Evaluating optimal diet models for an African browsing ruminant, the kudu: how constraining are the assumed constraints?

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Summary
The linear programming model (LPM) of Belovsky (1978, 1986) and modifications of the classical or contingency model incorporating a digestive constraint (CM) were tested using foraging data recorded for kudus (*Tragelaphus strepsiceros*) browsing savanna vegetation over the late wet season. Food choice was between the herbaceous and woody plant components for LPM and among plant species or categories for CM. The constraints considered were consumption (cropping) rate, foraging time and digestive capacity. Woody communities dominated by *Burkea* and *Acacia* represented alternative habitat types. Following a minor adjustment, LPM represented the overall average diet and predicted the dietary differences between habitat types. However, the kudus failed to respond dietarily to variations among days and foraging sessions (meals) in the parameters constraining intake. The kudus accepted a wider dietary range than predicted to be optimal by CM. Evidence suggested that neither foraging time, nor digestive capacity, formed an effective constraint under the study conditions. Thermal tolerance and gut space may become limiting only towards the extremes of environmental variability that animals experience. LPM is vulnerable to circularity if average parameter values are used to estimate constraint settings. The energy maximizer–time minimizer dichotomy fails to take into account the fitness consequences of alternative foraging responses. CM is less cryptic in its application than LPM and so has greater heuristic value, despite its predictive failures. However, there may be no consistent ranking of food types where multiple constraints that are variable in their effectiveness apply. Dynamic programming models offer a solution, but pose a formidable challenge in complex natural environments.

Keywords: digestive constraints; feeding ecology; foraging theory; linear programming; optimal diet; *Tragelaphus strepsiceros*.

Introduction
Optimal diet models for large mammalian herbivores generally incorporate multiple constraints. The basic constraints considered are (1) food intake, dependent on consumption rate while foraging in relation to available foraging time and (2) digestive processing capacity, dependent on gut space and the rate of turnover of material through it. The diet is optimized by maximizing net energy or nutrient gains, subject to the limitations imposed by these constraints. Models have been cast in two alternative formats: linear programming models (Westoby, 1974; Belovsky, 1978, 1986) and modifications of the classical or contingency model of optimal foraging theory (Owen-Smith and Novellie, 1982; Verlinden and Wiley, 1989). While these models are similar in approach, they differ in important ways that can influence their predictive success.

The degree of success of these models has been contentious. The linear programming model has predicted the dietary composition of a range of herbivores from grasshoppers and ground squirrels to moose and bison (Belovsky, 1984, 1986, 1987, 1990a, b; Ritchie, 1990; Schmitz, 1990). However, the application of this model to kudus by Belovsky (1984) was invalid, because...
the parameter values reported by Owen-Smith and Novellie (1982) were misinterpreted (see later). Nevertheless, Owen-Smith and Novellie (1982) claimed little predictive success, but much heuristic value, for their 'clever ungulate' version of the contingency model. Verlinden and Wiley (1989) proposed an alternative form of the contingency model, emphasizing digestive constraints, but failed to test their model. Hobbs (1990) suggested that the success of the linear programming model was serendipitous, because it used a biologically unrealistic formulation of the digestive constraint. Provenza and Balph (1990) expressed their belief that optimal foraging models had generated neither insightful research questions, nor understanding of processes governing the foraging behaviour of mammalian herbivores.

My aim in this paper is to critically reappraise the alternative forms of optimal diet model developed for large generalist herbivores. For this reassessment I will draw on a comprehensive data set on the foraging behaviour of kudus (*Tragelaphus strepsiceros*). These data were obtained under semi-natural conditions, in circumstances designed to allow the measurement of almost all of the relevant foraging parameters. The analysis presented here covers the late wet season (summer) months, a period during which food abundance and quality remained high and relatively constant. This allowed a large sample of data to be used for statistical comparisons.

The questions I consider are the following. (1) How successful are the models in predicting average dietary composition? (2) Are the models able to predict variations in diet composition under different conditions? (3) What is the appropriate level of consideration of food types? (4) What is the effect of alternative assumptions about the food dispersion pattern? (5) What is the influence of different formulations of the digestive constraint? (6) How effective are the putative constraints? (7) How heuristically useful are the models? (8) What improvements need to be made to these models?

**The models**

Linear programming models (LPM) and modifications of the classical or contingency model (CM) applied to large generalist herbivores differ in a number of features and assumptions (Table 1). Most notably these concern the level of detail of the food types considered, assumptions about the spatial dispersion of these food types and the specific formulation of the digestive constraint.

**Food types**

The LPM developed by Belovsky (1978, 1984, 1986) represents the choice between two alternative food types. In principle LPM can consider any number of food types, but computational time rises geometrically with number. The limitation to two is for simplicity in graphical representation. Hence, LPM has treated the choice between broad plant categories, e.g. monocots (graminoids) vs dicots (shrubs and forbs).

The version of CM developed by Owen-Smith and Novellie (1982) considers choice among several food types, equated with individual plant species or sets of species. Solving CM depends on ranking these food types in order of value. Classically, value is assessed in terms of energy gained per unit of handling time. Verlinden and Wiley (1989) proposed that, for large herbivores, digestive processing time is likely to override the effects of the handling time involved in plucking, chewing and swallowing food.

**Food dispersion**

For LPM it is assumed that the food types occur in different places, i.e. while searching for one food the animal does not encounter the other food type. This ensures that search is independent,