Norman Owen-Smith

Circularity in linear programming models of optimal diet

Abstract The linear programming model of optimal diet for herbivores has been criticized for being biologically unrealistic, for being too successful given statistical realities, and for being circular. I try to clarify the issue of circularity. Circularity arises if constraint lines are estimated from average values for governing parameters, when the assumed constraints are not effective. This may occur (1) under benign season conditions when consumers do not maximize their food intake, because of costs associated with food processing and storage, or (2) when an unidentified constraint limits intake. To evaluate hypotheses about the factors controlling diet composition, it must be shown that (1) consumers respond appropriately to variation in the parameters controlling constraint settings, and (2) the assumed constraints are close to their maximum (or minimum) settings.

Key words Optimal foraging · Linear programming · Diet selection · Constraints

Introduction

The linear programming model of optimal diet for herbivores (LPM, Belovsky 1978) has been criticized from three angles: (1) the formulation of the digestive constraint is biologically unrealistic (Hobbs 1990); (2) the high predictive success reported for this model (Belovsky 1986, 1987; Belovsky and Schmitz 1994) is statistically unlikely (Hobbs 1990; Huggard 1994); (3) the “success” of the model arises from a circularity (tautology) in how constraints were estimated (Owen-Smith 1993, 1994). In addressing these criticisms, Belovsky and Schmitz (1994) and Belovsky (1994) contended that I had withdrawn my criticism of circularity. Huggard (1994) stated that the methods used by Belovsky and co-workers to measure variables did not appear to be circular. However, I still believe that a tautology in parameter estimation underlies the apparent “success” of LPM. The basis for this belief has not been fully understood by Belovsky (1994), nor by Huggard (1994). I will attempt to clarify it.

In LPM, the optimal diet is generally determined by the intersection of a pair of constraints (Belovsky 1986). The baseline constraint is set by minimum energy requirements. Other constraints considered have been minimum needs for nutrients besides energy (Belovsky 1978), available foraging time relative to food cropping rate (Belovsky 1978, 1986), digestive processing capacity (Belovsky 1986), and maximum tolerable levels of potential toxins (Belovsky and Schmitz 1994). The objective is usually specified as either maximizing the daily intake of energy, or minimizing the time needed to obtain the maintenance need. Essentially LPM assesses which among a set of constraints effectively limits performance, given basic assumptions. In the version most frequently successful for large mammalian herbivores, the effective constraints seem to be available foraging time and digestive capacity (Belovsky 1984, 1986, 1987). Modifications of the classical diet breadth model for herbivores have incorporated similar constraints (Owen-Smith and Novellie 1982; Verlinden and Wiley 1989).

Constraint settings may be estimated in various ways. Cropping rates are invariably measured directly in the field as mean values for particular food types or patches. These are related to daily foraging time, to estimate the daily food intake that could potentially be obtained from each food. Belovsky (1986) used either an unpublished dynamic model (see Belovsky 1981), or observed daily feeding times, to determine the maximum feeding time in relation to ambient temperature conditions. Digestive processing capacity has been estimated in different ways. Belovsky (1986) used the measured wet mass/dry mass ratio for each food type, relative to gut capacity (specifically the rumen-reticulum volume for ruminants). Gut capacity was generally assessed from literature reports of gut contents mass, except for small herbivores, where ca-
Capacity was usually measured directly. A fixed passage rate for each herbivore species was assumed. Other workers have assumed a variable passage rate, determined by the fibre content of a food type, but with a fixed capacity in terms of dry mass of gut contents. Whatever the specific method, Belovsky (1990) contends that it is appropriate to use average measures of constraints to explain the average dietary composition over an extended period.

I challenged the basis for LPM by suggesting that the putative constraints are not effective under benign conditions when both food abundance and food quality are high (Owen-Smith 1993, 1994). During these times animals may fully obtain their energy needs within less time, and with lower digestive fill, than the maximum possible. To support this contention, I demonstrated that (1) kudus (*Tragelaphus strepsiceros*) did not respond to day-to-day variation in factors affecting foraging time and digestive capacity (Owen-Smith 1993), and (2) these animals increased their foraging time and digestive fill during adverse periods in the seasonal cycle (Owen-Smith 1994). Nevertheless, the LPM incorporating mean foraging time and digestion capacity closely predicted the mean dietary composition of kudus (Owen-Smith 1993). This raised the issue of circularity, which I will try again to explain.

**How circularity may arise**

Multiple weak constraints

Figure 1a depicts the typical LPM graphics. The consumer can choose between two food types, one high in quality but low in abundance (F1), the other more abundant but potentially saturating digestive capacity (F2). The diet maximizing energy gains is indicated by the intersection of the time and digestion constraints (point A). However, the costs of obtaining more energy than basic requirements may outweigh the benefits, if this energy contributes only to increased fat stores (see Tolkamp and Ketelaers 1992; Owen-Smith 1994). Minimizing the time spent foraging (indicated by point B) may be the best solution if the risk of predation while foraging is high (Schoener 1971), or when allocating more time to reproductive activities has a greater benefit for fitness (Belovsky 1986). When predation risk is of little consequence, it may be beneficial to minimize the amount of food ingested to meet requirements, rather than the time spent obtaining it, so as to reduce food processing costs (indicated by point C). Energetic costs associated with digestion or foraging activity would cause the energy-maximizing diet to deviate somewhat from point A.

However, all of these costs may be relatively weak, or only intermittently effective, so that the dietary intake could vary flexibly over the region indicated by the arrow-heads. In these circumstances, the mean foraging time and digestive fill fall below the true constraint regions, although still corresponding with the mean diet composition. I believe that this situation prevailed for the kudus that I studied during late wet season conditions. Notably, these animals were growing subadults, and thus not subject to reproductive demands.

Unidentified constraint

An unidentified constraint may determine the diet composition, e.g. costs of processing or detoxifying allelo-