ON THE SCALE DEPENDENCE OF FORAGING IN TERRESTRIAL HERBIVORES

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Abstract

Meaningful modeling of the spatial and trophic dynamics of terrestrial herbivores demands understanding of the constraints and fitness objectives that presumably underlie behavior. This is complex in terrestrial herbivores, because of scale-dependent constraints on nutrient or energy gain. Mechanistic processes of forage cropping, forage mastication, movements between feeding stations, and forage digestion each have unique constraints that apply on different time, size, and spatial scales. Moreover, competing activities are rarely taken into account. Experimental testing of foraging objectives is therefore clouded by uncertainty regarding which time scale is most relevant from the animal's perspective, leading to confusion and misrepresentation in the foraging literature. We illustrate these arguments from both theoretical and empirical points of view, based on our work with wild ungulates as well as the contemporary literature.

Introduction

Virtually every ecological phenomena is scale-dependent. This means, of course, that our perception of ecological patterns and the variables associated with those patterns depend on the

measurement units with which we measure the phenomena in the first place. If ecology is the study of organism distribution and abundance, clearly our answers necessarily depend on the yardstick we choose to use. Of the greatest interest, of course, are patterns whose interpretation or explanation changes across scales. In this paper, we examine how size, space, and temporal frames of reference might influence our perception of foraging behavior in large terrestrial herbivores, specifically with respect to optimality models.

We start by reviewing constraints on the herbivore functional response, emphasizing the key differences between herbivores and other consumers. We then point out how foraging patterns depend on the spatial distribution of resources relative to the body size of the herbivore. We then show how choice of time frame affects one's projection of foraging gains.

The second half of our missive will focus on the implications of these scale-dependent mechanisms on predictions of optimal foraging behavior. Temporal scaling is of particular importance in defining alternate fitness optima, generating alternate predictions that are testable using experimental or comparison methods. Our empirical examples demonstrate that it is far from obvious which temporal scale is most important in real life. These issues raise sobering questions about the possibility of ecological prediction, but potentially explain why foraging ecology is so often highly contentious, in spite of having a well-developed theoretical basis and a well-founded tradition of experimental hypothesis-testing.

Throughout our review, we concentrate on studies of wild ungulates rather than domesticated ungulates. We do this in part because we think it may be of interest for the livestock specialist to get a small taste of the kinds of thinking current among wildife biologists. We also emphasize wild species, because they might be expected to be particularly prone to natural selection. This is because of the importance of squeezing the most out of native plants of poor

nutritional quality available for short periods of the year, all the while combating a host of demographic challenges from predators, competitors, disease pathogens, and sometimes man.

Mechanistic constraints on foraging

Imagine a hypothetical hippo, grazing on hypothetical grass shoots as it wanders across a hypothetical landscape. Such is the idealized world of biomathematics, where we concentrate on simplified representations of complex phenomena, in order to make new predictions that can be rigorously assessed in experimental settings. For our subject, there are no competing interests: foraging is the only objective in life. Clearly, the rate that our hypothetical hippo can acquire food depends on its ability to find food, maneuver food into its mouth, masticate it, and finally swallow it.

An important milestone in our understanding of the ecological constraints affecting herbivore rates of intake under such hypothetical conditions was Spalinger and Hobbs' (1992) set of designer equations addressing the special characteristics of mammalian herbivores. They 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 surprisingly large impact on foraging, because of its consequences for the rate at which a foraging herbivore encounters food.

Ecologists have long recognized that prey encounter depends that on the velocity of predator movement across the landscape, as well as the predator's perception radius (Holling, 1959). In conventional predators, however, 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. Here the conventional mammalian herbivore has an advantage: the individual can move onward as soon as

it has made a bite, processing the bite as it moves on to the next feeding station. This can shorten the intervals between bites considerably, particularly when the forager can see the next bite as it departs from the last one. Nonetheless, even our hypothetical hippo must slow down or even stop as it obtains each bite, which implies that foraging reduces the velocity with which individuals move across the landscape.

Let's assume that our hypothetical hippo is searching for bites in a nearly barren landscape, hence many steps must be taken between bites. The rate of encounter with bites (λ) for our hypothetical hippo 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 (vwD) 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 our hypothetical hippo would have an average velocity of $v = v_{max} / (1+ \delta wD)$. It therefore follows that $\lambda = vwD = v_{max}wD/ (1+ \delta wD)$. Hence, forage intake (I) would equal bite size (S) multiplied by the encounter rate with bites (λ):

$$I = \frac{v_{max}\,wDS}{1+\delta wD} \qquad \text{eq. 1}$$

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 for process 1 foragers predicts that intake will be linearly related to bite (i.e. stem) size, but curvilinearly related to plant spacing, with a monotonically decelerating curve.

Exciting as it may be, this depiction of herbivore functional responses suffers from the fact that we can't actually measure bite size without explicit reference to the animal. If one is prepared to accept 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 (M). It readily follows that intake is a linear function of plant biomass under the conditions of process 1 grazing:

$$I = \frac{v_{max} wM}{1 + \delta wD}$$
<div align="right">eq. 2</div>

The scenario in which bites are widely spaced in space was termed process 1 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 spaced across the landscape. This kind of ecological circumstance, termed process 3 foraging, 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 for our hypothetical hippo? Bite size clearly must play a predominant role (Black and Kenney, 1984; 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, 1999). 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 behaviors 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 is compromised the same amount by each bite taken. It then follows that intake $I = R_{max} - \beta B$, where β is the effect of each bite on the rate of chewing and B = bites per unit time. If we presume, as before that I = BS, then substitution of the above expression yields the following functional response equation for process 3 herbivores:

$$I = \frac{R_{max} S}{\beta + S}$$

Eq. 3

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

$$I = \frac{R_{max} M}{\beta D + M}$$

Eq. 4

The cropping rate B can be obtained by dividing I by bite size (M/D), yielding

$$B = \frac{R_{max} D}{\beta D + M}$$

Eq. 5

Such inverse relations between bite rate and plant abundance have often been recorded in foraging studies with both wild species and domesticated ungulates (Black and Kenney, 1984;

Greenwood and Demment, 1986; Spalinger and Hobbs, 1988; Penning et al., 1991; Shipley and Spalinger, 1992; Gross et al., 1993; Bradbury et al., 1996; Wilmshurst et al., 1995, 1999).

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 becomes so short that there is no conflict with cropping, hence the functional response is linear, increasing proportionately with each unit increase in plant abundance (Fig. 1, dashed line). At ramet sizes above this threshold, the situation reverts to a process 3, and intake is curvilinearly related to plant abundance (Fig. 1, dotted line). 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. Similar conclusions have emerged from alternate mathematical formulations in which herbivore search can overlap with processing (Parsons et al., 1994; Farnsworth and Illius, 1996).

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 et al., 1995, 1999; 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 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,b). 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, 1994a), with profound impact on rates of depletion of swards (Laca et al. 1994b). This suggests that, although further adjustment of the mechanistic models of Spalinger and Hobbs (1992) may be useful, the fundamental soundness of the approach has been well demonstrated.

Digestive constraints

It has long been recognized that the rate of food intake per day is ultimately limited via either ingestive constraints, such as those in Spalinger and Hobbs' (1992) model, or digestive constraints on the amount of food passed through the gut (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 research and the underlying kinetics of digestion are well beyond our review. Suffice 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 could 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 tradeoffs often come into play in comparing the energetic gain obtainable from forages 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 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.

Wilmshurst et al. (1999) tested this prediction for Thomson gazelles in the Serengeti ecosystem of Tanzania. Digestibility of leaf and sheath tissue in sampled from areas occupied by territorial gazelles declined by ½ with a fourfold increase in grass abundance. Feeding trials on captive animals presented with forage of 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 *ab 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 (Wilmshurst et al., 1995) and woodland bison (Bergman et al., 2000, 2001). The logical conclusion is that daily rates of energy gain in mammalian herbivores are often controlled by constraints on digestion, rather than ingestion.

This has some sobering implications. Although we now understand a great deal about the factors influencing the rate of ingestion, this may of limited utility in evaluating animal performance, at least under the range of variation in plant quality applicable to wild ungulates. 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 costly 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). The reliability of its application to other species is an open question.

Patch preferences

Now that we are armed with some understanding about the constraints affecting the rates of food intake and energy gain in grazing mammals, we can consider patterns of patch preference. There are many potential points of view. One could evaluate use of patches of different community composition, use of patches varying according to resource abundance, or use of patches according to nutrient or energy gain. Given that we see strong selection in the wild for herbivore attributes that enhance energy gain (Illius et al., 1995), the latter seems the most promising perspective.

Given that nutritional quality in natural systems is often inversely related to resource abundance, we can ask whether grazing herbivores are capable of concentrating their foraging activity in patches that enhance long-term or short-term rates of energy or nutrient gain. Different solutions arise because of digestive constraints, which only affect gains over long-term time frames, but have no impact on short-term gains.

In the short-term, the rate of energy gain can be predicted by simply multiplying the instantaneous functional response by the digestible energy content of the sward (Fig. 2). Over a much longer time horizon, however, the herbivore can only feed to the minimum of the two constraints for ingestion versus digestion (Fryxell 1991; Fig. 3). Hence, the optimum sward depends on the time frame under consideration (Wallis de Vries, 1996; Bergman et al. 2001). Over short time frames, the optimum tends to occur at relatively high levels of biomass: bigger plants are generally better. Over a long time frame, lower biomass swards with shorter plants yield higher returns.

One common approach to testing such problems is to generate an experimental arena of patches of different resource levels. 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 80-300 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 *Cervus elaphus* in Norway (Langvatn and Hanley 1993), with results also indicative of long-term nutrient or energy maximization. These independent studies suggest that the behavior 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 107-419 g/m^2. Prior experimental work (Bergman et al. 2000, 2001) had indicated that daily energy gains should be maximized 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-maximizing 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 maximizing daily energy gain, bison were maximizing the short-term rate of energy gain, i.e. acting as though ingestive constraints were the sole determinant of fitness (Fig. 1). 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. Maximizing short-term gains allows foragers to minimize the time required to meet an arbitrary energetic target, while reserving time for other activities that might enhance fitness, such as social behavior, 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 the instantaneous rate of energy gain. They did not compare the predictive power of long-term vs short-term energy gain in explaining the pattern of space use. Wallis de Vries performed detailed calculations of daily and instantaneous energy gain for wild cattle (Wallis de Vries 1996). 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, 1994).

Hence, there is evidence that optimal foraging models, particularly those based on both ingestive and digestive constraints, can have reasonable success in predicting patch preferences by large herbivores. Nonetheless, predictions depend critically on temporal scale. Sometimes animals seem to maximize daily energy or nutrient gain, yet other trials suggest animals are maximizing short-term gains.

Future directions

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 habitat selection by grazers might occur (Senft 1987). Until we know the answer to this question, behavioral ecology has little to add to current approaches to population management and conservation.

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 habitat (i.e. resource) preference of muskoxen 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. 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 maximizing daily energy gain) or tall swards (as expected if animals are maximizing short-term gain). They found that the spatial distribution at large spatial scales was concentrated in areas of short grass, as predicted by the daily maximization model, but sward selectivity seemed to be more strongly related to grass greenness than grass height at smaller spatial scales.

There is substantial evidence that key factors influencing the foraging ecology of large herbivores scale allometrically in ways that could be very useful in practical applications. For example, the key parameters influencing ingestion rates have been well documented to vary predictably across body sizes (Illius and Gordon 1987, 1992; Shipley et al. 1994, 1996). Similarly, there is increasing evidence that digestive constraints are well predicted by dietary

properties and body mass (Demment and van Soest 1985; Illius and Gordon 1992; Meissner and Paulsmeier, 1995). Combining such relationships, Wilmshurst (2000b) derived an allometric relationship for optimal sward biomass, which predicts that small herbivores should do best in habitats with lower biomass, whereas larger species should prefer taller swards. These predictions are consistent with observational data from Serengeti National Park as well as other natural areas.

In a particularly exciting venture, Ritchie and Olff (1999) have recently used allometric scaling coefficients relating to patch use and resource concentration to predict variation in biodiversity across broad geographic spectra. The success of this approach in explaining observational patterns in herbivore diversity shows how our understanding of simple processes of resource acquisition and resource characteristics could have enormous conservation potential. Although Ritchie and Olff's model awaits rigorous experimental testing, there is clearly much to be gained in the undertaking!

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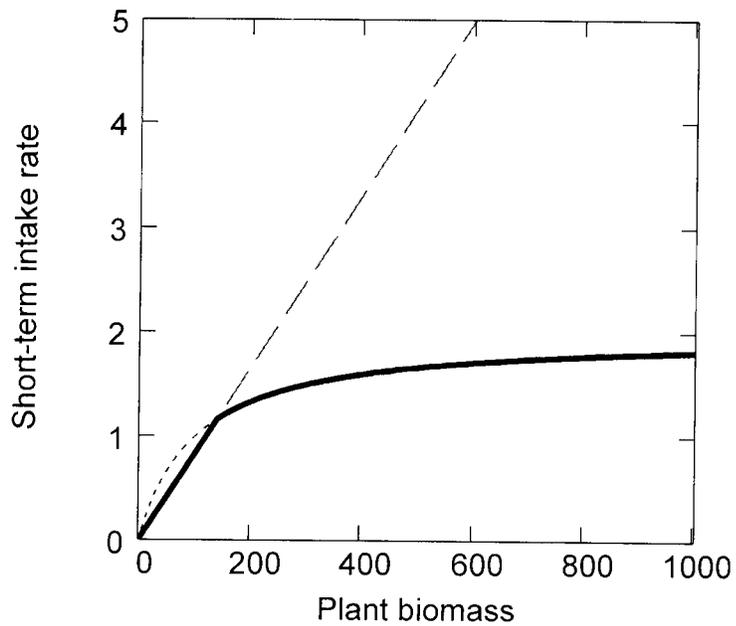
Figure 1 - Short-term rate of intake in relation to plant biomass, according to Spalinger and Hobb's (1992) herbivory model (eq. 1 and eq. 3). Note the discontinuity at the point at which process 1 conditions (dashed line) change to process 3 conditions (dotted line). Short-term intake is shown by the solid line. Model uses the following parameter values: $v_{max} = 0.5$, $\delta = 0.5$, $w = 0.1$, $D = 100$, $R_{max} = 2$, and $h = 0.5$.
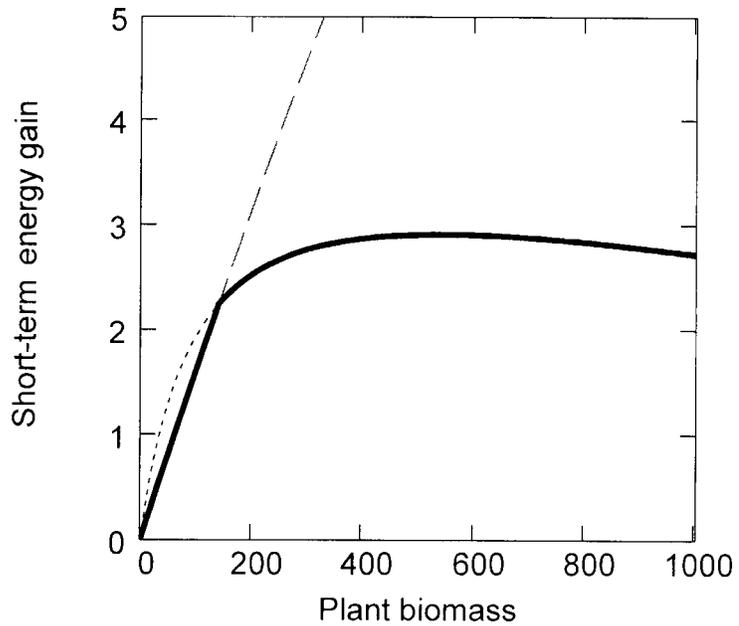
Figure 2 - Short-term rate of energy gain in relation to plant biomass, according to Spalinger and Hobb's (1992) herbivory model (eq. 6 and eq. 7). Note the discontinuity at the point at which process 1 conditions (dashed line) change to process 3 conditions (dotted line). Short-term energy gain is shown by the solid line. Energy gain is maximized at intermediate plant abundance when plant nutritional quality declines with plant abundance. Model uses functional response parameters as in Fig. 1 and assumes that digestible energy content is related to mass by $\varepsilon = 2.0 - 0.0005M$.
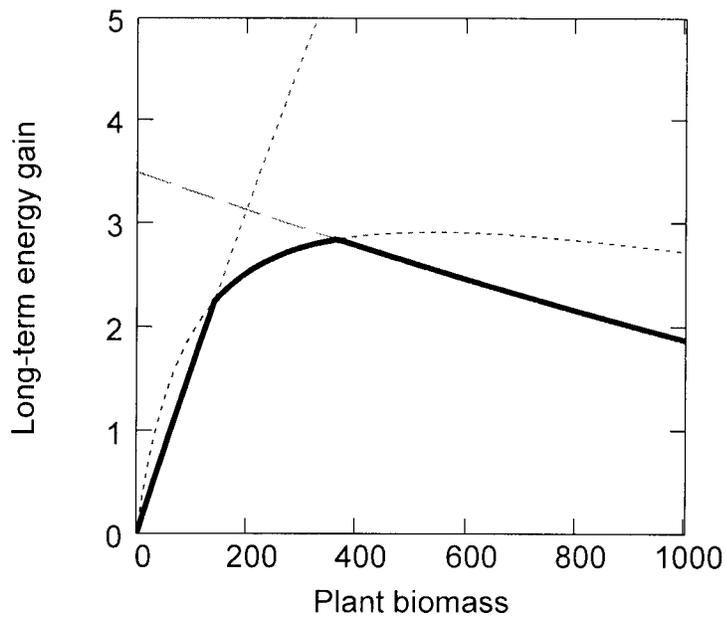
Figure 3 - Long-term rate of energy gain in relation to plant biomass, according to Fryxell's (1991) herbivory model. The dashed line corresponds to the digestive constraint, whereas the dotted lines correspond to the ingestive constraint. Long-term energy gain (solid curve) is maximized at low plant abundance when plant nutritional quality declines with plant abundance, whereas short-term gain (peak of the hump-shaped dotted curve) is maximized at much higher levels of resource abundance. Model uses parameters in Figs. 1 and 2, with additional assumption that digestive constraint = ε(1.75-0.0005M).