

Insights for caribou/reindeer management using optimal foraging theory

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Abstract: Optimal foraging theory is useful to wildlife managers, because it helps explain the nutritional value of different habitats for wildlife species. Based upon nutritional value, the use of different habitats can be predicted, including how factors such as insect harassment, predation and migration might modify habitat selection. If habitat value and use can be understood, then changes in habitat availability which are of concern to wildlife managers can be assessed. The theory is used to address diet choice and habitat use of caribou/reindeer. Diet choice is examined in terms of lichen composition of the diet and is demonstrated to be a function of daily feeding time, food abundance and digestive capacity. The diet choice model is then used to assess the nutritional profitability of different habitats and which habitat should be preferred based upon nutritional profitability. Caribou/reindeer use of habitats is demonstrated to be easily modified by insect harassment and predation which change the nutritional profitability of habitats differentially. The same type of approach could be used to explain migratory behaviour; however, the needed parameter values are unavailable. The results of this analysis lead one to question some common conceptions about caribou/reindeer ecology.

Keywords: Caribou, reindeer, foraging theory, habitat choice, modelling, habitat preference

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Introduction

Modelling the foraging behaviour of herbivores has been attempted by several ecologists (Westoby, 1974; Owen-Smith and Novellie, 1982; Stenseth and Hansson, 1979; Ritchie, 1988; Schmitz, 1990; Belovsky, 1978, 1984a, b, 1986 a, b, submitted; Ball, 1990). In most cases, these models have met with a high degree of predictive success (Belovsky, submitted), but none have dealt with mammals that normally migrate or are allowed to migrate today (e.g., bison). Therefore, modelling the foraging behaviour of a species like caribou/reindeer (*Rangifer tarandus*) that exhibits migratory behaviour in some populations might not be amenable to the same considerations that have been successfully applied to other species. In addition, the migratory behaviour of caribou/reindeer poses some interesting management considerations concerning why certain habitats are chosen within a given locale, why certain habitats are chosen seasonally, and how changing conditions (e.g., predator densities, human disturbance, etc.) might modify these choices.

I apply existing models of herbivore foraging that have proven successful for other species to the diet choices of caribou/reindeer employing data from the literature. With the potential value of these mo-

odels established employing the available caribou/reindeer data, I proceed to ask questions about what habitats these herbivores should utilize seasonally based on feeding efficiency, insect harassment and predation employing other aspects of foraging theory (Stephens and Krebs, 1986). This analysis provides insights into how changing environmental conditions might affect caribou/reindeer populations through habitat use in ways which might be of concern to managers.

What is foraging theory and what is its use to managers?

Foraging theory emerged in the mid-1960's as an attempt to link animal food choices with population carrying capacity (MacArthur and Pianka, 1966; Emlen, 1966). While this field of investigation developed into one of the few areas of ecology where mathematical theory and empirical tests were in accord (Stephen and Krebs, 1986), its successes were more in the arena of animal behaviour, especially psychobiology, than population ecology. A few studies have carried foraging theory into the realm of population dynamics (Werner, 1977; Werner and Mittlebach, 1981; Belovsky, 1984a, 1986a) with success. Recently, the theory has been specifically ap-

plied to questions of wildlife management, i.e., winter supplemental feeding of white-tailed deer (Schmitz, 1990).

How pertinent is the theory to the detailed investigation of wildlife management problems?

The theory has been invoked in a number of models directed towards managing wildlife populations (e.g., Hobbs and Swift, 1985; Hobbs and Hanley, 1990) based on predicting carrying capacity and/or habitat utilization. The potential use of such models appears to be high; however, some recent studies appear to have inappropriately applied the theory (Schmitz and Belovsky, submitted). One concern is that the detail required for wildlife management may be beyond the scope of current foraging theory. This arises from the inability of any study simultaneously to address generality, precision, and realism (Levins, 1967), as all studies are limited to attaining two of the three characteristics at any instant. Generality refers to the model's applicability to a wide range of species and conditions; realism refers to the model's ability to capture the specific details of a particular species and environment. Most foraging models seek generality and precision at the expense of realism.

The issue of generality vs. realism is of special concern to wildlife biologists and managers. Because foraging theory seeks generality at the expense of realism, it becomes very easy for individuals concerned with particular biological details to dismiss the theory. However, science seeks the general explanation of patterns rather than simply cataloguing specific details. Stephens and Krebs (1986) point out that foraging models by their general nature must simplify and treat many biological details in a perfunctory fashion; these are the same details that are the focus of a lifetime of research by other scientists (e.g., learning behaviour, digestive physiology, etc.).

Foraging models, however, may be of value to wildlife managers; it depends on the level of detail in the question being asked. If a manager is concerned with assessing the probability of survival of big game animals to a certain age or size based upon foraging conditions, then this question is far too detailed to be realistically addressed using foraging theory. If a manager is concerned with gross predictions of diet choice by a wildlife species in different habitats to assess the nutritional value of the habitats, or assess potential environmental changes on the species' nutritional ecology, then foraging theory has value.

Foraging theory, which is based upon concepts of natural selection and behavioral "plasticity", may provide wildlife managers with conceptual insights to design better management plans based upon the flexibility of individuals composing the wildlife population. Recently, Keppie (1990) criticized wildlife studies for their failure to address ecological concepts, so principles might be identified that would provide a broader application of information to different management situations. Keppie (1990) points out that we have a multitude of specific studies for wildlife species that are tied to particular locations, but their ability to provide insights for other sites and conditions is weak because the studies did not address conceptual issues that span all sites and conditions.

While foraging theory has been invoked by wildlife biologists working with caribou/reindeer (e.g., Kuropat and Bryant, 1980; White, 1983; Skogland, 1984), it has not been applied critically to assess the theory's predictive value. This is not unusual; the majority of studies that invoke foraging theory have failed to test it quantitatively for the species being examined (Stephens and Krebs, 1986; Belovsky, submitted). The only caribou/reindeer study that attempted to test a foraging model quantitatively was Skogland's (1984) study of reindeer in Norway. Unfortunately, a mathematically inconsistent foraging model (Stenseth and Hansson, 1979) was applied to the problem (Belovsky, 1984a). Additionally, serious problems in parameter estimation can be identified; it appears that food types may have been measured in a manner inappropriate to the modelling approach (i.e. food abundance), and digestibility values for lichen and non-lichen food types are not in accord with most literature values (see Table 3). Therefore, the apparently successful predictions of the model must be questioned.

Below I apply a foraging model to address whether caribou/reindeer choose food types consistent with the theory. Since the needed parameter values must be gleaned from the literature, and none were collected specifically to meet the requirements of the theory, some caution must be exercised in interpreting these results. Finally, the model is extended to examine habitat use patterns by caribou/reindeer.

The basic foraging model

Diet choice by mammalian herbivores has been predicted for a wide range of herbivore species and environments using the optimization technique called linear programming with more success than any other model yet applied (Belovsky, submitted). The

validity of these models has been questioned (Hobbs, 1990; Hanly, 1980), but no better alternative has been presented and most of the criticisms are as questionable as the points raised against the foraging models (Belovsky, 1990).

Linear programming is an optimization technique that explicitly includes constraints (limits) to actions. The constraints define a combination of actions that are feasible, i.e., sets of actions that do not violate the constraints. Linear programming then employs various mathematical algorithms (e.g., Simplex) that identify the combination of actions which maximizes or minimizes some goal within these constraints (Intriligator, 1972). This methodology is based upon the assumption that constraints can be written as linear functions.

From previous studies of mammalian herbivores, four classes of constraints can be considered: digestive processing, feeding time, nutritional requirements, and food toxicity. Justification of these constraints and how they are constructed are discussed by Belovsky (1984a, 1986a). How these constraints will be applied to caribou/reindeer using data from the literature are discussed below.

To develop a foraging model for caribou/reindeer, one detailed data set (White and Trudell, 1980a, b; Trudell and White, 1981) will be employed extensively, because it provides more of the needed parameters than any single study and presents these for specific habitats. Diet choices will be examined for late July in two distinct habitats, high-centre polygons and lake margins, that caribou/reindeer must choose between at this time. The diet will be defined in terms of two food categories, lichens and non-lichens (e.g., shrubs, grasses, forbs, and sedges). These two habitats are of interest given the seasonal and daily movements of caribou between them (White and Trudell, 1980a, b; Trudell and White, 1981, White *et al.*, 1975; White, 1983), and the special interest in lichen consumption by caribou given its poor nutritional value (Klein, 1970).

Digestive processing of plant tissues is often considered to constrain the amount of plant food that an herbivore can ingest in some fixed period (e.g., day) (Westoby, 1974). This requires knowledge of the ability of digestive organs to hold food (capacity: mass/day) and the rate at which digesta passes through these organs (turnover: times filled/day). Capacity multiplied by the number of times this capacity can be filled provides a simple estimate of the animal's ability to process foods. This digestive processing ability is differentially utilized by the consumption of different foods that fill this capacity to

varying extent (bulkiness: capacity filled/mass of food intake).

Digestive capacity might be defined either in terms of wet or dry mass. Hobbs (1990) argues that digestive processing ability should be measured in terms of dry, rather than wet, mass, and that bulkiness should be measured in terms of cell wall content (%/g-dry mass). However, using a digestive constraint based on dry mass in a linear programming model, Hobbs (1990) was unable to predict mammalian herbivore diets, as has been regularly found in other studies (Belovsky, 1990). There are physiological reasons and data to use dry matter and cell wall content (Hobbs, 1990; Belovsky, 1990), but there also are contrary physiological reasons and data to use wet mass (Belovsky, 1990). Therefore, choosing between these conflicting explanations for digestive capacity is not possible, and begs additional and redesigned physiological studies, but constraints based upon wet mass successfully predict mammalian herbivore diet choices in linear programming models (Belovsky, 1990).

The problem of defining the digestive capacity constraint based on dry vs. wet mass can be partially addressed using data for reindeer (Table 1). It can be demonstrated that daily food intake (g-dry/day/kg) is a significant negative function of food wet mass to dry mass, while cell wall content, measured as % fiber, is negatively correlated with intake, but not significantly. Therefore, wet mass appears to be a better basis for measuring the digestive constraint based upon this limited information, and was employed to construct the diet choice model presented here.

Table 2 presents the summary of data on caribou/reindeer that was used to construct a digestive constraint. Bulkiness (g-wet/g-dry) of the non-lichen foods in the two habitats differs, because the species composing those available in the lake margin tend to have a higher water content.

Feeding time seldom will encompass a complete 24 hr day, because animals are restricted in their feeding activity to time periods when digestive processing ability is not exceeded, thermal physiology is not limiting, and other activities are not being conducted (e.g., insect harassment, predator avoidance, mating, etc.). This feeding time is utilized differently in the acquisition of each of the foods (cropping time: min/g-dry). The parameter values for this constraint appear in Table 3.

For mammalian herbivores, digestive fill and thermal physiology seem to be most important in determining feeding time (Belovsky, 1986a). This may be the case for caribou/reindeer, as well. An important

Table 1. Daily food intake as a function of food bulk and cell wall contents using data from Syrjälä *et al.* 1983.

Parameter	Coefficient	t-value	P
Constant	27.19	8.23	0.004
Bulk	-2.35	-4.52	0.02
Cell wall content	-0.15	-2.1	0.13

Regression N=6, r=0.94, F=10.47, P<0.044

point is that thermal physiology may not limit activity via the animal being stressed to near lethal levels; rather activity may be limited by physiological changes relative to some set point chosen by the animal, and to times when activity may be least costly in terms of energy expended for thermoregulation (Belovsky, 1981, 1984b; Schmitz, in press). Winter feeding activity is often ascribed to heat loss limits (Gaare *et al.*, 1975), but is summer activity limited by thermal physiology?

Caribou/reindeer may be able to tolerate environmental conditions that lead to heat gains to the same extent as African ungulates, but to do so they must "work" harder at thermoregulation (Yousef and Luick, 1975), and they do demonstrate heat stress (Ryg, 1975). While insect harassment clearly restricts feeding activity on warm and still days (White *et al.*, 1975; Helle and Aspi, 1983; Wright, 1980), these weather conditions also lead to greater thermal stress. Therefore, without better studies, these two factors, insect harassment and heat stress, cannot be separated in explaining reduced summer activity.

This dilemma is further reinforced since caribou move towards the sea on warm, still days to escape insects (White *et al.*, 1975), but the coast will also provide thermally less stressful summer conditions, i.e., cooler and windier.

Cropping time (min/g-dry) should be a function of food abundance and distribution (Belovsky, 1986a), a prediction upheld for caribou/reindeer (Trudell and White, 1981; White and Trudell, 1980a; Skogland, 1980, 1984). However, Trudell and White (1981) argue that daily feeding time is limited by cropping rate, i.e., a constant intake of food that just satisfies nutritional requirements is sought, with the result that feeding time declines as food becomes more abundant. This can be explicitly tested using foraging theory and is the predicted outcome for the foraging goal called feeding time minimization (see below).

Nutritional requirements are the maintenance needs of an individual required to ensure survival. The maintenance requirements provide a set point against which discretionary additional intake by the forager can be compared. The additional intake can be allocated to growth, storage (i.e., fat) or reproduction. Three potential nutritional requirements are frequently listed for caribou/reindeer: energy, protein, and sodium.

Energy is the ultimate limiting factor in all ecological systems, and this is the best understood aspect of animal nutrition. The foraging model must include the individual's energy requirements to survive in the environment and how different foods satisfy this requirement (gross energy content x digestibili-

Table 2. Development of the digestive capacity constraint for a 70 kg female caribou/reindeer. L is lichen intake (g-dry/day) and NL is non-lichen intake (g-dry/day).

Parameter	References
Rumen/reticulum contents (g-wet) = 11293 ln (mass in kg)-35703 N = 25, r = 0.96, P < 0.001	Staaland <i>et al.</i> 1979, Egorov 1965
Fraction of rumen/reticulum contents that is food = 0.29	White and Gau 1975
Turnover of rumen/reticulum in both habitats = 1.68 X's/day	White and Trudell 1980a, b
Bulk - lichen: 2.54 g-wet/g-dry	Staaland <i>et al.</i> 1986, Syrjälä <i>et al.</i> 1980, Valtonen 1980
non-lichen: high centred polygon: 1.66 g-wet/g-dry	Batzli <i>et al.</i> 1981, A. Rodgers unpublished
lake margin: 2.05 g-wet/g-dry	Batzli <i>et al.</i> 1981, A. Rodgers unpublished
Constraint: high centred polygon habitat 5980 g-wet/g-dry ≥ 2.54L + 1.66 NL lake margin habitat 5980 g-wet/g-dry ≥ 2.54L + 2.05NL	

Table 3. Development of the feeding time constraint for a 70 kg female caribou/reindeer. L is lichen intake (g-dry/day) and NL is non-lichen intake (g-dry/day).

Parameter	References
Feeding time: high centred polygon – 305 min/day	White and Trudell 1980a, b
lake margin – 373 min/day	White and Trudell 1980a, b
Cropping time: lichen: 0.08 min/g-dry	White and Trudell 1980a, b, Trudell and White 1981
non-lichen: 0.15 min/g-dry	White and Trudell 1980a, b, Trudell and White 1981
Constraint: high centred polygon habitat 305 min/day $\geq 0.18L + 0.15 NL$	
lake margin habitat 373 min/day $\geq 0.08L + 0.15NL$	

ty). The energy constraint values are presented in Table 4. This does not imply that energy is limiting to survival, since other nutrients might limit survival and adequate energy is acquired along with other nutrients.

Protein is often considered important to the nutrition of herbivores, because plant tissue is frequently low in protein, especially proteins composed of the essential amino acids required by animals. This is of special concern for caribou/reindeer, because of their habit of frequently consuming large quantities of lichens that are low in protein (Klein, 1970). The protein constraint values are presented in Table 4. As with energy, protein may not be limiting survival, but adequate intake might be acquired along with other nutrients.

Sodium is often in low concentrations in plant tissue, especially in areas that have been glaciated and are located far from oceanic salt impaction (Botkin *et al.*, 1973; Belovsky and Jordan, 1981). Recent studies indicate that caribou/reindeer may experience and exhibit sodium deprivation in the summer months (Staaland *et al.*, 1983; Staaland and Jacobsen, 1983; Staaland *et al.*, 1980; Staaland *et al.*, 1981). The sodium constraint values are presented in Table 4. Again, sodium might not be limiting survival, but adequate amounts are acquired along with other nutrients.

Food toxicity from plant secondary compounds is often considered an important aspect of herbivore diet choice (Freeland and Janzen, 1974). Many plant secondary compounds (e.g., tannins) may reduce digestibility so their impact is incorporated in the nutritional constraints (Belovsky and Schmitz, 1991). However, plant secondary compounds that are potentially toxic to the herbivore must be explicitly built into the foraging model (Belovsky and Schmitz, 1991).

Lichens are known to contain many potentially toxic compounds (Rundel, 1978; Burkholder and Evans, 1945; Burkholder *et al.*, 1944). The importance of plant secondary compounds in caribou/reindeer foraging strategies has been argued (Kuropat and Bryant, 1980, 1983; Bryant and Kuropat, 1980). A constraint based on the ingestion of one of these compounds, pulvinic acid, is presented in Table 5. Pulvinic acid, a toxin peculiar to lichens, was employed because all of the necessary aspects of its actions on mammals (LD50 and concentration in plants) could be found in the literature (Rundel 1978).

Foraging goals are the outcome of foraging behaviour favoured by natural selection. This outcome could be determined either by the forager's variable behaviour ("plastic" response) or genetically fixed behaviour ("hard-wired" response). In the first case, selection would operate upon the flexibility in behavioral responses and learning ability of individuals, while in the latter case selection would operate directly upon an individual's foraging behaviour (e.g., a set of fixed diet choices). Most mammalian herbivores demonstrate a wide range of foraging behaviours ("plastic" response) and selection may operate on the ability to be flexible (Ritchie, 1990). In foraging theory, these foraging behaviours are often viewed to achieve two alternate goals: feeding time minimization and nutrient maximization (Belovsky, 1986a; Stephens and Krebs, 1986).

Feeding time minimization is the goal when the forager's fitness increases more with time spent in activities other than feeding (e.g., hiding from predators, mating, etc.). Because an individual must attain all of its nutritional requirements, this goal would have the forager attain these requirements in the least time spent foraging, so more time is available for other activities.

Table 4. Development of the nutritional requirements for a 70 kg female caribou/reindeer. L is lichen intake (g-dry/day) and NL is non-lichen intake (g-dry/day).

Parameter	References
Energy:	
maintenance metabolism = 4646 kcal/day	Holleman <i>et al.</i> 1980, Young and McEwan 1975, McEwan and Whitehead 1970, Steen 1968
gross energy content:	
lichen = 4.36 kcal/g-dry	Holleman <i>et al.</i> 1979, McEwan and Whitehead 1970
non-lichen = 5 kcal/g-dry	McEwan and Whitehead 1970
dry matter digestibility:	
lichen = 46%	Russell and Martell 1984, Jacobsen and Skjenneberg 1975, Person <i>et al.</i> 1975, 1980a, b, White <i>et al.</i> 1984, Thomas and Kroeger 1981, Thomas <i>et al.</i> 1984, Staalnd <i>et al.</i> 1983, Luick 1972.
non-lichen = 54%	Person <i>et al.</i> 1975, 1980a, b, White and Trudell 1980b, White <i>et al.</i> 1975, Thomas and Kroeger 1981, Thomas <i>et al.</i> 1984, Staalnd <i>et al.</i> 1983, Luick 1972, White <i>et al.</i> 1975.
Constraint:	
4646 kcal/day \leq 2.01L + 2.70NL	
Protein:	
Maintenance requirement = 115 g/day	Steen 1968, McEwan and Whitehead 1970, Holleman <i>et al.</i> 1980
Protein content:	
lichen = 2.8%	Person <i>et al.</i> 1980b, Wales <i>et al.</i> 1975, White <i>et al.</i> 1984, Pullianen 1971
non-lichen:	
high centred polygon = 14%	Scotter 1972, Staalnd <i>et al.</i> 1983, Luick 1972
lake margin = 14.6%	Scotter 1972, Staalnd <i>et al.</i> 1983, Luick 1972
Constraint:	
high centred polygon: 115 g/day \leq 0.028L + 0.14NL	
lake margin: 115 g/day \leq 0.028L + 0.146NL	
Sodium:	
Maintenance requirement = 1.1 g/day	Staalnd <i>et al.</i> 1981
Sodium content:	
lichen = 0.03%	Staalnd <i>et al.</i> 1981, 1983, Staalnd and Jacobsen, Luick 1972
non-lichen:	
high centred polygon = 0.05%	Staalnd <i>et al.</i> 1981, 1983, Staalnd and Jacobsen, Luick 1972
lake margin = 0.04%	Staalnd <i>et al.</i> 1981, 1983, Staalnd and Jacobsen, Luick 1972
Constraint:	
high centred polygon: 1.1 g/day \leq 0.0003L + 0.0005NL	
lake margin: 1.1 g/day \leq 0.0003L + 0.0004NL	

Nutrient maximization is the goal when the forager's fitness increases more with the additional intake of some nutrient that limits survival and reproduction, than time spent in nonfeeding activities. The nutrient most frequently addressed in foraging theory is energy, but could be protein, sodium, etc., or even minimization of toxin intake.

Nutrient maximization is usually seen as the expected goal when the intake of nutrients determines reproduction and survival, so that population density would increase with greater food intake by individuals. However, feeding time minimization does not imply that food availability is not important to individual survival and reproduction, and population density. A feeding time-minimizer's fitness increases if more food is available, even though food intake per se is not limiting, because acquisition of nutritional requirements in less time makes more time available for other fitness-increasing activities. Therefore, to argue that food availability is only important to nutrient maximizers is incorrect.

The above observation means that clear distinctions between food limitation, predator limitation, etc., of populations is not easy to assess. For example, if predation is limiting an animal's fitness, then we might expect the animal to be a time minimizer, because it may be more exposed to predators while foraging and need to spend more time hiding from predators. The forager and its population would benefit, greater fitness, when food is more abundant, since nutritional requirements will be obtained in less time which means less time exposed to predators. If exposure to predators does not increase with foraging, then there would be no benefit provided by a time-minimizing goal and the forager would always be a nutrient maximizer, even when predators reduce survival and reproduction. This is even more apparent when we realize that these foraging goals are endpoints along a continuum.

The above distinctions between fitness limits are important for caribou/reindeer. First, caribou/reindeer are known to have their survival and reproduction limited in some regions by nutrition (e.g., Adamczewski *et al.*, 1987, 1988; Leader-Williams, 1980; Skogland, 1985a, b; Roby, 1980). Other studies claim predation to be the principle limit to caribou populations, i.e., more food would not increase populations (Bergerud, 1980). From the above discussion, claims of predator limitation may not imply that food is unimportant to the caribou/reindeer population. This is why other investigators have argued that food availability and predation or insect harassment may be important at the same

time (Reimers, 1980; Haber and Walters, 1980; Helle and Aspi, 1983). Therefore, assessing the importance of food to caribou/reindeer populations, even when predators are abundant, cannot be accomplished without careful analysis of caribou/reindeer feeding behaviour and their foraging environment.

The simultaneous importance of food and predation to populations has been most evident in studies using foraging theory applied to bluegill (*Lepomis macrochirus*) in the presence and absence of their predator, the largemouth bass (*Micropterus salmoides*) (Werner, 1985). These basic ecological studies have forced sportfishery managers and aquaculturists to reevaluate their assessment of food limitation versus predator limitation. The same problem must be addressed for caribou and the foraging model developed below may provide some insights.

Solving the foraging model

Using the constraint equations developed in Tables 2-5, a graphical representation of the linear programming foraging model can be developed (Fig. 1). The graphical portrayal illustrates how the different constraints restrict the caribou/reindeer's diet choices in the two environments to define a feasible set of diets: these are the diet combinations of lichens and non-lichens that satisfy the constraints. The toxin constraint for pulvinic acid in lichens was incorrect or not operating, since it is apparent that caribou/reindeer consume a diet containing more lichen than expected from the toxin constraint. Most likely, the caribou/reindeer are better at detoxifying the pulvinic acid than rodents upon which the LD50 was based (Rundell, 1978). These results indicate the need for better measures of toxicity before the importance of secondary compounds can be quantitatively assessed via foraging models (*sensu* Belovsky and Schmitz, 1991).

The linear programming model can be used to solve for the two potential goals: feeding time minimization and nutrient maximization (Intriligator, 1972). The predicted diets are crude, since the model parameters were not measured to satisfy the foraging model's criteria (e.g., cropping rates were not measured instantaneously, g-dry/min for individual food types, but by food intake measured using fistulated animals, g-dry/longer time period, which can include behaviours other than foraging and can combine the intake of both food types). Nonetheless, certain possibilities can be identified.

1) If energy is the only limiting nutrient requirement, then a time-minimizing diet would consist of 100% lichens in both habitats (Point 1 in Fig. 1A, B),

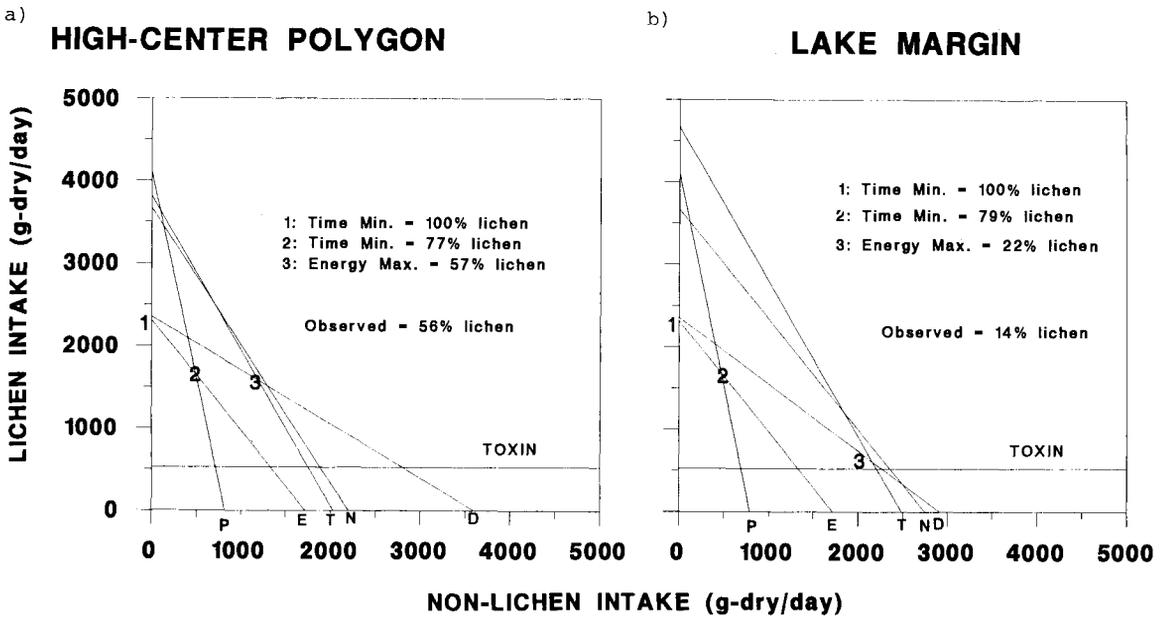


Fig. 1. The graphical representation of the linear programming diet model for caribou/reindeer is presented for the high-centre polygon habitat (a) and the lake margin habitat (b). The letters along the x-axis identify the constraints (Tables 1-4) (P is protein, E is energy, T is feeding time, N is sodium, D is digestive processing), and the flat line parallel to the x-axis is labelled TOXIN for secondary compounds. Each graph presents the observed diet and 3 solutions to the model (ignoring the toxin constraint, see text): 1) the time-minimized diet based only on an energy requirement; 2) the time-minimized diet based on energy and protein requirements; 3) the energy-maximized diet, ignoring the sodium requirement (see text).

but the observed diets are 56% in the high-centre polygon and 14% in the lake margin habitats. Therefore, either there are other nutrient requirements not satisfied along with energy requirements, or the caribou/reindeer are not time minimizers.

2) If energy and protein are limiting nutrients, then a time-minimizing diet would consist of 77-79% lichens in the two habitats (Point 2 in Fig. 1A, B). Again this is very different from the observed diets, indicating that the caribou/reindeer do not act as time minimizers or other nutrient constraints are operating.

3) The energy-maximizing diet consists of 57% lichens in the high-centre polygon and 22% lichens in the lake margin habitats (Point 3 in Fig. 1A, B). Both of these values are very close to those observed. Without detailed information on the diet samples which are not provided in the studies (White and Trudell, 1980a), a statistical comparison cannot be made. Nevertheless, it appears that these animals could be energy maximizers. But what about the maximization of other nutrients? It cannot be protein because a diet composed of 100% non-lichens would be predicted by protein maximization. This indicates that caribou/reindeer do not appear to be maximizing protein intake in anticipation of consumption of low-protein lichens during winter.

Thus, the idea that protein limits caribou populations (Klein, 1970) is brought into question. This leaves maximization of sodium intake as the only other possibility.

4) Using the sodium constraint, we find that the caribou/reindeer in either habitat cannot attain their minimum requirement measured in summer (Staal and *et al.*, 1981). The energymaximizing diet in this case also maximizes sodium intake, so either energy or sodium intake could be the goal. However, if sodium is in such short supply, how do the caribou/reindeer acquire adequate amounts of sodium in the summer? Possibly, this is achieved by the consumption of small amounts of aquatic vegetation that is high in sodium content (Staal and Jacobsen, 1983), as found for moose (*Alces alces*) (Belovsky, 1978).

It would be useful to determine the reliability of the model's predictions, given the confidence intervals of the model's parameters (sensitivity analysis). This can be done using Monte Carlo simulations (Belovsky, 1984b, submitted). However, most of the confidence limits for the parameters are not reported. Therefore, a sensitivity analysis could not be attempted.

An additional evaluation of the model can be performed by making qualitative predictions about

how diet composition will change with food depletion (White and Trudell, 1980a, b). White and Trudell (1980a, b) tethered caribou/reindeer in a small area for 3 days (314 m²) and the abundance of non-lichens was depleted more than lichens over this period. If a caribou/reindeer is a nutrient-maximizer (energy or sodium), it should: a) consume less lichens as feeding time increases, and b) consume more lichens as the more nutritious, in terms of energy, non-lichens decrease in abundance. The first prediction is affirmed by comparing diets in the two habitats. The second prediction also is affirmed. If the caribou/reindeer were time minimizers, the diet (77–79% lichens) would not have changed.

From the model, we can reach several conclusions, assuming that the parameter values are adequate to build a foraging model. First, the caribou/reindeer appear to be nutrient-maximizers. Second, the lake margin habitat is superior (1.13 times) to the high-centre polygon habitat from an energy intake perspective, and more so based on dry matter intake (1.33 times). Third, the major difference between the two habitats is due to differences in feeding time. Fourth, because the caribou/reindeer at these sites are nutrient-maximizers, this suggests that they would have greater survival and reproduction if food were more abundant, assuming that the observed feeding times reflect the maximum values for these habitats (see below).

The above points illustrate the importance of the feeding time constraint to developing a foraging model. Trudell and White (1981) originally argued that the difference in feeding time for the two habitats is due to the animal's maintaining a set nutritional intake which results in less time spent feeding when food is more abundant. Their argument is equivalent to a time-minimizing goal. Because the observed goal is energy maximization, we should seek explanations for the observed feeding time differences elsewhere (e.g., insect harassment, predators, thermal environment, etc.). Furthermore, it is very difficult to attribute feeding time differences to differences in food abundance, when the measures of different food abundances are based upon different seasons and habitats (Trudell and White, 1981). This means that many other factors that affect feeding time will be changing concurrently with food abundance.

Additional support for the foraging model is provided by solving it for caribou/reindeer at other sites where their diet and daily feeding time are known (see Fig. 2). This is done assuming that all model parameters presented in Tables 2–4 are the

same for these other sites, except for feeding time. The observed diets for these 6 additional sites are predicted very well ($r = 0.98$, Fig. 2), which illustrates the robustness of the model. The importance of feeding time is also reaffirmed, since it alone is varied in the diet model; feeding time in itself can explain the proportion of the diet composed of lichen very well ($r = -0.96$, $N = P \leq 0.01$), but not as well as the model. An interesting pattern emerges in Fig. 2. All the predicted diets contain more lichens than observed, this might arise if the toxins in lichens (Rundell, 1978) lead to reduced ingestion.

Habitat choice, predation and insect harassment

Foraging theory applications developed experimentally with fish (reviewed in Werner, 1985; Werner and Mittelbach, 1981; Werner and Gilliam, 1984; Gilliam and Fraser, 1987) can be used to address habitat use by caribou/reindeer. In the absence of natural enemies, a forager, whether an energy maximizer or time minimizer, will have its fitness determined by its energy intake rate (energy/time).

OTHER DIET STUDIES WITH FEEDING TIME

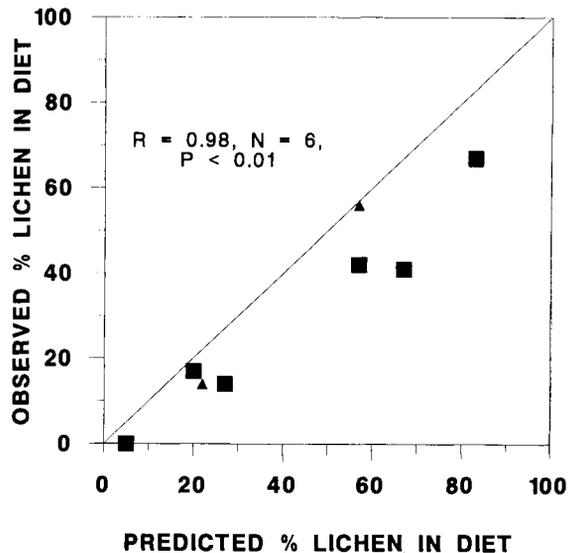


Fig. 2. The comparison of the predicted and observed proportion of the caribou/reindeer diet composed of lichens for 6 studies (squares: Wright, 1980; Skogland, 1984; Martell *et al.*, 1985, White *et al.*, 1975) is presented. The studies used to develop the linear programming diet model are also presented (triangles: White and Trudell, 1980 a, b).

With the greatest energy intake rate, a time-minimizer will satisfy its energy requirements in the least time, while an energy-maximizer will acquire the greatest energy intake in available feeding time. In this case, foragers, when presented with a variety of habitats, should choose to use the habitat that provides the greatest fitness. However, if natural enemies have an appreciable influence on an individual's fitness, then habitat selection based on energy intake rate can be modified, but energy intake rate will always be important.

The above conclusions are based upon the assumption that the habitat is neither depleted during the period of observation by the individual or by other individuals using the habitat during the same period. However, as the food becomes depleted, the individuals will distribute themselves according to the Ideal Free Distribution (Fretwell and Lucas, 1970; Fretwell, 1972). In the Ideal Free Distribution, individuals move or distribute themselves between habitats to maximize their fitness. Therefore, the second-best habitat in terms of fitness will be used only after a certain depletion of the best habitat

or a certain accumulation of individuals within the best habitat. The outcome is that the best habitat will contain more individuals or more time will be spent in it, and all habitats utilized will be equally depleted, i.e., provide equal fitness.

Assuming that natural enemies do not appreciably influence fitness, we can make some predictions about shifts in habitat use over the summer for caribou/reindeer, using White's (1983) seasonal comparison of habitats based upon food intake. Because daily food intake (g-dry) overestimates differences between the lake margin and high-centre polygon habitats (see above), daily food intake was converted into daily energy intake. To control for differences in daily foraging time, so the nutritional value of the two habitats can be compared, the energy intake (kcal/day) is divided by daily feeding time (min/day) to compute a rate of energy intake (kcal/min). The habitats are compared in Fig. 3 based on the rate of energy intake. The high-centre polygon would be used in May, then the lake margin would be used in mid-July, and then the high-centre polygon would be used again starting in late-August. At any one time, if a habitat cannot accommodate all individuals or is depleted, the other habitat would then be used. Energy intake rate declines because cropping rates (g-dry/min) decline, which reduces food intake and/or changes the diet so more of the less nutritious food types are ingested.

As predicted above, caribou in late-July preferentially use the lake margins (proportion of animal-hours spent in the habit relative to the proportion of area) (White and Trudell, 1980a, b). This preference is not absolute (only one habitat used), since the caribou also use the high-centre polygons, and this use occurs before the food in the lake margins is depleted. Therefore, caribou appear to utilize the high-centre polygons more frequently than expected, given energy intake rates. What other explanations might be invoked to explain this greater than expected use of the high-centre polygon habitat? Two potential causes could be insect harassment and predation.

Insect harassment reduces a caribou/reindeer's daily feeding time (White *et al.*, 1975; Helle and Aspi, 1983; Wright, 1980). White *et al.* (1975) examine reduced feeding time as a function of the intensity of insect harassment, and the habitats where insects are most abundant. This study indicates: a) insect harassment is greater in the lake margins than the high-centre b) insect harassment increases as air temperature rises and wind speed declines; c) at moderate levels of harassment, feeding time declines by 27%

HABITAT COMPARISON

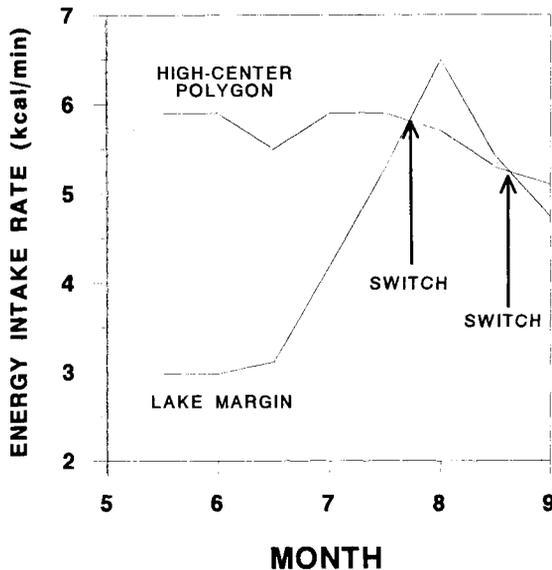


Fig. 3. The seasonal change in energy intake rate for caribou/reindeer in two habitats is presented. The optimum switching between habitats based upon energy intake rate is depicted. The relationship is adapted from White's (1983) representation of dry matter intake, and the linear programming diet model's conversion of dry matter intake into energy intake per minute.

HABITAT VALUE IN JULY

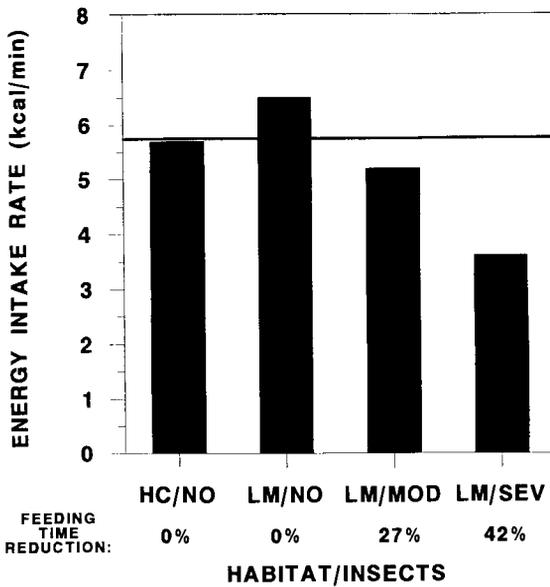


Fig. 4. The comparison between the energy intake rates in July for caribou/reindeer in two habitats, where one habitat (LM: lake margin) has higher biting insect abundances. The lake margin energy intake rate must fall below the horizontal line before the other habitat (HC: high-centre polygon) will be used. This occurs at moderate and worse levels of insect harassment in the lake margin habitat.

and at high levels of harassment the decline is 42%. The observed feeding times used in the foraging model cannot be attributed to insect harassment. First, the observed feeding times are not influenced by insect harassment, since White and Trudell (1980a, b) claim that the measures of feeding time were made on days of minimum harassment. Second, if harassment were important, we would expect less feeding time in the lake margin, not more as observed.

Using the above observations for reduced feeding time in the lake margin habitat, the foraging model can be solved using the reduced feeding time. At moderate and high levels of harassment, the caribou should prefer the high-centre polygon habitat, since energy intake rate (kcal/min) there becomes greater than in the lake margin habitat (Fig. 3). Therefore, insect harassment can influence habitat choice by modifying nutritional return. This may be the reason why the caribou do not demonstrate an absolute preference for the lake margin during summer.

Predation could also operate in a similar manner to insect harassment by reducing an individual's feeding time due to the need to spend time being vigi-

lant for predators (Lima *et al.*, 1985). Reimers (1980) makes this claim for wolves and human hunters on caribou/reindeer. Roby (1980) compared caribou/reindeer feeding time at two sites, one with wolves and the other without wolves. He found greater feeding time in the presence of wolves; however, this study compared two very different sites (Alaska vs. Greenland). To investigate these assertions, there must be much greater control over site differences that also might influence feeding time. Therefore, these data are not definitive, nor are there adequate data for other ungulates inhabiting open habitats in the presence and absence of predators.

In addition to decreased feeding time due to increased vigilance, predation can cause additional changes in foraging behaviour. If *healthy* individuals are killed (non-compensatory predation sensu Errington, 1956), predators reduce an individual's expected fitness through increased mortality. This effect of predation can be easily incorporated into foraging theory using linear programming and has been empirically tested using fish (Gilliam and Fraser, 1987; Gilliam, 1990). When presented with two habitats, as is the case investigated here, a set of simple predictions can be made based upon the ratio of mortality rate to energy intake rate:

- 1) if the forager can move between both habitats quickly (close proximity), then
 - a) the forager will only use the habitat with the highest energy intake rate, if it also has the lowest mortality rate (minimum ratio of mortality to energy intake rate);
 - b) if 1a is not the case and the forager seeks a set nutritional intake, the forager will feed in both habitats; this is accomplished by preferentially utilizing the habitat with the lowest mortality to energy intake ratio, but spending sufficient time in the other habitat to attain the set nutritional intake (non-feeding time will be spent in the habitat with the lower mortality, i.e., refuge);
- 2) if the forager cannot move easily between both habitats (not close proximity), then
 - a) it will spend all of its time in the habitat with the lowest ratio of mortality to rate of energy intake, if it can attain its set nutritional intake in this habitat;
 - b) if the set nutritional intake cannot be attained in the above habitat, but can be obtained in the other habitat, the animal will ignore the ratio of mortality rate to energy intake rate (i.e., select the habitat based solely on energy intake rate).

We know from the diet model that the caribou/reindeer do not forage to attain a set energy intake, because they are energy maximizers; therefore, case 1b and 2b can be discounted. This distinction is important, because the only condition left is selecting one habitat that minimizes the ratio of mortality rate to energy intake rate (cases 1a, 2a). This observation does not preclude the use of one of these habitats (or others) as refuges when the caribou are not feeding, which is observed (White and Trudell, 1980a, b). How much greater would the mortality rate due to predation have to be for a caribou/reindeer to shift its use of the lake margin to the high-centre polygon?

Wolves would have to be 14% more effective as predators in the lake margins than in the high-centre polygon to make the ratio of mortality rate to energy intake rate equal for the two habitats. This would eliminate any preference for the two habitats and illustrates how small a difference in predation is needed to cause habitat shifts. If the caribou avoided the habitat that provides a greater energy intake rate because of predation, the potential for food limitation of their population would be enhanced. Perhaps the killing of prey by predators is far less important to limiting prey populations than the ability of predators to enhance food limitation for their prey. Interestingly, Bergerud (1980) lists the caribou used in the foraging model (Western Arctic herd) as being limited by wolf predation.

Is there any evidence that wolves have differential predatory impacts on caribou in the two habitats? Miller (1982) argues that caribou are cautious when in areas of dense willow and brush, fearing ambush by a predator. Crisler (1956) and Kelsall (1968) indicate that caribou are more vulnerable to ambush by wolves, than to pursuit in the open. Shrubs are much more abundant in the high-centre polygon habitat, perhaps making wolf predation more effective there. Therefore, caribou may be more vulnerable in the high-centre polygon habitat.

The potentially greater predation risk in the high-centre polygon habitat may be the reason for the lower feeding time observed there, if the caribou spend more time being vigilant. If the caribou could increase their foraging time in the high-centre polygon in the absence of wolves, they *might* have a greater energy intake rate there than in the lake margin habitat and might preferentially use the polygon habitat. The lake margin habitat *is* preferentially used by the caribou. Caribou might prefer the lake margin because of its greater energy intake rate in the presence or absence of predators, but they might use

the high-centre polygon habitat less than the lake margin, because of predation. Without better data (mortality rates, and energy intake rates in the absence and presence of predation), this type of scenario cannot be evaluated, but will have important consequences for caribou management.

Migratory behaviour of caribou/reindeer is often attributed to the individuals' search for better food resources (Kuropat and Bryant, 1980; Whitten and Cameron, 1980; Skogland, 1980; Tyler and Oeritsland, 1989). This can be addressed using the same approaches developed above, where the energy intake rates for habitats that are far apart are compared after incorporating the amortized energy costs of migration. If the costs include reduced feeding time, this can be incorporated by discounting the energy gains obtained in each habitat after migration. Tyler and Oeritsland (1989) found that, during migration, daily feeding time is reduced by 21%. If the costs include increased mortality due to predators or exhaustion, this can be incorporated as was done above by using the ratio of mortality rate to energy intake rate. If the migratory benefit is in reproduction above that provided by better nutrition, this can be considered, but reproduction becomes the currency and energy intake will have to be converted into reproductive units. An attempt to perform such an analysis for migrating African ungulates was provided by Fryxell *et al.* (1988).

The data necessary to evaluate migratory behaviour are unavailable, but if they were, one could evaluate the impacts of reduced migration on caribou populations. This is an important management question given that migration routes are being disrupted and distinct habitats that are seasonally used are disappearing.

Conclusions

The utility of foraging theory to address questions about caribou/reindeer ecology is apparent from the above discussion. I do not wish to imply that the analyses that I presented above are definitive, because the available data were not collected to meet the parameter criteria of foraging models. These criteria include measurements made at the same site where the feeding studies were conducted, and over the time frame required for the constraints (e.g., instantaneous cropping rates on a single food type, see above). However, the results do illustrate the potential that the theory provides in understanding caribou/reindeer ecology. These ecological questions

are not only of scientific interest, but they have important implications for management decisions.

I used the linear programming diet choice model to investigate interactions (trade-offs) between digestive physiology, feeding time/food abundance, nutritional requirements and toxins, and the diet choice model was built into habitat selection models to investigate interactions between food intake, insect harassment, and predation. The results raise more questions than possibilities eliminated. For example, the foraging model only examined two food categories: lichens and non-lichens. Can the foraging model explain the variable intake of the plants composing the non-lichen category: grasses, sedges, forbs and shrubs? For example, the habitat choice model demonstrated how predator avoidance might reduce feeding time. Is feeding time reduced in the presence of predators or do other factors such as thermal physiology restrict feeding time more? These are but a few of the questions emerging.

Based upon foraging theory some basic explanations of caribou/reindeer ecology must be questioned. These include: feeding time being limited by food abundance (e.g., Trudell and White, 1981), summer food abundance and quality not being important (e.g., Reimers, 1980), and wolf predation, rather than food, limiting caribou populations (e.g., Bergerud, 1980). Rather than seeking a single explanation, the interactions between factors should be investigated (e.g., food and predation sensu Haber and Walters, 1980). Clearly, food limitation is not necessarily the simple observation of starving animals or overgrazed range, as sometimes claimed (Bergerud, 1978, 1980), and a better understanding of nutritional ecology is needed before other factors (e.g., predation) can be designated the most important limit to caribou/reindeer populations.

To make these types of comparisons, we need better data on wildlife. This will involve the manipulation and control of environmental conditions. When factors are not controlled, or at least measured for comparison (e.g., interplay between digestive physiology, thermoregulation, insect harassment and predatory risk in determining daily feeding time), it becomes very difficult to ascribe causality. I was able to formulate the diet choice model for caribou/reindeer because of a wide range of data already available, and even more importantly, the innovative *experimental* methods employed by Trudell and White (White and Trudell, 1980a, b; Trudell and White, 1981). These experimental methods are a first step toward eventually being able to distinguish among alternative explanations for feeding time, ha-

bitat usage, and a host of other caribou/reindeer attributes critical to effective management.

While ecologists such as myself are thrilled by the ability to predict quantitatively the biological details that represent species, populations and communities, this type of detailed understanding is just as critical for good management. Mautz (1978) argues that our ability to manage is limited by the weakest link in our knowledge. While this is in part true, I would also argue that we need to ask whether more detailed observations must be accumulated, or greater understanding might be achieved by developing and testing concepts; this is the dilemma of generality vs. realism.

Conceptual understanding might enable a manager to answer a priori how habitat changes, restricted migration, increased predator densities, etc., might affect the nutritional status of caribou/reindeer, and subsequently, their population densities. Even with detailed knowledge of species' biology, a manager might not be able to address these questions without a conceptual framework. Foraging theory provides this type of general conceptual framework with which fairly robust and valuable predictions can be made using the minimum of detailed information. The elegance of these general and minimal models in comparison to more complex approaches (e.g., simulation models) is that the underlying explanations are more easily identified, and can then be experimentally tested, so the model can be verified and validated (Jeffers, 1982).

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References

- Adamczewski, J. Z., Gates, C. C., Hudson, R. J. and Price, M. A. 1987. Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an arctic island with limited winter resources. - *Canadian Journal of Zoology*. 65: 1149 - 1157.
- Adamczewski, J. Z., Gates, C. C., Soutar, B. M. and Hudson, R. J. 1988. Limiting effects of snow on seasonal habit use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. - *Canadian Journal of Zoology*. 66: 1986 - 1996.
- Ball, J. P. 1990. Active diet selection or passive reflection of changing food availability: the underwater foraging behaviour of canvasback ducks. - In: Hughes, R. N. (ed.) *Behavioural mechanisms of food selection*. Springer-Verlag, Berlin. 95 - 107.

- Batzli, G. O., Jung, H.-J. G. and Guntenspergen, G. 1981. Nutritional ecology of microtine rodents: linear foraging-rate curves for brown lemmings. – *Oikos* 37: 112 – 116.
- Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. – *Theoretical Population Biology* 14: 105 – 134.
- Belovsky, G. E. 1981. Optimal activity times and habitat choice of a moose. – *Oecologia* (Berlin) 48: 22 – 30.
- Belovsky, G. E. 1984a. Herbivore optimal foraging: a comparative test of three models. – *American Naturalist* 124: 97 – 115.
- Belovsky, G. E. 1984b. Snowhoe hare optimale foraging and its implications for population dynamics. – *Theoretical Population Biology* 25: 235 – 264.
- Belovsky, G. E. 1986a. Generalist herbivore foraging and its role in competitive interactions. – *American Zoologist* 25: 51 – 69.
- Belovsky, G. E. 1986b. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. – *Oecologia* (Berlin) 70: 35 – 52.
- Belovsky, G. E. 1990. A reply to Hobbs. – In: Hughes, R. N. (ed.) *Behavioural mechanisms of food selection*. Springer-Verlag, Berlin. 415 – 422.
- Belovsky, G. E. submitted. Optimal diet choice studies in mammals.
- Belovsky, G. E. and Jordan, P. A. 1981. Sodium dynamics and adaptations of a moose population. – *Journal of Mammalogy* 62: 613 – 621.
- Belovsky, G. E. and Schmitz, O. J. 1991. Mammalian herbivore optimal foraging models and the role of plant defenses. – In: Palo, R. T., and Robbins, C. T. (eds.) *Plant defenses against mammalian herbivores*. CRC Publishing, Boca Raton.
- Bergerud, A. T. 1978. Caribou – In: Schmidt, J. L. and Gilbert, D. L. (eds.) *Big game of North America: ecology and management*. Stackpole Books, Harrisburg. 83 – 101.
- Bergerud, A. T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. – In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 556 – 581.
- Botkin, D. B., Jordan, P. A., Dominski, A., Lowendorf, H. and Hutchinson, G. E. 1973. Sodium dynamics in a northern forest ecosystem. – *Proceedings of the National Academy of Science* 70: 2745 – 2748.
- Bryant, J. P. and Kuropat, P. J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. – *Annual Review of Ecology and Systematics* 11: 261 – 285.
- Burkholder, P. R. and Evans, A. W. 1945. Further studies of the antibiotic activity of lichens. – *Bulletin of the Torrey Botanical Club* 72: 157 – 164.
- Burkholder, P. R., Evans, A. W., McVeigh, I and Thornton, H. K. 1944. Antibiotic activities of lichens. – In: *Proceedings of the National Academy of Science* 30: 250 – 255.
- Crisler, L. 1956. Observations of wolves hunting caribou. – *Journal of Mammalogy* 37: 337 – 346.
- Egerov, O. V. 1965. *Wild Ungulates of Yakutia*. (Translated by Isreal Program for Scientific Translations).
- Errington, P. L. 1956. Factors limiting higher vertebrate populations. – *Science* 124: 304 – 307.
- Emlen, J. M. 1966. The optimal choice in animals. – *American Naturalist* 101: 385 – 389.
- Freeland, W. J. and Janzen, D. H. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. – *American Naturalist* 108: 269 – 289.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton.
- Fretwell, S. D. and Lucas, H. L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. – *Acta Biotheoretica* 19: 16 – 36.
- Fryxell, J. M., Greever, J. and Sinclair, A. R. E. 1988. Why are migratory ungulates so abundant? – *American Naturalist* 131: 781 – 798.
- Gaare, E., Thompson, B. R. and Kjos-Hanssen, O. 1975. Reindeer activity on Hardangervidda. – In: Wiegolowski, F. E. (ed.), *Fennoscandian Tundra Ecosystems. Part 2. Animals and Systems Analysis*. Springer-Verlag, Berlin. 206 – 215.
- Gilliam, J. F. 1990. Hunting by the hunted: optimal prey selection by foragers under predation hazard. – In: Hughes, R. N. (ed.) *Behavioural mechanisms of food selection*. Springer-Verlag, Berlin. 797 – 818.
- Gilliam, J. F. and Fraser, D. F. 1988. Habitat selection under predation hazard: test of a model with foraging minnows. – *Ecology* 68: 1856 – 1862.
- Haber, G. C. and Walters, C. J. 1980. Dynamics of the Alaska-Yukon caribou herds and management implications. – In: Reimers, E., Gaare, E., and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 645 – 663.
- Hanley, T. A. 1980. *Nutritional constraints on food and habitat selection by sympatric ungulates*. Unpublished Ph. D. Thesis, University of Washington, Seattle.
- Helle, T. and Aspi, J. 1983. Does herd formation reduce insect harassment among reindeer? A field experiment with animal traps. – *Acta Zoologica Fennica* 175: 129 – 131.
- Hobbs, N. T. 1990. Diet selection by generalist: a test of the linear programming model. – In: Hughes, R. N. (ed.) *Behavioural mechanisms of food selection*. Springer-Verlag, Berlin. 395 – 413.

- Hobbs, N. T. and Swift, D. W. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. - *Journal of Wildlife Management*. 49: 814 - 822.
- Hobbs, N. T. and Hanley, T. A. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? - *Journal of Wildlife Management*. 54: 515 - 522.
- Holleman, D. E., Luick, J. R. and White, R. G. 1979. Lichen intake estimates for reindeer and caribou during winter. - *Journal of Wildlife Management*. 43: 192 - 201.
- Holleman, D. E., White, R. G., Luick, J. R. and Stephenson, R. O. 1980. Energy flow through the lichen-caribou-wolf food chain during winter in northern Alaska. - In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.). *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 202 - 206.
- Intriligator, M. D. 1972. *Mathematical optimization and economic theory*. Prentice-Hall, Englewood Cliffs.
- Jacobsen, E. and Skjenneberg, S. 1975. Some results from feeding experiments with reindeer. - In: Luick, J. R., Lent, P. C., Klein, D. R. and White, R. G. (eds.) *Proceedings of the First International Reindeer and Caribou Symposium*. Biological Papers, University of Alaska, Special Report. No. 1: 297 - 307.
- Jeffers, J. N. R. 1982. *Modelling*. Chapman and Hall Ltd., London. 80 p.
- Kellsall, J. P. 1968. *Continued barren-ground caribou studies*. Canadian Wildlife Service Management Bulletin Ser. 1. No. 12, pp. 148.
- Keppie, D. M. 1990. To improve graduate student research in wildlife education. - *Wildlife Society Bulletin*. 18: 453 - 458.
- Klein, D. R. 1970. Tundra ranges north of the boreal forest. - *Journal of Range Management*. 23: 8 - 14.
- Kuropat, P. and Bryant, J. P. 1980. Foraging behaviour of cow caribou on the Utukok calving grounds in northwestern Alaska. - In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 64 - 70.
- Kuropat, P. and Bryant, J. P. 1983. Digestibility of caribou summer forage in arctic Alaska in relation to nutrient, fiber, and phenolic constituents. - *Acta Zoologica Fennica*. 175: 51 - 52.
- Leader-Williams, N. 1980. Population dynamics and mortality of reindeer introduced into South Georgia. - *Journal of Wildlife Management*. 44: 640 - 657.
- Levins, R. 1967. *Evolution in Changing Environments*. Princeton University Press, Princeton.
- Lima, S. L., Valone, T. J. and Caraco, T. 1985. Foraging-efficiency-predation-risk trade-offs in the grey squirrel. - *Animal Behaviour*. 33: 155 - 165.
- Luick, J. R. 1972. Diets for freely grazing reindeer. - In: Rechcigl, M., Jr. (ed.) *CRC Handbook Series in Nutrition and Food, Section G: Diets, culture, media and food supplements*. Vol. 1. CRC Press, Cleveland. 267 - 278.
- McEwan, E. H. and Whitehead, P. E. 1970. Seasonal changes in the energy and nitrogen intake in reindeer and caribou. - *Canadian Journal of Zoology*. 48: 905 - 913.
- MacArthur, R. and Pianka, E. 1966. On optimal use of a patchy environment. - *American Naturalist*. 100: 603 - 609.
- Matrell, A. M., Nixon, W. and Russell, D. E. 1986. Distribution, activity and range use of male caribou in early summer in Northern Yukon, Canada. - *Rangifer* Special Issue. No. 1: 181 - 189.
- Mautz, W. W. 1978. Nutrition and carrying capacity. - In: Schmidt, J. L. and Gilbert, D. L. (eds.) *Big game of North America: ecology and management*. Stackpole Books, Harrisburg. 321 - 348.
- Miller, F. L. 1982. Caribou. - In: Chapman, J. A. and Feldhamer, G. A. (eds.) *Wild mammals of North America*. Johns Hopkins Press, Baltimore. 923 - 959.
- Owen-Smith, N. and Novellie, P. 1982. What should a clever ungulate eat? - *American Naturalist*. 119: 151 - 177.
- Person, S. J., White, R. G. and Luick, J. R. 1975. In vitro digestibility of forages utilized by *Rangifer tarandus*. - In: Luick, J. R., Lent, P. C., Klein, D. R. and White, R. G. (eds.) *Proceedings of the First International Reindeer and Caribou Symposium*. Biological Papers, University of Alaska, Special Report. No. 1. 251 - 256.
- Person, S. J., White, R. G. and Luick, J. R. 1980. Determination of nutritive value of reindeer-caribou range. - In: Reimers, E., Gaare, E., and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 224 - 239.
- Person, S. J., Pegau, R. E., White, R. G. and Luick, J. R. 1980. In vitro and nylon-bag digestibilities of reindeer and caribou forages. - *Journal of Range Management*. 44: 613 - 622.
- Pullianen, E. 1971. Nutritive values of some lichens used as food by reindeer in northeastern Lapland. - *Acta Zoologica Fennica*. 8: 385 - 389.
- Reimers, E. 1980. Activity pattern; the major determinant for growth and fattening in *Rangifer*? - In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 466 - 474.
- Ritchie, M. E. 1988. Individual variation in the ability of Columbian ground squirrels to select an optimal diet. - *Evolutionary Ecology* 2: 232 - 252.
- Ritchie, M. E. 1990. Optimal foraging and fitness in Columbian ground squirrels. - *Oecologia* (Berlin) 82: 56 - 67.
- Roby, D. D. 1980. Winter activity of caribou on two arctic ranges. - In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 537 - 545.

- Rundel, P. W. 1978. The ecological role of secondary lichen substances. – *Biochemical Systematics and Ecology* 6: 157 – 170.
- Russell, D. E. and Martell, A. M. 1984. Winter range ecology of caribou (*Rangifer tarandus*). – In: Olson, R., Hastings, R. and Geddes, F. (eds.), *Northern Ecology and Resource Management*, University of Alberta Press, Edmonton. 117 – 144.
- Ryg, M. 1975. Advances in the physiological studies in the reindeer/caribou in 1978–82. – *Acta Zoologica Fennica*. 175: 77 – 80.
- Schmitz, O. J. 1990. Management implications of foraging theory: evaluating deer supplemental feeding. – *Journal of Wildlife Management*. 54: 522 – 532.
- Schmitz, O. J. in press. Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. – *Holarctic Ecology*.
- Schmitz, O. J. and Belovsky, G. E. submitted. Wildlife management implications of foraging theory: assessment of carrying capacity. – *Journal of Wildlife Management*.
- Scotter, G. W. 1972. Chemical composition of forage plants from the Reindeer Preserve, Northwest Territories. – *Arctic* 25: 21 – 27.
- Skogland, T. 1980. Comparative summer feeding strategies of arctic and alpine *Rangifer*. – *Journal of Animal Ecology*. 49: 81 – 98.
- Skogland, T. 1984. Wild reindeer foraging-niche organization. – *Holarctic Ecology* 7: 345 – 379.
- Skogland, T. 1985a. The effects of food and maternal conditions on fetal growth and size in wild reindeer. – *Oecologia* (Berlin) 60: 156 – 168.
- Skogland, T. 1985b. The effects of density-dependent resource limitation on the demography of wild reindeer. – *Journal of Animal Ecology*. 54: 359 – 374.
- Staaland, H. and Jacobsen, E. 1983. Reindeer sodium and potassium metabolism in relation to ecology. – *Acta Zoologica Fennica*. 175: 185 – 187.
- Staaland, H., Jacobsen, E. and White, R. G. 1979. Comparison of the digestive tract in Svalbard and Norwegian reindeer. – *Arctic and Alpine Research* 11: 457 – 466.
- Staaland, H., White, R. G., Luick, L. J. and Holleman, D. F. 1980. Dietary influences on sodium and potassium metabolism of reindeer. – *Canadian Journal of Zoology*. 58: 1728 – 1734.
- Staaland, H., Holleman, D. F., Luick, J. R., and White, R. G. 1981. Exchangeable sodium pool size and turnover in relation to diet in reindeer. – *Canadian Journal of Zoology*. 60: 603 – 610.
- Staaland, H., Brattbakk, I., Ekern, K. and Kildemo, K. 1983. Chemical composition of reindeer forage plants in Svalbard and Norway. – *Holarctic Ecology* 6: 109 – 122.
- Staaland, H., Hove, K. and White, R. G. 1986. Mineral absorption in relation to nutritional ecology of reindeer. – *Rangifer*, Special Issue. No. 1: 279 – 287.
- Steen, E. 1968. Some aspects of the nutrition of semi-domestic reindeer. – *Symposium of the Zoological Society of London*. 21: 117 – 128.
- Stenseth, N. C. and Hansson, L. 1979. Optimal food selection: a graphical model. – *American Naturalist*. 113: 373 – 389.
- Stephens, D. W. and Krebs, J. R. 1986. *Foraging Theory*. Princeton University Press, Princeton. 247 p.
- Syrjälä, L., Salonen, L. and Valtonen, M. 1980. Water and energy intake and nitrogen utilization in reindeer. – In: Reimers, E., Gaare, E., and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 252 – 261.
- Syrjälä-Qvist, L. and Salonen, J. 1983. Effect of protein and energy supply on nitrogen utilization in reindeer. – *Acta Zoologica Fennica*. 175: 53 – 55.
- Thomas, D. C. and Kroeger, P. 1981. Digestibility of plants in ruminal fluids of barren-ground caribou. – *Arctic* 34: 321 – 324.
- Thomas, D. C., Kroeger, P. and Hervieux, D. 1984. In vitro digestibilities of plants utilized by barren-ground caribou. – *Arctic* 37: 31 – 36.
- Tyler, N. J. C. and Oeritsland, N. A. 1989. Why don't Svalbard reindeer migrate? – *Holarctic Ecology* 12: 369 – 376.
- Trudell, J. and White, R. G. 1981. The effect of forage structure and availability on food intake, biting rate, bite size and daily eating time of reindeer. – *Journal of Animal Ecology*. 18: 63 – 81.
- Trudell, J., White, R. G., Jacobsen, E., Staaland, H., Ekern, K., Kildemo, K. and Gaare, E. 1980. Comparison of some factors affecting the in vitro digestibility estimate of reindeer forages. – In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 262 – 273.
- Valtonen, M. H. 1980. Effects of dietary nitrogen and sodium chloride content on water intake and urine excretion in reindeer. – In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim. 274 – 277.
- Wales, R. A., Milligan, L. P. and McEwan, E. H. 1975. Urea recycling in caribou, cattle and sheep. – In: Luick, J. R., Lent, P. C., Klein, D. R. and White, R. G. (eds.) *Proceedings of the First International Reindeer and Caribou Symposium*. Biological Papers, University of Alaska, Special Report. No 1. 297: 307.
- Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. – *American Naturalist*. 111: 553 – 578.
- Werner, E. E. 1985. Species interactions in freshwater fish communities. – In: Diamond, J. and Case, T. J. (eds.) *Community ecology*. Harper and Row, New York. 344 – 357.

- Werner, E. E. and Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. – *Annual Review of Ecology and Systematics* 15: 393 – 425.
- Werner, E. E. and Mittlebach, G. G. 1981. Optimal foraging: field tests of diet choice and habitat switching. – *American Zoologist*. 21: 813 – 829.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. – *American Naturalist*. 108: 290 – 304.
- White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. – *Oikos* 40: 377 – 384.
- White, R. G. and Gau, A. M. 1975. Volatile fatty acid (VFA) production in the rumen and cecum of reindeer. – In: Luick, J. J., Lent, P. C., Klein, D. R. and White, R. G. (eds.) *Proceedings of the First International Reindeer and Caribou Symposium. Biological Papers, University of Alaska, Special Report*. No. 1. 284 – 289.
- White, R. G. and Trudell, J. 1980a. Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. – *Arctic and Alpine Research*. 12: 511 – 529.
- White, R. G. and Trudell, J. 1980b. Patterns of herbivory and nutrient intake of reindeer grazing tundra vegetation. – In: Reimers, E., Gaare, and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium. Direktoratet for vilt og ferskvannsfisk, Trondheim*. 180 – 195.
- White, R. G., Thomson, B. R., Skogland, T., Person, S. J., Russell, D. F., Holleman, D. F. and Luick, J. R. 1975. Ecology of caribou at Prudhoe Bay, Alaska. – In: Brown, J. (ed.) *Ecological investigations of the tundra biome in the Prudhoe Bay Region, Alaska, Biological Papers of the University of Alaska, Special Report*. No. 2, pp. 150 – 201.
- White, R. G., Jacobsen, E. and Staaland, H. 1984. Secretion and absorption of nutrients in the alimentary tract of reindeer fed lichens or concentrates during the winter. – *Canadian Journal of Zoology*. 62: 2364 – 2376.
- Whitten, K. R. and Cameron, R. D. 1980. Nutrient dynamics of caribou forage on Alaska's arctic slope. – In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium. Direktoratet for vilt og ferskvannsfisk, Trondheim*. 159 – 166.
- Wright, J. M. 1980. Spring and summer vegetation preferences of semi-domestic reindeer on the northwest Seward Peninsula. – In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium. Direktoratet for vilt og ferskvannsfisk, Trondheim*. 168 – 173.
- Young, B. A. and McEwan, E. H. 1975. A method for measurement of energy expenditure in unrestrained reindeer and caribou. – In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium. Direktoratet for vilt og ferskvannsfisk, Trondheim*. 355 – 359.
- Yousef, M. K. and Luick, J. R. 1975. Responses of reindeer, *Rangifer tarandus*, to heat stress. – In: Luick, J. R., Lent, P. C., Klein, D. R. and White, R. G. (eds.) *Proceedings of the First International Reindeer and Caribou Symposium. Biological Papers, University of Alaska, Special Report*. No. 1. 360 – 367.

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