Optimal foraging and fitness in Columbian ground squirrels

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Summary. Optimal diets were determined for each of 109 individual Columbian ground squirrels (Spermophilus columbianus) at two sites in northwestern Montana. Body mass, daily activity time, and vegetation consumption rates for individuals were measured in the field, along with the average water content of vegetation at each ground squirrel colony. I also measured stomach and caecal capacity and turnover rate of plant food through the digestive tract for individuals in the laboratory to construct regressions of digestive capacity as a function of individual body mass. Finally, I obtained literature estimates of average daily energy requirements as a function of body mass and digestible energy content of vegetation. These data were used to construct a linear programming diet model for each individual. The model for each individual was used to predict the proportion of two food types (monocots and dicots) that maximized daily energy intake, given time and digestive constraints on foraging. Individuals were classified as "optimal" or "deviating", depending on whether their observed diet was significantly different from their predicted optimal diet. I determined the consequences of selecting an optimal diet for energy intake and fitness. As expected, daily energy intake calculated for deviators (based on their observed diet proportion) was less than that for optimal foragers. Deviating foragers do not appear to compensate for their lower calculated energy intake through other factors such as body size or physiological efficiency of processing food. Growth rate, yearly survivorship, and litter size increase with calculated energy intake, and optimal foragers have six times the reproductive success of deviators by age three. Optimal foraging behavior, therefore, appears to confer a considerable fitness advantage.

Key words: Optimal foraging – Fitness – Ground squirrels – Energy intake – Growth rate

The development of optimal foraging theory (see Pyke 1984, Stephens and Krebs 1986) has been based on the assumption that foragers should choose the diet that maximizes their fitness, or lifetime reproductive success (Christiansen et al. 1977; Endler 1986). Optimal foraging theory explicitly assumes that there is some "currency" (e.g. energy, nutrients, or time) for fitness (Schoener 1971; Pyke 1984; Stephens and Krebs 1986). Maximizing acquisition of a particular "currency" can be viewed as a "goal" of the forager.

Energy maximization and feeding time minimization are two goals which have been proposed for foragers (Schoener 1971; Belovsky 1978; Hixon 1982). For energy maximizers, energy is the appropriate currency. In this case, foragers attempt to maximize their daily energy intake within their available feeding time. This goal is expected when fitness depends on the amount of energy that can be invested in survival or production of offspring. For time minimizers, time is the appropriate currency. In this case, foragers attempt to spend only enough time feeding to satisfy minimum energy or nutritional requirements so as to maximize the time available for other activities. This strategy is expected when fitness depends on the amount of time spent caring for young, searching for mates, avoiding predators, etc.

Survival and reproduction is associated with increased energy intake in a variety of taxa (e.g. Leslie et al. 1955; Lack 1966; Ayala 1967; Verme 1969; Morton and Sherman 1978; Porter et al. 1983; Dobson and Kjelgaard 1985a, b). In addition, many studies have also tested whether animals maximize their instantaneous rate of energy intake (e.g. Werner and Hall 1974; Krebs et al. 1974, 1977; Goss-Custard 1977; Elner and Hughes 1978). In these studies, the authors assume that energy is the currency for fitness, but cannot test this assumption by analyzing foragers' diets because both time minimizers and energy maximizers may attempt to maximize their instantaneous rate of energy intake (Schoener 1971; Belovsky 1984a). Nevertheless, there is evidence that some animals, particularly herbivores, maximize their daily energy intake [i.e. are true energy maximizers (Belovsky 1978, 1984a, b, 1986a, b; Belovsky and Ritchie 1990)]. None of these studies, however, demonstrate greater fitness for individuals that forage optimally. A major assumption of optimal foraging theory, therefore, remains untested.

In a previous paper (Ritchie 1988), I show that individual Columbian ground squirrels (Spermophilus columbianus) vary in their ability to consume diets that maximize their daily energy intake. The "optimal foraging ability" of an individual is measured as the absolute value of the difference between its optimal and observed diets. An individual's foraging ability is consistent over time within a season and is not affected by food abundance, thermal regime, or social environment. Consequently, foraging ability can be viewed as an individual behavioral character. I classified individuals into two groups: "optimal" and "deviator", based on whether an individual's observed diet was significantly different from its energy maximized diet. As a result, these individuals provide an opportunity to compare fitness components among individuals with different foraging abilities and therefore measure the consequences of deviating from an optimal diet.

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To demonstrate that optimal foragers have greater fitness, each of the following hypotheses must be tested.

**Hypothesis 1.** Deviators do not compensate for the energy intake lost due to incorrect diet choice through other factors, e.g. body size, cropping rates, activity time, or the physiological efficiency of processing food.

Testing this hypothesis shows that optimal and deviating foragers are alike in most characters other than foraging ability. If so, any difference in calculated energy intake among optimal and deviating foragers results only from their difference in optimal foraging ability.

**Hypothesis 2.** Individuals with greater energy intake will have greater growth, survival, and reproduction.

Testing this hypothesis shows that energy is an appropriate currency for fitness.

**Hypothesis 3.** Optimal foragers will have greater growth, survival, and reproduction than deviators.

Testing this third hypothesis ensures that the increment in fitness gained from greater energy intake is not overwhelmed by the increment in fitness gained or lost from other characters. For example, deviators might be subject to lower predation risk. The fitness gained by being an optimal forager might be exceeded by the fitness lost from predation risk.

**Methods**

The study was conducted during May–July, 1983–1986, using two populations of ground squirrels (JB and RJ-2, Belovsky and Ritchie 1990) on pasturelands near the National Bison Range, Montana. Detailed descriptions of the study site and vegetation characteristics are provided in Belovsky and Ritchie (1990). During the course of the study, 109 individuals (40 adults, 15 yearlings, and 54 juveniles) were trapped, marked, weighed, aged, and checked for reproductive condition. Each year, adults were trapped 3–10 days before juveniles were weaned and again, along with juveniles, 1–14 days after weaning.

In order to test Hypotheses 1–3 above, I calculated the energy budgets and measured the major fitness components of individuals whose optimal foraging ability was also measured (Ritchie 1988). Observations of individuals’ foraging behavior were made within 7 days of their last capture. Consequently, energy intake and foraging behavior were measured for all individuals at approximately the same point in the annual active period each year: 7–14 days after weaning in early June. In 1986, a subsample of 6 adult females were measured for foraging ability and energy intake 7 days prior to weaning to test whether individuals always attempted to maximize their daily energy intake or merely responded to immediate physiological demands (Millar 1975).

I examined potential relationships between optimal foraging ability, daily energy intake, and three components of fitness: daily growth, overwinter survivorship, and yearly reproduction by adult females.

**Deviation from an optimal diet**

Columbian ground squirrels eat primarily vegetation: herbaceous monocots (primarily grasses) and dicots (primarily forbs). In a previous study, I found that, in general, individual ground squirrels approached energy maximized diets rather than time minimized or random diets (monocots and dicots in their proportion in the environment) (Ritchie 1988). I consequently used the energy maximized diet for each individual as their optimal diet. In each case, the optimal diet provides a reference against which the individual’s observed foraging performance can be compared.

To determine the energy maximized diet for each individual squirrel, I used a linear programming optimization model (Westobay 1974; Belovsky 1978, 1984a; Karasov 1985). This model is appropriate because at my study site, monocots and dicots are distributed patchily relative to each other so that they cannot be searched for at the same time (Belovsky 1986a).

A linear programming model considers the impact of different constraints on a forager’s diet choice. The food intake of ground squirrels is constrained potentially by their (1) daily digestive capacity and its utilization by the bulk (wet wt/dry wt) of plant foods, and (2) maximum daily feeding time and its utilization by the time to crop plant foods (Belovsky 1986a; Belovsky and Ritchie 1990). The impact of these feeding constraints on food intake can be described with linear equations representing each constraint (Table 1) (Belovsky 1978, 1984a, 1986a). The equations describe the combination monocots and dicots that exactly satisfy the constraints (Fig. 1).

I estimated the parameters of the constraint equations for each individual (e.g. Table 2) [for details, see Ritchie (1988)]. Activity times (an upper limit to feeding time) and cropping times measured for each individual were used to calculate the feeding time constraint for each individual. Maximum daily activity time appears to be set by the thermal environment because only certain periods of the day have thermal conditions that allow ground squirrels to be above ground without overheating or becoming hypothermic. The activity time observed for ground squirrels is not significantly different from that predicted by thermal conditions (Belovsky and Ritchie 1990). Consequently, the observed activity time for an individual should correspond to an upper limit for feeding time.

**Table 1.** Equations to construct the linear programming models for each individual in the study

| Food Eaten | m = amount of monocot (dry mass) consumed per day |
| Time Constraint: | T ≥ c_m m + c_d d |
| Digestive Constraint: | D = (turnover rate) × (stomach + caecum capacity) |
| Hibernation Energy Requirement Constraint: | Adults: |
| | H = 5.72 × BMR = 5.72 (1.63 W^{0.75}) |
| | = 9.32 W^{0.75} |
| | Juveniles: |
| | H = 8.12 × BMR = 8.12 (1.63 W^{0.75}) |
| | = 13.23 W^{0.75} |
| | 11 ≤ c_m m + c_d d |