Snowshoe Hare Browse in North West Quebec: An Estimation of its Nutrient Composition and Use

By

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ABSTRACT

The use of tree and shrub browse by snowshoe hare (*Lepus americanus* Erxleben) in the James Bay region was evaluated by species, diameter, and height. Browse clippings were later collected for nutrient analyses to determine if a link existed between browse utilization and potential, and the nutrients contained therein. Potential referred to the estimated amount of browse available per plant while the estimated amount removed from the plant by hare was termed utilization. The amount of potential tree browse differed between species (black spruce, tamarack > jack pine). Browse digestibility (black spruce, jack pine > tamarack; willow > alder, birch) and the concentration of hemicellulose (black spruce > jack pine, tamarack; alder, birch > willow) also differed between species. The concentrations of cellulose, cell solubles, crude lignin, P, K, Ca, Fe and Mn in tree and/or shrub browse also differed between species, but to a lesser extent than the hemicellulose concentration or percent digestibility. Hare appeared to select browse which offered the best balance of digestibility and nutrient content, both between species and between heights. Browsing by hare was restricted to woody twigs when the snow was deep enough to cover the more succulent herbs. The availability, utilization, succulence, and concentrations of P and K in tree browse increased with height. Protein levels in shrub

browse also tended to increase in higher browse, whereas its percent cellulose content gradually decreased with height. The amount of hemicellulose in browse from height 3 (>80 cm) of black spruce and height 1 (0-40 cm) of tamarack were substantially different from the concentration at the same heights of other species. There were no apparent differences in the use, availability, or digestibility of browse from the four diameter classes of trees. The variability in crude protein and Ca concentration between the four diameter classes of black spruce were substantially different from those of the other tree species. Multiple regression modelling yielded four descriptive models for tree and shrub browse potential and its utilization by hare. Results of these models closely reflected those from other statistical analyses.

RESUME

L'utilisation des broutilles d'arbres et arbustes par le Lièvre d'Amérique (Lepus americanus Erxleben) dans la région de la Baie de James fut évaluée selon les essences, le diamètre (du tronc) et la hauteur. Des échantillons de broutilles furent ensuite prélevés en vue d'analyser les éléments nutritifs et de déterminer s'il existait une corrélation entre l'utilisation des broutilles (utilisation et potentiel) et les éléments nutritifs qu'elles contiennent. La quantité estimée de broutilles disponible sur chaque plante étant considérée comme le potentiel, alors que la quantité estimée de brout effectivement prélevée sur chaque plante était considérée comme l'utilisation. Les quantités potentielles de broutille d'arbre variaient selon les essences (épinette noire, mélèze > pin gris). La digestibilité du brout (épinette noire, pin gris > mélèze; saule > aulne, bouleau) et la teneur en hémicellulose (épinette noire > pin gris, mélèze; aulne, bouleau > saule) différaient également d'une espèce à l'autre. Les concentrations en cellulose, en solubles cellulaires, en lignine brute, en P, K, Ca, Fe et Mn dans la broutille prélevée sur les arbres ou arbustes variaient également selon les essences, mais à un degré moindre que la teneur en hémicellulose ou le pourcentage de digestibilité. Le Lièvre semblait sélectionner les broutilles offrant la digestibilité et la teneur en nutriments optimales, selon les essences aussi bien que selon la hauteur de brout. Le Lièvre se contentait de

brouter les brindilles ligneuses lorsque la neige était assez épaisse pour recouvrir les herbes plus succulentes. La disponibilité, l'utilisation, la succulence et les teneurs en P et K des broutilles d'arbres augmentaient en fonction de la hauteur. Les taux de protéines dans les broutilles d'arbustes tendaient également à augmenter en fonction de la hauteur, alors que le pourcentage de leur teneur en cellulose décroissait graduellement avec la hauteur. La quantité d'hémicellulose dans le broutilles, prélevées au niveau de hauteur 3 (>80 cm) sur des épinettes noires et à la hauteur 1 (0-40 cm) sur des mélèzes différait sensiblement de la concentration observée sur d'autres essences à la même hauteur. Il ne semblait exister aucune différence d'utilisation, de disponibilité ou de digestibilité des broutilles entre les quatre classes de diamètre d'arbres. Les variations dans les taux de protéine brute et de Ca entre les quatre classes de diamètre d'épinette noire différaient sensiblement de celles des autres essences. Une formulation de régression multiple fournit quatre modèles descriptifs du potentiel de brout des arbres et arbustes et de leur utilisation par le Lièvre. Les résultats de ces modèles correspondaient à ceux des autres analyses statistiques.

DEDICATION

To my family,
which was always behind me; and
to my wife, always beside me.

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LITERATURE REVIEW

The snowshoe hare (Lepus americanus) is a dominant species of the boreal forest community. It relies on several browse species, and in turn many avian and mammalian predators, particularly the lynx (Lynx canadensis), depend on it as a major year round food source (Grange 1932; Adams 1959; Nellis and Keith 1968; Banfield 1974). Early studies on hare were quite general and dealt with the more obvious aspects of their natural history, such as demography, cover requirements, habitat use and food habits. Recent studies have examined the nutritive composition, quality, and digestibility of hare browse, digestive tract anatomy and function, and physiology of the hare. All of these aspects are directly or indirectly related to hare demography.

Many studies have focused on the marked fluctuations in hare population density (MacLulich 1937; Green and Evans 1940; Keith 1963; Grange 1965; Keith 1974; Keith and Windberg 1978). Rowan (1948) stated that this population periodicity was an outstanding problem of Canadian conservation. The three categories of hypotheses developed to explain hare and small mammal population cycles are: the stress syndrome (Christian et al. 1965); genetic polymorphism (Chitty 1960, 1967); and hare-vegetation interactions (Keith and Windberg 1978; Bryant in press). These latter authors have postulated two separate, but similar, hare-vegetation interactions.

According to Bryant (in press) the population decline is due to the depletion of preferred browse, and the elevated level of anti-herbivore toxins produced in the browse in response to increased browsing pressure during the late incline and early peak phase of the cycle. Over the first three years of decline in hare density, the decreased browsing pressure initiates a decrease in toxin levels. By the time the population is at its lowest, the toxin-producing species are edible. This allows the browsing pressure to increase and thereby re-initiates the rapid growth phase of the hare population cycle.

The similar hypothesis of Keith and Windberg (1978) suggests that the depletion of the preferred browse, and the malnutrition that follows, initiates the population decline. This hare-vegetation interaction is further influenced by a subsequent hare-predator interaction that extends the duration of the decline. Eventually, there are too few hare to support the predator population and it also declines. This decrease in predators permits the hare population to increase once more and also leads to overbrowsing.

When hare overbrowse, strip bark from, or girdle preferred trees and shrubs, the recovery of these plants can be affected such that some never grow tall enough to escape from browsing (Adams 1959; Keith 1966; Lindlof _et al._ 1974a; Wolff 1977;

Keith and Windberg 1978; Pease et al. 1979; Bryant in press). Their vertical browse range of 50 - 60 cm (Wolff 1977; Pease et al. 1979) enables them to remove much of the understory. Hare's potential for overbrowsing increases with rising snow levels which shifts their browse range and augments their dependence on browse (Bider 1961; Wolff 1977, 1978a, 1978b). Overbrowsing associated with peak hare populations can also affect the quality of cover in the habitat (Keith 1966; Meslow and Keith 1968, Minke 1973, in Wolff 1977; Wolff 1978a).

Hare prefer patchy habitats with refuges of low, dense cover, particularly black spruce (Picea mariana), alder (Alnus spp.), or willow (Salix spp.) (Grange 1932; MacLulich 1937; Adams 1959; Keith 1966; Lindlof et al. 1974a). During winter they congregate in highly desirable habitat (refugia) then disperse into more marginal habitats in summer (Wolff 1977). Regardless of season, a habitat must supply hare with adequate cover and food (Grange 1932; Bider 1961; Wolff 1977).

Many of the authors who have studied hares' cover requirements have also investigated their food habits or home range, or both. Notable among these are Grange (1932), Adams (1959), Bider (1961), O'Farrel (1965), and Wolff (1977). These authors, and others, have established snowshoe hare home ranges to be between 8 - 10 ha with an active core of about 2 - 3 ha or less. Several hare can feed in the same general area since home ranges can overlap considerably (Bider 1961; Wolff 1977).

The food habits of snowshoe hare have been studied throughout its range, during all seasons, and by a variety of methods. The methods used fall into one or more of the following classes: browsing observations (MacLulich 1937; Dodds 1960; Bider 1961; Radwan and Campbell 1968), analysis of stomachs for occurrence of food by percent of total volume (Wolff 1978b), or fecal pellet analysis (Adams 1957). In his recent study, Wolff (1978b) found hare in Alaska ate fewer species of plants than previously reported in other areas and felt that this reflected the lesser diversity of plant species. Food habit studies during all seasons have shown that snowshoe hare and mountain hare (Lepus timidus) consume forbs, leaves and herbaceous plants, and some woody browse in summer, with the proportion of woody browse, bark, and needles gradually increasing with onset of winter (Grange 1932; Dodds 1960; Telfer 1972, 1974; Hewson 1973, Wolfe 1974; Lindlof et al. 1978; Wolff 1978b).

Food habit studies have led to the investigation of the nutrient composition or quality of major browse species. These studies have determined the nutrient composition of food items common to snowshoe hare and many other herbivores such as deer (Odocoileus virginianus and O. hemionus) (Hellmers 1940; Einarsen 1946; Atwood 1948; Dewitt and Derby 1955; Alkon 1961; Short and Reagor 1970; Robbins et al. 1975; Short 1975; Mautz et al. 1976), moose (Alces alces) (Kubota et al. 1970), grouse (Bonasa umbellus) (Kittams 1943; Treichler et al. 1946; Korschgen 1966; Hill et al. 1968), pheasants (Phasianus colchicus) (Errington 1936), turkeys (Meleagris gallopavo) (Beck and Beck 1955), and mountain hare (Pehrson, in press).

Both the quality and the quantity of browse eaten have been shown to affect the fitness of leporids. The size and fitness of rabbit (Sylvilagus floridanus) reproductive organs were deleteriously affected by a reduction in the quantity of food eaten (Kirkpatrick and Kibbe 1971). Pehrson (in press) has shown that during winter hares may lose weight depending on their rate of consumption (quantity) and the digestibility and diameter of browse (quality) consumed. He was also able to show that digestibility differed between browse species. The digestibility of aspen (Populus tremuloides), cedar (Thuja occidentalis), and red maple (Acer rubrum) browse for hare were evaluated by Walski and Mautz (1977), who also analyzed the proximate constituents of these foods to establish their nutritive value (i.e. quality).

More recently, the use of proximate analysis has been criticized and another analysis has to some extent replaced it, or is used in conjunction with it. Proximate analysis, the standard for decades, is claimed to analyze for food fractions that do not represent definable chemical entities and that are not realistic (Van Soest 1963). To solve this problem Van Soest (1963, 1964) and Goering and Van Soest (1970) developed a detergent fiber system (DFS) that separates plant tissues into more easily defined biochemical fractions. This approach, originally used for fodder analysis, is receiving wider acceptance as a wildlife research tool. Short and Reagor (1970) claim DFS fractions are more useful than proximate analyses for predicting utilization and suggest this system may also be used for predicting how deer utilize wild forages. It may be possible to expand this system to include analysis of browse for hare and other herbivores.

The most common use of the DFS has been evaluation of white-tailed deer (O. virginianus) browse nutrients and digestibility (Robbins and Moen 1975; Robbins et al. 1975). The DFS has also been applied to pronghorn (Antilocapra americana) foods by Schwartz et al. (1977). To evaluate the digestibility and nutritive value of certain seeds and fruits, Short and Epps (1976) used a cannulated goat, proximate analysis, and the DFS. They did not state why both methods of food analysis were used but it permitted comparison of the systems and a transition from one system to the other. Much data has undoubtedly been "lost" due to the inability to equate one system to the other.

The digestibility of browse to herbivores depends on the balance of compounds which promote or inhibit growth of gut flora (Longhurst et al. 1968). If this balance favours inhibiting compounds, digestion may be reduced. This encourages herbivores to select browse from several species (Klein 1970). Nutrients favorable to the growth of gut flora are proteins, carbohydrates, and cellulose (Van Soest 1977). Anti-quality factors have been separated (Van Soest 1977) into two categories: metabolic inhibitors (bacteriostatic toxins, resins), and plant structural matter resistant to animal enzymes (lignin and lignocellulose). No matter how nutritious a food is, these inhibitors limit its usefulness to the hare by their effect on their digestive tracts.

Some plant species rely on a constant level of toxicity for protection against browsing herbivores while in other species the concentration of toxins decreases to a palatable level when the plant matures. The latter species can revert to the toxic juvenile state if subjected to enough browsing pressure, but otherwise their nutrients are available to hare with little or no toxic effect (Bryant, pers. comm.).

The availability of the nutrients in browse to hare is difficult to study in the wild. Wild-caught hare have been used by some authors (Holter et al. 1974; Mautz et al. 1976; Walski and Mautz 1977) in attempts to determine the species' digestive efficiency when consuming natural foods. Six iso-caloric diets were used by Holter et al. (1974) to study the nutrition of wild-caught hare. Red maple browse was mixed with different amounts of commercial rabbit chow, soy bean meal, and ground shelled corn. The nutrient content of these diets were determined by proximate analysis, and showed that the protein concentrations of the diets ranged between 10 - 26%. The digestibilities of these diets were also discussed. A more recent study by Mautz et al. (1976) assessed the digestibility of three browses in pelleted and fresh-frozen forms. The proximate composition of each of three browse species was determined by Walski and Mautz (1977). The nutritive value of each browse to hare was then determined by means of feeding trials.

The acclimatization of hare to winter is also difficult to study in the wild. In an attempt to provide fairly natural surroundings, Hart et al. (1965) kept wild-caught hares in an outdoor enclosure when not testing these animals in a metabolic chamber. They measured many physiological parameters in order to assess metabolic rate, oxygen consumption, and insulation in the hare. Thermocouples were implanted to measure subcutaneous and substernal temperatures. It was noted that in winter hare had a lowered caloric intake and that their critical temperature dropped from 10° to -5° C. Hare consumed more O_2 in summer, when tested at temperatures below thermoneutrality, than they did in winter. All these findings contributed to a 35% greater heat conductance in summer, with the winter pelage accounting for at least 27% less heat loss. Another sign of the hare's acclimitization to cold was the broader thermoneutral zone during winter, and that this increase in thermoneutrality was entirely at the lower critical temperature.

Feist and Rosenmann (1974) felt the insulative effect of hare pelts only partially explained the species' adaptation to cold. They established that hare have a metabolic adjustment to cold as well as an enhancement of non-shivering thermogenesis. Their work supported that of Hart et al. (1965) by finding that the thermal conductance of hare was 33% lower in winter than in summer. When placed under analogous thermal stress, hare had much less activation of the sympathetic nervous system and adrenal medulla in winter than in summer. This implied a lower metabolic rate for hare during winter and hence, less expenditure of energy.

The above results partially explain why Hart et al. (1965) found food intake lower in winter than in summer. Winter is also the time of year when food is often scarcest.

Other reasons for the lower food demands in winter depend on hare behavior and physiology. During winter, hare do not have to cover the energetic demands of mating, reproduction, and rearing of young. Hare are also less active in winter (Grange 1932), spending most of their time resting in forms, protected from both predators and the elements.

INTRODUCTION

The selection of woody browse by many herbivores has been linked to its accessibility or digestibility, or its nutrient content (Einarsen 1946; Miller 1968; Tew 1970; Hewson 1973; Telfer 1974; Robbins et al. 1975; Wolff 1978b). However, limited attention has been given to the nutrient content of snowshoe hare browse and its digestibility (Walski and Mautz 1977), and no attempt has been made to relate these factors.

This study was designed to determine if relationships existed between snowshoe hare browse use, availability, digestibility and nutrient content. Four hypotheses were tested to disclose whether:

1) differences existed between species, or between heights, of trees or shrubs in the amount of potential browse, or the utilization of browse by hare;

2) differences existed between diameter classes of trees in the amount of potential browse, or the utilization of browse by hare;

3) the digestibility or nutrient content of browse differed with the species, height, or diameter class of tree sampled, or with the species, or height, of shrub sampled;

4) the amount of potential browse and/or the utilization of browse by hare were correlated with the digestibility and/or nutrient content of the browse.

Trees and shrubs known to be important winter browse species for snowshoe hare in other regions (Grange 1932; Adams 1959; Dodds 1960; Bider 1961; Wolff 1978b; and Pease et al. 1979) were selected for study. These species were jack pine

(*Pinus banksiana*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), willow (*Salix bebbiana* or *S. planifolia*), alder (*Alnus crispa*), and birch (*Betula glandulosa*).

Ancillary objectives were: 1) to use multiple regression models to describe browse utilization and potential in terms of the browse digestibility and nutrient content and 2) the establishment of a data base for the nutrient content of tree and shrub browse.

STUDY AREA

Location

The study area was located in the James Bay region of Quebec, 940 km north-northwest of Montreal (Fig. 1), with a base camp at Lac Hélène (53°27' N, 77°31' W).

Climate

The climate has been described by Trewartha (1954) as boreal subarctic, having a large annual range of temperature and sporadic permafrost. The area has a microthermal climate with humid winters, and short cool summers with less than four months over 10°C (Köppen, in Trewartha, 1954).

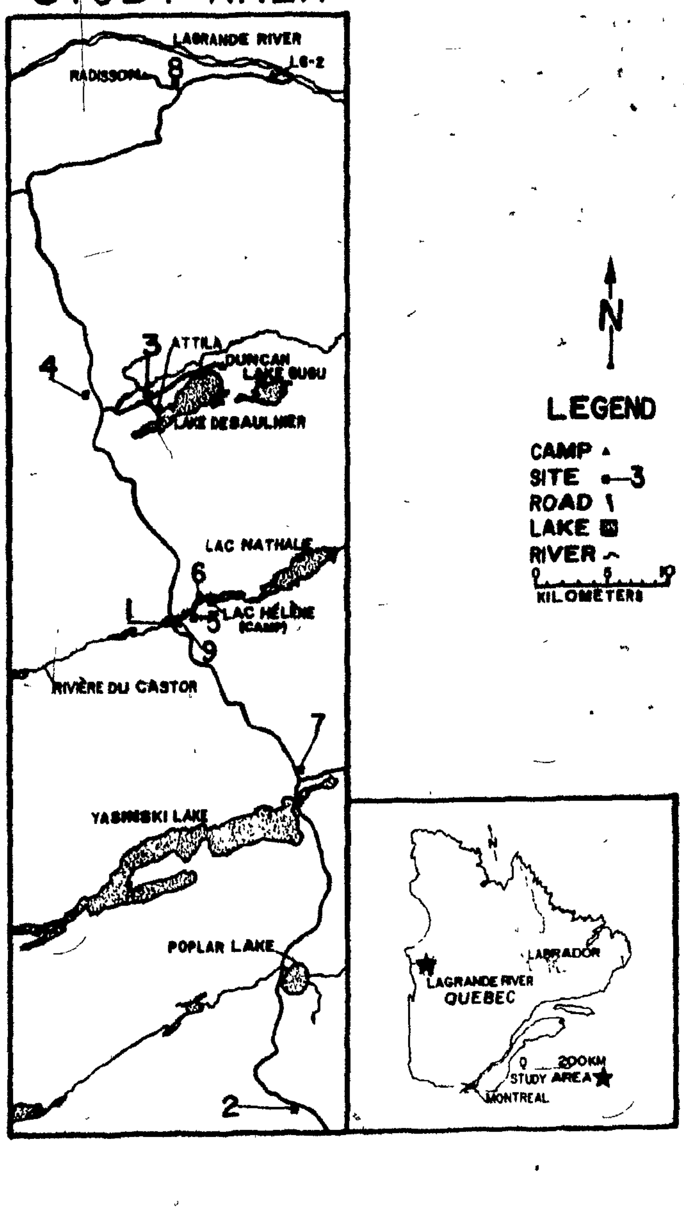
Soils

Many bogs, fens, eskers, and moraines, with their associated organic and till soils, dotted the area. Many rivers and lakes of various sizes were also scattered throughout the area. The soil was sampled at most sites and analyzed for pH and concentrations of elements (Soil test laboratory - Macdonald College). The pH of the soils ranged between 4.8-6.9. The concentrations of soil elements are summarized in Table 1.2, Appendix 1.

Vegetation

The vegetation in the study area was typical of subarctic boreal forest and has been classified by Rowe (1972) as Fort George, type B 13b. The open and closed stands provided good forest cover and several habitat types. Habitats of greatest importance to hare were sampled. Nomenclature used to describe flora follows Gleason and Cronquist (1963) or Marie-Victorin (1964). The floristic composition, soil pH, and mineral content of each site is described more fully in Appendix 1.

FIGURE I
STUDY AREA



METHODS

Estimation of Browse Potential and Utilization

Local hare normally consumed browse up to 5.0 mm in diameter. The estimated amount of this browse available per plant was termed potential while the estimated amount that had been removed from each plant by hare was termed utilization. These variables were estimated during the summer of 1975 at nine sites (Figure 1) selected on the bases of accessibility, stand homogeneity, and abundance of the dominant species. Estimates of tree and shrub browse potential and utilization were taken at three heights or strata (1, 0-40 cm; 2, >40-80 cm; 3, >80 cm) which roughly approximated the hare's usual summer, early winter and early spring, and late winter browse ranges. Most shrubs were between 1.2 and 1.4 m tall. The seasonal availability to hare of tree and shrub browse above height 1 depended on snow depth. Hare browse potential and utilization at each site were estimated to the maximum height that utilization was observed. Trees were allocated to one of four diameter classes (1, 0-1 cm; 2, > 1.0-2.5 cm; 3, >2.5-5.0 cm; and 4, >5.0 cm, measured immediately above the flare of the trunk). Trees of 5 cm trunk diameter or greater were not sampled due to their relative scarcity and the lack of browse within the hare's usual browsing range. In cases where there were two or more species codominant in the canopy and/or the understory, all of these species were sampled.

The species sampled at the sites were: 1, birch; 2, jack pine; 3, jack pine; 4, jack pine; 5, black spruce, willow; 6, tamarack, birch, willow; 7, tamarack; 8, tamarack, willow; 9, willow, alder. A 10 m-square plot was established at each site and 10 shrubs of each species, and/or up to 10 trees of each species per diameter class, were randomly selected. The amounts of potential and utilized browse were visually estimated and ranked (1.00, 0-20%; 2.00, 20-35%; 3.00, 35-50%; 4.00, 50-65%; 5.00, 65-80%; 6.00, 80-100%) at each height of the selected plants. Estimated potential and utilization rank values for a given species were pooled and averaged by height, diameter class, and site.

Chemical Analyses

Collection and Preparation of Samples

Collection of browse samples was facilitated by use of a template notched with the maximum dimensions of the browse, and the tree diameter classes. Sampling variability was also minimized by using this template. Browse clippings were placed in watertight bags, labelled, and kept near 0°C until weighed.

Samples were weighed, dried, and ground in preparation for chemical analyses. Samples were weighed to within 0.001 g on a top loading balance and then air dried at 45°C until weights were constant. Drying temperatures in excess of 50°C would have caused the formation of significant amounts of artifact lignin due to non-enzymatic browning (Van Soest 1973). The percent dry matter at 45°C was obtained by reweighing each sample. The percent dry matter at 100°C was obtained by drying 1.000 g subsamples overnight in a vacuum oven and then reweighing. Each sample was ground and mixed in macro- and micro-Wiley mills (2.00 mm and 0.85 mm mesh screen, respectively) and then bottled and labelled.

Determination of Elemental Content

A sulfuric-peroxide wet digestion method was used to prepare samples for analyses (Thomas et al. 1967). Digests were diluted 10:1 with deionized distilled water instead of 50:1 as suggested so that the same digests could be used for both major (N, P, K, Ca, and Mg) and trace (Cu, Fe, Mn, and Zn) element analysis. Concentrations of major elements were determined by automated analyses while trace elements were determined by atomic absorption spectrophotometry using standard techniques.

The results for Cu and Zn were inconclusive due to technical difficulties.

Determination of Browse Digestibility and Tissue Fraction Concentrations

The digestibility and concentrations of most tissue fractions (cell wall, lignocellulose, lignin, cellulose, hemicellulose and cell solubles) were determined by the forage fiber analysis method (Goering and Van Soest 1970). The N values obtained in elemental analyses were multiplied by 6.25 to yield a crude protein value for each sample. All variables were expressed on a 100% dry matter basis. The formulae (Van Soest, pers. comm.) used to calculate browse digestibility were:

1) %CSOL=100 - (CW x 100)
2) DIGT=[(CW x 100) x 0.2] + %CSOL
3) DIGA=DIGT - 9.0%

where CW is the sample's average percent cell wall value
CSOL is the sample's average percent cell solubles value
DIGA is the sample's average percent apparent digestibility value
DIGT is the sample's average percent true digestibility value
9.0% is the sample's estimated metabolic fecal loss value

Statistical Analysis

An analysis of variance using Winer's (1971, pp 539-559) three-factor repeated measures model was followed by multiple comparisons. The use of the Waller-Duncan multiple range test (Barr et al. 1976) allowed for the unbalanced design.

Four multiple regression models that best estimated the browse potential and utilization of trees and shrubs were developed by using a stepwise procedure with dummy variables (Barr et al. 1976; Chatterjee and Price 1977). Residuals were examined to determine if deficiencies existed in the structure of the final models.

Further details on chemical (elemental and fiber) and statistical (variance and multiple regression) analyses can be found in Appendix 2.

RESULTS

Browse Potential and Utilization

Hare appeared to have browsed all trees and shrubs fairly evenly (Table 1). A moderate amount of tree and shrub browse remained available to hare although jack pines had significantly less browse than other trees. The amount of potential browse, and its utilization by hare, increased with height in trees but not in shrubs. The tree diameter classes used were rough indicators of age. Hare did not seem to prefer to browse any particular diameter class ($p > 0.05$). The amount of potential tree browse also appeared to be uniform among diameter classes ($p > 0.05$).

Browse Digestibility and Composition

The concentrations of several nutrients in the browse, and its digestibility, differed among both tree and shrub species (Table 2). However, no particular species of tree or shrub browse contained the highest concentrations of all the nutrients.

The concentrations of most browse nutrients did not differ between sampling heights (Table 3). However, the concentrations of some nutrients important to the hare diet did differ between heights. In particular, the amounts of crude lignin, P, and K in tree browse increased with height while the cellulose content of shrub browse decreased with height. Shrub browse had generally more crude protein in the upper strata. The most succulent tree browse (as shown by percent dry matter) was from the uppermost stratum (Table 4). Several other variables did show direct or inverse relationships to the height of tree or shrub browse but were not significantly different.

The concentrations of three nutrients (crude protein, calcium, and hemicellulose) were affected by the simultaneous interaction of two of the factors (species and diameter or height) (Table 5). Crude protein was most concentrated in tree browse from diameter class 2. Slightly less was found in browse from other diameters. The crude protein content of black spruce browse varied most between diameters. This species generally had less protein than other trees. Browse from trees of diameter class 1 had the most Ca, with significantly less Ca content in browse from diameters 4, 2, and 3 respectively. Black spruce contained by far the most Ca and hemicellulose while tamarack browse had the least hemicellulose (Table 2). Browse from the highest stratum of black spruce and the lowest stratum of tamarack had noticeably more hemicellulose than browse from other strata of these two species.

Description of Browse Parameters by Multiple Regression

Multiple regression models were developed to describe tree and shrub browse potential and utilization in terms of the other variables (Table 6). Examination of the residuals indicated no significant deficiences existed in the structure of the final model. The adjusted multiple correlation coefficients (R) for three models were 0.93 while the model for the browse potential of shrubs had an R value of 0.73 (Table 6). As Mn concentrations increased, the utilization of tree browse decreased. A test for interaction of the independent variables showed this relationship to be slightly stronger for Site 6 tamarack than for trees at other sites. Willows at Site 5 were used slightly more by hare than willow elsewhere.

TABLE 1. Relationship of average browse potential and utilization ranks to species and heights sampled.

	TREES			SHRUBS		
	BS[2] (N=11)	JP (N=21)	TA (N=10)	AL (N=3)	DF (N=4)	SA (N=10)
Potential[1]	4.04[a][4]	1.91[b]	3.19[a]	3.80[d]	4.43[d]	3.73[d]
Utilization	1.24[a]	2.05[a]	3.38[a]	2.30[d]	1.10[d]	2.70[d]

	TREES			SHRUBS		
	1[3] (N=10)	2 (N=15)	3 (N=17)	1 (N=7)	2 (N=7)	3 (N=3)
Potential	2.02[c]	2.70[b]	3.27[a]	3.80[d]	3.79[d]	4.43[d]
Utilization	1.09[c]	1.95[b]	2.95[a]	2.30[d]	2.31[d]	2.00[d]

[1] Browse Potential and Utilization ranked from 1.00-6.00, with an increase in rank denoting an increase in the variable.

[2] SPECIES: BS, black spruce; JP, jack pine; TA, tamarack; AL, alder; DF, dwarf birch; SA, willow.

[3] HEIGHTS: 1, 0-40 cm; 2, >40-80 cm; 3, >80 cm.

[4] Waller-Duncan Test results at $\alpha = 0.05$. For each variable the tree or shrub means for species or heights sampled are not significantly different if they have the same superscript.

TABLE 2. Relationship of mean apparent digestibility and mean concentrations of nutrients, as expressed on a dry matter basis, to species of browse sampled.[1]

	TREES			SHRUBS		
	BS[3] (N=11)	JP (N=21)	TA (N=17)	AL[4] (N=3)	DF (N=3)	SA (N=11)
Digestibility (%)	54.69[a 2]	53.60[a]	45.65[b]	39.49[e]	38.03[e]	44.03[d]
Cellulose (%)	21.30[a]	22.97[a]	23.39[a]	23.66[e]	24.33[e]	33.22[d]
Hemicellulose (%)	9.46[a]	7.71[b]	4.09[c]	9.26[d]	8.57[d]	3.83[e]
Cell solubles (%)	54.61[a]	53.23[a]	43.31[b]	35.61[e]	33.79[e]	41.28[d]
Crude Protein[5] (%)	2.01[a]	2.89[a]	2.59[a]	5.02[d]	3.74[d]	3.78[d]
Crude Lignin (%)	14.73[b]	16.08[b]	29.21[a]	31.47[d]	33.30[d]	21.67[e]
Phosphorus (ppm)	758[a]	806[a]	937[a]	759[e]	753[e]	921[d]
Potassium (ppm)	3613[a]	3732[a]	3955[a]	2671[e]	2399[e]	3677[d]
Calcium (ppm)	6842[a]	1699[b]	1425[b]	7108[d]	3367[d]	7719[d]
Magnesium (ppm)[5]	1267[a]	1423[a]	1551[a]	1101[d]	1316[d]	1608[d]
Iron (ppm)	71[a]	331[a]	604[a]	384[d]	90[e]	63[e]
Manganese (ppm)	774[a]	411[b]	568[a,b]	278[d]	171[d]	334[d]

1 Using Waller-Duncan Multiple Range Test at $\alpha = 0.05$.

2 Means for each variable having same superscript are not significantly different.

3 BS, black spruce; JP, jack pine; TA, tamarack

4 AL, alder; DF, dwarf birch; SA, willow.

5 No. of observations for crude protein and magnesium in shrub samples = AL, N=3; DF, N=5; SA, N=10.

TABLE 3. Relationship of mean apparent digestibility and mean concentrations of nutrients, on a dry matter basis, to heights of browse sampled.[1]

	TREES			SHRUBS		
	1[3] (N=12)	2 (N=18)	3 (N=19)	1 (N=7)	2 (N=7)	3 (N=5)
Digestibility (%)	52.04[a2]	51.23[a]	50.34[a]	40.22[d]	42.21[d]	43.19[d]
Cellulose (%)	23.06[a]	22.54[a]	22.72[a]	30.87[d]	29.30[d,e]	27.37[e]
Hemicellulose (%)	7.12[a]	7.02[a]	6.51[a]	6.04[d]	6.25[d]	5.35[d]
Cell solubles (%)	51.30[a]	50.28[a]	49.18[a]	36.52[d]	39.01[d]	40.24[d]
Crude Protein[4] (%)	2.40[a]	2.64[a]	2.65[a]	3.41[e]	4.59[d]	3.88[d,e]
Crude Lignin (%)	18.60[c]	20.16[b]	21.59[a]	26.57[d]	25.44[d]	27.05[d]
Phosphorus (ppm)	781[b]	834[a,b]	844[a]	833[d]	923[d]	776[d]
Potassium (ppm)	3564[b]	3624[b]	4071[a]	3218[d]	3354[d]	2894[d]
Calcium (ppm)	3519[a]	3126[a]	1930[a]	5051[d]	7302[d]	7320[d]
Magnesium (ppm)[4]	1354[a]	1415[a]	1499[a]	1351[d]	1461[d]	1526[d]
Iron (ppm)	361[a]	336[a]	401[a]	104[d]	119[d]	148[d]
Manganese (ppm)	541[a]	555[a]	526[a]	254[d]	289[d]	312[d]

[1] Using Waller-Duncan Multiple Range Test at $\alpha = 0.05$.

[2] Means for each variable having the same superscript are not significantly different.

[3] Browse sampling heights: 1, 0-40 cm; 2, >40-80 cm; 3, >80 cm.

[4] No. of observations for Crude protein in shrub samples: 1, N=7; 2, N=7; 3, N=4.
No. of observations for Magnesium in shrub samples: 1, N=6; 2, N=7; 3, N=5.

TABLE 4. Relationship between % dry matter and drying temperature for browse samples from different species and heights.[1]

	TREES			SHRUBS		
Species[2]	BS (N=11)	JP (N=16)	TA (N=16)	AL (N=3)	DF (N=5)	SA (N=11)
% DM (45°C)	59.6[a]	53.5[a]	60.0[a]	54.5[d]	63.5[d]	55.7[d]
% DM (100°C)	55.8[a]	50.5[a]	55.8[a]	51.2[d]	59.8[d]	52.2[d]

	TREES			SHRUBS		
Heights[3]	1 (N=10)	2 (N=16)	3 (N=17)	1 (N=7)	2 (N=7)	3 (N=5)
% DM (45°C)	59.0[a]	57.9[a]	56.2[b]	57.6[d]	57.1[d]	58.2[d]
% DM (100°C)	55.3[a]	54.2[a]	52.6[b]	54.1[d]	53.6[d]	54.7[d]

[1] Waller-Duncan Test Results using $\alpha = 0.05$. For each variable, the means for the species or heights sampled are not significantly different if they have the same superscript.

[2] SPECIES: BS, black spruce; JP, jack pine; TA, tamarack; AL, alder; DF, dwarf birch; SA, willow.

[3] HEIGHTS: 1, 0-40 cm; 2, >40-80 cm; 3, >80 cm.

[4] % Dry Matter for browse dried at 45°C or 100°C; Temperatures >50°C produce significant amounts of artifact lignin.

TABLE 5. Species means for interacting factors of treatment combinations calculated on a dry matter basis.

		DIAMETER[1]						HEIGHT[2]		
		1	2	3	4			1	2	3
Crude Protein (%)	BS	2.03(2)[3]	2.43(3)	1.99(3)	1.61(3)	Hemi-cellulose (%)	BS	8.04(4)	9.19(4)	11.71(3)
	JP	2.76(2)	3.08(7)	2.90(8)	2.59(4)		JP	7.18(6)	8.33(8)	7.46(7)
	TA	2.42(2)	2.78(6)	2.52(6)	2.46(3)		TA	5.11(2)	3.83(6)	4.04(9)
Calcium (ppm)	BS	11119(2)	7919(3)	3688(3)	6066(3)					
	JP	1002(2)	1652(7)	1844(3)	1840(4)					
	TA	1276(2)	1287(6)	1235(6)	2181(3)					

DIAMETER: 1, 0-1.0 cm; 2, >1.0-2.5 cm; 3, >2.5-5.0 cm; 4, >5.0 cm.
HEIGHT: 1, 0-40 cm; 2, >40-80 cm; 3, >80 cm.
SPECIES: BS, black spruce; JP, jack pine; TA, tamarack.

[1] Diameter and Species-diameter interaction were both significant (P>F<0.05).

[2] Species-height interaction was significant (P>F<0.05) while height effect was not significant (P>F>0.05).

[3] Sample size appears in parentheses ( ).

TABLE 6. Results of the multiple regressions of browse species, diameter class, height, and nutrient content, on a dry matter basis, on tree and shrub browse potential and utilization.

	POTENTIAL					UTILIZATION				
	Variables	Coefficient	Probability	R	MSE	Variables	Coefficient	Probability	R	MSE
TREES				0.93	0.19				0.93	0.20
	Intercept	0.67				Intercept	3.62			
	Tamarack*	-0.61	<0.01			Tamarack*	1.37	<0.01		
	Jack pine*	-0.82	<0.01			Jack pine*	-0.40	0.03		
	Height	0.75	<0.01			Height	0.42	<0.01		
	Diameter 1*	-0.33	0.02			Diameter 1*	-0.04	0.76		
	Diameter 2*	-0.37	<0.01			Diameter 2*	0.49	<0.01		
	Diameter 3*	-0.45	<0.01			Diameter 3*	0.22	0.06		
	Fe	-0.23	<0.01			Mn	-0.58	<0.01		
						Site 6 TA[1]	-1.12	<0.01		
						Site 3 JP	0.88	<0.01		
SHRUBS				0.73	0.34				0.93	0.08
	Intercept	5.58				Intercept	2.70			
	Alder*	-0.17	0.46			Alder*	-0.02	0.83		
	Birch*	0.25	0.26			Birch*	-0.66	<0.01		
	Height	0.46	0.05			Height	-0.16	0.15		
	P	-0.003	0.02			Site 5 SA	0.73	<0.01		

* Denotes dummy variables.

[1] JP = jack pine; SA = willow; TA = tamarack.

DISCUSSION

It was expected that one or two species, heights, or diameter classes would have had more potential browse, and/or utilization by hare than the others. The assumption was that while hare browsed several species, they would attempt to optimize their nutrient intake by favoring some species, heights, or diameter classes that offered the best balance of digestibility and nutrient content.

Browse Potential and Utilization

The results (Tables 1-6) partially support the study's four hypotheses. Hare apparently attempted to optimize their diet, although not entirely in the manner that was expected. Reasons for the results can be suggested after considering how the hare population probably interacted with their habitat during the period prior to sampling.

When hare are scarce, as was the case when sampling occurred, they occupy only the best parts of optimal habitat (refugia) (Keith 1963: 88-89, 1966; Wolff 1977) and therefore can be very selective of food and cover. This opportunity to select the best browse and cover was augmented by the nearly complete recovery of the habitat at the time of sampling.

Areas of dense food and cover are preferred by hare during winter, particularly those with black spruce (Grange 1932; Wolff 1977). This preference for food and cover is reflected in the availability of browse and its use (Table 1). Shrubby areas appeared to be used moderately by hare throughout the year, as shown by the uniform availability and use of browse from different heights and species. This uniform use of shrub browse by hare and their increased use of tree browse in winter implies that tree browse was the most necessary source of winter food (Table 1). Dense stands of tamarack usually grow near or amongst dense black spruce and appear to have afforded a good source of potential food and cover (Table 1) during winter.

On the other hand, jack pine had less potential browse than other trees. This was likely due to the combined effect of 1) summer use of jack pine by hare, 2) the time at which jack pine received heaviest use, and 3) the long recovery period required by overbrowsed jack pine. Whereas hare prefer dense stands during winter, they migrate to more open (jack pine) habitat in summer to capitalize on the better seasonal food and cover (Adams 1959; Wolff 1977). During summer, hare could deplete the available browse in the lower strata. Only a small amount of the preferred browse species remained during the peak and post-peak phase of the cycle. Jack pine and black spruce were probably the most abundant species of winter browse then and the combined effect of summer and winter use would have reduced their potential considerably. Those overbrowsed jack pine that were able to recover would have required three to five years to do so and regrowth would have been primarily in their actively growing crowns (MacArthur, pers. comm.). Regrowth was probably not browsed by hare due to increased concentrations of toxins in accessible browse (Klein 1970, 1977; Bryant, in press), inaccessibility of browse in taller pines, and greater abundance of available browse in more preferred species.

Seasonal availability of food and tree growth patterns may have been responsible for the greater relative abundance of tree browse as height increased. Cumulative snowfall data (Bulletin Meteorologique 1975, vol. XIV, 1976, vol. XV) indicated that for hare the period of accessibility to browse in a stratum decreased as the sampling heights increased. These differences in browse availability, and the quicker recovery of the more actively growing upper strata, might explain the lower amount of potential tree browse in the lower strata (Table 1).

However, the heavier use of browse in the upper strata felt to be due to hare actively selecting the best browse when deeper snow made it accessible. The importance of woody browse increases when other foods are buried by snow (Wolff 1978b) and it is logical to assume that snowshoe hare would attempt to select the most beneficial browse available.

Relationship of Browse Quality to its Use by Hare

The results (Tables 2, 3, and 4) largely agree with previous studies (Lindlof *et al.* 1974b; Lindlof *et al.* 1978; Pease *et al.* 1979) that found the greatest differences in browse digestibility and nutrient content occurred between species.

It has been well established that snowshoe hare and mountain hare select browse with high concentrations of several nutrients. These nutrients include reducing sugars (a component of cell solubles) (Radwan and Campbell 1968), protein (as N x 6.25), phosphorus (Miller 1968; Lindlof et al. 1974b), and calcium (Lindlof et al. 1978). Mountain hare are also known to select the most digestible browse (Pehrson, in press) and snowshoe hare are suspected of doing likewise.

Given the previous research, this study's results suggest that hare did select quality winter browse with the best available balance of digestibility, nutrient content, and succulence (as shown by percent dry matter) (Tables 1, 2, 3, and 4). Tamarack browse appeared to meet these criteria.

Tamarack browse was expected to have been in the toxin-relaxed phase when sampled and therefore it could have been freely included in the hare diet. Browse of other nutritious species of variable or constant toxicity may also have been included in the hare diet but tamarack appeared to be the most important source of nutrients. Black spruce browse is toxic but is also highly digestible and nutritious (Table 2). Ingestion of sufficient quantities of tamarack browse could have diluted the adverse effect of black spruce or other toxic browse.

It is felt that the majority of winter browsing by hare took place in tamarack-black spruce refugia due to their density and quality of food and cover. The increased use of portions of successively higher tree browse during the short time it was available further suggests that hare selected browse. While not ignoring the possibility that the increased use of higher tree browse may have been related to availability, it is felt that this use was at least partially due to the elevated concentrations of phosphorus and potassium in the upper strata of tree browse (Table 3). The greater succulence of browse from the uppermost stratum of trees may have been a further factor that encouraged increased browsing by hare (Table 4).

Hare's choice of food could also have been affected by the higher levels of crude protein, calcium, and hemicellulose contained in browse from particular diameter classes or heights of jack pine or tamarack (Table 5). Snow depth, the availability of browse, and its use by hare are known to be interrelated (Bider 1961). The overall height of trees is generally related to their diameter class. If hare selected browse from certain species-diameter or species-height combinations that contained these nutrients, they could have increased the utilization of browse in the upper strata while capitalizing on an otherwise inferior or unavailable resource.

Differences in the amounts of several variables did not appear to occur between browse from the species, heights, and diameter classes examined. It is possible that these differences did not exist. Insufficient sample size, or deficiencies in the method, may have been responsible for those differences that did exist but were not brought to light.

Descriptive Use of Multiple Regression Models

The models closely reflected the F- and Waller-Duncan test results. However, unlike the analyses of variance, the models were able to disclose three cases in which the utilization of browse by hare differed slightly from the average (Table 6). This increased (Site 3 jack pine, Site 5 willow) or decreased (Site 6 tamarack) use by hare may have been due to subtle differences (site age, vegetation composition and structure, location) between these sites and the other sites at which these species were sampled. Year-round use of these sites by hare may have been encouraged by the increased abundance of ground cover plants usually eaten during summer, and the freer movement afforded by the moderate density of trees and shrubs at Sites 3 and 5. The high density of trees at Site 6, relative lack of summer foods, and use of this site only during winter might have contributed to the lower use of tamarack browse.

Hare appear to have optimized their nutrient intake by selecting the most digestible and nutritious browse. The selection and use of tree browse by hare was also affected by its availability. The limited availability of food in winter was reflected by the increased use of woody browse when snow was deepest. There is also evidence that when hare were able to reach the higher strata of trees and shrubs, they ate the most succulent browse with the greatest concentrations of many nutrients. The concentrations of several nutrients in the browse, and its digestibility, were shown to vary. This variability occurred mainly between species but in several instances occurred in browse from different heights or diameter classes. It appeared that the amount of potential browse, its utilization by hare, digestibility, and nutrient content were interrelated.

CONCLUSIONS

The amount of potential hare browse differed between tree species and increased with sampling height. Utilization of tree browse by hare also increased with height. Hare did not appear to browse trees of one particular diameter class more heavily than other ones, nor did the rank of potential tree browse vary between diameter classes. In many instances, the digestibility and nutrient content of trees and/or shrubs differed between species. These differences were less apparent between browse from the various sampling heights and diameter classes.

The results (Tables 1-6) suggest that even though hare and their browsing were affected by several ecological factors, they still appear to have optimized their nutrient intake by the selective use of available browse. Tamarack browse was less digestible than browse from other trees but appears to have offered hare the best nutrient combination of all browse species available. Since it is advantageous for herbivores to select browse from several species (Klein 1970), it is possible that hare benefitted by ingesting browse of other species that grew nearby the tamarack refugia and were more digestible or contained more of specific nutrients. If any of these other species contained toxins, these toxins would likely have been diluted by the non-toxic species. The increased use of browse from the higher strata is further evidence of browse selection by hare, especially if one considers the short period during which this browse is available, its greater succulence, and its elevated concentrations of P and K. Snow depth was an important factor in determining which browse was available to hare but they appeared to have selected to most nutritious browse from among the strata that were accessible.

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APPENDIX 1

STUDY AREA

APPENDIX 1

Study Area

The sites shown in Figure 1 have been described separately in order of increasing soil humidity. Each site has been described in general to give the reader an understanding of its floristic composition. Consult Table 1.1 for a more detailed list of species and their abundance.

Site 1: Glandular birch heathland -- clumps or clump-aggregates of glandular birch spotted this level moraine. A scattering of fifty-year-old jack pine grew in the open patches between clumps. The birch clumps were 1.0 - 1.5 m tall while the jack pine were 6 - 9 m tall and over 10 cm in diameter.

Although birch clumps were the main component of the understory, several ericaceous species as well as tamarack saplings were also present. The ground cover consisted of a mat of reindeer moss (Cladonia sp.) (Cunningham 1974), with several species of forbs. Twenty percent of this cover was littered with deadfalls. This ground cover was underlaid by a thin (4 cm) mat of humus which was in turn underlaid by medium coarse sand and the occasional rock.

Site 2: Dense regeneration of jack pine -- this stand was the densest secondary succession sampled. Trees in this mesophytic stand were up to 2.5 m tall and 29 years old.

The understory was heavily browsed, with many branches stripped of needles. Chlorotic needles may have indicated deficiencies due to leaching. This is probable since this level moraine had sandy soil.

The ground cover consisted of reindeer moss, ericaceous plants and a few willow (Salix planifolia). Deadfalls, which covered 10% of the lichen (Cladonia sp.), were scattered amongst the ground cover.

Site 3: Jack pine sapling stand -- a 27-year-old stand of mesophytic jack pine saplings dominated this site. This site was not as dense as Site 2, but was floristically similar.

The understory had a sparse growth of ericaceous plants. A mixture of ericaceous and forb species grew on the lichen mat which was littered with several deadfalls.

Site 4: Mature jack pine -- this stand was dominated by 33-year-old jack pine. Mixed with these pine were several black spruce of varied ages. Cover density was approximately 60% but dropped as low as 30% in adjacent areas. The jack pine and black spruce were up to 5.0 m and 3.5 m tall, respectively.

The understory was sparsely vegetated. The pine was defoliated between ground level and 1 - 2 m. This may have been due to browsing, soil deficiencies or both, since chlorotic needles were evident and willow and Labrador tea (Ledum groenlandicum) were stunted.

Lichen, on fine sandy soil, dominated the ground cover. Needles littered 25 - 30% of the lichen mat while deadfalls covered an additional 15%. Blueberry (Vaccinium sp.) and the occasional basidiomycete were the only other flora at this site.

Site 5: Mixed coniferous regeneration -- this was a secondary succession of jack pine and black spruce which grew on a flat gravelly sand moraine. This mesic site was located between a willow-alder bottomland and Rivière du Castor. The approximate age of this sere was 40 - 45 years.

The 5 - 8 m tall jack pine, and black spruce up to 4.5 m tall, formed a moderately dense (60%) canopy in a 65% - 35% mix. The understory, dominated by young spruce, supported a variety of ericaceous plants. Ground cover consisted of several forb species on a continuous lichen mat.

Site 6: Hygrophytic conifers -- this hygric site of 25-year-old black spruce and tamarack grew on a slight slope. The loamy soil at the crest of the slope graded into a clayey soil at the base.

These trees, up to 6 m tall, covered 80% of this site. Much of this cover was saplings in the understory. The rest of the understory was composed of Labrador tea and shrubs.

As the soil graded from loam to clay, the ground cover changed from lichen to a carpet of Sphagnum sp. Several herb species were present but scattered. Needles littered the lichen.

Site 7: Riparian conifers -- this mixed stand of tamarack

(60%) and black spruce (40%) grew on a sandy clay between a small lake and the roadside. Part of the ground cover had been scalped, exposing the soil. Trees and shrubs occurred in patches over 70% of the site.

Six-meter tall conifers formed the canopy. The understory of treed patches had saplings and some shrubby plants. The opposite was true of the understory in shrubby patches. The scant ground cover was composed of grasses, sedges and some sphagnum.

Site 8: Hygrophytic tamarack -- this site, at the base of a hill, supported tamarack, black spruce, and several species of shrubby plants up to 39 years old. The majority of trees were 3 - 5 m tall, although some reached 7 m in height. Fifty percent cover was provided by these trees.

The understory consisted of conifers and shrubby plants. Ground cover was dominated by hummocks of sphagnum with a few lichen patches. Several forbs and tufts of grass grew on these hummocks. More shaded spots supported ascomycetes and basidiomycetes.

Site 9: Willow-alder association -- this association of willow (*Salix bebbiana*) and alder (*Alnus rugosa*) inhabited an overgrown stream bed and was about 10 m wide. A thick layer of silt covered the stream bottom and was in turn covered by a meter of sphagnum. The age was estimated at 35 years, assuming the site burned at the same time as the trees on both sides of the ravine.

The canopy afforded 90% cover, with the willow contributing 60% of this and the alder 40%. The understory had roughly the same composition, except that Viburnum edule was scattered throughout.

The ground cover was dominated by sphagnum. Grasses, sedges and several forbs grew amidst the shrubs.

TABLE 1.1 Floristic Composition of Sites. (Amounts expressed as % cover)

Species (plants)	Site 1	2	3	4	5	6	7	8	9
Canopy									
Alnus rugosa									36
Betula glandulosa									
Larix laricina						36	42	30	
Picea mariana				5	21	44	28	20	
Pinus banksiana	20	80	60	55	39	5			54
Salix bebbiana									
Understory									
Alnus rugosa						2			28
Betula glandulosa	25					10	8	6	
Kalmia angustifolia	20				1				
Larix laricina	3					20	30	15	
Ledum groenlandicum	10	5	3	4	5	15	12	2	
Picea mariana				5	20	25	20	20	
Pinus banksiana		55	70		5				
Salix planifolia		2		2	3				
Vaccinium angustifolium	17	12	10	15	20				
V. myrtilloides						3			
V. oxycoccus						2			
V. uliginosum					1				9
Salix bebbiana						16		4	38

TABLE 1.1 Cont'd.

Species (plants)	Site 1	2	3	4	5	6	7	8	9
Ground Cover									
Ascomycetes								1	
Basidiomycetes				1				2	
Caltha palustris									2
Carex aquatilis							5		6
Chiogenes hispidula						2			
Cladonia sp.	96		96	65	88	35		10	
Cornus canadensis	10	98	5		8				
Deschampsia cespitosa							5	5	3
Epigaea repens	25		8		10				
Epilobium angustifolium					1			1	
Equisetum arvense						1			3
Linnaea borealis					12				
Lycopodium sp.	1				4				
Maianthemum canadense			2		18				
Petasites palmatus					2	5	8	2	8
Potentilla tridentata	10				22				
Rubus chamaemorus						3			10
Smilacina trifolia									2
Sphagnum sp.						65	42	85	80
Polytrichum sp.				2					

TABLE 1.2. Soil pH and concentrations of elements at sites sampled[1,2]

Site No.	pH	P	K	Ca	Mg	Fe	Mn
1	5.00	55.00	8.00	80.00	6.00	3.20	0.12
2	6.90	71.00	20.00	320.00	20.00	9.68	1.84
3	4.80	58.00	15.00	90.00	6.00	4.48	0.20
4	6.00	65.00	26.00	80.00	6.00	13.92	0.48
5	5.30	48.00	10.00	70.00	5.00	3.72	0.15
6	5.50	63.00	160.00	860.00	148.00	21.76	2.54
7	N/A	N/A	N/A	N/A	N/A	N/A	N/A
8	5.60	73.00	36.00	500.00	42.00	16.80	0.88
9	5.50	45.00	125.00	2000.00	190.00	30.00	N/A

[1] Concentrations measured in parts per million (ppm).

[2] N/A - information not available.

APPENDIX 2

METHODS

APPENDIX 2

Determination of Nutrient Concentrations

The determination of elemental concentrations in browse was performed in duplicate on batches of 15 samples, plus a blank containing only the reagents used in wet digestion. The automated analysis used the Auto Analyzer (Technicon Ltd.) system which consisted of sampler, pumping unit, colorimeter, flamephotometer, atomic absorption (AA) spectrophotometer (Perkin-Elmer model 290) and three chart recorders. The sampler and pumping unit were used for analysis of all major elements. The colorimeter was used for N (as ammonia) and P analysis. The flame photometer was used for Ca and K analysis while AA spectrophotometry was used for Mg determinations. The ammonium molybdate indicator for P did not develop properly due to excess acidity. This was easily remedied by changing the deionized distilled water and sampling tubes so that they yielded the final dilution of 50:1 as suggested by Thomas et al. (1967). Microelemental concentrations in the digests were determined on a Perkin-Elmer model 303 AA spectrophotometer using standard techniques.

The forage fiber analysis methods (Goering and Van Soest 1970) used to determine concentrations of tissue fractions and the digestibility of the browse samples consisted of three tests: neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL). Samples were run in duplicate as well as standards of known composition which served as controls.

Statistical Methods

Analyses of Variance

F-statistics were determined in the first part of the analysis of variance based on a three-factor repeated measures model (Winer 1971: 539-559). The design of this study was not balanced and so slight modifications were made. The model used is shown below:

$$Y_{ijml} = u+n_i+e_{j(i)}+g_m+ng_{im}+e_{jm(i)}+k_l+kn_{il}+e_{jl(i)}$$

where Y_{ijml} was the j^{th} site on the i^{th} species, measured at diameter m and height l. The error terms are denoted by e's.

u	the overall mean
$e_{j(i)}$	error term associated with a species' variability from site to site
$e_{jm(i)}$	error term associated with the variability of a species of given diameter from site to site
$e_{jl(i)}$	error term associated with the variability from site to site at a given height
n_i	parameter associated with the i^{th} species
g_m	parameter associated with the m^{th} diameter
k_l	parameter associated with the l^{th} height
j	index associated with site
n	number of sites, assumed constant for a species

The following additional assumptions were necessary:

1) species, diameter, and height error terms were independent

2) error was identically distributed with mean zero and a constant variance

3) errors were normally distributed

If the design was balanced, within-site errors would have been easily calculated. The model was not balanced and so SAS type IV sums of squares were used (Barr et al. 1976). Possible reasons for significant F-statistics were then found from an examination of the marginal means. Means were differentiated by using the Waller-Duncan multiple range test, which included Kramer's adjustment due to the unbalanced design (Kramer 1956, in Barr et al. 1976). The tests were performed on all variables for all main effects.

Descriptive Use of Regression Analysis

Multiple regression models were developed to describe browse potential and utilization in terms of the apparent digestibility and nutrient composition variables. The model used to estimate the browse potential and utilization of trees differed slightly from that used for shrubs.

The main effects (species, diameter, and height) were included in the tree model so as to account for their effects on browse potential and utilization. Interactions of these main effects were not included in the model since they were of limited significance in the previous analyses and it was desirable to minimize the number of descriptive variables. Dummy variables were created for site, species, and diameter and used in the description of browse potential and utilization (Chatterjee and Price 1977). The species and diameter dummy variables were forced (i.e., all descriptive models included these terms) into the tree model. For each effect there were as many dummy variables as there were degrees of freedom and hence, singularity was avoided. There was no height dummy variable in the tree model. Instead, the means of potential and utilization were presumed describable in terms of a constant, β, times height, so that a linear function with estimated regression coefficient was used.

Shrubs had no diameter effect and the height effect was omitted from the model since it was thought to be less important.

After having described browse potential and utilization in terms of the main effects in both models, apparent digestibility and nutrient composition variables, if significant, were allowed to enter the models. In this manner, the models with the best sets of descriptive variables that had the best R^2 statistics were chosen. Only linear terms were used. In developing the tree and shrub models it was impossible to compute all possible models and so a stepwise procedure (Barr et al. 1976; Chatterjee and Price 1977) was used. The R values were adjusted using the method outlined by Zar (1974: 260) and a test for interaction of the independent variables was also performed. The structure of the residuals was examined, using criteria outlined by Chatterjee and Price (1977), and showed no significant deficiencies existed in the final models.

APPENDIX 3

ANALYSIS OF VARIANCE TABLES

TABLE 3.1. Relationship of tree sampling factors (species, height, and diameter class) to browse potential, digestibility, nutrient content, and utilization by hare.

	POTENTIAL (17)[1]		UTILIZATION (17)		% DM[4][45°C](16)		% DM[100°C](16)	
	df[2]	Prob.[3]	df	Prob.	df	Prob.	df	Prob.
Species	2	0.02	2	0.34	2	0.07	2	0.09
Site (species)	3	-	3	-	4	-	4	-
Diameter	3	0.37	3	0.16	3	0.54	3	0.49
Species*Diameter	6	0.64	6	0.56	6	0.54	6	0.44
Site*Diameter (species)	5	-	5	-	5	-	5	-
Height	2	<0.01	2	<0.01	2	<0.01	2	<0.01
Species*Height	3	0.10	3	0.12	4	0.15	4	0.16

	% APPARENT DIGESTIBILITY (20)		CELLULOSE (20)		HEMICELLULOSE(20)		CELL SOLUBLES (20)	
	df	Prob.	df	Prob.	df	Prob.	df	Prob.
Species	2	<0.01	2	0.16	2	<0.01	2	<0.01
Site (species)	4	-	4	-	4	-	4	-
Diameter	3	0.23	3	0.36	3	0.62	3	0.23
Species*Diameter	6	0.07	6	0.34	6	0.47	6	0.07
Site*Diameter (species)	7	-	7	-	7	-	7	-
Height	2	0.07	2	0.28	2	0.29	2	0.07
Species*Height	4	0.06	4	0.07	4	<0.01	4	0.06

TABLE 3.1. Cont'd..

	CRUDE PROTEIN (20)[1]		CRUDE LIGNIN (20)		PHOSPHORUS (20)		POTASSIUM (20)	
	df[2]	Prob.[3]	df	Prob.	df	Prob.	df	Prob.
Species	2	0.28	2	<0.01	2	0.58	2.	0.96
Site (species)	4	-	4	-	4	-	4	-
Diameter	3	0.02	3	0.37	3	0.41	3	0.77
Species*Diameter	6	0.02	6	0.35	6	0.29	6	0.16
Site*Diameter (species)	7	-	7	-	7	-	7	-
Height	2	0.06	2	<0.01	2	0.02	2	<0.01
Species*Height	4	0.42	4	0.09	4	0.91	4	0.36

	CALCIUM (20)		MAGNESIUM (20)		IRON (20)		MANGANESE (20)	
	df	Prob.	df	Prob.	df	Prob.	df	Prob.
Species	2	<0.01	2	0.52	2	0.43	2	0.04
Site (species)	4	-	4	-	4	-	4	-
Diameter	3	<0.01	3	0.93	3	0.91	3	0.27
Species*Diameter	6	<0.01	6	0.77	6	0.80	6	0.06
Site*Diameter (species)	7	-	7	-	7	-	7	-
Height	2	0.19	2	0.88	2	0.06	2	0.15
Species*Height	4	0.90	4	0.82	4	0.08	4	0.32

1 Error degrees of freedom
2 df Source degrees of freedom
3 Probability of a greater F value (P>F<0.45)
4 DM - Dry Matter

SPECIES: black spruce, jack pine, and tamarack
DIAMETER: 1, 0-1.0 cm; 2, >1.0-2.5 cm; 3, >2.5-5.0 cm; 4, >5.0 cm.
HEIGHT: 1, 0-40 cm; 2,>40-80 cm; 3, >80 cm.

TABLE 3.2. Relationship of shrub sampling factors (species and height) to browse potential, digestibility, nutrient content, and utilization by hare.

	POTENTIAL (5)[1]		UTILIZATION (5)		% DM[4][45°C](6)		% DM[100°C](6)	
	df[2]	Prob.[3]	df	Prob.	df	Prob.	df	Prob.
Species	2	0.43	2	0.11	2	0.16	2	0.15
Site (species)	4	-	4	-	4	-	4	-
Height	2	0.07	2	0.13	2	0.10	2	0.12
Species*Height	3	0.06	3	0.76	4	0.10	4	0.14
	APPARENT DIGESTIBILITY (6)		CELLULOSE (6)		HEMICELLULOSE(6)		CELL SOLUBLES (6)	
Species	2	0.02	2	<0.01	2	0.03	2	0.02
Site (species)	4	-	4	-	4	-	4	-
Height	2	0.06	2	0.02	2	0.75	2	0.06
Species*Height	4	0.62	4	0.91	4	0.70	4	0.62

TABLE 3.2. Cont'd.

	CRUDE PROTEIN (5)[1]		CRUDE LIGNIN (6)		PHOSPHORUS (6)		POTASSIUM (6)	
	df[2]	Prob.[3]	df	Prob.	df	Prob.	df	Prob.
Species	2	0.19	2	<0.01	2	0.03	2	0.02
Site (species)	4	-	4	-	4	-	4	-
Height	2	0.05	2	0.05	2	0.45	2	0.08
Species*Height	4	0.31	4	0.14	4	0.42	4	0.08

	CALCIUM (6)		MAGNESIUM (5)		IRON (6)		MANGANESE (6)	
	df	Prob.	df	Prob.	df	Prob.	df	Prob.
Species	2	0.53	2	0.09	2	0.02	2	0.39
Site (species)	4	-	4	-	4	-	4	-
Height	2	0.02	2	0.70	2	0.81	2	0.35
Species*Height	4	0.05	4	0.30	4	0.56	4	0.14

1 Error degrees of freedom
2 Source degrees of freedom
3 Probability of a greater F value (P>F<0.05)

SPECIES: alder, dwarf birch, and willow
HEIGHT: 1, 0-40 cm; 2,>40-80 cm; 3, >80 cm.