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A penny saved is a penny earned: lean season foraging strategy of an alpine ungulate

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Lean season foraging strategies are critical for the survival of species inhabiting highly seasonal environments such as alpine regions. However, inferring foraging strategies is often difficult because of challenges associated with empirically estimating energetic costs and gains of foraging in the field. We generated qualitative predictions for the relationship between daily winter foraging time, body size and forage availability for three contrasting foraging strategies including time minimization, energy intake maximization and net energy maximization. Our model predicts that for animals employing a time minimization strategy, daily winter foraging time should not change with body size and should increase with a reduction in forage availability. For energy intake maximization, foraging time should not vary with either body size or forage availability. In contrast, for a net energy maximization strategy, foraging time should decrease with increase in body size and with a reduction in forage availability. We contrasted proportion of daily time spent foraging by bharal, *Pseudois nayaur*, a dimorphic grazer, across different body size classes in two high-altitude sites differing in forage availability. Our results indicate that bharal behave as net energy maximizers during winter. As predicted by the net energy maximization strategy, daily winter foraging time of bharal declined with increasing body size, and was lower in the site with low forage availability. Furthermore, as predicted by our model, foraging time declined as the winter season progressed. We did not find support for the time minimizing or energy intake maximizing strategies. Our qualitative model uses relative rather than absolute costs and gains of foraging which are often difficult to estimate in the field. It thus offers a simple way to make informed inferences regarding animal foraging strategies by contrasting estimates of daily foraging time across gradients of body size and forage availability.

Alpine and temperate regions are characterized by a short summer with abundant nutrient-rich forage, and a severe, often long, winter when much of the forage is of poor quality (post leaf senescence), and often inaccessible because of snow (Goodson & Stevens, 1991; Parker, Barboza, & Gillingham, 2009). Ruminants inhabiting such regions often face food-related stresses during the lean season (Parker et al., 2009). Furthermore, the energetic costs of foraging associated with thermoregulation and locomotion increase owing to low ambient temperatures and snow, making foraging relatively costly (Dailey & Hobbs, 1989; Murray, 1991; Sabine et al., 2002). Animals often lose body condition during the winter months and have to rely on body reserves built over the productive summer season to see the lean winter season through (Parker et al., 2009; Taillon, Sauvé, & Côté, 2006). Lean season foraging strategies supplement body reserves built over summer and are thus crucial for the survival of species inhabiting highly seasonal environments.

Despite having received much attention, there is still disagreement over lean season foraging strategies of ungulates. While some suggest that ruminants should behave as time minimizers to reduce thermal exposure and minimize predation risk (Bergman, Fryxell, Gates, & Fortin, 2001), others support an energy intake maximization (feeding time maximization) strategy (Belovsky,

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1986; Schmitz, 1990, 1991). Others, still, have found no evidence for either (kudu, *Tragelaphus* spp.: Owen-Smith, 1994; musk ox, *Ovibos moschatus*: Forchhammer & Boomsma, 1995), and suggest that during the lean season, ruminants in extreme environments should employ an energy saving or net energy maximization strategy (Kie, 1996; Loe et al., 2007; Murray, 1991).

We generated predictions regarding foraging time for the time minimization, energy intake maximization and net energy maximization foraging strategies. In particular, we examined how lean season foraging time is influenced by body size and forage availability, factors that are known to explain within- and across-species differences in foraging behaviour. Body size plays a critical role in mediating the foraging behaviour of animals as it determines the energy required to maintain basal metabolic rate (Illius & Gordon, 1987) and the intake rate of food (Gross, Hobbs, & Wunder, 1993; Shipley, Gross, Spalinger, Hobbs, & Wunder, 1994). For ruminants, body size assumes even more significance as rumen volume and gut capacity, factors that determine the amount of food a ruminant can eat and how well it can digest it, are linked closely with body size (Clauss, Schwarm, Ortmann, Streich, & Hummel, 2007; Illius & Gordon, 1987). Although the role of body size in shaping foraging behaviour has been investigated across species (Mysterud, 1998; Owen-Smith, 1992), its role within species, even highly dimorphic ones, has rarely been explored (but see Pelletier & Festa-Bianchet, 2004).

CONCEPTUAL MODELS AND PREDICTIONS

Time Minimization

Animals seeking to minimize foraging time should maximize short-term intake rate. Given that minimum energy required (E) to maintain basal metabolic rate (BMR) scales with body weight (W) as $W^{0.75}$ (Clarke, Rothery, & Isaac, 2010; Kleiber, 1932), while maximum intake rate (I) of dry matter scales as $W^{0.71}$ (Shipley et al., 1994), time to meet minimum energy requirements,

$$T_{\min} \propto E/I = pW^{0.75} \Big/ qW^{0.71} = aW^{0.04} \tag{1}$$

where 'p' can be conceptualized as energy required per unit body weight, 'q' as intake rate of energy per unit of body weight and 'a' as the amount of time required to meet energy requirements of unit body weight. Intake rate of energy per unit of body weight, 'q', will depend on forage availability and increase with increasing forage availability. Hence 'a' will increase linearly as forage availability decreases (see Andersen & Saether, 1992).

For a fixed availability of forage, $T_{\min}$ scales very gradually with body size (equation (1), Fig. 1) especially for within-species size differences. Although our model predicts that foraging time should scale with body size with an exponent of 0.04, it is likely that this exponent is indistinguishable from zero based on empirical data (Shipley et al., 1994). At the level of a species, this implies almost equal foraging times across body size classes. For a given body size, however, as forage availability decreases, the time required to meet minimum energy requirements increases (Fig. 1). Therefore, a time minimization strategy predicts almost equal foraging times for all body size classes, and an increase in foraging time for all size classes with decreasing forage availability.

Energy Intake Maximization

Energy intake maximizers are likely to be constrained by the daily time available for foraging (Belovsky, 1981; Forchhammer & Boomsma, 1995; but also see Owen-Smith, 1994) when either encounter rate of food is low or ingestion time is high (owing to prolonged cropping and chewing processes). Ruminants may also be constrained by digestive processes (rumen volume/turnover rate). Foraging time for ruminants should then be determined by which of the two processes, ingestive or digestive, is more limiting. When forage availability is limited and/or forage quality is poor, animals will be limited by the total time available for foraging (Fortin, Fryxell, & Pilote, 2002). As our study is restricted to the winter season, we limit our discussion to the latter scenario. In this case, animals seeking to maximize energy intake are likely to forage for as much time as possible. Thus, foraging time should not vary with body size or forage availability, and should approximate the total time available for foraging in a day.

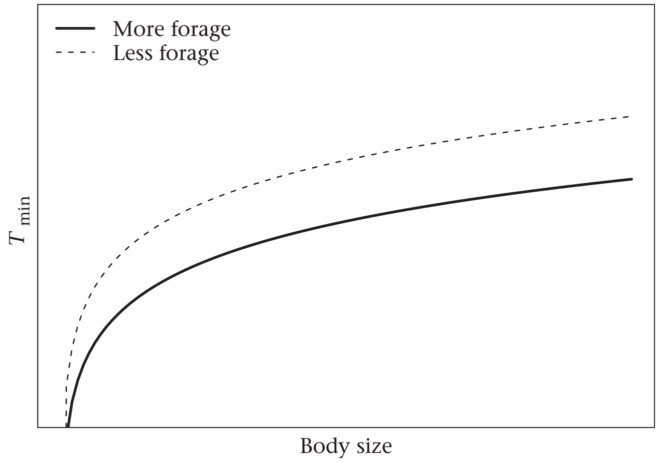

Figure 1. Time required to meet minimum energy requirement, $T_{\min}$, as a function of body size. Body size varies over two orders of magnitude for ease of interpretation. For a fixed body size, $T_{\min}$ increases as forage availability decreases.

Net Energy Maximization

Gross energy accumulated, E_a, in time T spent foraging in a patch is a type II functional response (Laca, Distel, Criggs, & Demment, 1994; but also see Searle, Hobbs, & Shipley, 2005) whereas energy spent foraging or the cost of foraging, E_c, is a linear function of the time spent foraging (Fig. 2). The net energy gained, E_{net}, is, then, the difference between gross energy gained and energy spent, i.e.,

$$E_{\text{net}} = E_a - E_c = b\left(1 - e^{-cT}\right) - dT, \tag{2}$$

where b, c and d are functions of body size and the environment (Fig. 2). Specifically, 'b' reflects the total energy contained in a patch (the asymptote in Fig. 2) and increases as forage availability increases (Laca et al., 1994). For a fixed availability of forage, 'c' reflects the rate at which the patch is depleted (asymptote is reached), and increases with body size; 'd' is the cost of foraging (locomotory and thermoregulatory) per unit foraging time and increases with body size (Murray, 1991). Also, 'd' increases with decreasing forage availability as the costs of locomotion increase because of an increase in searching effort (Murray, 1991).

Graphically, E_{net} is the difference between the gain and cost curves and the solution for optimum foraging time, T_f, lies where this difference is greatest (vertical lines in Fig. 2c, d).

For a fixed availability of forage, the cost of foraging increases with body size, that is, the slope of the cost curve is steeper for larger animals (Fig. 2a). At the same time, larger animals deplete patches faster which means that their returns reach an asymptote sooner relative to smaller animals (Fig. 2a). Thus, the optimal