer patches with highest nutritional quality but lowest abundance, whereas others have reversed preferences. There is an inherent difficulty, however, in interpreting most of the experiments in the published literature. If trials are conducted only on swards below the hump in the daily-intake function, then daily energetic intake is maximised by selecting patches with high abundance – that is, animals should apparently prefer quantity to quality. The opposite would be true for trials conducted for sward abundance to the right of the hump in the intake curve. Clearly, such trials call for non-linear model evaluation (Hobbs et al. 2003). Without careful parameter estimation, it is difficult to know which situation might apply, because the shape of daily energy intake in relation to plant biomass varies with herbivore body mass (Wilmschurst et al. 2000). To make modelling even more problematic, maturational changes in plant quality can vary enormously across sites (Albon and Langvatn 1992). The sensitivity to local parameter values and the non-linear form of the alternate gain functions present sizeable challenges to predictive patch-use modelling in large grazing herbivores.

Rigorous quantitative tests of patch preference by ungulates have been largely confined to tightly controlled experimental trials at small spatial scales. It is less clear whether these experiments can be used to predict patterns of space use of free-ranging herbivores at large spatial scales. This is important, because resource heterogeneity occurs at all spatial scales in the environment and we cannot say *a priori* at which spatial scale resource selection by grazers might occur (Senft et al. 1987a). Until we know the answer to this question, optimal foraging theory has little to add to current approaches to population management and conservation of large herbivores.

Very little work has addressed this key question in large grazing mammals. Schaefer and Messier (1995) performed one of the most detailed analyses to date on



Resource heterogeneity occurs at all spatial scales and we cannot say a priori at which spatial scale resource selection by grazers might occur

habitat (i.e., resource) preference of musk oxen at a multitude of spatial scales ranging from the population level to that within feeding stations of individuals. They found that patterns of food selection were generally consistent across spatial scales, although there were some reversals at different scales for marginal species. Nellemann (1997) found that musk

oxen in Greenland preferred areas of high graminoid abundance (over 100 g m^{-2}), suggesting that they valued short-term over long-term intake rates.

In an elegant set of experiments, Wallis de Vries and co-workers (1999) evaluated the effect of scale on decision-making by cattle feeding on a mosaic of patches of high and moderate grass biomass. In one set of trials, each patch in the mosaic measured $2 \times 2 \text{ m}$, whereas in another set of trials the patches measured $5 \times 5 \text{ m}$. Their results showed that selectivity was demonstrably higher in the coarse-grained than in the fine-grained environment, and as a consequence animals maintained higher levels of energy gain. Surprisingly, however, there was little evidence that animals altered the tortuosity of foraging trajectories to keep themselves longer in favoured patches or that they fed longer in favoured patches. Animals sought out preferred patches, but once there did little to stay in preferred patches.

Ward and Salz (1994) measured use of patchy madonna-lily plants by dorcas gazelles in the Negev Desert. During the dry part of the year, all live plant material was below ground, necessitating digging by the gazelles, whereas emergent plant tissue was fed upon during the growing season. Gazelles concentrated feeding activity in areas with high lily-bulb density, as evidenced by short move lengths between feeding stations and depth of digging. At the level of single bulbs, which could also be considered a 'patch', requiring an extended period of digging versus cropping, gazelles selected plants with large leaves during the growing season, but preferred small bulbs during the dry season. The latter was interpreted as an adaptive response to increased energetic costs relative to minor rewards associated with digging up large, deep bulbs.

Wilmshurst et al. (2000) evaluated patterns of habitat selection by radio-collared wildebeest in Serengeti, to test whether wildebeest preferred short swards (as expected if animals are maximising daily energy gain) or tall swards (as expected if animals are maximising short-term gain). They found that the spatial distribution at a large spatial scale was concentrated in areas of short grass, as predicted by the daily maximisation model, but sward selectivity seemed to be more strongly related to grass greenness than grass height at smaller spatial scales.

Seasonal patterns of migration by red deer in Norway show that use of specific ranges by deer was linked to seasonal and spatial variation in forage quality (Albon and Langvatn 1992). Animals wintered close to the coast, where nutritional quality of graminoids and herbs was higher than that of dormant plants in the summer range. Migration to higher elevations was apparently timed to coincide with the

emergence of nutritious immature plants. By migrating seasonally between the coast and the mountains, animals maintained a considerably higher nutritional plane than would be possible by sedentary behaviour in either coastal or upland areas.

In a more recent study (Fryxell et al. 2004), we used direct experimental data (Wilmschurst et al. 1999a) to parameterise the four foraging functions shown in Figure 6.3 (short-term food intake, short-term energy intake, long-term food intake and long-term energy intake) for Thomson's gazelles in Serengeti National Park. We then evaluated the ability of each of these models to predict the spatial distribution of gazelles across a 40×40 -km expanse of the Serengeti Plains. Predictions of gazelle spatial distribution were generated in relation to samples of grass abundance collected at several hundred sample points spread around the study area. At the same sites where grass abundance was sampled, we also counted all large herbivores in a semi-circle with a radius of 1 km. This exercise was repeated at roughly bi-weekly intervals during the growing seasons of 1995 and 1996, yielding 16 separate replicates of gazelle density relative to plant biomass. We then regressed observed gazelle density against relative fitness (Figure 6.2) predicted by each of the foraging models. Results clearly demonstrated that Thomson's-gazelle distribution was best predicted by long-term rate of energy intake, with animals preferring swards of 20-30 g m^{-2} . These data offer perhaps the strongest evidence to date that foraging gain can be used to predict patch preference at large spatial scales.

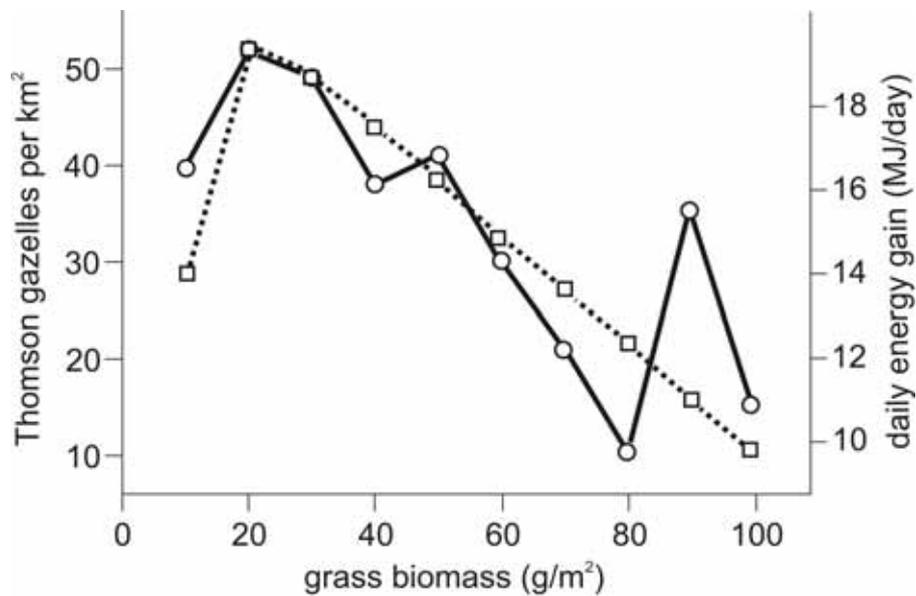


Figure 6.3. Observed (solid line and filled symbols) versus predicted (dotted line and open symbols) densities of Thomson's gazelles, based on a daily energy-matching strategy (Fryxell et al. 2004)

PATCH DEPARTURE RULES

A second bio-mathematical approach to understanding patch use is to consider whether foragers depart patches in a predictable manner. There is a well-developed body of theory that relates to patch departure, based on the so-called marginal-value theorem (Charnov 1976). The basis of the model is straightforward. Imagine that an animal forages indiscriminately within a patch for a given period of time. The longer a forager stays in a particular patch, the more the abundance of food items (bites, for a herbivore) within that patch declines. Changes in food abundance translate into slower rates of short-term food intake, according to the functional response, so there have to be diminishing energetic or dry-matter returns the longer a forager stays in each patch.

In principle, one could keep score of the cumulative gain obtained by the forager over time since it left the previous patch. For simplicity, we first concentrate on gain with respect to dry matter, rather than energy or nutrients. There is an initial period of time spent on travelling from the previous patch, during which no gain occurs. After the forager settles in the patch, gain increases at fast rate. Over time, however, the rate of gain decelerates, ultimately levelling off at an asymptote (maximum value) set by the total resource abundance initially present in the patch.

Now, let's calculate the long-term rate of yield, by dividing the cumulative gain at any particular residence time ($G[t]$) by the total elapsed time since the forager left the last patch (search time $[\tau]$ plus time in the current patch $[t]$). Charnov (1976) elegantly showed that the optimal decision for the forager would be to stay in the patch until the instantaneous rate of food gain ($dG[t]/dt$) equals the long-term rate of yield ($G[t]/[\tau+t]$). This is graphically shown by drawing onto the cumulative gain curve, the tangent going through the origin (Figure 6.4a). The optimal patch residence time is obtained by finding the point of intersection of this tangent and the cumulative-gain curve, and projecting downwards to the horizontal axis (Figure 6.4b).

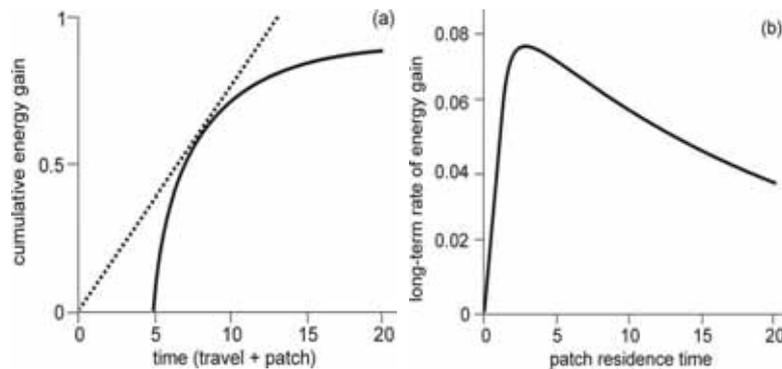


Figure 6.4. Cumulative energy gain within a patch (a) and long-term rate of energy gain (b) as a consequence of different patch residence times. The optimal decision is to stay in the patch until the marginal rate of cumulative energy gain (decelerating curve in a) equals the tangent to the curve rooted at the origin

The marginal-value theorem predicts that the more widely-spaced patches are, the longer should foragers stay in each patch. That is, the greater the time investment to relocate, the less picky should a 'clever' animal be. A relevant example of this kind of scenario is moose feeding on saplings or small trees. Astrom et al. (1990) tested whether animals spent longer at each sapling when saplings were widely spaced than when they were close together, having first shown that cumulative gain from a given sapling tended to decline over time. Results demonstrated that animals were in some sense sensitive to changing gain rates over time, as predicted.

Rigorous tests of the marginal value theorem with grazing ungulates are rare. Some experimental trials with cattle clearly suggest that patch departure can be well predicted by the marginal-value theorem, at least sometimes. Laca et al. (1993) and



Rigorous tests of the marginal-value theorem with grazing ungulates are rare

Distel et al. (1995) conducted an elegant series of trials with livestock grazing on small sward patches of given height (varying between 5-15 cm height) and bulk density (sparse versus dense), created by mowing an initially uniform pasture to desired levels. Because the sward was uniform before cutting, forage quality should vary little among patches, whereas

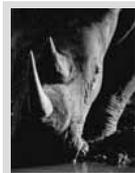
intake rates would positively scale with height and bulk density. Results of these trials clearly suggest preference by livestock for the patches with highest instantaneous intake. As predicted by the marginal value theorem, residence time within patches increased with distance between adjacent patches and with the degree of variation between good and poor patches.

Using the same data on Thomson's gazelles described earlier, we also tested alternate behavioural responses to the shifting mosaic of grass abundance across the Serengeti Plains (Fryxell et al. 2004). We found that gazelle distribution was best predicted by a mechanistic model that animals leave a given 10×10 -km patch when the long-term rate of energy gain in that patch fell below the mean value recorded across the rest of the landscape. Moreover, animals settled in adjoining patches at a rate proportionate to the rate of daily energy gain. These empirical results offer support for the marginal-value theorem. Departure was scaled to local rates of gain relative to the expectation elsewhere in the environment, as predicted. On the other hand, emigrating animals did not settle evenly in adjoining patches, but rather the tendency to settle was matched to relative energy gains. In other words, both patch departure and patch selection rules apparently influence patterns of spatial redistribution of Thomson's gazelles from week to week.

As indicated earlier, plant abundance varies spatially at every meaningful scale. This implies that food resources do not occur necessarily in discrete patches that are readily definable (Skidmore and Ferwerda, Chapter 4). The marginal-value theorem can be extended to situations in which resource abundance varies continuously over space (Arditi and Dacorogna 1988; Focardi and Marcellini 1995). The outcome of this modification is that animals should exhibit a threshold response, grazing at

every site encountered with a rate of food intake exceeding the expectation derived over the home range. Animals should locally deplete resources until intake rates reach the marginal value, at which point the grazer should move on.

There is limited evidence consistent with this continuous version of the marginal-value theorem. Wallis de Vries et al. (1999) found no evidence that cattle foraged longer in preferred patches, despite showing a strong preference in seeking



When resource abundance varies continuously over space, the marginal-value theorem predicts that animals should exhibit a threshold

those patches out. On the other hand, Jiang and Hudson (1993) showed data on captive wapiti suggestive of a threshold response at the feeding-station level. Focardi et al. (1996) made detailed observations of foraging trajectories of fallow deer and patterns of foraging over the course of those trajectories in relation to local resource abundance. In captive

deer, feeding in a fenced-in area, there did seem to be a threshold response to local food abundance, in accordance with the model. In a wild population of deer in another area, however, there was no apparent evidence of such a threshold response. The reason for this discrepancy is unclear, but may stem from differences in the motivational state of animals, differences in the degree of familiarity of foragers with resource distribution, and/or greater demands on informational processing by free-living animals living in the wild site. It is interesting that here again the evidence for strategic behavioural response is most compelling in captive, rather than wild, herbivores.

SYNTHESIS

A new generation of spatially-explicit models of herbivore movement behaviour has emerged in the past decade (Turner et al. 1993; Moen et al. 1997; Grünbaum 1998; Farnsworth and Beecham 1999; Fryxell et al. 2005), capitalizing on rapid growth in micro-computing power needed to consider detailed spatial processes. To varying degrees, these models incorporate patch-use criteria, either in the form of patch preference rules that influence patterns of movement with respect to neighbouring patches (Turner et al. 1993; Farnsworth and Beecham 1999; Illius and O'Connor 2000), patch departure rules (Moen et al. 1997), or both (Fryxell et al. 2005). A general result that has emerged from such modelling is that decision criteria (optimal versus sub-optimal), spatial scale on which decision-making is based (local versus regional), and motivational objectives (daily versus hourly rate maximisation) have profound impact on modelled rates of intake, animal performance and sustainability in heterogeneous environments.

For example, we have recently shown that Thomson's gazelles in Serengeti National Park may require much larger grazing areas (on the order of 2500 km²) than one might have expected in order to sustain themselves during the inevitable periods of drought and superabundance of rainfall that they experience (Fryxell et al. 2005). This shows that spatially-explicit modelling of large herbivores, based in

large part on patch-use decisions, can have important implications for understanding ecological interactions and in shaping wise management decisions (Fryxell et al. 2005).

A key impediment to such progress, however, is a pronounced gulf between the sophistication of models versus empirical data. Part of the problem is in finding appropriate ways to compare the explanatory power of alternate models, although



Modelling shows that decision criteria, spatial scale on which decision-making is based, and motivational objectives have profound impact

recent advances in information-theoretic approaches have great promise (Burnham and Anderson 2002). It is also enormously difficult to gather data at relevant scales to parameterise spatially-explicit models. Movement rates and transition probabilities among patch categories (e.g., high, medium and low vegetation biomass) are notoriously difficult to measure in

the field. As mentioned earlier, appropriate experimental measurement of animal performance criteria (intake rates of energy versus dry matter at hourly versus daily time frames) is similarly rare. Without these parameters, models are limited to showing the potential importance of biological features, not using models as tool to enhance understanding of even more complex ecological processes at the community or ecosystem scale. Until this occurs, utility of spatially-explicit models for management purposes will be necessarily limited. We see particular need for strong research linkages among modellers, spatial statisticians, GIS specialists, experimental behavioural ecologists and field ecologists in tackling spatially-explicit foraging processes in large herbivores. Without such a team approach, solutions of these intractable problems will be slow in coming.

Box 6.1. *Testable hypotheses for future research*

Hypothesis 1. Forage processing in the digestive tract may be more commonly limiting to energy intake than forage availability.

Hypothesis 2. Herbivores that value social needs or security ahead of energy gain should choose patches to maximise short-term intake rather than long-term intake.

Hypothesis 3. Energetic gain influences patch use more than other constraints, such as predation or risk of parasitism.

Several key hypotheses would seem to be of particular relevance. Some hypotheses for future research are formulated in Box 6.1. The first hypothesis is so central to other questions with respect to herbivore patch use that it must be of high priority.

Enormous strides have been made in the past two decades in understanding and predicting patterns of patch use by large herbivores, although there is insufficient replication and insufficient consistency in experimental methods to allow definitive conclusions. Most trials suggest that grazing herbivores trade forage quality against

abundance, in a manner that favours long-term rates of energy gain. Due to covariation between digestible energy and nutrient composition, energy maximisation probably succeeds in maximising intake of important nutrients as well.

This can be achieved either through seeking out patches of high energy gain or by staying in such patches whenever encountered. On balance, the experimental evidence for optimal patch departure is much less compelling than is the evidence that animals seek out adjacent patches with the high rates of energy gain. The pattern of selection is rather all-or-nothing, but much more commonly proportionate scaling of patch selectivity with energy gain. As a consequence, energy matching is a consistently more realistic description of observed patch-use patterns than is energy optimisation.

Predictive modelling of herbivore patch preferences has often proven highly successful at a small spatial scale (1-100 m²), using manipulated patch conditions in experimental arenas. On the other hand, predictive modelling of patch use at the larger spatial scale (100-10,000 m²) is needed for management decisions. Such large-scale patch-use modelling is in its infancy, although recent work points to enormous strides in this direction (Turner et al. 1993; Moen et al. 1997; Illius and O'Connor 2000; Farnsworth and Beecham 1999; Fryxell et al. 2005). Given the success of predictive modelling at smaller spatial scales, we suspect that there are enormous opportunities for application of behavioural models of patch use at larger spatial scales. The current limitation is not so much ingenuity in formulation of models, but rather finding innovative and informative ways to link models meaningfully with empirical data. Such a step is needed to winnow out non-useful models and to apply herbivore movements to more complex ecological interactions (i.e., predation, competition and host disease) on spatially-realistic landscapes.

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