Oecologia (1997) 112:331–332

Norman Owen-Smith

How successful was Edwards' linear programming model for marmots?

Received: 20 March 1997 / Accepted: 12 June 1997

Edwards (1997) believes that a linear programming (LP) model successfully predicted the observed dietary composition of yellow-bellied marmots (*Marmota flaviventris*) during early spring and summer, but acknowledges that it underestimated the monocot:dicot proportion later in the summer. Nevertheless, the correlation between observed and predicted diets early in the season depended on data points for one month (June 1991), when an exceptionally high proportion of monocots was eaten by the marmots.

Edwards tried to avoid the inherent circularity in previous applications of LP to herbivore diets (Owen-Smith 1993, 1996) by assessing the wet mass of gut contents only for animals 'with obviously distended stomachs'. He assumed that the observed active time during daylight represented maximum levels for feeding activity. Marmots spent the night inactive in burrows.

I accept that marmots were probably active for close to the maximum time allowed by thermal conditions, and that their gut fill at the end of the day probably represented maximum capacity. This is because I recognize the need of these hibernators to acquire as much energy as possible during summer, since their overwinter survival is dependent upon stored fat reserves. Accordingly, the finding that the data are in accordance with energy maximization rather than time minimization principles (at least during early summer) is hardly a revelation.

Nevertheless, I suspect any matching between model predictions and observations is somewhat fortuitous, given the questionable assumptions made in estimating the digestion constraint. Marmots began their morning and, for part of the year, afternoon foraging sessions with mostly empty guts, because of preceding periods of inactivity. Hence, for much of the time, their digestive fill was substantially less than capacity. Moreover, the throughput rate estimated from the retention time of an indigestible cotton thread marker is not representative of the faster turnover of the cell-soluble component of the diet. The overestimation of gut fill could have been compensated by the underestimation of digestive turnover rate. The contentious assumption that gut fill is limited by the wet bulk of food components (see Hobbs 1990) was not substantiated.

By raising the potential influence of variation in nocturnal foraging on daytime diets, Edwards recognizes that constraints vary dynamically in their effects. Consequences of varying gut fill on diet choice over the daily cycle should be more extreme for marmots, which cease foraging completely at night, than for kudus. In time-varying environments where gains and costs vary non-linearly, predicting diets from average values for constraining factors could be misleading.

The heuristic value of LP models lies in assessing the influence of multiple potential constraints on the achievement of some objective. Edwards assumed a priori that foraging time and digestive capacity were the only constraints, relative to an objective of meeting energy requirements. The basic problem confronted with regard to herbivore diets is why they include a varied mix of food types. Westoby (1978) suggested possible additional explanations: (1) savings in search costs where food types are interspersed; (2) changes in relative value of food types over time; (3) need to sample different food types to assess value; (4) need to balance intakes of various nutrients relative to energy, and (5) need to restrict intakes of specific toxins.

Edwards recognised point 4 above as a possible reason for the discrepancy between the predicted and observed diets of marmots during late summer, with regard to polyunsaturated oils. This was a no more than a post hoc suggestion without supporting evidence. I suspect that explanations 2 and 5 were also influential. From

N. Owen-Smith
Centre for African Ecology, Department of Zoology,
University of the Witwatersrand, Private Bag 3,
Wits 2050, South Africa
Fax: +339-3407; e-mail: norman@gecko.biol.wits.ac.za

this perspective, I question whether forcing multiple plant species with diverse properties into categories as broad as monocots versus dicots is appropriate.

The danger of circularity arises when certain constraints are assumed a priori to be limiting without considering other possible restrictions on diet choice. To be illuminating, linear (or non-linear) constraint models must assess alternative hypotheses. To support their claim to be mechanistic, such models must be able to explain short-term variability in diet choice, in relation to changes in benefits, costs and limitations. Judging from his concluding summary, Edwards (1997) recognizes this need for a more dynamic approach to optimality analysis.

References

Edwards GP (1997) Predicting seasonal diets in the yellow-bellied marmot: success and failure for the linear programming model. Oecologia 112:320–330

Hobbs NT (1990) Diet selection by generalist herbivores: a test of the linear programming model. In: Hughes RN (ed) Behavioural mechanisms of food selection NATO ASI Series, vol G 20. Springer, Berlin Heidelberg New York, pp 395–414

Owen-Smith N (1993) Evaluating optimal diet models for an African browsing ruminant, the kudu: how constraining are the assumed constraints? Evol Ecol 7:499–524

Owen-Smith N (1996) Circularity in linear programming models of optimal diet. Oecologia 108:259–261

Westoby M (1978) What are the biological bases of varied diets? Am Nat 112:627–631