

## CHAPTER 8B

### COMMENTS ON “EFFECTS OF TEMPORAL VARIABILITY IN RESOURCES ON FORAGING BEHAVIOUR”

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Owen-Smith (Chapter 8) describes the current state-of-the-art of the foraging models in relation to different temporal scales. He argues that the static, equilibrium approach of the traditional optimal foraging models does not seem to hold for real-life foraging studies, as trait plasticity is needed to cope with changes in foraging conditions over time. Addressing different temporal scales, from the variability on a certain day to day-to-day changes, and seasonal fluctuations of foraging conditions, it becomes clear that present-day models must be improved in order to be able to accommodate the variability in environmental conditions. Apparently, current models cannot yet fully cope with the importance of scale in foraging models. Indeed, the effects of both temporal and spatial scales on foraging behaviour need to be incorporated in the available models. An important gap is that few studies have been carried out that implicitly study the impact of these scale issues on foraging theory, let alone the hierarchy of different scales. There is an urgent need for studies that address the effect of scale on foraging behaviour.

One of the major problems in these foraging studies is that the thresholds (e.g., the marginal value, or thresholds used in the diet breadth analyses) or optima are dynamic as well; there is probably no fixed optimal intake rate or fixed optimal diet composition. They will change, depending on the changing local conditions, and fluctuate over time. Stephens and Krebs (1986) showed that the variation of the thresholds or of the expected intake rate can have important consequences for foraging choices, thereby explaining partial preferences. Moreover, Bailey and Provenza (Chapter 2, but see also Bryant et al. 1991) highlight the importance of a

balanced diet, the satiety hypothesis, as an alternative explanation for partial preferences. In the real world, probably all these processes influence foraging choices simultaneously, so we have to develop elegant studies that are able to disentangle the effect of these different variables. Due to the complexity, experiments under controlled conditions are certainly required. One should be careful with testing new ideas by searching for evidence in studies that were not aimed at addressing these multiple scales, such as done in Chapter 8 in the rhino home-range contraction example.

In contrast to Owen-Smith we would like to argue that the equilibrium concept in the description of systems is very important. Models without an equilibrium cannot persist over long time whether or not accompanied by variation around the equilibrium. Therefore, animal numbers never reach equilibrium. The equilibrium-modelling approach can therefore be of limited use and could miss the patterns we want to understand. On the other hand, the concepts of equilibrium and stability should not be dismissed. Even though the equilibria themselves might not be reached, the system nonetheless tracks these equilibria, even when varying over time. Savanna systems are highly dynamic. It is important to identify a stable point to which a system is inclined to move, the point of attraction, irrespective of the starting conditions. There exists an intriguing degree of constancy in nature; a good example is the constancy in the bison population that lived for over 5 million years in America under highly variable conditions. Sometimes individual species seem to fluctuate erratically, but the biomass of the whole grazer community appears to be remarkably constant (e.g., the Ngorongoro crater or Manyara National Park; Prins and Douglas-Hamilton (1990)). The question rises whether constancy necessarily implies stability.

A dynamic optimisation approach could be a useful alternative for the classic optimal foraging models, or neural networks or genetic algorithms could be used. These are probably only part of the alternative modelling approaches; others include multiple criteria or multiple objective optimisation, or approaches that include conflicting demand (Schmitz et al. 1997) or evolutionary modelling. Moreover, the concept of satisficing (Ward 1992), i.e., maximising the probability of exceeding a moving target (Parlar and Weng 2003) could be useful in modelling the diet choices of herbivores that have so many objectives and constraints. Realism urges us to consider the effect of imperfect information of the animal, or decaying spatial memory and risk aversion strategies as well. The latter approach seems essential; decreasing the probability of poor decisions might be an evolutionarily more promising strategy than just nutrient optimisation that could include some poor decisions under imperfect information or just from the stochasticity in resource availability. However, it might be true that these approaches may not give more insight into diet selection and optimisation of intake. These new models might be able to detect optimal solutions under a set of local conditions, but not be able to describe the mechanisms behind the underlying selection process. A first step would be to test this, and Owen-Smith clearly shows that we lack studies addressing different temporal scales simultaneously, studying the variability of the resource availability over time, and addressing the hierarchy of these different scales for the foraging decisions taken at a specific moment in time. These studies are essential to

parameterise and test new models. However, building in more and more biology and realism in the models does not necessarily lead to more insight and to more reliable diet predictions. Conclusions about partial food preferences maybe slightly altered, but might not be fundamentally different from what one could infer using more simple models. Moreover, there is the problem of the enormous number of parameters needed and dimensionality. A simulation model incorporating even some simple biologically sound rules may already generate enormous complexity. Incorporation of all relevant biological variables yields results as inconceivable as reality itself, as Owen-Smith also clearly underlines. Simulation hides the applied optimisation rules and might results in nothing more than what was already stated by the formulation of the model rules; much more work should therefore be done on the objective function. Even more so, the first priority should be to develop a theoretical framework that combines scale issues with foraging theory. This would certainly be a prerequisite if one wants to extrapolate field study results for the understanding of population dynamics.

One of the testable hypotheses put forward in this paper is that, due to Jensen's inequality, adverse periods are more important in shaping foraging behaviour than times of plenty. This is an elegant, attractive theory, but how useful is it when studying foraging behaviour? Can we test this? We think that these studies seem feasible, but also here controlled intake experiments are being called for. Moreover, the classical approach of presenting foods to animals and recording selection and intake, could be extended to address the effect of multiples scales, another topic of Owen-Smith's chapter. These experiments seem also the most appropriate to disentangle the effect of spatial and temporal scales, which in field studies are so often confounded.

Owen-Smith's chapter is very valuable in that it clearly pinpoints the shortcomings of the classical foraging theories. It stimulates our creativity, and urges us to start planning to test new ideas, in order to be able to incorporate scale in foraging theory.

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