CHAPTER 2B

COMMENTS ON "MECHANISMS DETERMINING LARGE-HERBIVORE DISTRIBUTION"

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How many prey to take of a certain type or how long to stay in a patch are key questions of a foraging animal according to the optimal foraging theory (OFT) (Krebs and Davis 1986). Within the OFT, the goal for herbivores generally is some form of energy maximisation within the limits of certain constraints. Although the application of energy as single currency has had some success, it is widely recognised that focusing on energy alone is not sufficient to explain the foraging behaviour of herbivores. Especially the complex, and ever changing, nature of their diet, together with the many constraints to be taken into account, poses problems (Krebs and Davies 1986; Simpson et al. 2004; Illius et al. 2002; Bailey and Provenza, Chapter 2). Essential here is that herbivores tend not to stay in a patch as long as predicted, and/or do not select a diet which provides maximal energy gain (Van Wieren 1996; Bailey and Provenza, Chapter 2). Because of this, alternative models have been developed, among them the sufficing principle (defined by Ward (1992) as choosing between different options when information-processing limits the ability of an animal to make optimal decisions), and the satiety hypothesis. The question here is if and/or how the satiety hypothesis fits into the OFT. Interestingly, the satiety hypothesis is not formally stated in the chapter. The closest we can get to a definition is that, according to the satiety hypothesis, "the behavioural mechanisms for switching between feeding sites involve satiating on a particular food or foraging location as they become increasingly less adequate (deficient, excessive, or

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imbalanced) relative to needs”. A key concept in the satiety hypothesis is ‘aversion’ due to flavours, toxins and nutrients, leading to a decrease in preference of food just eaten and to satiation, after which the animal stops eating a particular food. Despite the lack of a clear definition, the satiety hypothesis leads to three testable predictions. All tests require some measurement of aversion in relation to some ‘nutrient’ level. How this exactly needs to be done does not become clear. In some experiments, with only a few forage species, the satiety hypothesis did ‘help’ to explain the preference patterns found. It may, however, be very difficult to estimate the relative effects of individual forage species when herbivores take a mixed diet, a problem in common with the analysis using predictions derived from the OFT. More problematic is that the satiety hypothesis is not directed at a specific goal. Basically it deals with *a posteriori* effects after food has been ingested and, as such, is more related to the ‘giving-up rules’ or even ‘constraints’ which are part of the OFT. For the satiety hypothesis really to be(come) an alternative for the OFT, it should formulate clear goals for the foraging animal. Moreover, according to the satiety hypothesis animals can also choose among different forage types, and maximisation principles (not only aversion) are expected also to operate when deciding what to eat. It is, however, not clear if the authors have the intention to formulate an alternative theory or that they feel that the satiety hypothesis should in one way or the other be incorporated in OFT.

The ultimate goal of foraging animals is to maximise Darwinian fitness, and, as this is still the ruling paradigm, any foraging theory should at least in principle be embedded in this paradigm. Although energy maximisation has frequently been used as a proxy for fitness, it is clearly a special case, since fitness maximisation and energy maximisation subject to constraints are in general not equivalent (Illius et al. 2002; Simpson et al. 2004). Although still far away from a new foraging theory, some concepts of the OFT are presently being rethought. Is there, for instance, an alternative for energy maximisation? The complex nature of both the food base and the requirements for a number of nutrients that constitute the herbivore’s world, calls for the inclusion of more nutrients in the ‘goal’ than energy alone. There is growing evidence that some herbivores regulate the intake of multiple nutrients independently and, instead of maximising intake, avoid ingesting surpluses and deficits relative to regulated points (Simpson et al. 2004). The goal, then, becomes the regulation of a multidimensional ‘intake target’. Regulation implies that the animal strives to a certain state and it is only a small step to relate this state to the concept of ‘homoeostasis’, another fundamental paradigm in biology (Bradshaw 2003). There are approaches such as multiple criteria or multiple objective optimisation, or approaches that include conflicting demand (Schmitz et al. 1997). We suggest that the satiety hypothesis could, perhaps, find a place within the homoeostasis concept, because it, too, deals with balancing the intake of nutrients and tolerance levels, while requirement levels could be included. If it is possible to predict the requirements for homoeostasis properly, then it will become possible to predict at least part of the optimal behaviour of animals. In testing the predictions, indicators of performance like body weight could be used as a common currency.

Although striving for homoeostasis may be used as a convenient substitute for fitness maximisation, it is likely not equivalent to it? How does the struggle for life works out if all the members of a population (only) strive towards homoeostasis? It is possible that competitive and evolutionary processes have shaped the 'regulation points' to a higher level than that strictly required for maintaining homoeostasis? In that case some maximisation principle, again, needs to be invoked, and included in the models. Whatever that may be, the homoeostasis concept enables us to understand much of the behaviour of animals over a relatively short time span. It also makes animal performance the currency to evaluate, and this is a much more encompassing and integrative evaluation criterion than energy intake only.

If the regulation of a certain state is the goal rather than energy maximisation, the expected behaviours of animals are somewhat relaxed. The so frequently observed 'non-optimal' behaviour of herbivores can then be more realistically understood from the viewpoint of sufficing, than from being 'suboptimal' because either not all the constraints have apparently been included or because some basic assumptions (e.g., complete knowledge of the home range) have not been met. As the greater part of the regulation mechanism deals with evaluations across relatively short time periods, it is expected that much insight can be gained from studying foraging herbivores relative to these short periods. Selection of feeding sites (1-10 ha) within a daily range of 10-100 ha seems to be appropriate.