

## ORIGINAL PAPER

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**Foraging strategies and seasonal diet optimization of muskoxen in West Greenland**

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**Abstract** Various aspects of optimal foraging and seasonal diet composition of bulls (bachelor and dominant), cows, subadults, and yearlings of muskoxen *Ovibos moschatus* were investigated in West Greenland during the following seasons: calving, post-calving, summer, rut and mid-winter. The following hypotheses were tested: (1) muskoxen maximize daily energy intake during spring and summer, (2) dominant bulls monopolizing cows during the rutting season shift from an energy maximizing to a time minimizing foraging strategy in order to maximize the time available for reproductive activities, and (3) muskoxen employ a time minimizing foraging strategy during winter to conserve energy. As forage quality changed throughout the short Arctic growing season, muskoxen responded by changing the proportions of daily time spent feeding on graminoids (Cyperaceae, Poaceae) and dicots (*Salix*, *Betula*), respectively. This seasonal variation in the relative proportion of daily feeding time spent ingesting graminoids followed approximately the energy maximization prediction over the periods calving to rut. Neither time minimizing nor random foraging could explain the observed diets in this period, thus confirming hypothesis 1. Dominant bulls did not shift to the time minimizing strategy as predicted by hypothesis 2. However, during the pre-rutting and rutting seasons bulls deviated from the other sex/age classes by failing to obtain the daily maximum energy predicted by the model, as a result of a higher proportion of time allocated to agonistic and sexual behaviour. During winter, none of the sex/age classes employed a time minimizing strategy, so rejecting hypothesis 3. Instead, muskoxen were found to maximize Na intake, indicating that Na is of major importance for winter survival. The results emerging from a linear programming model

with constraint settings varying over seasons confirm that the constraint parameters applied are indeed important limiting factors for muskoxen in natural populations.

**Key words** Diet optimization · Foraging strategies · Herbivore · Linear programming · Muskox

**Introduction**

The muskox *Ovibos moschatus* is, apart from caribou/reindeer *Rangifer tarandus*, the only ungulate adapted to survive and reproduce under the severe constraints of the Arctic and the high Arctic. As herbivores in habitats with marginal conditions for plant growth, muskoxen are exposed to an extreme seasonal variation in forage quality and availability (Olesen 1987; Thing et al. 1987; Klein and Bay 1990, 1991; Forchhammer 1992; Olesen et al. 1994). They can therefore be expected to show large seasonal differences in applied foraging strategies.

The variation in forage quality and availability apparently causes a concomitant variation in the foraging behaviour of muskoxen. In comparison to the winter season, muskoxen generally increase the daily feeding time during summer whereas a larger proportion of time is allocated to resting and ruminating during winter (Jingfors 1980; Olesen 1987; Klein and Bay 1990; Forchhammer 1992). This difference in activity budget could be a functional response (sensu Andersen and Sæther 1992) to the change in quality and availability of forage, since time spent feeding is dependent on the forage digestion rate, a consequence of the rumen fill theory (Moen 1973). In this respect, the reduction in feeding time from summer to winter is to some extent a result of increased allocation of time to rumination (digestion) caused by the low forage digestibility (i.e. quality) during winter. However, the time spent resting (i.e. the non-ruminating lying period)

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also increases from summer to winter (Forchhammer 1992). Consequently, during winter muskoxen do allocate time to inactive periods otherwise available for foraging, implying that the observed seasonal differences in feeding/lying activity of muskoxen cannot be explained as a simple functional response only. Thus, an alternating energy maximizer – time minimizer foraging strategy in summer and winter is considered as an alternative explanation for the above-mentioned seasonal variations in muskox activity budgets.

Since the development of the linear programming model (Westoby 1974; Belovsky 1978), it has been successfully applied to several herbivore species to model the energy maximizer – time minimizer dichotomy of foraging strategies (e.g. Belovsky 1978, 1984a, b; Ritchie 1988; Owen-Smith 1993a). However, the linear programming approach has only once been used in the study of arctic grazers (Belovsky 1991), even though this model is highly suitable for such environments. Considering the marginal habitat of muskoxen with its extreme seasonal variations in abiotic and biotic factors, the linear programming currency (maximize daily energy intake or minimize daily energy consumption) becomes an important fitness parameter. The same fluctuating nature of the muskox habitats makes it very likely that the constraints of the linear programming model (i.e. energetic requirement, available feeding time, digestive capacity and mineral requirement) are real limitations on the foraging options of muskoxen.

Previous studies on the foraging strategies of herbivores have applied the optimization technique of linear programming on average individuals within one season (usually the summer season), keeping constraint parameters constant (Westoby 1974; Belovsky 1978, 1984a, b; Owen-Smith 1993a; but see Ritchie 1988). However, in order to assess and discuss the importance of foraging strategies applied by Arctic grazers in one season, it is necessary to consider foraging strategies throughout the year, since the constraints on foraging decisions vary significantly throughout the seasons (Thing et al. 1987; Forchhammer 1992). In fact, one of the main criticisms of the linear programming approach in modelling herbivore foraging strategy is that previous studies have implicitly assumed, but not demonstrated, that animals respond to variation in the factors controlling the linear programming constraint settings (Owen-Smith 1993a, b).

Furthermore, in using an optimization approach to explain the foraging behaviour of muskoxen, one has to consider the individual sex/age classes. In addition to sex/age variation found in feeding time (Jingfors 1980; Olesen 1987; Forchhammer 1992; Oakes et al. 1992), time allocated to feeding on different forage species also varies between sex/age classes (Forchhammer 1992; Oakes et al. 1992), reflecting a possible sex/age specific variation in nutrient requirements. This paper presents and analyses such sex/age and season specific optimal foraging models with four

feeding constraints: maximum daily feeding time, rumen capacity, daily minimum energy requirement, and daily minimum sodium requirement. It is hypothesized that all sex/age classes forage as energy maximizers during the spring and summer when forage quality and availability are high. During winter, when forage quality and availability are low, muskoxen are expected to be time minimizers. Since foraging activities are in conflict with reproductive behaviour (e.g. Prins 1989; Dunbar et al. 1990; Komers et al. 1992) dominant bulls in mixed herds are also expected to shift from an energy maximizing strategy towards a time minimizing strategy in the rutting season (late summer). In contrast, bulls not monopolizing cows should maintain an energy maximizing strategy. These hypotheses are tested by comparing observed foraging dynamics with those predicted by the model.

As in earlier studies of large herbivores (e.g. Belovsky 1978, 1984b; Belovsky and Jordan 1981), Na uptake through forage is investigated as a separate constraint factor, because Na is known to be a potentially limiting mineral in muskoxen as well (Thing et al. 1987; Klein and Thing 1989; Staal and Thing 1991; Forchhammer 1992). However, in contrast to previous studies, the relative proportions of daily time spent feeding on selected forage categories (i.e. diet composition) which maximize Na intake is discussed in relation to actual forage intake, and compared with the energy maximizing and time minimizing strategies.

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### The model

Given a theoretical maximum available daily feeding time (cf. Belovsky 1978), which may vary throughout the seasons, foraging muskoxen face two extremes of a continuum: (1) muskoxen can either choose to forage through the entire period and thereby increase energy intake above the daily minimum requirement, or (2) stop foraging just after obtaining sufficient energy for daily physiological maintenance. Given a set of available forage categories, each characterized by a specific energy content, muskoxen applying feeding strategy 1 can maximize daily energy intake through selection of forage categories. Daily energy maximization can also be viewed as that particular division of maximum daily feeding time, where the relative proportions of time spent feeding on available forage categories result in maximum energy intake. In contrast, by applying feeding strategy 2, the relative proportions of time spent feeding on forage categories can minimize the daily feeding time of muskoxen.

Though not strict alternatives, the distinction between energy maximization and feeding time minimization is important. Basically, the energy maximizer – time minimizer dichotomy can be viewed as a trade-off. First, considering present versus future reproduc-

tion, energy maximization provides muskoxen with the greatest amount of energy for maintenance, growth, survival, and thus future reproduction. In contrast, time minimization leads to some minimum energetic intake and more time available for reproductive activities, thus increasing present reproductive output. Second, considering the marginal habitat of muskoxen, an energy maximizing strategy will increase exposure to deleterious environmental factors (e.g. result in excessive loss of energy), whereas a time minimizing strategy reduces deleterious exposure.

In Greenland, muskoxen utilize two major forage categories, graminoids (Cyperaceae and Poaceae) and dicots (mainly dwarf shrubs) (Thing et al. 1987; Klein and Bay 1990; C. R. Olesen, unpublished data). Four constraints are assumed to be of primary importance for the foraging strategies of muskoxen. First, a given maximum time period is available for foraging due to thermal and ruminating limitations (Belovsky 1978) and can be expressed as:

$$T_g + T_d \leq T_{MAX} \quad (1)$$

where  $T_g$  and  $T_d$  are the time (min/day) allocated to foraging on graminoids and dicots, respectively, and  $T_{MAX}$  the maximum available feeding time (min/day).

Second, muskoxen need a daily minimum intake of energy for maintenance and survival. This energetic constraint can be written as:

$$(E_{g, net} c_g)T_g + (E_{d, net} c_d)T_d \geq E_{MIN} \quad (2)$$

where  $E_{g, net}$  is the net energy obtained from one gram of graminoids ingested (kJ/g dry wt),  $E_{d, net}$  the net energy obtained from one gram of dicots ingested (kJ/g dry wt),  $c_g$  and  $c_d$  are the cropping rates (g dry wt/min) of graminoids and dicots, respectively, and  $E_{MIN}$  is the daily minimum energetic requirement for maintenance and survival (kJ/day).  $E_{MIN}$  is proportional to live body weight,  $W^{0.75}$  (Frisby et al. 1984; White et al. 1984a, b; Tyler and Blix 1990).

Third, muskoxen, as ruminants, are dependent on both their rumen capacity and specific digestive turnover rates, which set an upper limit to the daily amount of forage that can be ingested. This constraint can be written as:

$$(b_g c_g)T_g + (b_d c_d)T_d \leq R_c D_t \quad (3)$$

where  $b_g$  and  $b_d$  are the bulk values (wet weight/dry weight) of graminoids and dicots, respectively,  $R_c$  is the rumen capacity (g wet wt; proportional to body weight: J. Adamczewski, unpublished data), and  $D_t$  the daily digestive turnover rate.

Finally, Na content is low in forage relative to the physiological requirements of muskoxen and is known to be a potential limiting mineral, emphasized by mineral licking behaviour (Thing et al. 1987; Klein and Thing 1989; Staal and Thing 1991; Forchhammer 1992). The Na constraint can then be

written as:

$$(Na_g c_g)T_g + (Na_d c_d)T_d \geq Na_{MIN} \quad (4)$$

where  $Na_g$  and  $Na_d$  are the Na content (g/g dry wt) in graminoids and dicots, respectively, and  $Na_{MIN}$  is the daily minimum Na requirement (g/day).

The above-mentioned constraints determine the limits of possible foraging strategies of muskoxen. It must be stressed, however, that the constraints are by no means fixed values. There is seasonal variation in the parameters included in the constraint equations, resulting in a variable 'parameter space' within which foraging strategies can be adjusted. The model thus allows a simultaneous analysis of both the endogenous variation (i.e. sex/age variation) and environmental variation (i.e. seasonal variation in forage quality and availability) of muskox foraging in West Greenland.

## Material and methods

Study area, forage quality and muskox sex/age classes

Data needed for the presented model were collected during a study of muskox feeding ecology in Ammalortup Nunaa (66°58' N, 50°15' W), the northeastern region of Angujaartorfiup Nunaa in the low Arctic region of West Greenland. Field work was carried out in four 2–3 week periods from 12 May to 3 September 1992. Winter field work took place between 25 January and 27 February 1993. Data collection included the following seasons of the muskox life cycle: calving (25 April to 31 May), post-calving (1–30 June), summer (1 July to 14 August), rut (15 August to 14 September), and mid-winter (1 December to 14 February). During each of the first three summer field periods, the collected data covered all 24 h equally, but increasing darkness in August/September allowed data collection only between 0600–2300 hours. During the winter field period a light-gathering attachment was used on a spotting scope so that data could be obtained during all hours of the day and night.

In Angujaartorfiup Nunaa, muskoxen feed on two major forage categories, graminoids (Cyperaceae, Poaceae) and dicots (*Salix* and *Betula*). This division was made because muskoxen use these forage categories complementarily (Thing et al. 1987; Klein and Bay 1990; C. R. Olesen, unpublished data). Forage categories were sampled at 10-day intervals throughout the field seasons by cutting the current year's growth of graminoids and top shoots of dicots. Fresh samples were weighed and then pre-dried in the field in a pan at low heat (using a stove) and stored in paper envelopes. Further nutritional analyses were done at the Wildlife Habitat Management Laboratory, Washington State University, Washington, D.C., and included analyses for gross energy (bomb calorimetry), in vitro dry matter digestibility (Tilley and Terry method) and Na content.

Muskoxen were divided into four categories: bulls, cows, subadults and yearlings. During the rut, bulls were subdivided into 'dominant' bulls (bulls monopolizing cows) and 'bachelor' bulls (bulls not monopolizing cows). Calves were not included in the present analyses as they supplement their plant diet with an unknown amount of milk. Based on data from Olesen (1990) and Olesen et al. (1994) the following average total body weights (TBW<sub>kg</sub>) were used in the model: TBW<sub>bull</sub> = 310 kg, TBW<sub>cow</sub> = 250 kg, TBW<sub>subadult</sub> = 228 kg and TBW<sub>yearling</sub> = 142 kg. These average body weights were used for all summer seasons (i.e. calving to rut). During winter the averages were TBW<sub>bull</sub> = 280 kg,

TBW<sub>cow</sub> = 231 kg, TBW<sub>subadult</sub> = 247 kg and TBW<sub>yearling</sub> = 170 kg [data from Olesen (1990) and Olesen et al. (1994)].

Daily maximum feeding time ( $T_{MAX}$ ) and cropping rate ( $c_i$ )

In order to solve the linear programming model, an estimate of the theoretical maximum daily feeding time is needed (Belovsky 1978, 1986). Belovsky (1981) developed a thermodynamic model, using dynamic programming (Belmann and Dreyfus 1962) to determine the maximum time a herbivore can forage at minimum energetic cost. The data needed to compute the theoretical daily maximum feeding time (cf. Belovsky 1981) for muskoxen are not available at the present time. However, previous comparative data on the observed and theoretical daily maximum feeding time of several ruminant species, covering the body size range of muskoxen, show high agreement and consistency across species (Belovsky 1981, 1984a, 1986). Observed daily feeding time was therefore used as an estimate for the theoretical maximum daily feeding time ( $T_{MAX}$ ). Data on  $T_{MAX}$  were collected using instantaneous scan sampling (Altmann 1974) on randomly chosen herds. Individuals in herds were scanned at 15-min intervals. Observations were made with a 30 × 60 spotting scope at a distance between 200 to 500 m depending on the prevailing topography. Herds were followed for as long as possible and data on herds disturbed by any human activity were excluded from the analyses. Within each season,  $T_{MAX}$  for a given age/sex class  $c$  was calculated as:

$$T_{MAX} = 60 \sum_{h=1}^{24} \frac{f_c(h)}{N_c(h)} \quad (5)$$

where  $f_c(h)$  is the number of individuals of class  $c$  recorded feeding in the  $h$ 'th hour, and  $N_c(h)$  is the total number of individuals of that class scanned in the  $h$ 'th hour.

Forage intake rates, defined as grams dry weight ingested per time unit of cropping forage, were calculated as the product of bites/minute and grams dry weight/bite for each forage class. Bites/minute were measured in the field by counting the number of bites during a period of forage cropping, using a counter and electronic stopwatch with timer. Measurements of bites/minute were done in mid-June and at the end of July. In order to estimate the amount of forage obtained per bite, bites of muskoxen were simulated in the field. Muskoxen feed on graminoids by using the lower incisors against the upper pad and pulling with the head. Foraging on shrubs of *Salix* and *Betula* is different and involves an additional, sharp upward head movement breaking off the outer twigs (Gray 1973, M. C. Forchhammer, personal observation). Simulation of foraging on graminoids was done as follows: (1) the width of lower incisors was obtained for the sex/age classes; (2) the 'length' of a bite (i.e. how much the mouth opens) was estimated by observing the proportion of a yawn in relation to the height of muzzle; this was done at close range ( $\leq 100$  m) using a 30 × 60 spotting scope without disturbing the foraging muskoxen; (3) a plastic plate with the width of the measured lower incisors was constructed such that it could mimic the length of a bite when bowed as a 'V'; and (4) the 'V'-shaped plastic plate was placed over the forage in the habitat where muskoxen had been observed foraging, the two sides pushed against each other and the vegetation 'caught' was clipped.

A different technique was applied on the other forage class – dicots: (1) number and length of top shoots pulled ('zero-point' to top) were observed in the field; and (2) the plastic 'V' was placed at the 'zero-point' of the observed topshoot length taken and the two sides pressed together, before being pulled up to peel off cortex and leaves. Remaining current year top shoots were removed by clipping, in the same way as done by grazing muskoxen. The simulated bite samples were field-dried and later dried at 100 °C for 24 h and weighed. Bite simulation on graminoids was made both in mid-June and at the end of July, whereas simulation on dicots was made only at the end of July.

The simulation technique was developed in Greenland and data on width of lower incisors were available only from adults (one cow, five bulls) and one subadult. Measurements of lower incisors of yearlings (five individuals) were done at the Zoological Museum, Copenhagen. Assuming linear proportionality between amount of forage taken and width of lower incisors, cropping rates for yearlings were obtained by extrapolating the data on adults/subadults using the ratio between incisor width of the two sex/age classes. Data on effective cropping rates were not obtained in January/February and values from the period May to September were applied to the winter data. Snow cover results in lower cropping efficiencies during winter (see below). However, once snow has been removed by muskoxen, access to forage in winter is the same as during the summer periods, and since the morphology of forage ingested does not change significantly (M. C. Forchhammer, personal observation) the cropping rates are likely to be approximately the same throughout the seasons.

Cropping efficiency of forage class  $i$  ( $C_i$ ), defined as the fraction of time actually spent ingesting forage class  $i$ , was measured as the cumulative time spent cropping forage during a 5-min interval while the animals were feeding. The muskoxen were defined as cropping when their lips (or lower part of muzzle) moved. Observations were made at close range ( $\leq 100$  m) using a 30 × 60 spotting scope.  $C_i$  is needed to convert forage intake rates (i.e. gram dry weight ingested/minute of cropping forage) to the cropping rates ( $c_i$ ) defined as gram dry weight of forage  $i$  ingested/minute of feeding time. Thus, cropping rates of graminoids ( $c_g$ ) and dicots ( $c_d$ ) used in the model were obtained by multiplying forage intake rates with the respective cropping efficiencies.

#### Energetic calculations

The daily minimum energy requirement for maintenance and survival ( $E_{MIN}$ ) was calculated using the equations  $E_{MIN} = 544.0W^{0.75}$  (kJ/day) for May to September and  $E_{MIN} = 425.0W^{0.75}$  (kJ/day) for January to February (White et al. 1984b). These allometric relationships were obtained for young muskoxen ( $W$  range: 200–240 kg) fed ad libitum with a mixture of brome hay and pellets (White et al. 1984b). However, the relationships were used for all the sex/age classes in the present study since no data were available from wild muskoxen. The net energy obtained from 1 g dry wt of forage class  $i$  ( $E_{i,net}$ ) was calculated as:

$$E_{i,net} = E_{i,gross} DMD - E_{i,cost} \quad (6)$$

where  $E_{i,gross}$  is the gross energy obtained from 1 g dry wt of forage category  $i$  (kJ/g dry wt), DMD is the in vitro dry matter digestibility of forage category  $i$ , and  $E_{i,cost}$  the energetic cost of cropping 1 g-dry wt of forage category  $i$ .  $E_{i,cost}$  was calculated from the equations:

$$E_{i,cost} = M_i c_i E_{M,cost}, \quad E_{M,cost} = 0.0115W^{-0.41} \quad (7a, b)$$

where  $M_i$  is movement rate (m/min) associated with cropping forage category  $i$  (Forchhammer 1992),  $c_i$  the cropping rate of forage category  $i$  (min/g dry wt), and  $E_{M,cost}$  the energy spent moving 1 m (kJ/m), calculated from data presented by Schmidt-Nielsen (1972). However, the energetic cost of cropping 1 g dry wt calculated from Eq. 7a and b was negligible for both forage groups (range:  $1.36 \times 10^{-4}$ – $4.10 \times 10^{-4}$  kJ/g dry wt) and thus assumed to be zero in the further calculations.

Rumen capacity, digestive turnover rate, bulk value, daily minimum sodium requirement and sodium content in forage

Rumen capacity ( $R_c$ ) was defined as the reticulo-rumen content and the digestive turnover ( $D_c$ ) as 24 h/MRT, where MRT (mean retention time) is the mean time that a food particle stays in the reticulo-rumen (Holleman et al. 1984). Since data on  $R_c$

from muskoxen in Greenland were sparse, data from Canada were used to calculate the allometry of  $R_c$ . On the basis of unpublished summer and winter data provided by J. Adamczewski the following allometric relationships were calculated for bulls (summer):  $R_c = 0.014W^{1.50}$  ( $r = 0.93$ ,  $t_{49} = 17.4$ ,  $P < 0.001$ ); bulls (winter):  $R_c = 0.22W^{0.97}$  ( $r = 0.97$ ,  $t_{10} = 13.2$ ,  $P < 0.001$ ); cows (summer):  $R_c = 0.008W^{1.60}$  ( $r = 0.96$ ,  $t_{163} = 43.3$ ,  $P < 0.001$ ); cows (winter):  $R_c = 0.38W^{0.86}$  ( $r = 0.92$ ,  $t_{47} = 17.1$ ,  $P < 0.001$ ); all sexes (used for yearlings) (summer):  $R_c = 0.007W^{1.63}$  ( $r = 0.96$ ,  $t_{214} = 49.6$ ,  $P < 0.001$ ); all sexes (winter):  $R_c = 0.29W^{0.91}$  ( $r = 0.94$ ,  $t_{57} = 22.5$ ,  $P < 0.001$ ).

Mean retention time for each sex/age class was calculated from the equation  $MRT = 15.3W^{0.251}$  (Illius and Gordon 1992). Bulk values ( $b_i$ ) were calculated as wet weight measured in the field divided by dry weight measured after 24 h at 100 °C. Data on bulk values were obtained during post-calving, rut, and mid-winter.  $Na_{MIN}$  was calculated from the equation  $Na_{MIN} = 0.002W$  (Church et al. 1971) and data on seasonal variations of sodium content in forage ( $Na_i$ ) were obtained from the collected forage classes (graminoids and dicots) analysed at the Wildlife Habitat Management Laboratory, Washington State University.

Predicted and observed proportion of daily feeding time spent feeding on the forage classes

The predicted proportions of daily feeding time spent foraging on graminoids and dicots,  $T_g$  and  $T_d$ , respectively, for an energy maximizing, time minimizing, and Na maximizing strategy were calculated as follows. The solution ( $T_d, T_g$ ) for an energy maximizing strategy was found by maximizing  $(E_{g,net}c_g)T_g + (E_{d,net}c_d)T_d$  subject to Eqs. 1–4. Likewise, the solution for a time minimizing strategy was found by minimizing  $T_g + T_d$  subject to Eqs. 1–4. The solution for a Na maximizing strategy was found by maximizing  $(Na_gc_g)T_g + (Na_dc_d)T_d$  subject to Eqs. 1–4 [see Thie (1988) for a detailed description of the linear programming algorithm].

Observed daily time spent foraging on graminoids and dicots was obtained by instantaneous scan sampling (Altmann 1974) of individuals in herds, with an interval of 15 min between scannings. Observed daily proportion of time spent feeding on forage class  $i$  was then calculated as:

$$T_i = 60 \sum_{h=1}^{24} \frac{f_{c,i}(h)}{N_c(h)} \quad (8)$$

where  $f_{c,i}(h)$  is the number of individuals of age/sex class  $c$  feeding on forage class  $i$  in the  $h$ 'th hour, and  $N_c(h)$  the total number of individuals scanned in the  $h$ 'th hour. The data collected on  $T_{MAX}$  (Eq. 5) and  $T_i$ , respectively, were randomly divided during each season into two groups of individuals, e.g. when 2–4 herds were followed in the field simultaneously, the data from the first 1–2 herds were used to estimate  $T_{MAX}$ , and data on the other 1–2 herds were used to calculate  $T_d$  and  $T_g$ . This procedure avoids the circularity arising in applying the same data set in both predicted and observed proportions of daily time allocated to foraging on graminoids and dicots. However, since both groups of individuals respond to the same environment, one can argue that the data collected are not truly independent. In this more philosophical perspective, circularity is not totally avoided but minimized as much as possible (see Discussion).

Two-level nested ANOVA and single classification ANOVA (Sokal and Rohlf 1981) were used in the statistical analyses. Homoscedasticity was confirmed by Hartley's  $F_{max}$ -test (Sokal and Rohlf 1981). Throughout the text, mean values are given  $\pm 1$  SD.

**Results**

The parameters used to calculate the constraint equations ( $T_{MAX}$ ,  $b_i$ ,  $c_i$ ,  $R_c$ ,  $D_t$ ,  $E_{MIN}$ ,  $E_{i,gross}$ ,  $DMD$ ,  $E_{i,net}$ ,

$Na_{MIN}$ ,  $Na_i$ ) and observed daily proportions of time spent feeding on graminoids ( $T_g$ ) and dicots ( $T_d$ ) are given in Tables 1 and 2, respectively.

There were no significant differences in cropping efficiencies during summer ( $C_i$ ) between the sex/age classes (ANOVA:  $F_{3,226} = 0.98$ ,  $P > 0.25$ ). Additionally, no significant differences in cropping efficiencies were found between the two forage classes graminoids and dicots ( $F_{4,222} = 1.03$ ,  $P > 0.25$ ) nor between summer seasons ( $F_{3,4} = 0.36$ ,  $P > 0.75$ ) (two-level nested ANOVA: cropping efficiencies nested within seasons). The average  $C$ -values (graminoids:  $75.2 \pm 3.9\%$ ,  $n = 191$ ; dicots:  $72.5 \pm 5.7\%$ ,  $n = 39$ ) were therefore used to convert forage intake rates to cropping rates ( $c_i$ ) throughout the four summer seasons. In mid-winter, cropping efficiencies averaged  $70.9 \pm 7.9\%$  ( $n = 39$ ) for graminoids. Cropping efficiency on dicots was not obtained during the winter season. However, since the differences in cropping efficiencies of graminoids and dicots are apparently minor, the average value for graminoids obtained in mid-winter was applied in the calculation of the winter cropping rates.

Mean values of bites/min were  $115.0 \pm 17.5$  ( $n = 163$ ) and  $56.4 \pm 15.9$  ( $n = 50$ ) for foraging on graminoids and dicots, respectively. When foraging on graminoids, no significant differences in bites/min were found over seasons (ANOVA:  $F_{1,163} = 0.71$ ,  $P > 0.25$ ). The amount of forage taken in one bite was  $0.14 \pm 0.03$  g dry wt for graminoids ( $n = 120$ ) and  $0.55 \pm 0.06$  g dry wt for dicots ( $n = 120$ ). No significant seasonal difference in g dry wt graminoids/bite was found (ANOVA:  $F_{1,120} = 0.03$ ,  $P > 0.75$ ), hence average values were used to calculate forage intake rates (g dry wt/min of cropping).

Bulk values ( $b_i$ , Table 1) did not vary significantly within each forage category (i.e. graminoids and dicots), either between summer seasons ( $F_{1,2} = 0.06$ ,  $P > 0.75$ ) or between the genera Poaceae and Cyperaceae ( $F_{2,8} = 1.51$ ,  $P > 0.25$ ) (two-level nested ANOVA: bulk values nested within seasons), and these mean values (Table 1) were used through all four summer seasons. Bulk values of graminoids and dicots, respectively, are given in Table 1.

Energy maximizing, time minimizing, and Na maximizing solutions to the model ( $T_d, T_g$ ) were calculated for each season (Table 2) with Eqs. 1–4 using the model parameters in Table 1. Solutions for energy maximization and Na maximization were indistinguishable in all seasons, except for mid-winter (Table 2). Observed proportion of time spent feeding on graminoids and dicots for the sex/age classes – bulls, cows, subadults and yearlings – are also shown in Table 2. In the period calving to rut, the observed time allocated to graminoids and dicots for cows, subadults and yearlings correlated well with the diet predicted by an energy maximizing strategy ( $r = 0.73$ ,  $t_{11} = 3.51$ ,  $P < 0.01$ ) (Fig. 1a) and the regression equation was not significantly different from the perfect prediction ( $y = x$  in Fig. 1; slopes:  $t_{12} = 0.15$ ,  $P > 0.5$ ; intercepts:  $t_{12} = 0.53$ ,  $P > 0.5$ ). However, the

**Table 1** Model parameters used in Eqs. 1–4 and 6 (see text for details): maximum available feeding time ( $T_{MAX}$ ), bulk value ( $b_i$ ), cropping rate ( $c_i$ ), rumen capacity ( $R_c$ ), daily digestive turnover ( $D_i$ ), daily minimum energetic requirement for maintenance and survival ( $E_{MIN}$ ), gross energy obtained from 1 g dry wt forage ( $E_{i, gross}$ ), in vitro dry matter digestibility ( $DMD$ ), net energy obtained from 1 g

dry wt of forage ( $E_{i, net}$ ), daily minimum sodium requirement ( $Na_{MIN}$ ), and sodium content in 1 g dry wt forage ( $Na_i$ ) (BBU bachelor bulls, SUB subadults, YEA yearlings, DBU dominant bulls, gram graminoids, dic dicots). Horizontal lines indicate that the value is used throughout all seasons

Model parameters	Season				
	Calving	Post-calving	Summer	Rut	Mid-winter
$T_{MAX}$ (min/day) <sup>b</sup>					
BBU/DBU	784.2	786.0	732.0	689.4	656.7
COW	792.0	606.0	672.0	744.0	616.7
SUB	699.0	653.4	666.6	738.0	594.5
YEA	810.6	552.6	594.0	752.4	557.5
$b_i$ (wet wt/dry wt) <sup>a</sup>					
Gram		1.88 ± 0.26 (12)			1.46 ± 0.16 (9)
Dic		3.06 ± 0.04 (3)			1.87 ± 0.04 (3)
$c_i$ (g dry wt/min) <sup>a</sup>					
AD/SUB-gram		12.19 ± 1.84 (163)			11.49 ± 1.74 (163)
-dic		24.44 ± 3.94 (50)			23.89 ± 3.85 (50)
YEA-gram		7.20 ± 1.09 (163)			6.79 ± 1.03 (163)
-dic		14.45 ± 2.33 (50)			14.12 ± 2.28 (50)
$R_c$ (g wet wt)					
BBU/DBU			76414		52020
COW			54928		40970
SUB			48357		46060
YEA			23204		31050
$D_i$ (/day)					
BBU/DBU			0.37		0.38
COW			0.39		0.40
SUB			0.40		0.39
YEA			0.45		0.43
$E_{MIN}$ (kJ/day)					
DBU/BBU			40210		29090
COW			34220		25180
SUB			31940		26480
YEA			22390		20010
$E_{i, gross}$ (kJ/g dry wt) <sup>a</sup>					
Gram	18.26 ± 0.59 (6)	18.93 ± 0.63 (6)	19.34 ± 0.25 (6)	18.97 ± 0.50 (6)	18.93 ± 0.46 (12)
Dic	21.94 ± 1.76 (4)	21.86 ± 0.92 (4)	21.48 ± 0.84 (4)	21.73 ± 0.92 (4)	22.02 ± 1.21 (5)
$DMD$ (%) <sup>a</sup>					
Gram	41.73 ± 8.41 (6)	63.31 ± 10.53 (6)	65.73 ± 6.03 (6)	62.22 ± 7.17 (6)	40.65 ± 1.66 (12)
Dic	29.26 ± 1.82 (4)	40.35 ± 8.68 (4)	46.35 ± 7.25 (4)	46.90 ± 11.92 (4)	32.31 ± 4.22 (5)
$E_{i, net}$ (kJ/g dry wt) <sup>a</sup>					
Gram	7.58 ± 1.51 (6)	11.98 ± 1.93 (6)	12.73 ± 1.17 (6)	11.85 ± 1.54 (6)	7.66 ± 1.09 (12)
Dic	6.41 ± 0.54 (4)	8.79 ± 1.72 (4)	9.92 ± 1.30 (4)	10.13 ± 2.22 (4)	7.08 ± 0.84 (5)
$Na_{MIN}$ (g/day)					
BBU/DBU			0.620		0.560
COW			0.500		0.462
SUB			0.456		0.494
YEA			0.284		0.340
$Na_i$ (µg/g dry wt) <sup>a</sup>					
Gram	205.0 ± 63.6 (2)	177.2 ± 154.1 (6)	80.0 ± 49.8 (6)	75.7 ± 35.2 (6)	286.7 ± 131.4 (12)
Dic	112.5 ± 12.6 (4)	97.5 ± 20.6 (4)	65.0 ± 23.8 (4)	57.5 ± 20.6 (4)	104.0 ± 33.8 (5)

<sup>a</sup>Values given as mean ± SD with sample size in brackets

<sup>b</sup>Sample size:  $n_{BBU} = 5922$ ,  $n_{DBU} = 601$ ,  $n_{COW} = 4802$ ,  $n_{SUB} = 1720$ , and  $n_{YEA} = 1584$

observed percentages of daily time allocated to graminoid intake by bulls during the calving and summer seasons and by all sex/age classes during winter were generally higher than predicted by an energy maximizing strategy (Fig. 1a). Bulls foraged as energy maximizers only during the post-calving season (Fig. 1a). Through all seasons the observed diet correlated with the diet predicted by the Na maximizing strategy

( $r = 0.80$ ,  $t_{15} = 5.14$ ,  $P < 0.001$ ) and the regression equation did not deviate significantly from perfect predictions (slopes:  $t_{16} = 0.20$ ,  $P > 0.5$ ; intercepts:  $t_{16} = 0.61$ ,  $P > 0.5$ ) (Fig. 1b). A time minimizing strategy did not explain the observed diet for any of the four sex/age classes ( $r = 0.19$ ,  $t_{19} = 0.78$ ,  $P > 0.4$ ) (Fig. 1c).

The observed diets (expressed as the daily feeding time allocated to graminoids and dicots, respectively)

**Table 2** Observed daily proportion of time spent foraging on graminoids and dicots (*obs*) compared to the predicted daily proportion of time spent foraging on graminoids and dicots assuming an energy maximizing strategy (*pred EMax*), time minimizing strat-

egy (*pred TMin*), or Na maximizing strategy (*pred NaMax*) under the given constraints (Eqs. 1–4). (*BBU* bachelor bulls, *SUB* subadults, *YEA* yearlings, *DBU* dominant bulls,  $T_g$  daily time spent foraging on graminoids, and  $T_d$  daily time spent foraging on dicots)

	BBU		COW		SUB		YEA		DBU	
	$T_d$ (min)	$T_g$ (min)	$T_d$ (min)	$T_g$ (min)	$T_d$ (min)	$T_g$ (min)	$T_d$ (min)	$T_g$ (min)	$T_d$ (min)	$T_g$ (min)
<b>Calving</b>										
Pred EMax and NaMax	199.0	585.0	63.2	728.8	64.2	634.8	0.0	771.4	–	–
Pred TMin	256.7	0.0	218.5	0.0	203.9	0.0	230.8	19.1	–	–
Obs	0.0	792.0	0.0	786.0	0.0	708.0	0.0	793.8	–	–
<b>Post-calving</b>										
Pred EMax and NaMax	198.1	587.9	145.5	460.5	84.4	569.0	96.8	455.8	–	–
Pred TMin	261.4	0.0	210.8	0.0	193.7	0.0	202.7	0.0	–	–
Obs	185.2	592.9	100.8	529.2	162.3	489.7	129.7	423.3	–	–
<b>Summer</b>										
Pred EMax and NaMax	222.0	510.0	116.3	555.7	78.5	588.1	78.5	515.5	–	–
Pred TMin	366.6	38.6	258.8	91.2	230.9	92.1	170.8	214.7	–	–
Obs	58.1	668.5	102.6	581.4	92.1	573.3	64.2	521.2	–	–
<b>Rut</b>										
Pred EMax and NaMax	240.9	448.5	84.1	659.9	46.9	691.1	8.4	744.0	240.9	448.5
Pred TMin	323.4	179.3	226.2	197.4	201.1	187.6	143.9	302.6	323.4	179.3
Obs	6.8	671.8	42.5	665.5	45.3	710.1	59.6	685.0	5.2	512.6
<b>Mid-winter</b>										
Pred EMax	314.3	342.4	217.0	399.7	286.9	307.6	475.5	82.0	–	–
Pred NaMax	0.0	656.7	0.0	616.7	0.0	594.5	0.0	557.5	–	–
Pred TMin	136.8	67.8	125.0	46.1	129.3	52.6	180.5	38.2	–	–
Obs	7.6	634.8	7.4	595.6	9.1	584.5	12.5	598.8	–	–

Sample size:  $n_{BBU} = 5431$ ,  $n_{DBU} = 531$ ,  $n_{COW} = 4034$ ,  $n_{SUB} = 1815$ , and  $n_{YEA} = 1927$

of the muskox sex/age classes cannot be described in simple common terms. As illustrated in Fig. 2 and 3, size and location of the possible ‘diet space’ (hatched area limited by the constraint equations) varied considerably both between sex/age classes and between seasons. Specific responses of sex/age classes to the seasonal variation in forage quality occurred, and the observed diets were found to vary both between sex/age classes and between seasons (Figs. 2, 3). During calving, bulls foraged as energy maximizers, whereas in the remaining seasons they deviated by having a diet of mainly graminoids (Fig. 2). Although some deviations from an energy maximizing diet occurred in cows (Fig. 3), they did approach an energy maximizing diet better than bulls. The optimal diets predicted from an energy maximizing or Na maximizing strategy were the same in all seasons except for mid-winter, since the slope of both the *E*- and Na-constraint equations (Eqs. 2, 4, respectively) were steeper than the *T*-constraint equation (Eq. 1). However, during mid-winter the slope of the Na-constraint equation did become less steep than the *T*-constraint equation, and the optimal diet for a Na maximizing strategy consisted solely of graminoids (i.e. 100% of  $T_{MAX}$  allocated to graminoid intake) whereas the energy maximizing optimal diet was a mixture of graminoids and dicots (Fig. 2e, 3e). Seasonal variation in diets for subadults and yearlings was similar to cows in all seasons (Fig. 4). The shift to a pure Na maximizing diet during mid-winter is obvious and the observed diet for all sex/age classes fitted

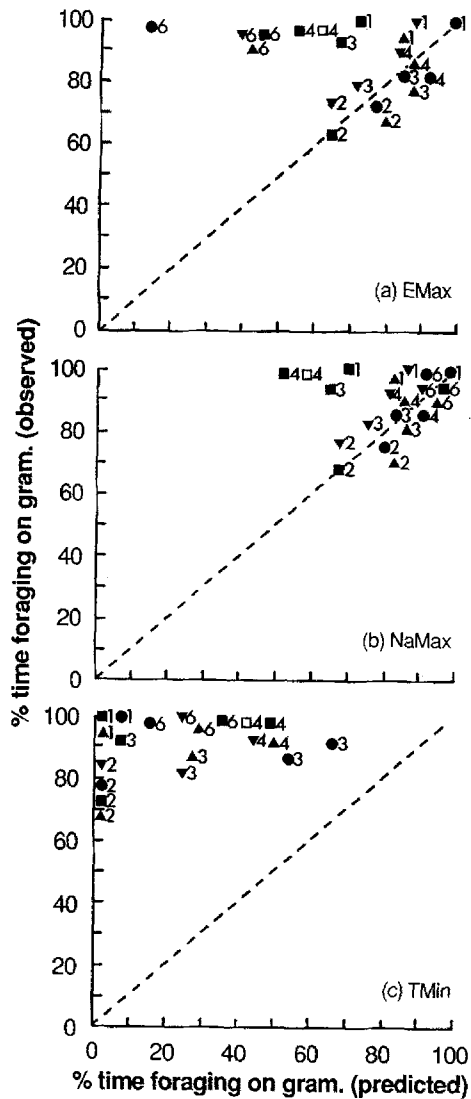
the model predictions quite well, given a Na maximizing strategy (Fig. 4).

### Discussion

#### Foraging strategies and seasonal diet optimization

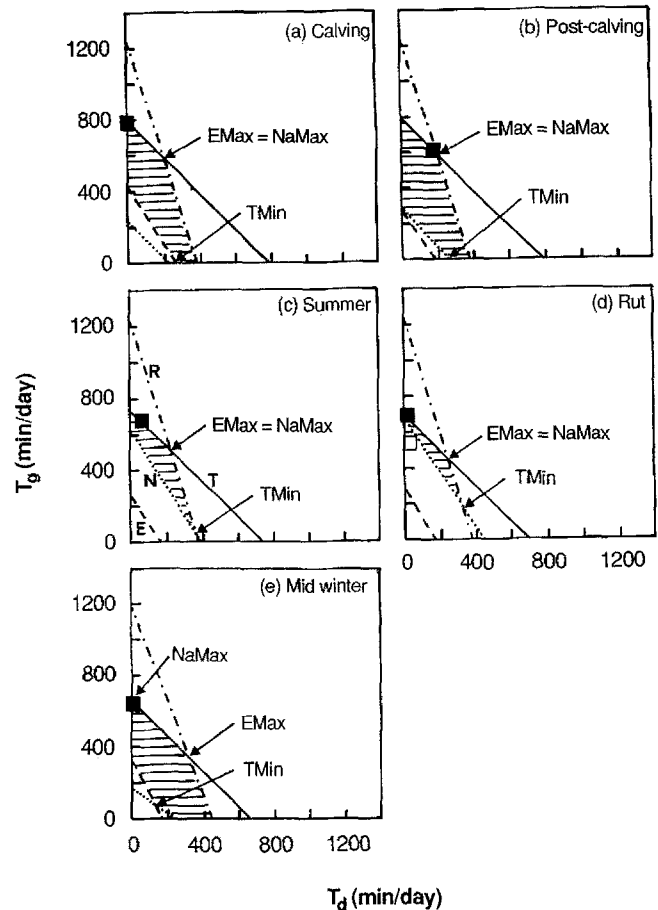
Within the limits of the presented model, the results emerging do indeed, as hypothesized, show that muskoxen in West Greenland maximize daily energy intake most of the year. This happens by allocating the optimal proportions of daily feeding time to graminoid and dicot intake (Table 2; Figs. 1a, 2–4). By doing so, the muskoxen also maximize the intake of Na, and in winter Na intake appears to get priority over energy maximization. In contrast, the time minimizing strategy does not explain the observed proportions of time allocated to intake of graminoids and dicots (i.e. diet compositions), either seasonally or on average (Table 2; Figs. 1c, 2–4). In addition, no correlation was found between seasonal graminoid availability and relative proportion of feeding time spent on graminoids ( $r = 0.19$ ,  $t_{14} = 0.71$ ,  $P > 0.4$ ), indicating that muskoxen do select forage across vegetation types.

Although all sex/age classes generally forage in an energy maximizing manner during the summer seasons, some consistent relationships with sex and age were found. As seen in Figs. 1a and 4, the observed relative proportion of time allocated to graminoid-intake of



**Fig. 1a–c** The predicted relative proportion of time spent feeding on graminoids in relation to the observed, relative proportion of time spent feeding on graminoids. The line  $y = x$  indicates the perfect correlation between predicted and observed. **a** Energy maximizing strategy (*EMax*), **b** sodium maximizing strategy (*NaMax*), and **c** time minimizing strategy (*TMin*). Symbols used for the sex/age classes: ■ bull, □ dominant bull, ▼ cows, ▲ subadult, and ● yearling. Number accompanying symbols indicate seasons: 1 calving, 2 post-calving, 3 summer, 4 rut, 6 mid-winter

bulls (except during post-calving: symbol '■2' in Fig. 1a) was consistently above that of the other sex/age classes, indicating that bulls were not 'perfect' energy maximizers. The deviation from the energy maximizing strategy was expected, a priori, to occur for dominant bulls (symbol '□4' in Fig. 1a) in the period around the rutting season due to conflict between foraging and reproductive activities. However, bulls monopolizing cows did not, as hypothesized, show a strict shift from an energy maximizing strategy to a time minimizing strategy during the rut (Table 2; Fig. 2d). The allocation of time to reproduction seen



**Fig. 2a–e** Graphical solution of the model for bulls. Shaded areas represent the proportions of time spent feeding on dicots ( $T_d$ ) and graminoids ( $T_g$ ) subject the constraints: maximum daily feeding time ( $T$ ), rumen capacity ( $R$ ), daily minimum energy requirement ( $E$ ), and daily minimum Na requirement ( $N$ ). The observed allocation of time to dicot and graminoid intake (■ bachelor, □ dominant bulls), and the predicted diet from energy maximization (*EMax*), time minimization (*TMin*), and Na maximization (*NaMax*), respectively, are also shown. Seasons: **a** calving, **b** post-calving, **c** summer, **d** rut, and **e** mid-winter

in dominant bulls is thus apparently not all-consuming, such that foraging ceases after obtaining  $E_{MIN}$  as assumed by the time minimizing hypothesis. This further emphasizes the need to consider the energy maximizer – time minimizer dichotomy as a continuum and not as strict alternatives.

The fact that bachelor bulls during the pre-rutting and rutting seasons show similar deviations from pure energy maximization, as do dominant bulls (symbols '■3' and '■4' in Fig. 1a), indicates that these bulls also allocate time to reproductive activities. Bachelor herds are apparently not groups of non-breeding bulls only, and additional observations (Olesen 1987; M. C. Forchhammer, personal observation) suggest that potentially breeding bulls 'flow' through these herds. Since the data used in the model are based on means (within sex/age classes), a high 'flow' of bulls through bachelor and mixed herds would result in the observed



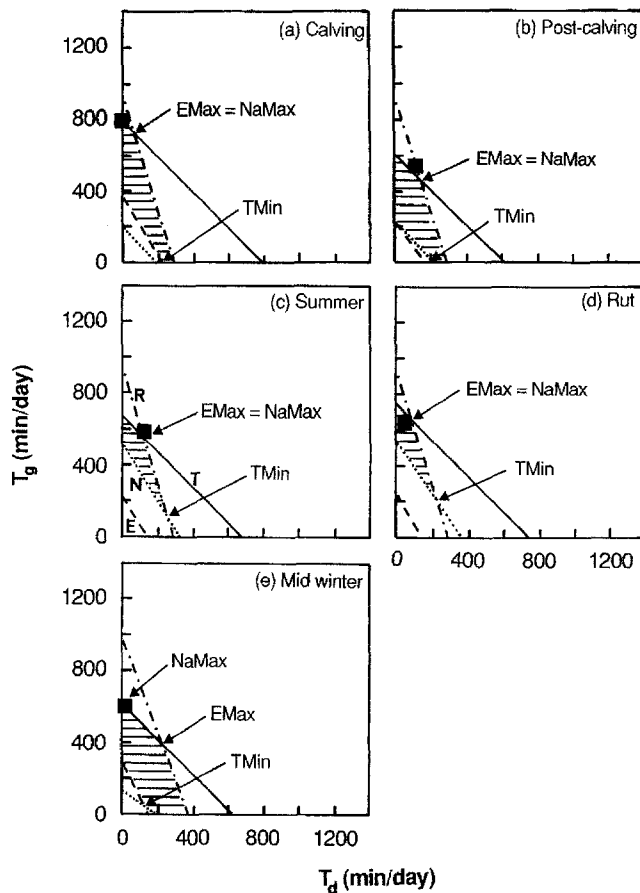
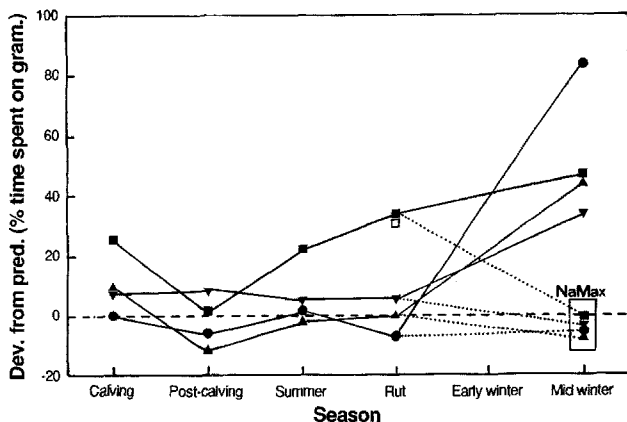


Fig. 3 Graphical solution of the model for cows. For further explanation see Fig. 2. The graphical results for subadults and yearlings are similar to those observed for cows

pattern, i.e. all potentially breeding bulls would do about the same. Flow of breeding males has been observed for bison *Bison bison*, where breeding individuals improve body conditions in the bachelor herds

Fig. 4 Seasonal deviations in observed percentage of graminoids in the diet (i.e. relative proportion of time allocated to graminoid intake) from predicted diet given energy maximization (solid lines). Dotted lines connecting deviations in rut and mid-winter seasons show the shift to Na maximization (NaMax) seen in mid-winter. Symbols used for the sex/age classes: ■ bull, □ dominant bull, ▼ cows, ▲ subadult, ● yearling



after a period of monopolizing females (Komers et al. 1992).

However, bulls during calving (symbol '■1' in Fig. 1a) were expected to be energy maximizers, as was observed for bulls during post-calving (symbol '■2'). The deviation in this period cannot be explained by allocation of time to other activities (Forchhammer 1992, unpublished data). Since the energy maximizing and Na maximizing strategies predict the same optimal diet during calving (Table 2; Fig. 2a), a trade-off between energy and Na maximizing also cannot explain the observed deviation of bulls in the calving season. Whether this deviation is due to other nutrients or minerals not specified in the model is at present unknown.

Although muskoxen allocate relatively more time to lying (rumination and non-ruminating resting) during winter (Forchhammer 1992), a shift from energy maximizing to time minimizing was not observed for any of the four sex/age classes (Table 2; Figs. 1c, 2-4). Instead, muskoxen were found to be Na maximizers throughout winter (Figs. 1b, 2-4). Na is known to be an important constraint factor and muskoxen are known to lick mineral soil during the summer seasons (Klein and Thing 1989; Staal and Thing 1991). However, mineral licking has not to our knowledge been observed in winter, probably because snow cover prevents easy access to mineral soil. Without additional Na supply from soil licking during winter, Na intake through forage becomes important. Na intake through forage is probably also important during summer seasons (Figs. 1b, 2-4). However, since optimization of energy and Na intake are synonymous in this period, additional controlled experiments are needed to assess a possible energy - Na trade-off in summer.

Model parameters

A number of comments can be made with regard to the precision of the parameters applied in the model equations and in the calculation of observed diet. Cropping efficiencies in the present study are up to 20% less than those obtained in previous studies on muskoxen (e.g. Olesen 1987). This deviation is most likely due to differences in observation methods. Previously, cropping efficiency has mostly been measured as the proportion of foraging time when a focal individual has its muzzle down in vegetation (Jingfors 1980; Olesen 1987). However, the detailed observations of the present study indicated that ingestion is not continuous and that 'muzzle-down' measurements thus overestimate actual forage intake. Cropping rates have not been previously calculated for muskoxen. However, one additional independent estimate on daily forage consumption does exist from Alaska ( $102 \pm 7 \text{ g dry wt/kg}^{0.75} \text{ day}^{-1}$  for young muskoxen in summer; White et al. 1984b), and is similar to the daily forage intake

calculated in the present study (115.3 g dry wt/kg<sup>0.75</sup> day<sup>-1</sup> for a subadult in summer). This suggests that the bite simulation rates approximately reflect the actual forage intake of muskoxen.

During calving and mid-winter, crude protein content of forage averaged 6–7%, whereas the crude protein content in the plant growing season (post-calving to rut) averaged 11–15% (Forchhammer 1995). Estimated daily crude protein requirements of muskoxen averaged 3–5% for yearlings and subadults, 2–3% for adult males and non-lactating females, and 7–8% for lactating females (M. C. Forchhammer, unpublished data). Since lactation of calves are concentrated from post-calving to rut (Jingfors 1980; Olesen 1987; M. C. Forchhammer, personal observation), estimated crude protein requirements of all muskox sex/age classes were considerably below the crude protein content in selected forage. Hence, protein constraint was not considered to be an important influence on the foraging strategies of muskoxen and was thus not included in this study.

Although the observed daily feeding time correlates with the theoretical maximum value (Belovsky 1986). The possibility that the observed value is less than the theoretical maximum cannot be excluded. If so, the observed foraging strategy of muskoxen would be limited by factors other than daily feeding time. However, the energy (and Na) maximizing foraging strategy as generally observed in muskoxen (Table 2; Fig. 1) would still be valid in a relative sense, because the energy and Na maximizing strategies as opposed to the time minimizing strategy should be perceived as end points of a continuum and not as strict alternatives (Belovsky 1986).

An independent estimate of the observed diet (expressed as actual daily forage intake or proportion of daily time allocated to feeding on different forage categories) of herbivores can be achieved in various ways. Nevertheless, several of the methods previously employed will bias the estimates in some way. Observed diets expressed as proportion of graminoids or dicots have often been calculated by using microhistological analyses of plant fragments in faeces (e.g. Ritchie 1988). However, this does not seem to be a valid alternative in muskoxen as the relative proportions of dicots and graminoids seen in faeces deviate by up to 47.1% from those ingested (i.e. observed in the rumen-reticulum) due to the different degree of digestion (e.g. Thing et al. 1987; M. C. Forchhammer and J. J. Boomsma, to be published). Consequently, such an estimate will cause deviations from, for example, a pure energy maximizing diet, for spurious reasons. Controlled enclosure experiments can also be applied to estimate observed diet. This method, however, is likely to affect the behaviour of the herbivore species investigated, and forage ingested in enclosures could deviate significantly from in situ measurements in natural habitats. Reticulo-rumen sampling provides the most correct independent

estimate of observed diet, if applied to individuals in the population (and season) under study. Using comparative reticulo-rumen data from other populations in other habitats would impose deviations from pure optimal diets, since environmental constraints differ not only seasonally but also geographically (Forchhammer 1992). Moreover, existing data from rumen-reticulum samplings of muskoxen (C. R. Olesen, unpublished data) give the same estimate for diet composition as found in the present study (M. C. Forchhammer and J. J. Boomsma, to be published). Finally, independent observations of daily proportion of time allocated to various forage categories (e.g.  $T_d$ ,  $T_g$ ) can be used as a measure of actual diet composition. Basically, this method is the same as rumen-reticulum sampling, since time spent feeding on a given forage is proportional to the corresponding intake of forage, and both procedures would give approximately the same plant proportions ingested (M. C. Forchhammer and J. J. Boomsma, to be published).

Despite making the measurements of  $T_{MAX}$ ,  $T_d$  and  $T_g$  independent by collecting data simultaneously on two independent groups of individuals, one can still argue that since the two groups of individuals do respond to the same environment, the measurements of  $T_{MAX}$ ,  $T_d$  and  $T_g$  are not truly independent. However, the modelling results with data indicate no inconsistencies, and while the proportion of daily time spent feeding on graminoids and dicots *must* sum to  $T_{MAX}$ , the daily allocation of time to one forage category is largely independent of  $T_{MAX}$ . Thus, a comparison of predicted and observed times spent foraging on, for example, graminoids is largely free of circularity.

#### Linear programming: optimal foraging of herbivores

Linear programming has been successfully applied in describing the optimal foraging decisions of several herbivore species (e.g. Belovsky 1978, 1984b, 1986; Ritchie 1988; Vulink and Drost 1991). However, the linear programming optimization approach has been critically debated (Belovsky and Schmitz 1993; Owen-Smith 1993a, b). One of the major criticisms is whether the mean constraint values used in linear programming modelling are actually upper limits to the foraging of herbivores: previous studies having implicitly assumed but not demonstrated this (Owen-Smith 1993a, b). Consequently, animals living in a fluctuating environment should only respond to the variation in the factors controlling the linear programming constraint settings, if the applied constraints are really limiting. From this perspective, Arctic herbivores are very interesting study animals because they have a relatively simple diet composition, with Arctic environmental factors likewise being relatively simple and showing a large seasonal variation. The results emerging from the presented linear program-

ming model confirm that the constraint parameters normally applied are indeed limiting the foraging decisions of muskoxen and thus support the general validity of the linear programming approach to modelling herbivore foraging strategies. In addition, the present study shows that a year-round analysis of varying foraging constraints may be required to describe and assess the future consequences of the foraging strategy applied by herbivores in each single season (or equivalent time period).

Although optimality predictions from linear programming fit the foraging strategy patterns of average individuals (e.g. sex and age classes) fairly well, deviations from the energy maximization – time minimizing dichotomy are observed (e.g. Figs. 1–4). Na maximizing does explain some of the residual variation seen in muskoxen, especially during winter (Fig. 4). However, individuals are different and do not necessarily need to approach a single optimal diet, since potential constraints on diet choice differ among individuals (Ritchie 1988). This is probably the case in muskox bulls. Although the analysis presented here shows that bulls forage as energy maximizers and/or Na maximizers during certain periods, additional behavioural and physiological constraints may become limiting during other periods. Further studies are needed to unravel the details of individual foraging dynamics of muskoxen.

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