# CHAPTER 7B

# COMMENTS ON "ASSEMBLING A DIET FROM DIFFERENT PLACES"

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Prins and Van Langevelde (Chapter 7) use a linear-programming model to assess the extent to which ruminants of different size are able to satisfy their nutrient, energy and protein requirements from a landscape composed of two 'food' patches that differ in their relative densities of these important nutritional variables. Amongst their findings they conclude that, overall, small species are less able to balance their nutritional requirements when patches are widely dispersed than are large species, and are, therefore, more likely to be found in fine-grained (i.e., more closely dispersed food patches) than in course-grained ecosystems. Whilst this is an interesting and testable hypothesis, I will argue that it is the 'foodscape', not the landscape, that foraging animals respond to. My view is that the conclusions are an artefact of the model description rather than an actuality of the real world in which ruminants forage for a living. I posit that the dispersion of food in the landscape is a species-specific construct with the result that the foodscape of two species foraging in the same landscape will differ because of their differing views of food and their differing ability to select that food from the array of non-food on offer (see also Underwood 1983).

Belovsky (1978 and others) was the first person to use the linear-programming methodology to describe the diet selection of herbivores; in his studies he used the constraints of foraging time and digestive capacity to determine the optimal mix of two food types in the diet. He then went on to test his predictions against actual diet composition with, often, remarkable results. Whilst there have been many arguments and debates about the application of linear programming in Belovsky's studies (e.g., Hobbs 1990; Owen-Smith 1996), it still provides a valuable framework for conceptionalising simple foraging decisions and outcomes. I applaud Prins and Van Langevelde (Chapter 7) for using linear programming to develop hypotheses concerning the effects of food patch distribution on the ability of animals of



*Herbert H.T. Prins, Frank van Langevelde (eds.), Resource Ecology: Spatial and Temporal Dynamics of Foraging*, 157-158.

different size to balance their diet. In their model, Prins and Van Langevelde add a distance-travelled constraint to those originally developed by Belovsky (e.g., foraging time and digestive capacity). They then model the effects of varying the distance between patches on the 'feasible region'[1] in the linear-programming model for animals of different size. As already mentioned, they conclude that small species are only likely to be found in fine-grained landscapes.

I would argue, however, that body size will have an effect, not only in the movement costs between patches, but also on the ability of animals to select the nutritionally relevant food from the non-food matrix in the landscape (see also Jarman 1974). I (Gordon and Illius 1988) and others (Janis and Erhardt 1988) have shown that the foraging-apparatus size scales allometrically with body size in herbivores; this shows that small animals have mouths that will allow them to be more selective than will large animals (a gazelle vs. a buffalo; a roe deer vs. a moose). Field studies have also shown that small animals consume a higher-quality diet than large animals, even when feeding in the same landscape (Jarman and Sinclair 1979; Gordon and Illius 1996). This suggests that smaller species are able to make more fine-scale selection of food than are large species, which require relatively large patches of acceptable food to forage from. In effect, small species forage in a more fine-grained foodscape than do large animals. Counter to this, large animals are able to digest poorer-quality food items more efficiently than are small ones (Illius and Gordon 1991), and so will have more of the food on offer that is acceptable to them than are smaller animals. As such the model of Prins and Van Langevelde, by varying the distance between acceptable food patches, without taking body size differences in food dispersion into account, is not reflecting the reality of food distribution for small and large species. I, therefore, disagree with the conclusions drawn by Prins and Van Langevelde and argue that the grain size of a foodscape is defined by the animal itself and not by human-defined arbitrary food patches that can be seen and measured by ground survey on remote sensing. Until we can see the foodscape through the eyes of the animal we will not be able to clearly define hypotheses about the way in which the structure of the landscape affects animals of different size.

I may be wrong, Prins and Van Langevelde may be right, or we both may be wrong, but the wonder of science is to stand on the shoulders of others and scan the horizon.

## NOTES

[1] The area in a linear-programming model that satisfies an animal's nutritional requirements, bounded by the constraints.