AN OPTIMAL FORAGING MODEL FOR WILD HERBIVORES

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Summary

An optimization model predicts the diets of 15 wild mammalian herbivores at different seasons in their native habitats, for 56 case studies.

I. INTRODUCTION

What determines the choice of food plants by herbivores has received much study and debate (Belovsky 1978, 1984a). One approach to this investigation is optimal foraging theory (Stephens and Krebs 1986). This mathematical theory is used to predict an animal's diet in different environments. Different herbivore optimal foraging models have been advanced and have been compared using a common data set (Belovsky 1984a). One model appears most predictive, linear programming; it defines an herbivore's solution to its feeding goal e.g., maximizing energy intake) within physiological and behavioral constraints (Belovsky 1984a). These findings for wild mammalian herbivores are summarized here.

II. METHODS

The construction of a linear program foraging model for a wild herbivore requires the measurement of a number of its behavioral, physiological and anatomical characteristics in each habitat and time of the year. The methods for measuring these parameters and the model's construction have been described in detail elsewhere (Belovsky 1978, 1984a, b, c, 1986a; Belovsky and Slade 1986; Belovsky, submitted; Belovsky and Ritchie, submitted). Studies conducted in temperate and tropical grasslands, temperate forest, and alpine tundra using 15 species of mammals provide 56 tests of the model.

Three herbivore foraging constraints are hypothesized as being important in constructing the model. The first is daily digestive capacity (g wet/day). Digestive capacity is the amount of food that the organ(s) for plant digestion holds (e.g., rumen for ruminants, stomach and caecum for caecal digestors, etc.) times the rate of food passage. Organ fill depends on each food's bulk (wet wt/dry wt).

The second constraint is daily feeding time (min/day). Feeding times were found in these studies to be set by the herbivore's thermal physiology and the thermal environment and are utilized by ingesting foods with different cropping rates (min/g dry wt). Cropping rates depend on the abundance and distribution of plants in the habitat. In these studies, the herbivores are unable to search for different types of plants (e.g., grasses, forbs, shrubs) at the same time, because they are distributed in different places in the habitat (i.e., non-simultaneous search).

The third type of constraints are nutritional (e.g., energy,, protein, sodium, etc.). Nutritional constraints are average daily minimum requirements for the forager (e.g., energy metabolism/day) and are satisfied by ingesting foods with different nutritional values (e.g., digestible energy).

Using the Simplex algorithm of linear programming (Strum 1970) and an herbivore's constraint equations, a diet that optimizes a foraging goal can be predited. Two foraging goals may be important: nutrient maximization and feeding time minimization (Stephens and Krebs 1986). Nutrient maximization is the goal if survival and reproduction increase with nutrient intake; energy may be the critical nutrient. Feeding time minimization is the goal if survival and reproduction decrease with time spent foraging (e.g., increased time

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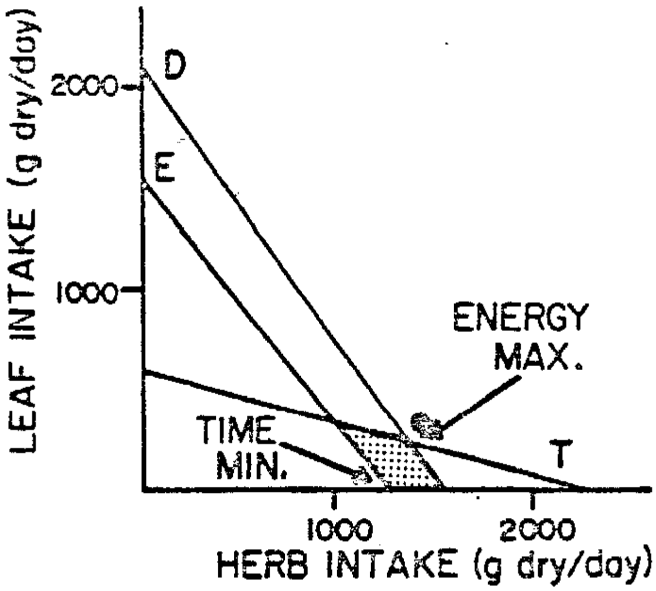
for mating, care of young, hiding from predators, etc.) after minimum nutrition is satisfied. These predicted diets are compared with the observed diet, measured using microhistological techniques for feces or stomach contents.

III. RESULTS AND DISCUSSION

A simple (i.e., 2 food types) diet model from my 56 studies is presented in the figure. This example demonstrates how the foraging constraints lead to different diets for different goals. The observed diet is not different from the nutrient (energy) maximized diet. Using χ^2 goodness of fit tests, it is different from the time-minimized diet and from a random diet composed of plants in proportion to their relative abundances of plants in the habitat.



A graphical linear programming model for Odocoileus virginianus in summer at the George Reserve, Michigan (Belovsky, submitted). The goal solutions are noted for comparison with the observed diet (●). The shaded region denotes feasible diets that satisfy the constraints: digestive (D), time (T) and energetic (E).

In all 56 cases studied, energy maximization predicts the observed diet very well ($r=0.96$, $p<0.001$) compared with time minimization ($r=0.02$, N.S.). Except in one case, the observed diets are different from the relative abundances of plants in the habitat, a random diet. Therefore, this wide range of wild herbivores appears to be highly selective foragers that maximize their daily energy intake [body mass: 0.035-636 kg; each species and number of studies: Microtus pennsylvanicus - 8, Spermophilus columbianus - 24, Sylvilagus nutalli - 2, Lepus americanus - 2, Marmota flaviventris -8, Castor canadensis - 1, Antilocapra americana - 1, Odocoileus virginianus - 2, O. hemionus - 1, Ovis canadensis - 1, Tragelaphus strepticeros - 1, Cervus elaphus - 1, Alces alces - 2, Bison bison - 1, Equus caballus - 1]. These herbivores studied in a diversity of habitats appear to be food limited because nutrient maximization is the foraging goal when survival and reproduction are limited by food intake. Therefore, the foraging model shows promise in explaining aspects of diet choice by diverse herbivores in a wide range of habitats.

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