CHAPTER 6B

COMMENTS ON "PREDICTIVE MODELLING OF PATCH USE BY TERRESTRIAL HERBIVORES"

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Fryxell's aim (Chapter 6) is to evaluate the current understanding of forage intake and patch selection by herbivores across temporal and spatial scales, where resource (food) heterogeneity is large. His approach starts at a description of the functional response, i.e., the food intake response of consumers to quantitative changes in the resource supply. Re-developing several models of food and energy intake applicable at the detailed level of feeding station, he places bite size or bite processing central to short-term food procurement. This is then developed into longer-term (daily) food or energy intake functions, where digestive rather than bite-size or bite-processing constraints may operate.

In developing both instantaneous- and daily-intake functions, he makes use of so-called multiple piecewise formulas. Essentially, they read as minimising functions, where the objective function, i.e., food or energy intake in the short or the long term, is the minimum of either summed bite size, summed bite procurement, or digestion (long-term only) achieved. For instance, daily energy intake can be calculated as the intake of lab-determined energy from ramets over one day of feeding, or as the energy intake from ingestive processes, or as the energy intake of lab-determined total daily food, the latter subject to digestive constraints. If the energy intake calculated from, say, daily food digested is lower than any of the other calculated intake values, then digestion is considered to be the rate-determining

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parameter. The merit of this approach is that it clearly shows which of the most rate-limiting functions determines resource intake at various temporal scales. Indeed, the 'forage maturation hypothesis', which explains foraging behaviour with instantaneous and daily time-scale minimum functions, has also been corroborated by recent work on cattle foraging in complex tropical swards (Drescher et al. 2006b). However, the drawback of this likelihood approach is that the demonstration rests on one major assumption, namely that bite size is known and is considered to be synonymous with ramets.

Bite size is one of the most evasive variables in foraging ecology. It can be estimated and deduced, but not appropriately measured. Not only is this problematic in swards with one tissue (leaf) of one height in production grasslands, but even more so in complex swards, the other 50% of the world's grazing areas, where leaves mingle with bite-deterrent stems, in various densities and heights, and at various stages of maturation. One of the consequences of Fryxell's assumption is that intake increases to an asymptote with increasing resource biomass. In this case, an increase in ramet mass evokes one maximum functional response. In reality, herbivores select – or at least prefer – leaves from among leaf-and-stem swards, and mature swards show increased stem biomass that may in fact reduce resource intake at high values (type-4 functional response). That the basic assumption on ramets being equal to bite size appears to be supported by most of the results from the experimental studies cited in this chapter says more about the experimental conditions that were created than about the harvesting processes in nature's grasslands. Drescher (2003), and Drescher et al. (2006a) showed that stems in swards consistently depressed the functional response across the tested resource biomass (up to 220 g m^{-2}).

Another assumption in the reasoning developed in this chapter is that 'scaling up' from instantaneous to daily intake is a matter of multiplication by time. However, the digestive constraint does not emerge from scaling up, but is separately introduced as an add-on to the reasoning. This is, for obvious reasons, understandable, but it emphasises the scaling problem when it comes to food intake predictions. Linked to this, and still on the subject of temporal scales, various experiments with large herbivores show conflicting results in terms of the rate-limiting resource ingestion. While this may be a herbivore species effect, it is not satisfactory from a theoretical point of view to see the ecology of scale being subject to effects of natural history or taxonomy. One issue here may be that the tests on rate-limiting factors have not been rigorously executed, and that too many assumptions (like ramets as bite size, limited or no variability in bite size or bite rate, etc.) were included. This does not necessarily call for more details in the testing, but rather for more tractable testing *per se*. This underlines the problems that ecologists face in their quest for a tractable, low-scale – high-scale explanation of resource consumption.

Moving from the temporal to the spatial scale, Fryxell then addresses an arbitrary 'next' level, one above feeding station, and terms it 'patch', in line with many others. Patches are not spatially defined, but are presumed to consist of feeding stations. In experimental situations, patches are created and defined in structure and

space. In natural situations, one patch is left and another one entered when some distance needs to be covered before entering a next feeding station. This makes contrasts among patches arbitrary, even though we may pre-define how patches should differ. Even though Fryxell refers to a recent study (Fryxell et al. 2004) to lend support for theoretically derived patch departure rules at the landscape level (10×10 km), that study basically correlated field data with several foraging and animal-movement models to determine the best fit, and thus the most likely strategy employed by the animals in question, Thomson's gazelles. Variation among sub-populations of gazelle was large, but the best fit appeared to be with the model describing movements of Thomson's gazelles from patch to patch ruled by their daily rate of energy intake. We do not downplay the value of such studies, but we do note that the likelihood method should be seen as delivering an interim product, a rough approximation of the possible underlying processes determining patch use and patch departure rules. Correlating field data with model predictions does not provide the rigorous testing of hypotheses that we still require in this field.

Like with other chapters described in this book, Fryxell's chapter on predictive modelling of patch use by terrestrial herbivores provides a thought-provoking, up-to-date review on theory development and underlines the need for rigorous testing of these theories.