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.

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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,
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, Ortman, 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, Rothey, & 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,

$$T_{min} = E/I = pW^{0.75}/qW^{0.71} = aW^{0.04}$$

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.

**Net Energy Maximization**

Gross energy accumulated, $E_a$, in time $T$ spent foraging in a patch is a type II functional response (Laca et al., 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.,

$$E_{net} = E_a - E_c = b(1 - e^{-cT}) - dT$$

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
foraging time, $T_f$, decreases as body size increases (Fig. 2c). For a fixed body size, an increase in forage availability leads to an increase in the amount of energy gained per unit time. It also leads to a decline in the searching time which means that the cost of foraging per unit time decreases (Fig. 2b). Accordingly, the optimal foraging time, $T_f$, will increase with increasing forage availability (Fig. 2d).

The three different strategies thus lead to contrasting predictions regarding how time spent foraging should vary with body size and forage availability. A time minimization strategy predicts that foraging time remains largely invariant across body sizes but increases as forage quality decreases (Fig. 3). In contrast, an energy intake maximization strategy predicts that foraging time is not influenced by either body size or forage availability, while a net energy maximization strategy predicts a decrease in foraging time with increasing body size and with decreasing forage quality (Fig. 3).

We tested these predictions on bharal, *Pseudois nayaur*, a medium-sized (mean adult body weight 55 kg; Mishra, Van Wieren, Heitkönig, & Prins, 2002) grazing ruminant, in a high-altitude (>4000 m) trans-Himalayan region of India. The species shows high sexual dimorphism in body size with adult males weighing 60–75 kg and adult females 35–45 kg (Schaller, 1998; Weckerly, 1998). Specifically, we examined how time spent foraging by bharal in winter varied as a function of body size and forage availability. In addition, we quantified how time spent foraging within sites changed over the course of the winter as forage availability decreased.

**METHODS**

**Study Species**

Adult male bharal show considerable variation in size with age, with the youngest adult males nearly the size of adult females while the largest ones grow up to twice this size (Schaller, 1998). Morphologically, the species is graze-adapted (specialized to feed on graminoids), and while its summer diet comprises almost

![Figure 2.](image-url)  
*Figure 2.* Gross energy gained (type II curve) and spent (straight line) and net energy gained with time spent foraging for (a, c) varying body size and (b, d) varying forage availability. The thicker lines represent larger size classes (a, c) or increased forage availability (b, d). In (a), foraging cost increases with size and larger animals also deplete the patch sooner. Optimum foraging time (indicated by vertical lines), where net energy is maximized, decreases with increasing size (c). In (b), with increasing availability of forage, foraging cost decreases while energy accumulated in time $T$ increases. Optimum time increases with increase in forage availability (d).

![Figure 3.](image-url)  
*Figure 3.* Graphical summary of predictions from the three strategies showing relationship between foraging time and body size of the animal and availability of forage: (a) time minimization, (b) energy intake maximization and (c) net energy maximization. Dashed lines represent conditions of lower forage availability.
entirely of graminoids, it has a mixed diet in winter (Mishra, Van Wieren, Ketner, Heitkönig, & Prins, 2004; Suryawanshi, Bhatnagar, & Mishra, 2010).

**Study Area**

The study was carried out in the Kibber region of Spiti Valley (32°N, 78°E), Himachal Pradesh, India. The area is a cold, mountainous desert characterized by a mosaic of rolling and steep hills, rocky cliffs and outcrops with the altitude varying from 3800 to 5000 m. Temperatures during winters drop below –35 °C and vegetation growth is restricted to a short spring—summer window from May to August. Precipitation is predominantly in the form of winter snow most of which falls during December to March.

The vegetation of this region is classified as dry alpine steppe. Much of the landscape is bare rock and scree slopes where no vegetation grows. Dominant species include shrubs such as *Caragana versicolor*, *Lonicer a spinosa*, *Eurotia* (short shrub) and *Rosa webbiana*. Graminoids found here include species of *Stipa*, *Carex*, *Poa*, *Elymus* and *Festuca*. Commonly occurring herbs include *Scorzoner a* and *Bupleurum*.

Native herbivores in the study area include bharal, ibex, *Capra sibirica*, and woolly hare, *Lepus oiiostulus*. While the domestic component comprises sheep, *Ovis aries*, goat, *Capra hircus*, horse, *Equus caballus*, donkey, *Equus asinus*, cow, *Bos indicus*, yak, *Bos grunniens*, and ‘dzomo’ which is a cow—yak hybrid. Large tracts of the study area are utilized by both wild herbivores and domestic livestock in the summer. However, in some areas, as part of a conservation initiative, villagers are compensated for keeping domestic livestock off tracts of land which are thus ‘reserved’ for wild herbivores (Mishra, Prins, & Van Wieren, 2003). Areas outside the reserve that are extensively grazed by livestock in summer tend to be characterized by lowered forage availability for bharal in the winter, whereas ‘reserve’ areas typically support higher forage biomass (Suryawanshi et al., 2010). To investigate how variation in forage availability affects bharal foraging in the lean winter months, we chose two study sites: one within the ‘reserve’ area and another in an area intensively grazed by livestock. The two sites were similar in altitude and aspect.

**Estimating Forage Availability**

Difference in forage availability between sites was quantified between 26 December 2011 and 4 January 2012 by harvesting above-ground herbaceous biomass from 37 and 38 randomly located 3 × 3 m plots in the high and low forage sites, respectively. Shrubs were not clipped but their percentage cover in plots was recorded. Harvested biomass was air-dried, separated into grass and forb components, and weighed to within 10 mg using an electronic scale.

**Quantifying Bharal Foraging Behaviour**

In each of the two study sites, bharal time activity budgets were constructed through scan samples of herds (St-Louis & Côté, 2012). Bharal herds were observed using a 45–60× spotting scope and 8 × 40 binoculars from a distance of 20–150 m. During each scan, the age–sex class of each individual of the herd and its activity were noted. A scan of the herd was usually completed within 2 min. For larger herds, or where herds were far off, scans were restricted to a maximum of 5 min. Successive scans were separated by 10 min intervals. The number of scans in a day varied from 10 to 47. Age–sex classification was done following Mishra et al. (2004). Animals were classified as kid (<12 months old), yearling (12–24 months), adult female (>24 months), Class 1 male (24–48 months), Class 2 male (48–72 months), Class 3 male (72–96 months) and Class 4 male (>96 months old). Size classes were later grouped into four major classes reflecting a size gradient, namely kids (kids + yearlings), females (adult females), small males (Class 1 + Class 2 males) and large males (Class 3 + Class 4 males). Females and small males represented the same size class but were kept independent to ensure that body size-related patterns were not confounded by sex differences.

Bharal activities were classified into feeding, resting, walking, social interactions, standing and vigilance. ‘Feeding’ included time spent biting and chewing food and moving from one plant to another within a feeding patch. This movement from one plant to another while feeding was different from ‘walking’ as the former was usually slow and deliberate with the head held below the shoulder whereas the latter was faster with the head held above the shoulder. Animals that were lying down were classified as ‘resting’. An animal was recorded as ‘standing’ when it was standing but not vigilant. ‘Vigilance’ (most often while standing; rarely while resting) involved the animal being alert with the head and shoulders tensed and could be easily differentiated from ‘standing’. Any activity involving more than one animal was classified as a ‘social interaction’, including male–male, male–female and female–female interactions.

A total of 632 and 730 5 min scans were performed and averaged daily over 27 and 26 sampling days in the high and low forage sites, respectively. Care was taken to ensure similar sampling effort across all times of day, from first light to a little after sunset, and to sample across a range of group sizes in both sites. Data were collected on sequential days as far as weather permitted. The observation team was split into two to collect data from the two sites. The two teams spent sufficient time together to calibrate classification of animals and activities. Importantly, team members were rotated across sites to avoid any observer bias.

**Analyses**

Proportion of daily time spent foraging (and resting) by bharal in each site was estimated as the proportion of individuals within each size class in a scan that were foraging (and resting), averaged over all scans in a day. We used a general linear model (GLM) to examine how proportion of daily time spent foraging by bharal varies over time as the winter progresses as a function of site and body size class. We included days since the start of the study as a predictor variable since forage depletion with the advance of the winter season is likely to affect foraging time. Although our response variable is a proportion, we used a GLM with normal errors and identity link function since inspection of residuals indicated homogeneity of variance with normally distributed errors. Starting with a global model that included all interaction terms, we sequentially dropped nonsignificant model terms using F tests until a minimum adequate model was achieved. All statistical analyses were done using the statistical software R version 2.14.2 (R Development Core Team, http://www.R-project.org).

**RESULTS**

**Forage Availability**

Mean above-ground graminoid biomass in the ‘reserve’ area was higher (3.23 ± 0.41 g/m²; hereafter ‘high-forage’ site) than that in the livestock-grazed area (0.56 ± 0.15 g/m²; hereafter ‘low-forage’ site). In contrast, mean above-ground biomass of forbs was similar in both areas (reserve: 4.41 ± 0.59 g/m²; livestock grazed: 4.19 ± 0.80 g/m²). Mean percentage cover of shrubs, which are
typically avoided by bharal, was 37% (median 30%) and 16% (median 5%) in the reserve and grazed sites, respectively.

**Time Activity Budget**

Our final minimum adequate model included the main effects of time, forage availability and body size, but did not include any interaction terms (see Table 1 for foraging time, Table 2 for resting time). Proportion of daily time spent foraging was highest for kids, followed by small males, females and large males in that order (Appendix Table A1, Fig. 4). Kids spent a significantly higher proportion of time foraging compared with all other size classes ($P < 0.05$, Table A1). Small males spent significantly more time foraging than large males ($P < 0.05$). There were no significant differences between small males and females, which represent the same body size class, or between females and large males. For each size class, the proportion of daily time spent foraging was 6.8% higher ($P < 0.001$; Table A1, Fig. 4) in the high-forage ‘reserve’ site than in the low-forage availability site, and declined by 0.3% per day with advance of the winter season in both sites ($P < 0.001$; Table A1, Fig. 4).

The proportion of daily time spent resting showed the opposite trend: it was almost 5% less in the high-forage ‘reserve’ site ($P = 0.018$; Table A2, Fig. 5) and increased by 0.25% per day with advance of the winter season ($P = 0.0001$; Table A2, Fig. 5). Bharal kids rested the least followed by small males, females and large males in that order (Table A2, Fig. 5). Proportion of daily time spent resting by kids was lower than for other classes ($P < 0.05$ for differences with females and large males, $P = 0.08$ for kids and small males), while small males spent less time resting than large males ($P < 0.05$). Time spent resting by females was not significantly different from that for either small or large males.

**DISCUSSION**

Our results suggest that bharal behave as net energy maximizers during winter. In accordance with the predictions of this strategy, the mean proportion of daily time spent foraging decreased with increasing body size and was lower in the site where forage availability was lower. The fact that bharal fed less where there was less forage available, and that this trend was consistent across body size classes, was not in accordance with the predictions for the time minimization strategy, wherein bharal should have compensated for reduced foraging and resting according to body size and forage availability related reasons.

Earlier work in the study area has shown that forage quality during winters falls below maintenance level (mean crude protein content for graminoids = 2.1% Suryawanshi et al., 2010) and forage availability is generally low in comparison with other grasslands in the world (Mishra, 2001). Like many other temperate and alpine ungulates (e.g. black-tailed deer, *Odocoileus hemionus*; Parker, Gillingham, Hanley, & Robbins, 1993; white-tailed deer, *Odocoileus virginianus*; DelGiudice, Mech, Kunkel, Gese, & Seal, 1992; red deer, *Cervus elaphus*; Loison, Langvatn, & Solberg, 1999; moose, *Alces alces*; Milner, van Beest, Solberg, & Storaas, 2013; but see Couturier, Côté, Huot, & Otto, 2008), bharal lose body condition as winter advances. This implies that average daily net energy intake over winter is lower than the energy required to meet the basal metabolic rate, and hence time minimization, which implies curtailment of foraging once the minimum energy requirement is met (Hixon, 1982), would be an unachievable strategy. Instead of minimizing foraging time, animals may maximize daily energy intake during winter to minimize their energy deficit (e.g. white-tailed deer: Schmitz, 1990, 1991). However, if the costs of foraging are high and gains low, maximizing feeding time (hence maximizing intake of energy) could increase the daily energy deficit instead of reducing it (Murray, 1991). Bharal seem to balance foraging and resting according to body size and forage availability such that net energy gained daily is maximized and, hence, daily energy deficit minimized. Although this still means a daily loss in body condition, the strategy can potentially minimize the rate of this loss. This could be a critical overwintering strategy of bharal. During winters, death caused by loss of body reserves is perhaps the greatest risk facing temperate and alpine ungulates and this risk can be reduced by minimizing daily energy deficit (Parker et al., 2009).

While it is accepted that foraging strategies form a continuum between end points represented by time minimization and energy maximization, few studies have explored this continuum or proposed a framework to understand and model them (Bergman et al., 2001). In the qualitative framework presented here, net energy maximization offers an explanation for such a continuum. As it is responsive to changes in both the energetic costs and gains of foraging, a change in foraging conditions can cause the optimum foraging time (where net energy is maximized) to vary. Factors that alter the energetic gains and/or cost of foraging (e.g. forage depletion, snow cover, extreme weather, large group sizes) will affect the optimum solution and lead to a gradient in predicted foraging time (see Fig. 2). Natural selection would favour such a strategy (Bergman et al., 2001) rather than a restrictive choice between a minimum (as per time minimization) or a maximum (as per energy intake maximization). This is an important aspect as in many conditions neither time minimization nor energy intake maximization may be optimal for the animal. For example, northern ungulates reduce their foraging time when harassed by biting flies (e.g. Toupin, Huot, & Manseau, 1996), but unless the selection on this reduction is very strong, animals may not benefit by

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**Table 1**

ANOVA table showing significant main effects of body size class, forage availability (site) and advance of winter season (day) on daily foraging time

<table>
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<th>Mean square</th>
<th>F</th>
<th>P(&gt;F)</th>
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</table>

**Table 2**

ANOVA table showing significant main effects of body size class, forage availability (site) and advance of winter season (day) on daily resting time

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<tr>
<th>df</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>F</th>
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adopting a time minimization strategy at the cost of extra energy intake. Within the framework of net energy maximization, increased costs of foraging because of biting flies would mean that animals must reduce their foraging time without adopting the extreme time minimization solution.

Although we have dealt only with winter foraging across two sites differing in forage availability, our qualitative model can provide insights into foraging behaviour across seasons. In the productive season, when costs of foraging are relatively low and gains high, optimal foraging time for net energy maximizers may lie beyond the total time available for foraging in a day (see Fig. 2). In such a situation, net energy maximizers are likely to forage for all the time available and may, therefore, appear to behave as energy intake maximizers. With the onset and advance of the lean season (and therefore of forage depletion), the energetic costs of foraging increase and gains decrease. While energy intake maximization would still predict that animals forage for all of the time available, net energy maximization will predict a continuous decline in

Figure 4. Proportion of time spent foraging by bharal in winter in relation to the advance of the season (sampling day). (a) The low-forage ‘grazed’ site. (b) The high-forage ‘reserve’ site. Different letters over regression lines indicate significant difference between intercepts.

Figure 5. Proportion of time spent resting by bharal in winter in relation to the advance of the season (sampling day). (a) The low-forage ‘grazed’ site. (b) The high-forage ‘reserve’ site. Different letters over regression lines indicate significant difference between intercepts.
foraging time and time minimization a continuous increase. Our results show proportion of time spent foraging and resting by bharal decreased and increased, respectively, through our study period (Fig. 4), providing further support to the net energy maximization hypothesis. The extent of depletion of forage (or advance of the lean season) at which predictions from energy intake and net energy maximization strategies diverge will depend on the environment and species concerned.

While the patterns we have observed suggest that body size plays an important role in foraging behaviour, there are other differences between individuals and groups that must be inspected in future work. Body condition at the start of winter is one such important factor that is likely to affect winter foraging behaviour in combination with body size (Monteith et al., 2013). Animals are likely to regulate body reserves during the lean season in accordance with the amount of somatic reserves available at the start of the lean season and this may vary between individuals as a result of differences in body size, physiological state and other factors. For example, large rutting males may enter winter in the poorest nutritional condition owing to the energetic costs of mating (Barboza, Hartbauer, Hauer, & Blake, 2004). Including such factors that operate at the level of an individual may explain the observed patterns better. Although other studies have found evidence for two energy maximization during the lean season (reindeer, Rangifer tarandus: Loe et al., 2007; black-tailed deer: Kie, 1996; kudu: Owen-Smith, 1994), a more widespread application of this concept in ungulate foraging studies has presumably been limited owing to difficulty in estimating energetic costs and gains of foraging for free-ranging wild herbivores which makes it difficult to generate testable quantitative predictions. A qualitative framework, such as the one presented here, using ‘quasi experimental’ differences in forage availability and the natural variation in body size, generates contrasting predictions which can be easily tested in the field. The challenge for the future is to incorporate energetic costs other than locomotion and thermoregulation, and effects of group foraging in our model of net energy maximization and to test it in a broad array of foraging conditions. Finally, changes in foraging behaviour of animals can have significant population-level impacts mediated through changes in energy intake. Bharal are not migratory and inhabit more-or-less the same area throughout the year. It is thus likely that animals in areas of more forage availability enter the winter season in better body condition. Bharal in areas grazed by livestock may, therefore, be doubly disadvantaged; first, they enter winter in poorer body condition and, second, are less able to supplement their body reserves during winter. This may affect the productivity of bharal herds in areas with very poor forage conditions.

Acknowledgments

We thank the Department of Science and Technology, Ministry of Science and Technology, India for funding the field work and the Forest Department, Himachal Pradesh for providing necessary work permits. The National Centre for Biological Sciences provided crucial institutional, financial and infrastructural support. The Nature Conservation Foundation helped with logistics in the field and we are grateful to the Whitley Fund for Nature for support. We thank Dr Ajith Kumar and Dr Anindya Sinha for their valuable suggestions at various stages of the study, Dr Kavita Isvaran for much help with statistical analysis, and Mr Sumanta Bagchi and two anonymous referees for comments on the manuscript. We thank Tenzin Thukten, Lobzang Chhupil, Tandup Chhering, Rinchen Tobge, and Chhunit Kesang and other villagers of Kibber, Spiti for their immense help with field work.

References


### Appendix

#### Table A1

| Estimate | SE    | t     | P(>|t|) |
|----------|-------|-------|---------|
| Intercept| 0.7299| 0.03154| 23.141  | <0.001  |
| SiteR    | 0.0680| 0.02003| 3.394   | 0.001   |
| Class2small | -0.0583| 0.02711| -2.151  | 0.033   |
| Class3female | -0.0807| 0.02697| -2.994  | 0.003   |
| Class4large | -0.1198| 0.0277 | -4.324  | <0.001  |
| Day      | -0.00285| 0.00066| -4.298  | <0.001  |

#### Table A2

| Estimate | SE    | t     | P(>|t|) |
|----------|-------|-------|---------|
| Intercept| 0.1834| 0.03257| 5.631   | <0.001  |
| SiteR    | -0.04939| 0.02009| -2.387  | 0.018   |
| Class2small | 0.04825| 0.02800| 1.723   | 0.087   |
| Class3female | 0.05735| 0.02785| 2.059   | 0.041   |
| Class4large | 0.11475| 0.02863| 4.008   | <0.001  |
| Day      | 0.002466| 0.00068| 3.598   | <0.001  |