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BODY CONDITION AND FOOD RESOURCES OF WHITE-TAILED DEER ON
ANTICOSTI ISLAND, QUEBEC

University of Alaska

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BODY CONDITION AND FOOD RESOURCES OF WHITE-TAILED DEER
ON ANTICOSTI ISLAND, QUEBEC

A
THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

Jean Huot

Fairbanks, Alaska

December 1982

BODY CONDITION AND FOOD RESOURCES OF WHITE-TAILED
DEER ON ANTICOSTI ISLAND, QUEBEC

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ABSTRACT

A study was conducted on relationships between seasonal variation in body condition of white-tailed deer (*Odocoileus virginianus borealis*) and food resources on Anticosti Island, Quebec.

Results of the vegetation surveys show that food resources are extremely limited in abundance and variety as snow covers the ground vegetation in winter. Excluding *Picea spp.*, *Abies balsamea* is by far the most available browse species, accounting for approximately 95% of the available browse biomass in February and March. Analysis of rumen contents suggests that this species accounts for 98.5% of the browse eaten by inland deer between February and mid-April. Lichens account for 9.5% of the dry weight of the rumen content at that time. During the snow-free period, forbs dominate the diet.

Both sexes and all age classes show a well-defined pattern in body composition with maximum fat levels occurring between September and mid-December and minimum levels between mid-April and mid-June. Fat reserves (ether extraction) in fawns vary from a maximum of 15.3% in

fall to a minimum of 0.2% in spring as they lose 41% of their ingesta-free body weight. Composition of the winter body weight loss varies according to sex and age. Fat represents 31.7 to 58.9% of the loss and protein 17.8 to 23.0%. Water is inversely correlated with fat, and ash is a minor part of the loss. The caloric content of the weight loss on an ingesta-free weight basis is lowest in 3-year-old males (3.95 kcal/g) and highest in 2-year-old females (6.86 kcal/g).

It is concluded that, in association with their low productivity in summer, Anticosti deer must base their winter survival strategy primarily on energy conservation and secondarily on food acquisition during that season.

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INTRODUCTION

The white-tailed deer (*Odocoileus virginianus*) is the most widely distributed wild ungulate of the New World. Its behavioral and physical characteristics are responsible for its success in the most varied climates and habitats from the tropical lowlands of South America and Panama to the boreal forests of Canada. Its efficiency in the selection of nutritious forages from a wide variety of plant species and habitats and its high reproductive potential enabled it to take rapid advantage of the early successional stages of vegetation created as white settlers altered the woodlands of the north. However, as the deer expanded its distribution into the northern forests it had to cope with deeper snows and longer winters. This small, nervous, and fine-legged animal was now invading the range of the long-legged and powerful moose and the large-hoofed and cold-resistant caribou.

Among the strategies that must be used by herbivores inhabiting the northern environment, one of the most important is the ability to take advantage of the abundance of food in summer and to live on a minimum budget in winter. In the northern part of its distribution, the

potential winter range of deer is less than 10% of the summer range in surface area, the quantity of food available is probably less than one per cent as compared to summer food and the quality of the food is also greatly reduced. For some species, the solution to such seasonal extremes in resources availability has taken the form of hibernation or dormancy. However the accumulation of fat reserves during the period of moderate temperatures and high food abundance and the reduction of basal and active metabolism associated with the utilization of reserves are not restricted to true hibernators such as the woodchuck (*Marmota monax*) or animals capable of long periods of *stuporous* sleep (*sensu* Kayser, 1965), such as the black bear (*Ursus americanus*). Many wild ruminants also show similar cycles in their physiology. Although part of this cyclic pattern may be imposed directly by the low availability and poor quality of food in winter as opposed to summer conditions, it appears that many species have their own internal mechanisms controlling these cycles.

The studies on growth of white-tailed deer in captivity by French et al. (1955) and by Silver and Colovos (1957) and of four races of black tailed deer (*Odocoileus hemionus*) by Wood et al. (1962) were the first indications that these cyclical patterns could be independent of food availability and quality. Even when kept on constant rations, these species showed a weight stasis or decline in winter followed by a rapid increase in summer. Winter weight losses increased during each successive winter of life and were more pronounced in males (Nordan et al. 1968; Bandy et al. 1970). The weight losses for adult males of four

rates of *O. hemionus* ranged between 18% and 31% of the maximum fall weights computed after the equations given by Wood et al. (1962). A similar growth pattern has been reported for caribou (*Rangifer tarandus*) in captivity (McEwan and Wood 1966; McEwan 1968), but the cyclical pattern in muskoxen (*Ovibos moschatus*) (McEwan 1975) and Rocky Mountain bighorn sheep (*Ovis canadensis*) (McEwan 1975; Chappel and Hudson 1978) is less pronounced.

In the wild, although occasional severe cases of malnutrition and deteriorated physical condition are reported in wild ungulates, generally, weight losses do not exceed those reported from animals kept in captivity. In captive male caribou the loss of body weight during the reproduction season varies from 13% to 36% while in wild species the difference between peak summer and minimum winter weights increases gradually from 8% at 5 months to 36% at 5 years of age according to McEwan (1975). According to the weights given by Franzmann et al. (1978) for Alaskan moose during winter, adult wild males and females loose close to 30% of their autumn weight. Mautz (1978b) suggests that it is common for white-tailed deer to loose 20% to 30% of their weight in their first winter while Ullrey et al. (1970) estimate that a loss of 23% would approach the critical point for the life of an adult doe. In red deer Mitchell et al. (1976) report an over winter weight decline of 31.1% for adult stags, 16.8% for hinds unaccompanied by calves, 14.4% for milk hinds and relatively constant weights for calves. It seems apparent that the winter weight loss phenomenon is not merely a consequence of lower plane of nutrition in winter but is also an innate capacity to

utilize reserves accumulated during the super abundance of resources in summer. This is also confirmed by the fact that animals maintained on a low plane of nutrition in summer do not experience the pronounced characteristic weight loss of deer on a high plane diet or in the wild (French et al. 1955; Nordan et al. 1968).

Closely associated with the annual cycle in body weight in northern ungulates is a cycle in voluntary dry matter intake. This pattern has been best documented in captive cervids (French et al. 1955; Silver and Colovos 1957; Wood et al. 1962; Nordan et al. 1968; Bandy et al. 1970) and is also known to occur in bighorn sheep (Chappel and Hudson 1978). French et al. (1955) were the first to suggest that the decrease in food consumption and the consequent weight loss was an "inherited adaptation to winter shortage of food normally experienced by deer in the wild." This interpretation is now generally accepted and it is believed that the bases of this phenomenon are physiological mechanisms that permit both laying down of adipose tissue in summer when there is a surplus of nutrient energy and the conservation of energy in winter.

Seasonal change in basal metabolic rate is apparently the primary mechanism controlling the seasonal cycle in body weight and energy expenditure. Silver et al. (1969, 1971) reported that the fasting metabolic rates of white-tailed deer were over 80% higher in summer than in winter. McEwan and Whitehead (1970) reported similar findings for caribou, Nordan et al. (1970) for young black-tailed deer, Weiner (1977) for roe deer, Segal (1962) (in Weiner 1977) for Siberian reindeer, and Chappel and Hudson (1978) for bighorn sheep. However, in

red deer despite the presence of a cycle in body condition and weight (Mitchell et al. 1976), Brockway and Maloiy (1967) and Maloiy et al. (1968) did not detect any seasonal change in the metabolic rate of this species.

Although most authors associate these seasonal cycles with changes in the activity of the endocrine system, the relative importance of the different hormones and the role of external factors such as food quality and temperature is not clearly understood. In most cases for cervid males, the rut seems to mark the timing point, the food intake sharply decreases and the weight loss during this period may exceed 30%, this led McEwan (1975) to stress the importance of testosterone level in the annual cycle of body weight. Yousef and Luick (1971) did not find any significant seasonal change in the thyroid indices and concluded that the thyroid gland appears to play a relatively minor role in acclimatization of reindeer to the Arctic. Yousef et al. (1971) reported, however, that winter acclimatization in this species was accompanied by increased adrenocortical activity. In white-tailed deer, Silver et al. (1969, 1971) suggested that the most important factors in seasonal variation in heat production were coat change and endocrine activity. These authors with Ozoga and Verme (1970) also indicated that there was a close agreement between the cycle in body weight, food intake and metabolism and the variation in thyroid gland weight and activity reported by Hoffman and Robinson (1966). Seal et al. (1972) concluded that the normal winter hypothyroid state in deer can be intensified by nutritional deprivation. Similar changes in thyroid activity in beaver (*Castor canadensis*) were interpreted as an hibernator pattern in a non-

hibernator species by Aleksasuk and Cowan (1969). They stressed the difference between this intrinsic rhythm and the increased thyroid activity in winter noted by several researchers on other non-hibernating rodents when there is an increased thermoregulatory demand. The similarities in the seasonal physiological rhythms of the white-tailed deer and hibernators have also been recognized by Sauer (1973) and Moen (1978).

The value of this cycle has been recognized by many researchers as an adaptation to maintain a positive energy balance during periods of food shortage under wild conditions. Fat has been readily identified as the main source of seasonal variation in the body weight and its value as a source of energy became evident. For some researchers body weight changes after maturity were synonymous with fat deposition, and the degree of fatness became an index of physical condition. The level of fat reserves appeared to be a good indication of the recent energetic history of the animal and its ability to cope with its future needs. Therefore a series of methods to assess rapidly body fat reserves were designed for wild ungulates. However very few studies have attempted to explore the exact nature of the changes in body weight during the year and the exact amount of the constituents gained or lost over a given season. Even seasonal weight changes have not been quantitatively examined to any extent under wild conditions. The most detailed study on these aspects was conducted on Scottish red deer (Mitchell et al. 1976), the authors followed the cycle of body condition of well defined classes of animals, utilizing body weights, fat indices, and weight of selected organs. Dauphiné (1976) studied the effect of seasonal changes

on the growth and fat reserves of a large number of caribou of the Kaminuriak herd and Bear (1971) described the seasonal variations of fat levels in Colorado pronghorns. Holl et al. (1979) studied the relationship between the seasonal variation of the energy reserves in California mule deer does and the composition of their diet. Caughley (1970, 1971) related seasonal levels of fat indices to the demographic performances of Himalayan thar (*Hemitragus jemlahicus*) and of the red deer in New Zealand. These studies mainly used body weight and fat indices proposed by Riney (1955) as indicators of body condition.

Estimates of the fat content of the whole body or of the eviscerated carcass in wild ungulates are not frequently encountered in the literature. Anderson et al. (1969, 1972) related several fat indices to the seasonal fat content of the eviscerated and skinned carcass of both sexes of mule deer. Øristsland (1970) estimated the total fat reserves of a male reindeer in fall. In roe deer, Weiner (1973) investigated the body composition and caloric value of eight individuals killed in winter, these estimates were used in the study of the energy budget of this species by Drozdz et al. (1975) and Weiner (1975). The first study of the body composition of white-tailed deer was conducted by Robbins et al. (1974b). They estimated the amount of water, fat, protein and ash present in the ingesta-free body of captive deer killed from June through October and they calculated the total caloric value of these animals. More recently, Finger et al. (1981) estimated the seasonal variation of the total amount of body fat of free ranging deer in South Carolina. Although the determination of body fat provides one of the best simple indices of energy balance (Cameron et al. 1975) and

of general physical condition (Hammond 1942; Riney 1955; Smith 1970), the estimation of the total amount of fat in the animal is usually not required and fat indices are commonly used successfully for the appraisal of the condition of wild ungulates (Harris 1945; Cheatum 1949; Riney 1955; Ransom 1965; Anderson et al. 1969, 1972a; Hesselton and Sauer 1973; and many others). Body weights frequently have also been used as condition indicators (Park and Day 1942; Severinghaus 1955; Taber and Dasmann 1958; Roseberry and Klimstra 1975). However, Klein (1964) pointed out the problem of discriminating the effect of genetic variations from the effect of the range quality on body weight especially with small sample sizes and suggested the use of skeletal ratios. The apparent stability of the weight despite considerable changes in body composition due to the inverse relationship between fat and water content as reported in reindeer (Cameron and Luick 1972; Cameron et al. 1975) may also limit the use of body weight as an indicator. The use of blood parameters as an index of physical condition has been investigated by many researchers during recent years as baseline values have become available (LeResche et al. 1974a; Franzmann and LeResche 1978; Seal et al. 1978). Recent studies on white-tailed deer fawns in captivity suggest that the state of nutrition clearly affects the size of the thymus gland despite a normal seasonal cycle (Ozoga and Verme 1978). These studies have also shed more light on the effect of protein and energy content on body growth and lipogenesis (Verme and Ozoga 1980a, 1980b).

These indirect approaches to the assessment of the relative quality of the range are valuable indicators and are usually more

appropriate than a study of the vegetation itself as they integrate the quality of the vegetation with the performance of the animal in the environment. However at the northern limits of the white-tailed deer's range the nitrogen and energy balance during critical periods and on an annual basis (Seal et al. 1978; Mautz 1978b; Moen 1978; Verme and Ozoga 1980a, 1980b) are often limiting factors, therefore the fat and protein reserve cycle must be quantified in relation to the environmental conditions in order to understand the survival strategy of deer.

The present study is part of a larger research program on the ecology of deer of Anticosti Island. Its main objectives were to describe the seasonal body condition cycle and to estimate its role in the survival and the performance of this population. Other related studies dealt with the quality of the summer range, the reproductive performance and dynamics of the population and the winter activity budget.

In the present work on the seasonal variations of the condition of deer in relation to the resources, the following aspects were considered:

1. The first part deals with the food resources of the island and with the general characteristics of the habitat. Special attention has been given to estimation of the food availability and quality during winter to assess the importance of the nutritional stress that the animals face during this season.

2. In order to understand how the deer exploited the food resources a detailed analysis of the diet was performed and the protein

content of both rumen contents and material eaten were estimated throughout the year. This approach gives a better idea of the quality of the food resources than a survey of the vegetation as it includes the resource and the ability of the animal to use it.

3. The seasonal variation in total weight of the deer and in the weight of several organs and glands as well as in the composition and caloric content of the live animal were analyzed in relation to the first two aspects. The survival value of body weight changes can be clearly understood only when the variations of each constituent of the body are known and can be correlated to changes in total energy reserves. Moreover it is important to know how much the weight of the internal organs as well as the carcass itself are influenced by this annual cycle.

The research helps to understand better the energetic aspects of white-tailed deer ecology but it also explores an important aspect of the adaptability of the wonderful animal that is the white-tailed deer.

ANTICOSTI ISLAND

Known as a large, remote, private estate open only to selected visitors for nearly 300 years, Anticosti Island became accessible to the general public after its purchase by the Quebec Government in December 1974. Named the *Gulf graveyard* because of the numerous ship wrecks that occurred along its coasts, it is also reputed as a *hunting and fishing paradise* and has been a source of curiosity for many years. Despite its relative inaccessibility Anticosti has been the subject of detailed biogeographical descriptions (Huard 1897; Guay 1902; Schmitt 1904; Mackay 1979; McCormick 1979) and, although there are as many descriptions of Anticosti as there are reasons to describe it, all the recent accounts place heavy emphasis on the presence of the introduced white-tailed deer population. The location of Anticosti Island with respect to the general white-tailed deer distribution in Quebec and in North America is shown in Figure 1. The presence of high densities of deer at the extreme limit of its range is in itself intriguing and presents a unique opportunity to study the adaptability of this widespread species.

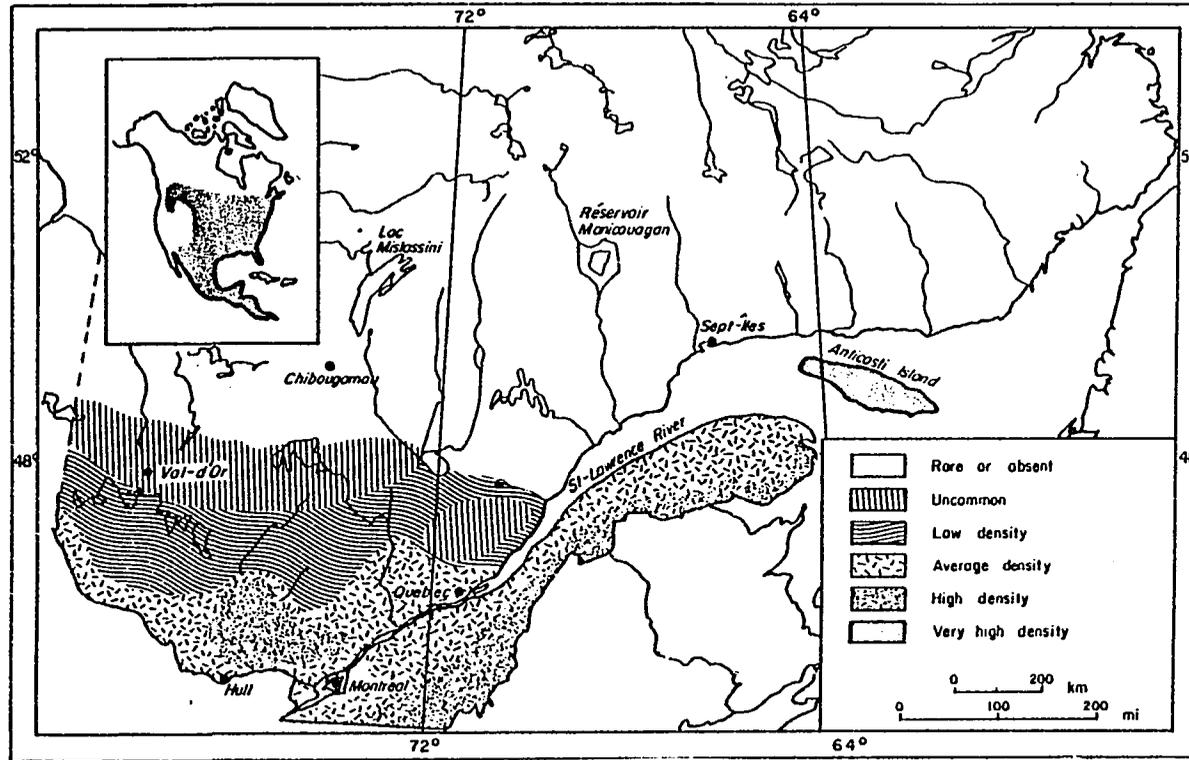


Figure 1. Location of Anticosti Island with respect to the distribution of white-tailed deer in Quebec and North and Central America, (modified after Huot 1973)

General Characteristics

Anticosti Island is located in the Gulf of St. Lawrence between latitudes 49°03' and 49°55'N and longitudes 61°45' and 64°35'W. It is separated from the mainland to the north by the Jacques-Cartier Passage, 35 km of sea water cooled by the Labrador currents coming from the north; the nearest mainland to the south is the Gaspé Peninsula, some 70 km away. The island extends in a general north-west and south-east direction, with a length of about 220 km, and a breadth, in its broadest part, of about 56 km, covering 7,900 km². The northern coast presents cliffs ranging from 60 to 120 m in height, cut in places by deep canyons. The interior of the island consists of a series of plateaus gradually descending to the south shore. The eastern third of the island is mostly low and swampy, and characterized by the presence of extensive peat bogs. The underlying bedrock is mainly Ordovician limestone in the north-west half of the island and Silurian limestone and shales in the south-east half (Canada 1957). Marine deposits cover the lower areas, about two thirds of the total, while glacial till is found at higher altitudes (Legget 1961). The soils have not been studied extensively but the most important types have been identified. Brown soils, highly podzolized, are widely distributed in areas covered by fine deposits and are associated with a good forest productivity. Podzols are characteristic of coarser deposits and are mainly associated with moraines. On the very fine marine deposits, gleisols have developed and when adequately drained, these are very productive (Ministère des Terres et Forêts 1974).

The human population is concentrated in only one permanent village, Port Menier with 235 residents in 1974 (Ministère des Terres et Forêts 1974). More than 1,500 km of roads give access to the interior of the island. A main road runs from the village to the north-east coast of the island and many secondary roads go to the hunting and fishing camps. Another series of innumerable logging roads can also be used for hunting. Only the southeastern portion of the island is not accessible by roads (Figure 2).

Climate

The climate of the island is considered sub-arctic (Canada 1957), its main characteristics are summarized in Table 1 and Figure 3. The summers are cool and short due to the maritime influence and the growing season does not exceed 150 days (Wilson 1971). The maritime influence is most apparent on the number of growing degree-days (1,844) which is just above half of the figure for Montreal (3,600). The winters are long, 156 days, but the temperatures are usually as mild or even milder than within the rest of the deer range in Quebec. The mean temperature of the coldest month (February) is -11.0°C at Port Menier.

The total annual precipitation averages 836 mm, the proportion of it falling as snow reaches 43 per cent at the western extremity of the island but decreases to 27 at the east point (Ministère des Terres et Forêts du Québec 1974). The total snowfall is less than throughout most of the deer range in Quebec averaging only 250 cm (Villeneuve 1967), this characteristic is however highly variable from year to year.

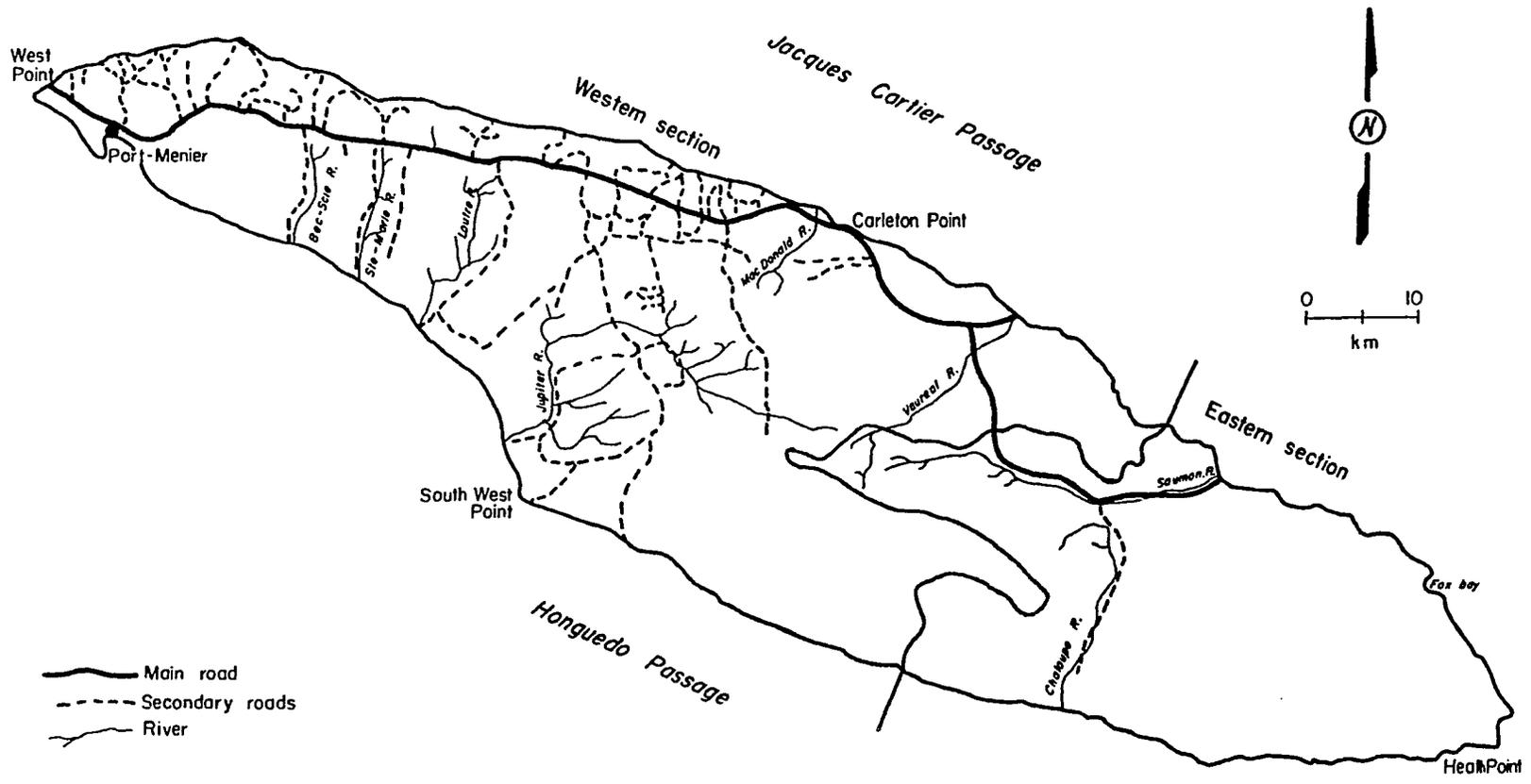


Figure 2. Places mentioned in the text and main road system

TABLE 1. Main characteristics of the climate of Anticosti Island as compared to other locations within the deer range in Quebec

Climatic Characteristics	Anticosti ¹	Quebec	Montreal
Mean July Temperature ²	15.7°C	19.9°C	21.4°C
Mean January Temperature ²	-10.2°C	-10.6°C	-10.1°C
Length of Winter ³	Nov 12-Apr 17 156 days	Nov 15-Apr 5 140 days	Nov 20-Mar 21 120 days
Growing season ³	May 16-Oct 12 150 days	Apr 25-Oct 21 180 days	Apr 15-Oct 31 200 days
Growing Degree-Days ³	1,844	3,000	3,600
Total Precipitation ²	836 mm	1,157 mm	1,067 mm
Snowfall ⁴	300 cm	300 cm	250 cm
Snow accumulation ⁵	62.5 cm	32.5 cm	20.8 cm

¹ Port Menier

² Source: Villeneuve 1967

³ Source: Wilson 1971

⁴ Source: Ministère des Richesses naturelles, Quebec 1978

⁵ Approximated from monthly snow accumulation maps (Canada 1974):

Apr	
Σ	Normal snow depth on last day of the month
Dec	

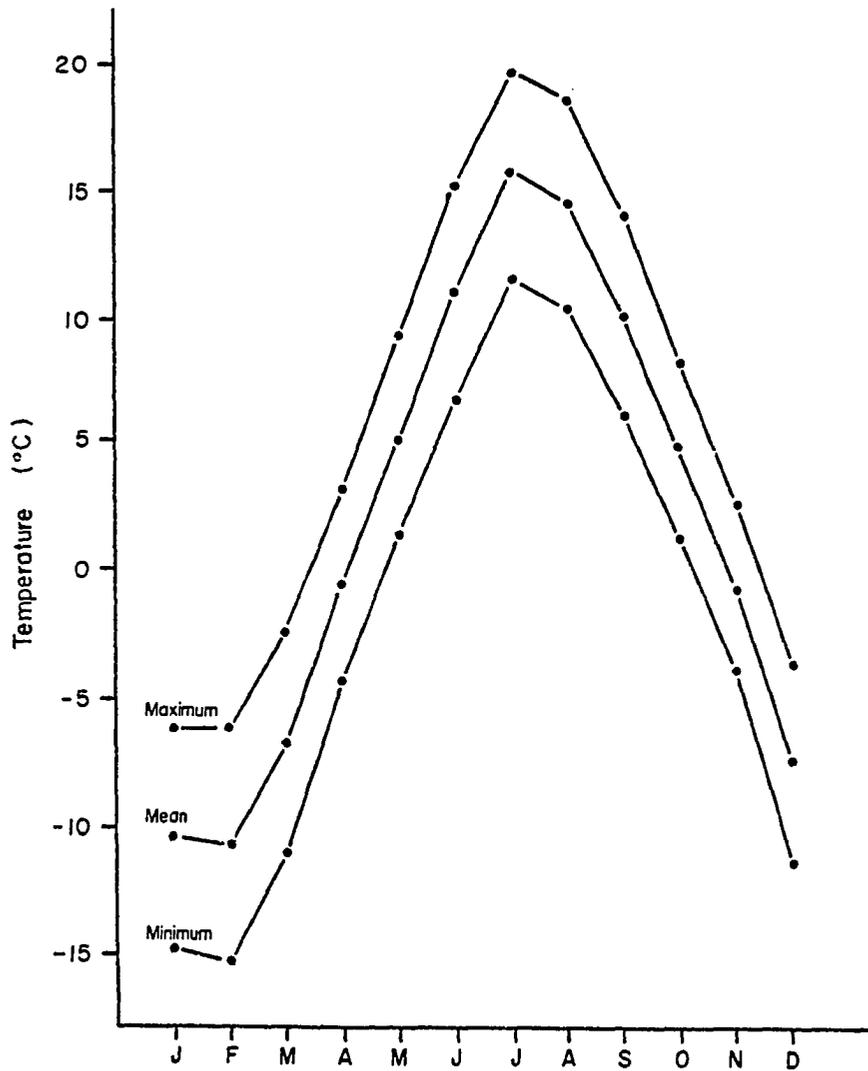


Figure 3. Mean monthly temperatures at the west end of Anticosti Island, 1931-1960, (from Villeneuve 1967)

Vegetation

The forest of the island is typically boreal and is characterized by extensive stands of white spruce (*Picea glauca*), black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). At first, the forests appear as a homogeneous coniferous cover interspersed by openings of various origins. However the cover is far from being homogeneous and consists of a multitude of stands of varied ages and densities which can be grouped in larger units mainly according to the forest composition and the origin of the last major perturbations (Figure 4). Forest exploitation started as early as 1898 and was at first limited to the western end of the island. Logging was very active between 1946 and 1972 and covered a surface area of 48,800 ha. In all, 67,000 ha were logged and this was one of the most important factors responsible for opening the forest (Ministère des Terres et Forêts 1974). Most of the logging consists of large clearcuts and as a general rule forest regeneration has been very poor or has not occurred. According to Pimlott (1954a, 1954b) this situation is mainly due to overbrowsing by deer.

Large portions of the virgin forests of the island have been killed by insect outbreaks but the last outbreak of Hemlock looper (*Lambdina fuscicollaria*) that ended in 1972 was probably one of the most important. It covered some 220,000 ha resulting in a potential loss of over 3 millions cords of wood (Jobin 1973). The hemlock looper, which appears to be mainly limited to islands and coastal areas, attacked balsam fir and white spruce on Anticosti. According to Jobin (1973), a previous major attack had occurred between 1926 and 1935 resulting in an

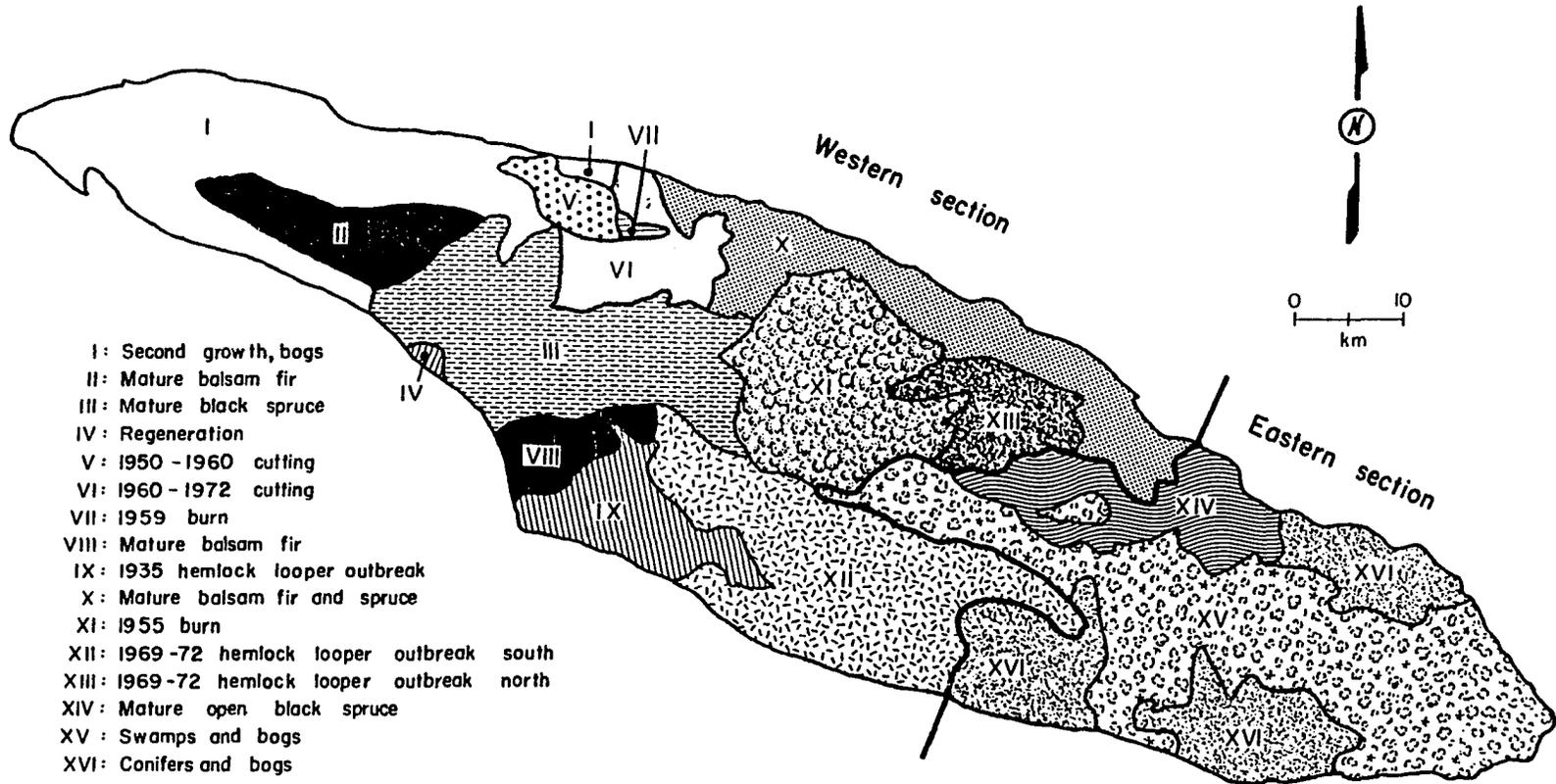


Figure 4. The vegetation zones of Anticosti Island

estimated loss of 500,000 cords of wood. The spruce budworm (*Choristoneura fumiferana*) has also been active on the island but its effects have been much less important and have resulted in the creation of smaller openings.

During the last 30 years several forest fires also affected significantly the cover of the island but their impact was much more concentrated than the effects of the insects or of the forest cutting activities (Figure 4). The two major recent fires are the one of 1955 which covered 67,000 ha and a second much less important fire in 1959 which covered approximately 2,500 ha. In both cases the regeneration of conifers has been very slow and most of these areas are still only covered by herbaceous vegetation. In the first case some lowland areas with deeper soils regenerated in dense stands of trembling aspen (*Populus tremuloides*) whereas in the second area a more diverse regeneration has occurred during the last five years and trembling aspen, paper birch (*Betula papyrifera*) and white spruce seem to be progressively invading the favorable sites.

Natural openings are also common on the island, the most important in size and frequency of occurrence are the peat bogs which are scattered throughout the area. They differ significantly in dimension and vegetation. Some are mainly covered with sedges and other herbaceous plants, while others are dominated by ericaceous shrubs, dwarf birch (*Betula glandulosa*) or even alder-leaved buckhorn (*Rhamnus alnifolius*). Dolines (sink holes) are responsible for the second type of natural openings. Associated with limestone areas, these depressions are

scattered over the island. Their dimensions vary but most of them are probably smaller than one hectare. Their vegetation is strictly herbaceous and usually dominated by grasses. All the ones which we have visited had been flooded in spring and some were flooded after rains. The latter appeared to have deeper and better formed soils and a more luxuriant vegetation including a greater abundance of forbs.

The rest of the forested parts of the island is mainly covered by decadent stands of balsam fir (over 100,000 ha) and black spruce (110,000 ha). The only area where deciduous species such as paper birch appear to be a significant component of the original forest composition is on the northern fringe of the island along the coast, elsewhere the presence of deciduous species is associated mainly with fire and logging operations.

Finally 230,000 ha are covered by a mosaic of stunted black spruce stands and peat bogs. In some areas stunted white spruce and balsam fir may also form important stands. The abundance of trees decreases eastwardly and large prairie-like bogs cover the eastern end of the island. Most of the research was conducted in the portion of the island readily accessible from the road system and for that reason description of the vegetation of the eastern end of the island is less detailed.

Mammalian Fauna

According to Cameron (1958) the only native mammals of the island were the black bear (*Ursus americanus*), river otter (*Lutra*

canadensis), pine marten (*Martes americana*), white-footed mouse (*Peromyscus maniculatus*) and red fox (*Vulpes vulpes*). One of these species, the pine marten, was probably exterminated in the 1930's by over trapping (Cameron 1958) and the black bear, once numerous, is now very scarce. Cameron suggested that the paucity of mammalian fauna native to this large island indicates that no post-glacial connection existed with the mainland, or at the most one of only brief duration.

At the turn of the century the owner of the island, Henri Menier, proceeded to stock it with various species of wildlife. Among the main species introduced to this private fishing and hunting reserve, the white-tailed deer proved to be the most successful. However, other species such as the snowshoe hare and the beaver (*Castor canadensis*) also established and spread rapidly. Moose were introduced at the same time but their numbers seemed to remain very low until recent years when they appear to have increased. Mink (*Mustela vison*) were introduced in 1912 (Newsom 1937) and increased rapidly but by 1936 they had apparently become extinct (Cameron 1958). Muskrats (*Ondatra zibethicus*) were introduced in 1930 (Cameron 1958) but apparently never became very abundant. Unsuccessful introductions were those of the bison (*Bison bison*), caribou (*Rangifer tarandus*) and wapiti (*Cervus canadensis*).

Although several naturalists visited the island after the introduction of deer the early history of the white-tailed deer population of Anticosti is largely unknown and those reports that do exist are often contradictory. Schmitt (1904) stated that 100 deer were introduced a few years prior to 1896 while Townsend (1934), in Pimlott (1954a),

reported that 150 were introduced in 1897. Finally Newsom (1937) mentions that a total of 220 deer were introduced in 1896 and 1897. All reports appear to agree on the origin of the animals and indicate that these were captured on the south shore of the St. Lawrence between l'Islet and Cap-Chat, the western extremity of the island appears to have been the only point of release.

Before the visit of the Newsom-Watson Expedition of the American Museum in fall 1936 (Newsom 1937) there was very little published information on the deer population of Anticosti. Twenhofel (1928) who studied the geology of Anticosti in 1909 and 1919 indicated that deer existed in great numbers on the island. Marie-Victorin and Rolland Germain (1969) who did botanical collecting in the area mentioned in 1926 that deer trails were apparent in the bogs of Rivière la Loutre; one year later they report having trouble finding an intact specimen of *Habenaria unalascensis* in the Fox Bay area as most plants were grazed by deer.

M.C. McCormick (Pers. Com.) who was the chief game warden of the island during many years mentioned that when he arrived on Anticosti in 1926 deer were already plentiful. He did not notice signs of winter mortality however before spring 1934 when he estimated the number of dead deer to be approximately 10 per square mile (2.3/km²). Townsend (1934) in Pimlott (1954a) estimated the deer density at 15 per square mile (5.8/km²) for the wooded portion of the island. In July 1942, Rousseau (1950) crossed the island for a botanical survey and estimated the population at 15,000, he also reported that in many areas, especially

in the *natural prairies*, the vegetation was so intensively clipped by deer that species such as *Viburnum edule* had become rare and that it was hard to obtain complete botanical specimens. Cameron (1958) visited the island in 1952 for a study of terrestrial mammals and stated that the total population could not be less than 350,000.

In 1954 Pimlott (1954b, 1963) spent one month on Anticosti to investigate the effects of deer on the vegetation. He estimated that the population had dropped to 15 to 20 deer per square mile (9-12/km²) after a major irruption and had probably been relatively stable between 1934 and 1954. He and Lachance (1958) concluded that deer had serious effects on the forest regeneration. Some ten years later the owner of the island at that time the Consolidated Paper Corporation Ltd. inaugurated a research program on deer (Letourneau 1965; Dixon 1968; Free and Severinghaus 1967). Dixon (1968) stated that the deer population could be "guessed at anywhere between 50,000 and 100,000 head" and the research being done was aimed at obtaining basic information on the physical condition of the deer. This study, based on the examination of over a thousand of hunter-killed animals, some 300 deer killed in winter as part of the research and live-tagged deer is the only major investigation of the deer of Anticosti prior to the present study.

Finally a series of four aerial surveys were conducted on the island in winter in order to map the distribution of deer, to estimate their number or to follow the possible important population variations in time. The first aerial survey was conducted in 1969 and the

population was then estimated at 65,000 head (A.B. Stephenson, biologist responsible for the survey, pers. comm.). Following another aerial survey conducted in 1972, Pichette et al. (1972) set three density classes ($< 3.86/\text{km}^2$, 3.86 to $11.58/\text{km}^2$ and more than $11.58/\text{km}^2$) and estimated the number of deer at 75,000. In 1978 (Morasse and Beauchemin 1979), estimated the number of deer at 60,000 and following another aerial survey in winter 1979, Morasse (1980) concluded that the population had increased significantly as compared to 1978.

To summarize, since the introduction of deer to Anticosti Island little research has been conducted on this population. Most reports are unpublished and based on short investigations in very restricted areas. For this reason and also because the estimation of numbers of forest ungulates is normally an imprecise undertaking little is known on past deer numbers. Population estimates made before aerial surveys could be conducted appear to be guesses and are probably as unreliable as they are erratic. A generally accepted explanation of the population history of the Anticosti deer is that after the introduction of some 150 animals at the turn of the century there was a very rapid irruption-like increase of the population followed by periodical heavy winter mortalities. Deer have had pronounced effect on the vegetation of the island and have in turn been limited almost exclusively by winter starvation.

GENERAL METHODS OF THE STUDY

The main objective of this research was to assess energy reserves of deer and to relate these to the annual cycle in food resources. For that purpose we attempted to obtain complete deer specimens killed at different times of the year mainly for body composition analysis and diet determination. A series of measurements and analyses were used to estimate the state of growth of the animal, the length measurements with age information were especially useful for that purpose (total length, femur length, hind foot length, ...). The estimation of fat deposits, which was used as the main condition index, is based on total fat content determination as well as fat indices. The weight data are ambivalent as they give an assessment of condition but are also related to the stature of the animal and its age. These are probably affected by individual genetic variation, long term body condition, immediate body condition and age. Finally a series of measurements were aimed at the description of the digestive tract especially the components of the stomach and their contents. In summer 1975 and 1976, a large portion of time was spent on vegetation surveys mainly to evaluate winter food resources.

Deer Studies

Collection of the specimens

Selecting individuals of a given sex and age, or reproduction status for collection according to a defined sampling procedure was often not possible on Anticosti Island except during certain periods of the year. For that reason emphasis in sampling the population was placed on adult females but young of the year and bucks were also included in the study. For example, it is difficult to distinguish between adult and yearling females in summer except on the basis of size, so any attempt to include only adult does would have resulted in the selection for the larger ones. In winter, adult females were often killed while accompanied by yearlings that looked and behaved like fawns.

Collection of specimens was based on intensive two week sampling periods, selected in relation to the main events of the annual life cycle of deer (Figure 5). Between these intensive collection periods specimens were also obtained, mainly road-killed animals, and for that reason the data are usually grouped into periods of one month or more. Period 1 (February 03-March 08) corresponds to mid-winter conditions, herbaceous plants are not available, and body condition should be deteriorating but reserves should be sufficient for survival for another month and a half to two months. Period 2 (April 13-April 18) is the last period when deer are accessible for collection before spring break up. Spring break up, when rivers, streams and bogs are flooded, is probably the period of maximum deer mortality and when deer

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Life cycle	Reproduction						Fawning					Rutting	
	Lactation												
	Antlers	Casting							Velvet shedding				
	Coat								Summer			Winter	
Environment	Snow												
	Growing season				Apr 13-18								
Collection period			Feb 3 - Mar 8			May 15 - Jun 14	Jun 18 - Jul 13	Jul 14 - Aug 26	Sep 2 - Nov 4			Nov 5 - Dec 12	
Reference number			1		2	3	4	5	6			7	
Deer collected for body condition analyses	Does		8		6	2	4	11	4			5	
	Bucks				3	2	5	3	2			2	
	Yearling		1		5	5	7	11	4				
	Fawns		7		5	2		4	7			3	
	Total (118)		16		21	11	16	29	17			10	

¹ Goudreault and Huot (unpublished)

² Goudreault (1979)

Figure 5. Sampling schedule in relation to the life cycle of deer and the seasonal environmental changes. Only the specimens that could be included in the body composition analyses are taken into account, other specimens (27) were used only for rumen content identification or anatomical measurements

are in poorest body condition. Period 3 (May 15-June 14), this is also a period of poor body condition but it corresponds to the emergence of new vegetation and beginning of fawning. Period 4 (June 18-July 13) includes fawning to the peak of lactation and is a period of high quality of forage. Period 5 (July 14-August 26) covers the last stage of high milk production and forage remains high in quality. Period 6 (September 02-November 04) includes the decline in forage quality and probably the last weeks during which improvement in body condition is possible. Period 7 (November 05-December 12) encompasses the rutting period and probably includes peak condition for does. Most of the 145 (118 ± 27) deer specimens were collected between May 1976 and April 1977, but 28 were obtained in summer and fall 1975, 6 in fall 1977 and 4 in winter 1978.

Most of the deer were shot in the neck to avoid damage to internal organs but in fall and winter when hunting was more difficult, animals had to be shot in the thorax. In summer, hunting started as early as light permitted and was terminated when at least two deer had been collected, usually within 2 to 4 hours. This procedure became impossible to follow in fall and in winter as hunting success dropped sharply. On several occasions one to two days of hunting were required to obtain a single deer. In summer and fall, most deer could be collected from a vehicle along secondary roads or even from the main road, however in fall and in winter most deer moved to other habitats and we had to hunt on foot, searching what appeared to be the best areas. Figure 6 gives the locations where the specimens were collected on the island.

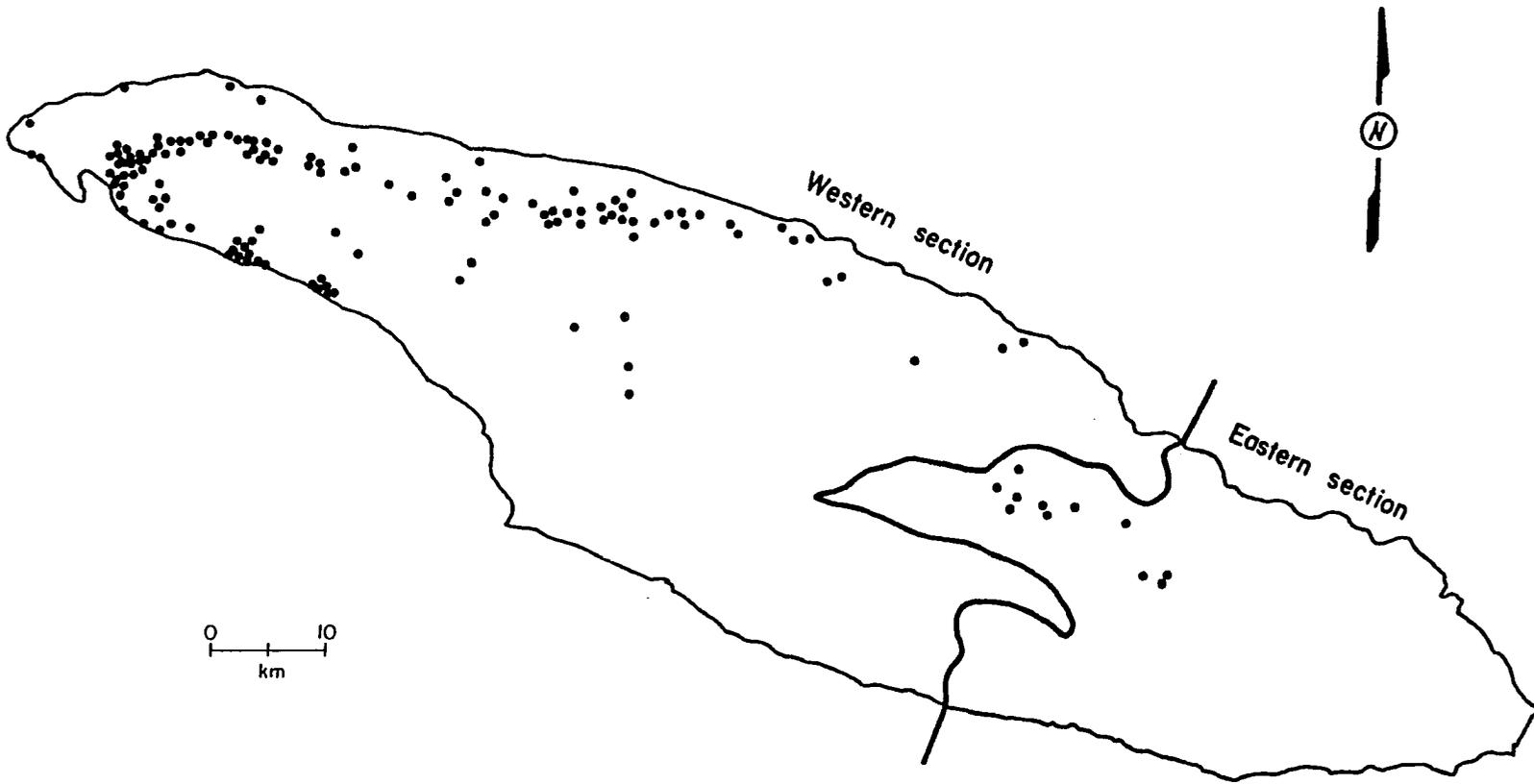


Figure 6. Distribution of deer specimens collected on Anticosti Island, 1975-1978

We also included as specimens several fresh road-killed deer. These specimens generally provided the same measurements and specimen material as the field shot animals with the exception that rumen contents were not used for chemical analyses.

Some data were also obtained from deer that had died of starvation within a few hours of being found or while they were still alive but could not escape due to extreme weakness. These specimens represent the extreme in exhaustion of body reserves.

Processing and measurements

The whole deer were taken to a processing room adjacent to a freezer at Port Menier. A summary of the various measurements and weights taken during the autopsies is given in Table 2. External measurements and total body weight were taken on arrival. After that the animal was skinned, paying attention to leave the subcutaneous fat on the carcass, the skin was immediately weighed. The depth of the fat on the rump was measured according to Riney's (1955) method. A cut was made anteriorly from the base of the tail at a 45° angle from the spine, then a series of 7 measurements of the depth of the fat was taken with a ruler to the nearest mm every 25 mm. The mean of the seven measurements was then recorded as the depth of back fat (DBF).

The body cavity was opened, all the viscera were removed, and the carcass was weighed and sawed longitudinally through the center of the vertebrae. One half of the carcass was weighed, usually the right,

TABLE 2. Main observations and measurements made on deer at the field station ¹

Observation or measurement	Abbreviation	Unit and precision ¹	Objective	Remarks
Spring molt	-	% completed nearest 10% visual estimation	Spring-early summer condition	-
Total body weight	TBW	kg (0.5 kg)	Growth and condition	Does not include blood loss due to bullet wound (usually less than 1% of live weight according to our estimation)
Corrected total body weight	CTBW	kg (0.5 kg)	Growth and condition	TBW minus uterus and content; (C)TBW: when a list includes pregnant and non pregnant deer
Dressed body weight	DBW	kg (0.5 kg)	Growth and condition	TBW minus all viscera
Ingesta-free body weight	IFBW	kg (0.5 kg)		Sum of all parts (content of stomach and intestines removed)
Corrected ingesta-free body weight	CIFBW	kg (0.5 kg)	Growth and condition	IFBW minus uterus and content; (C)IFBW: when a list includes pregnant and non pregnant deer

TABLE 2 (continued)

Observation or measurement	Abbreviation	Unit and precision ¹
Total length	TL	mm (10 mm)
Hind foot length	HFL	mm (5 mm)
Femur length	FL	mm (1 mm)
Brain weight	Br W	g (0.1 g)
Lung weight	Lu W	g (0.1 g)
Spleen weight	Spl W	g (0.1 g)
Heart weight	Hea W	g (0.1 g)
Kidney weight	Kid W	g (0.1 g)
Adrenal weight	Ad W	g (0.1 g)
Intestine weight	Int W	g (0.1 g)

Objective	Remarks
Growth	Extended (from nose to last vertebra)
Growth	Extended (calcaneum to tip of longest hoof)
Growth	-
Growth and condition	Pericardium removed and blood drained
Growth and condition	-
Growth and condition	-
To be included in IFBW	Empty

TABLE 2 (continued)

Observation or measurement	Abbreviation	Unit and precision ^a
Rumen-reticulum weight	-	g (0.1 g)
Abomasum weight	-	g (0.1 g)
Omasum weight	-	g (0.1 g)
Content of rumen-reticulum weight	-	g (0.1 g)
Volume of rumen-reticulum content	-	mL (100 mL)
Volume of abomasum content	-	mL (1 mL)
Volume of omasum content	-	mL (1 mL)

Objective	Remarks
Assess the size of digestive organs	Empty
Assess the size of digestive organs	Empty
Assess the size of digestive organs	Empty
Assess the size of digestive organs	-
Assess the size of digestive organs	-
Assess the size of digestive organs	-
Assess the size of digestive organs	-

TABLE 2 (continued)

Observation or measurement	Abbreviation	Unit and precision ¹	Objective	Remarks
Volume of rumen-reticulum (capacity)	-	mL (10 mL)	Assess the size of digestive organs	-
Peritoneum weight	-	g (0.1 g)	Mainly condition	-
Depth of back fat	DBF	mm (1 mm)	Condition	-

¹ The International System of Units (SI) has been used throughout the thesis with the exception of kilocalories (kcal) for energy instead of joules (J) (1 kcal = 4.184 J).

and frozen for further analysis. The femur of the other half was removed and measured and a sample of 30 mm of marrow in the central part was removed, weighed to the nearest 0.01 g and frozen for fat content determination. For does, the uterus and ovaries were removed and weighed. The uterus and its contents were frozen while the ovaries were fixed and preserved for another study. The peritoneum covering the digestive tract was removed and weighed fresh and frozen. The liver, heart and lungs were isolated, weighed and frozen. The adrenals were also weighed separately to the nearest 0.01 g. The kidneys and perirenal fat were removed including fat adhering along the dorsal part of the abdominal cavity on each side of the vertebrae. Each kidney with its fat was weighed, the fat anterior and posterior to the kidney was trimmed and weighed, finally all the surrounding fat was peeled and the kidney was weighed (Figure 7). The following formulae gave us the total kidney fat index (KFI-T) and the Riney fat index (KFI-R) (Riney 1955). In both cases, the left and right indices were calculated separately and the mean value of both is given as the index.

$$\text{KFI-T} = \frac{\text{Total kidney fat weight} \times 100}{\text{Kidney weight}}$$

$$\text{KFI-R} = \frac{\text{Trimmed kidney fat weight} \times 100}{\text{Kidney weight}}$$

The intestines were isolated, washed of their content under running water, the excess of water was removed and they were weighed. The abomasum and omasum were separated and weighed separately. The rumen-reticulum was weighed with its contents, the contents were emptied into a graduated beaker, weighed and volume determined. The volume of the

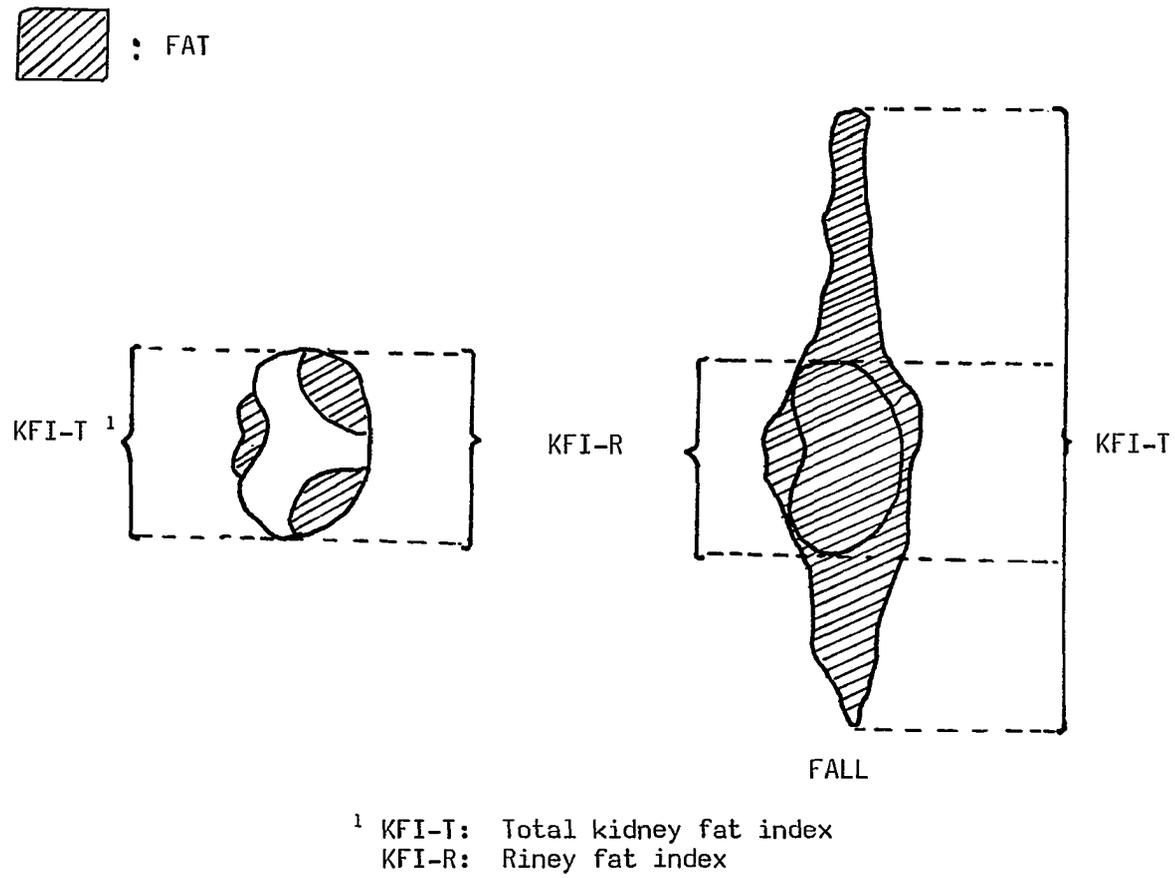


Figure 7. Trimming of the fat for kidney fat indices

rumen-reticulum was estimated following the method described by Short et al. (1965). The emptied rumen-reticulum was placed on a flat surface and filled with water to its normal shape, avoiding excessive distention. Although this method appears crude the results obtained from 10 repetitions on the same organ gave a standard error smaller than 2% of the mean.

Rumen contents analyses

The contents of the rumen-reticulum were separated into three samples. Approximately one liter was preserved by adding 50 mL of 10% formalin and kept for diet determination. Another sample of 500 mL was weighed, preserved with formalin, and later dried to obtain the dry weight of the total contents and kept for chemical analysis. The rest of the content was washed on a sieve with 5.6 mm openings in order to retain only the large vegetation fragments. It was also preserved with 10% formalin for chemical analysis. These last two samples will be referred to as the washed and unwashed fraction of the rumen contents. This procedure was based on the method described by Klein and Schönheyder (1970).

The analysis of the seasonal food habits of deer is based on the examination of rumen content samples collected from deer killed by accident on the road or for research purposes. The contents from the snow-free period, were analysed following the point sampling method suggested by Chamrad and Box (1964). The rumen material was washed through a 5.66 mm mesh size sieve and the retained particles were spread in a standard

enamelled laboratory pan (17 x 28 cm). A five pin frame was advanced along this pan in 1 cm increments, 5 pin drops being made at each time (Figure 8). One hundred hits of particules were used per sample. A dissecting microscope and a reference collection were used for the identification of the items.

The rumen contents obtained between January and late April were treated differently. As the density of the particles of the winter diet (twigs as compared to lichens for instance) differed markedly and as the diet was much more simple all the items retained in the sieve were identified, oven dried at 70°C and weighed. Most items of this period were very easy to identify except the twigs without bark. The total weight of these items was later attributed proportionally to the abundance of the identified browse species in the content examined.

Body composition analyses

The viscera and one half of the carcass of deer collected were kept frozen and transported to the university laboratories. The parts were subsequently partially unfrozen, cut into manageable pieces and ground three times through a large commercial meat grinder. Between each grinding the minced material was thoroughly mixed in a large container. Finally, three subsamples (≈ 30 grams) were taken, weighed and frozen for subsequent analyses. A smaller grinder was used to homogenize the liver and lungs which were analysed separately. The peritoneum was either kept intact, when small, or cut into small pieces ($\approx 1 \text{ cm}^3$) and subsampled for analysis.

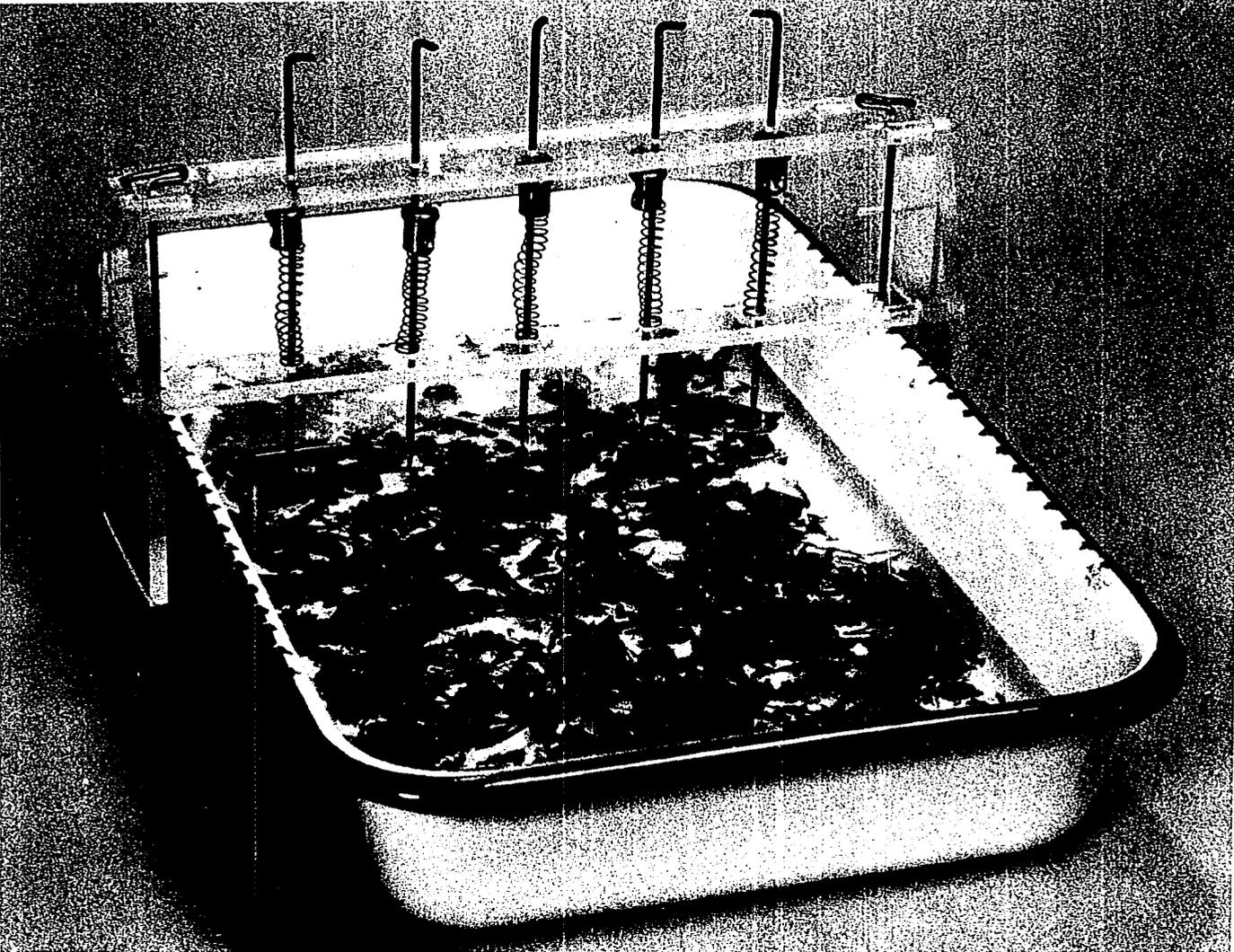


Figure 8. Sampling set up for the study of rumen contents

The subsamples were freeze-dried and subjected to continuous petroleum ether extraction in a Soxhlet apparatus. The remaining part after extraction was freeze-dried again, weighed and ashed in a muffle furnace for 12-16 hours at 600°C. The difference between dry weight of the sample before extraction and its dry weight after extraction is referred to as *fat content*. Protein content was estimated by difference after combusting the fat-free sample.

The results of the analysis of the three subsamples of 25 different individuals showed that variations among the subsamples were so small that only two subsamples would be sufficient, the third one was conserved to be used only if the difference between the two results exceeded 5% of their means. Pieces of skin ($\approx 4 \text{ cm}^2$) were cut from different parts and analysed according to the same procedure.

The weights of the different parts were summed to obtain the total (C)IFBW. Similar summations were made to obtain the weight of the different chemical components. Caloric value of the body tissue was estimated using protein and fat contents of the animal and the caloric value of protein (5.413 kcal/g) and fat (9.490 kcal/g) reported for deer by Robbins et al. (1974a).

Vegetation Studies

The approach

The general approach to assessing deer range quality for deer on Anticosti Island was first to identify some of the key habitat types

from which units were selected for field surveys using forest maps and aerial photographs. Sample plots were randomly chosen within these selected units and various vegetation measurements were made within these plots. Most of the selected units were located in the western half of the island (Figure 9).

The first step, identification of key habitats, was primarily based on our experience with deer and from two previous winter aerial surveys. We decided to use the dominant tree species, the percentage of canopy closure, the age of the stand and its origin (fire, insect, logging, ...) as the main criteria to determine key habitat types. These characteristics were thought to be the primary ones determining quality of the cover, the food species present and food quality. Topography is presumed to be unimportant as the island is a nearly flat plateau. Soil moisture was included as a criterion for some types.

The second step, selection of units for field studies, was accomplished with the aid of 1:20,000 forest maps (Ministère des Terres et Forêts 1974) and 1:70,000 infra-red aerial photographs made in 1971. An habitat unit was defined as a continuous area covered by vegetation of homogeneous structure, age, species composition, and origin (e.g. a forest stand, a bog, a logged area, ...). Most of the sample units varied in size between 50 and 150 ha. The selection was based mainly on accessibility and size, the time required to sample large units would have been prohibitive while the border effect could have affected the results in small units. The sampling method in each unit was based on a simple random allocation of thirty sample points. At each point

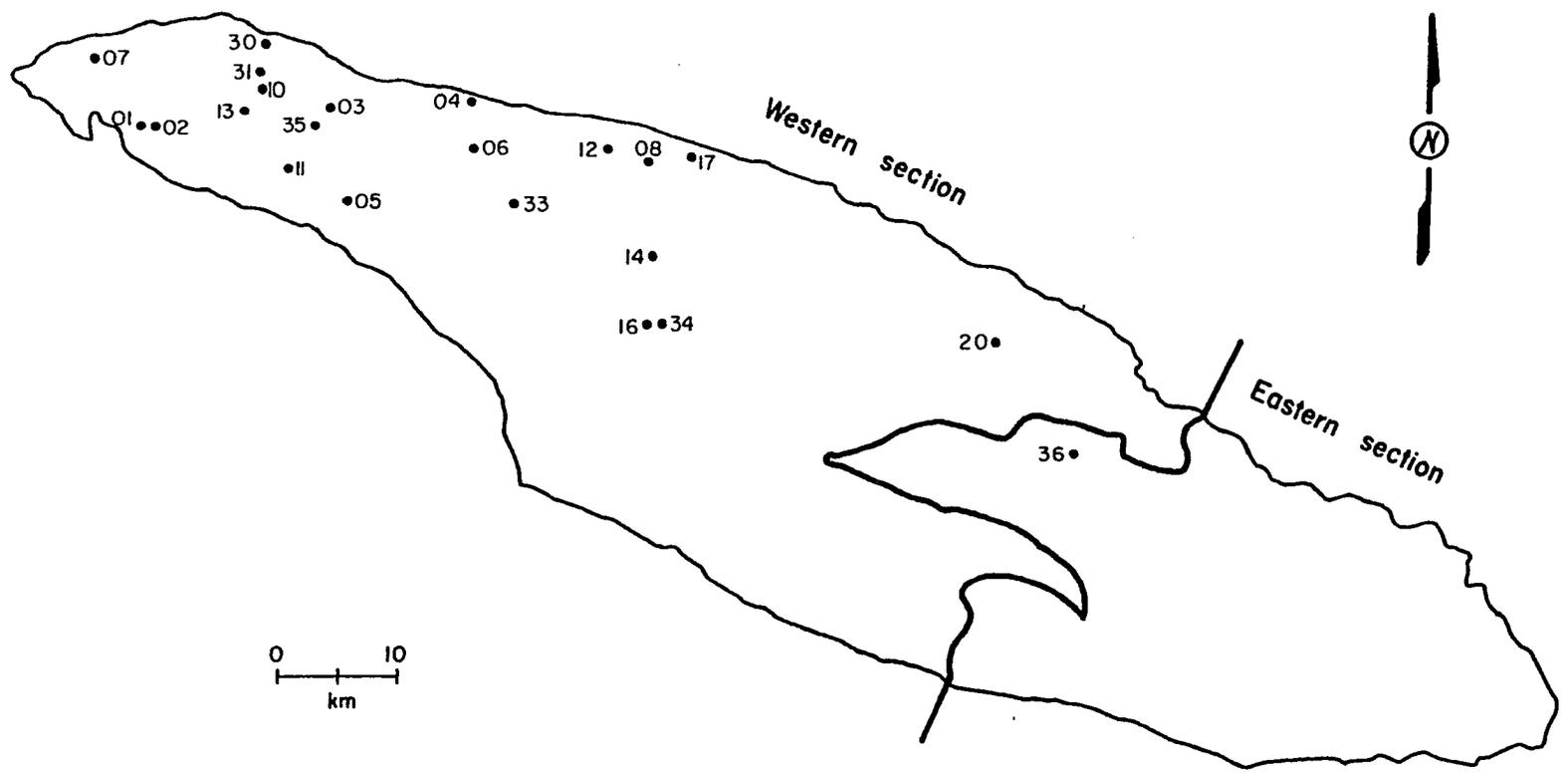


Figure 9. Location of the deer habitat units surveyed on Anticosti Island

sample plots of different sizes and shapes were established depending on the characteristic studied (Figure 10, Table 3).

General description of the habitat units

At each randomly selected point visited in the field the following general characteristics of the habitat were noted:

1. slope in percent;
2. exposure;
3. percent of total canopy cover and conifer cover;
4. the three main tree species present.

Three trees, representative of the dominant stratum of the stand were selected, their DBH and height were measured and their age was estimated.

The stand composition, structure, density, basal area, and mean DBH were estimated according to the Bitterlich's method using a factor 10 wedge prism (Grausenbaugh 1952). This method, based on the variable probability sampling of trees according to their DBH, is currently used as a time saving method in forest surveys, and was also used in previous deer habitat studies by Telfer (1967) and Huot (1972). In the present study only trees with a diameter larger than 4 centimeters were tallied.

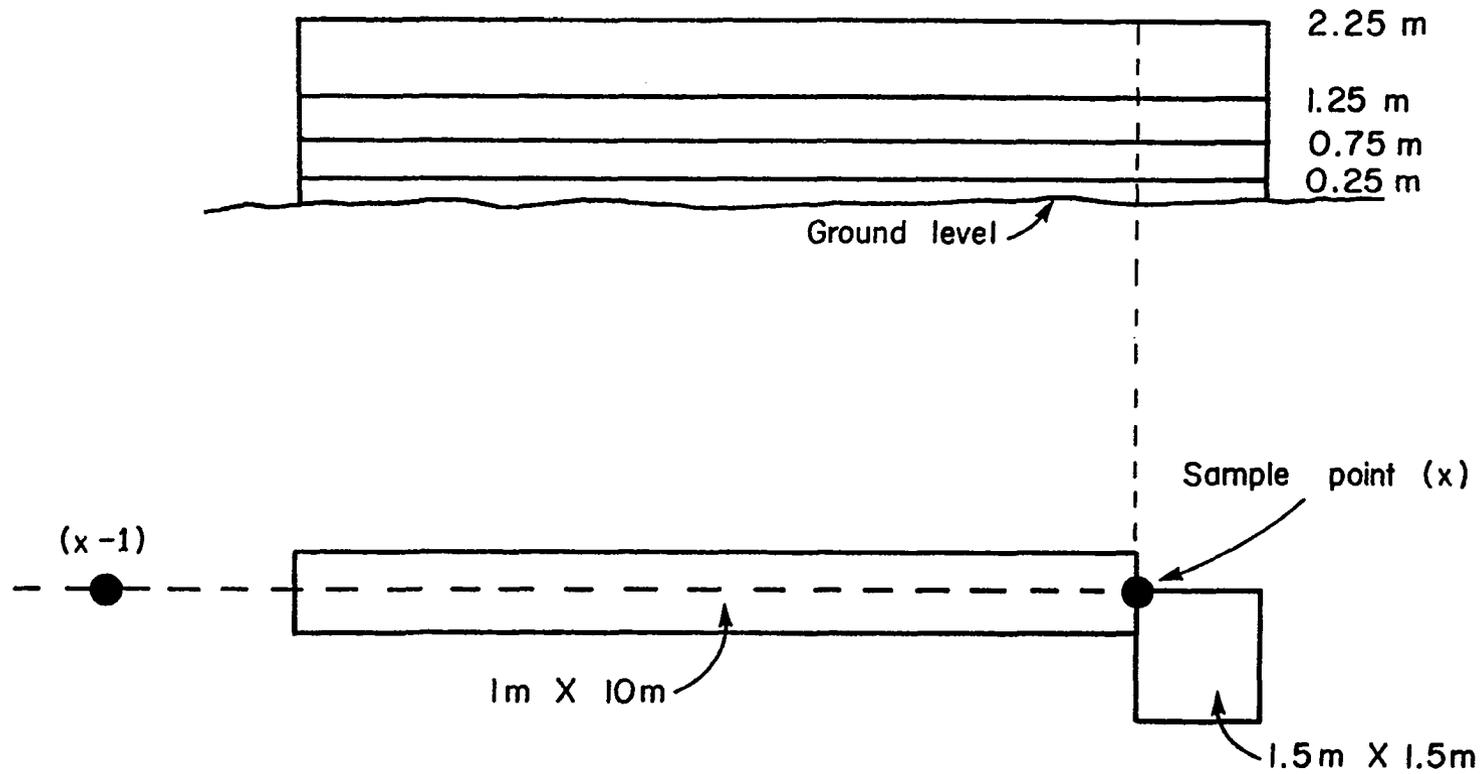


Figure 10. Layout of the sampling plot used for the study of the vegetation

TABLE 3. Sizes and shapes of the sampling plots used for the vegetation surveys

Characteristic studied	Plot shape and Dimension
Stand Composition and Structure (Trees > 4 cm DBH)	Bitterlich's method-factor 10 x prism (Plot size variable)
Woody Browse Availability (stems/ha)	Rectangular, 1 m x 10 m
Woody Browse Availability and Utilization (twigs/stem, percentage of use...)	Square, 1.5 m x 1.5 m
Summer forage	Square: 10 m x 10 m, primary 1 m x 1 m, secondary unit

Winter feeding stratum

The vertical stratum of the habitat that deer can utilize directly in winter was considered to be comprised between 0.25 and 2.25 m from the ground. All the twigs longer than 25 mm, and the arboreal lichens present in this stratum were considered potential food, although some species are rarely utilized because of their low palatability or digestibility. The limits of this stratum were fixed after examining the vertical distribution of browsing on preferred species, the present limits appear to include most of the stratum utilized by deer in winter although in exceptional winters the snow cover may reach 2 meters, as recorded for one month in 1976, and under these conditions deer may reach branches higher than 3 meters. The limits used in other studies vary and any comparison of food

availability must take this into account. Anderson et al. (1972b) considered all twigs below 1.52 m as available to mule deer, Stiteler and Shaw (1966) working in Pennsylvania and Virginia included all twigs between 0.30 and 1.52 m, while in previous works in Quebec the limit was set at 0.46 and 2.13 m (Huot 1972) for deer, and 0.60 and 3.00 m for moose (Crête and Bédard 1975).

In order to take into account the change in food accessibility as snow depth increases, the feeding stratum was further divided into three substrata as follows: substratum I, 0.25-0.75 m; substratum II, 0.75-1.25 m; substratum III, 1.25-2.25 m. Two different sampling units were used to estimate the amount of browse available and used. A plot 1 m x 10 m in size was used to estimate the number of stems with twigs in each substratum. After the limits of the plots had been first established on the ground, all the woody stems originating within the limits were identified and tallied. In the present study *Rubus idaeus* and *Ribes spp.* were considered as woody species available in winter.

In order to estimate more precisely the relative amount of food available by species, a 1.5 m x 1.5 m plot was established adjacent to each 1 m x 10 m plot. All twigs on the stems originating within this plot were counted and tallied according to their substratum as browsed or unbrowsed by deer or hare.

The abundance of lichens available within the feeding stratum was also estimated using the 1.5 m x 1.5 m sampling unit. In all mature stands surveyed, the lichen was stripped from the bole and the lower branches of the coniferous trees present in the 1.5 m x 1.5 m plots.

The lichen picked by hand was put in plastic bags, each bag containing the lichen of one substratum of one tree. The species and the diameter of the tree were also recorded. The content of the bags was oven dried at 100°C during 12 hours and weighed to the nearest mg.

Nutritive quality of browse and lichens

The main plant species available as browse to deer and samples of arboreal lichens were analysed for their nutritive quality. A first series of analyses was performed to estimate the N, Ca and P contents of the browsed parts. These analyses were made in duplicate by the regional laboratory of Ministère de l'Agriculture, des Pêcheries et de l'Alimentation in Alma, Que. A conversion factor of 6.25 was used to estimate protein from the N values.

A second series of analyses was performed in laboratories at Laval University in order to estimate the digestibility of the plant material collected. Tests were first conducted using the cell wall constituents technique (Goering and Van Soest 1970). The samples were dried in a vacuum oven at 70°C and then ground in a Wiley mill through a 40 mesh sieve. The neutral detergent, acid detergent and H₂SO₄ treatment were done according to the original method in duplicate, and the NDF, ADF and ADL values were incorporated in the following formula:

$$\text{TDMD} = \left| 0.98 (100 - \text{NDF}) \right| + \left| \text{NDF} \left(147.3 - 78.9 \log \frac{\text{ADL} \times 100}{\text{ADF}} \right) \right| - \text{SiO}_2$$

TDMD: True dry matter digestibility
NDF: Neutral detergent fiber
ADF: Acid detergent fiber
ADL: Lignin
SiO₂: This element was not included in the present study

As this technique was developed taking into account the digestibility of soluble carbohydrates, hemicellulose, and cellulose by ruminants and the inhibiting effect of the lignin, a second series of independent analyses was conducted based on the direct action of the microorganisms of the rumen. In our study, we suspected that the above formula based on ruminants feeding mainly on grasses might not apply as our forage material contained substances that could inhibit rumen microorganisms, such as resins or complex carbohydrates in lichens. For that reason we submitted subsamples of the same material to 48 hours of *in vitro* digestion according to the method described by Tilley and Terry (1963). For the proteolytic digestion step we used the neutral detergent as suggested by Goering and Van Soest (1970). This accelerated the procedure and permitted the results to be compared with the detergent method. Four digestions were conducted on the same material in two different lots of digestion and for each lot two Whatman No. 1 filter papers (100% cellulose) were digested to test the efficiency of the inoculum. The inoculum was obtained from fistulated sheep fed daily with 1 kg of dry alfalfa hay and 0.5 kg of concentrate containing 13.7%CP. The animals were fed at 8:00 and the inoculum was taken at 9:30.

The material included in these analyses was collected in January and February while following deer tracks, only a few twigs were collected on each tree so that a wide variety of conditions would be included. Field observations and the analyses of rumen contents indicated that for most browse species deer took only the current year growth and only this part was included in the samples. However in the case of *Abies balsamea* deer consumed much older twigs and most bites included two or three years of growth, therefore we analysed separately a sample of twigs of the current year and a sample of material similar to what was eaten by deer. Lichens were handpicked within the stratum accessible to deer on *Picea spp.* and *Abies balsamea*.

Foods during the snow free period

Although the abundance of forage varies from habitat to habitat during the snow free period, green vegetation is probably available in abundance to all deer of Anticosti between early June and mid-November. The quality of the available vegetation is however quite variable according to the species of plants, the parts of plants, the time in summer and the site where these plants grow.

A study of these aspects was conducted in conjunction with the present study and the result will be presented in detail in Tremblay and Huot (in prep. a, b). Because some of the results will be used in the following sections a summary of the methods used and the most pertinent results will be presented here.

Eight habitat units were selected for the study including units 01, 17, 03, two sites (humid and dry) in unit 04, an abandoned field, and a doline. Seven collection periods were equally distributed from late May to mid-October in each habitat unit in 1976. In two units, the doline and unit 10, the harvest was delayed until the snow had melted in mid-June. *Cornus canadensis*, *Hieracium spp.* and *Graminae spp.* were collected in 1976. In 1978, *Taraxacum officinale*, *Vicia cracca*, *Anaphalis margaritacea*, *Fragaria virginiana* and *Rubus pubescens* were added to the list.

The plants were collected on seven rectangular plots corresponding to the seven periods of collection in each unit. The size of the plot was decided according to the density of the plants and every stem encountered in the plot was collected until a maximum weight of 200 g of fresh material was accumulated. The analyses were performed in the same laboratories and according to the same methods used for the analyses of the winter forages presented earlier.

RESULTS AND DISCUSSION

PART I - The Food Resources and their Utilization

Introduction

Browse is usually considered the staple food of white-tailed deer in winter and its availability or lack of it is often reported as the key factor in deer population dynamics. However, nonbrowse forage may also contribute significantly to the winter diet and may even become the main food during the snow free period. Moreover, grazers and browsers will suffer more frequently from deficiencies in food quality than food lack in a quantitative sense (Dasmann 1964: 61). The presence of high quality forage during the snow free period for instance is probably much more important than the mere abundance of green vegetation of fair quality. As suggested by Blaxter (1962: 291) an increase in digestibility of forage from 50% to 60% may result in daily energy retention five times greater due to the interrelationships existing

between food composition, voluntary intake, food digestion and utilization.

This section deals with the availability of food, its quality and its utilization as aspects of deer nutrition. Although there exist many published methods to estimate the availability and utilization of browse these apply mainly to winter yard surveys or to the assessment of the effects of specific forest perturbations such as logging and fire. Because Anticosti deer do not show a well defined yarding behavior and also because of the large size of the island it was impossible to attempt to estimate total food resources. However, because deer were collected over a large sector of the island, the selection of only a small sample area for the study of the vegetation would have been misleading and inappropriate. Moreover deer do not use the habitat nor feed at random but are considered selective in these activities and for that reason the evaluation of the quality of the various habitats and of the food had to take this selectivity into account. For these reasons the survey plan for the study of winter habitat units was largely based on a subjective selection of habitats while the study of food quality had to be based on a method taking into consideration the selection by the deer.

The Habitat Types and Habitat Units

Based on the examination of aerial photographs and forest maps, as well as on field surveys and reconnaissance visits the vegetation of the island was stratified into the habitat types described in Table 4. The

TABLE 4. Main habitat types defined and habitat units surveyed

Habitat type	Characteristics			Units surveyed
	Origin and age (nearest 5 years)	Dominant trees and canopy cover \pm s.d. (nearest 10%)	Main shrubs	
Mixed Regeneration - Logging	Clearcutting 5-25	<i>A. balsamea</i> 20% \pm 20%	<i>P. glauca</i> <i>A. balsamea</i> <i>B. papyrifera</i>	6-year cutting (14) ¹ 15-year cutting (17) 20-year cutting (01) 20-year cutting (07) 20-year cutting (12) 25-year cutting (31)
Second Growth Conifer	Clearcutting 35-50	<i>P. glauca</i> 50% \pm 50%	Absent	35-year white spruce (03) 50-year white spruce (10)
Uneven aged Conifer - Logging	Partial cutting 40-120	<i>A. balsamea</i> 60% \pm 30%	<i>P. glauca</i>	40-year partial cutting (13)
Open Hardwood - Conifer	Partial cutting 30-100	<i>B. papyrifera</i> <i>A. balsamea</i> <i>P. glauca</i> 50% \pm 20%	<i>P. glauca</i>	Paper birch-conifer (30)
Mixed Regeneration - fire	Fire 15	Absent 0%	<i>P. glauca</i> <i>P. tremuloides</i> <i>B. papyrifera</i>	1959 - burn-S (04) 1959 - burn-N (08)

TABLE 4 (continued)

Habitat type	Origin and age (nearest 5 years)
1955 Burn	Fire 20
Mature Irregular Balsam Fir	Hemlock looper outbreak 1929-1934 40-120
1969-1972 Insect Outbreak	Hemlock looper outbreak 5 and 120 +
Irregular Black Spruce	- > 100

Characteristics		
Dominant trees and canopy cover \pm s.d. (nearest 10%)	Main shrubs	Units surveyed
Absent 0% \pm 10%	<i>P. tremuloides</i> <i>B. papyrifera</i> <i>P. glauca</i>	None
<i>A. balsamea</i> <i>P. glauca</i> <i>B. papyrifera</i> 70% \pm 20%	<i>P. glauca</i> <i>A. balsamea</i>	1929 - insect outbreak-moderate (16) 1929 - insect outbreak-light (06)
<i>A. balsamea</i> <i>P. glauca</i> 50% \pm 30%	Absent or <i>P. tremuloides</i> <i>P. mariana</i>	1969-1972 - Insect outbreak high moderate (20) 1969-1972 - Insect outbreak moderate-severe (34)
<i>P. mariana</i> <i>A. balsamea</i> 40% \pm 20%	<i>P. mariana</i>	Mature irregular black spruce (11) Open black spruce - balsam fir (33)

TABLE 4 (continued)

Habitat type	Characteristics			Units surveyed
	Origin and age (nearest 5 years)	Dominant trees and canopy cover \pm s.d. (nearest 10%)	Main shrubs	
Mature - Regular Balsam Fir	- 80-120	<i>A. balsamea</i> 80% \pm 10%	Absent	Mature regular balsam fir (5)
Lowlands - Bogs	-	<i>L. laricina</i> <i>P. mariana</i> 0% \pm 10%	Ericaceous shrubs <i>P. mariana</i>	Peat bog (2)
Mixed Conifer - East	-	<i>P. mariana</i> <i>A. balsamea</i> <i>L. laricina</i> 20% \pm 20%	Ericaceous shrubs <i>P. mariana</i> <i>L. laricina</i>	Salmon river conifer (36)
Bogs - East	-	<i>P. mariana</i> <i>A. balsamea</i> <i>L. laricina</i> 0% - 10%	Ericaceous shrubs <i>P. mariana</i> <i>L. laricina</i>	None

relative importance of the habitat types in each vegetation zone was estimated by the line intercept method using 1:20,000 forest maps. Lines were traced on the maps perpendicular to the long axis of the island every 3.2 km. The length of line crossing each forest stand was recorded and subsequently these stands were reclassified according to the habitat types already defined. Considering the whole island, the most common habitat types on the basis of surface covered, are bogs and lowlands (including lowland-bogs and bogs-East) which are present in every zone and cover 18.9% of the island. They are followed by black spruce stands (17.2%) and conifer stands affected by the 1969-1972 insect outbreak (14.4%). In the western sector, the irregular black spruce stands come first (22.8%) and are well dispersed in all zones, they are followed by the conifer stands affected by the 1969-1972 insect outbreak (14.6%) and logged areas (13.4%). The bogs are also present in all zones of the western sector (12.5%) and the 1929 insect outbreak affected 10.9% of this sector. The hardwood-conifer stands are important in only one zone (14.4% of zone X), the uneven aged conifer stands following partial cuttings are also unimportant (0.1%) as well as the burned areas (10.5%) which are concentrated in two zones (VII: 70.8% and XI: 73.1%) (Table 5).

The Winter Food Resources

Browse availability and utilization

Four expressions have been used to give an account of the availability of browse:

TABLE 5. Percent of area covered by habitat types in each vegetation zone of Anticosti Island

Vegetation zone	Mixed regeneration - Logging	Second growth - Conifer	Uneven aged conifer - Logging	Open hardwood - Conifer	Mixed regeneration - Fire	1955 Burn	Uneven aged conifer - 1929 Insect outbreak	1969-1972 Insect outbreak	Irregular black spruce	Mature regular balsam fir	Lowlands-bogs	Mixed conifer - East	Bogs-East	Others (Lakes, rivers, roads)	Total area (km ²)
I	36.4	21.4	0.2	0.2	2.1	-	4.6	-	13.2	1.2	14.8	-	-	5.6	957
II	23.8	3.1	-	0.4	-	-	6.3	-	39.9	15.7	9.9	-	-	0.9	223
III	3.7	0.6	0.1	1.5	1.2	-	10.7	1.2	60.0	3.9	12.9	-	-	3.9	961
IV	43.9	9.8	-	-	-	-	14.6	-	21.9	-	9.8	-	-	-	41
V	52.6	12.5	0.7	-	8.6	-	2.6	-	7.2	-	13.2	-	-	2.6	152
VI	57.4	2.6	-	-	11.3	-	4.1	-	8.7	1.5	12.8	-	-	1.5	265
VII	-	-	-	-	70.8	-	-	-	4.2	-	25.0	-	-	-	24
VIII	17.1	3.4	1.4	1.4	-	-	19.9	-	21.9	17.8	4.8	-	-	12.3	146
IX	7.0	1.5	-	-	-	-	27.2	16.8	15.0	22.9	7.0	-	-	2.4	327
X	2.7	5.2	0.3	14.4	1.2	-	48.3	3.4	20.2	3.4	13.5	-	-	3.7	380
XI	-	-	-	0.4	-	73.1	2.5	-	2.5	0.1	12.9	-	-	8.3	672
XII	0.5	0.4	-	0.3	0.1	-	5.4	55.0	20.0	0.6	11.3	-	-	6.3	1,177
XIII	0.7	-	-	1.0	2.4	-	25.3	33.6	14.2	-	19.7	-	-	3.1	289
XIV	2.1	1.2	-	3.6	-	-	43.8	3.0	26.4	-	15.3	-	-	4.5	333
XV	-	-	-	-	-	-	-	11.4	-	-	-	29.8	54.3	4.4	1,190
XVI	-	-	-	-	-	-	-	21.6	-	-	-	53.2	12.8	12.3	787
(I-XIII) ¹	13.4	5.0	0.1	1.3	1.8	8.7	10.9	14.9	22.8	3.7	12.5	-	-	5.0	5,614
(XIV-XVI) ¹	0.3	0.2	-	0.5	-	-	6.3	13.7	3.8	-	2.2	33.5	32.3	7.1	2,310
(I-XVI) ¹	9.6	3.6	0.1	1.1	1.3	6.2	9.6	14.4	17.2	2.6	9.5	9.8	9.4	5.6	7,924

¹ (I-XIII): western sector; (XIV-XVI): eastern sector; (I-XVI): whole island

1. the frequency of occurrence by species in the 1 m x 10 m plots;
2. the number of stems per unit of area;
3. the number of twigs per unit of area; and
4. the oven-dry biomass of browse per unit of area.

The 22 habitat units surveyed are listed in Table 4. The results are given in Tables 6, 7 and 8.

Table 6 gives the relative importance of the species in the upland sites of the western sector (excluding lowland units 2, 35 and 36). *Picea glauca* and *Picea mariana* are the dominant species of the feeding stratum. They account for 99.1% of the twigs and biomass in substratum I, 96.6% of the twigs and 96.7% of the biomass in substratum II and 91.8% of the twigs and 92.9% of the biomass in substratum III. *Picea glauca* is more widespread than *Picea mariana* as its frequency of occurrence in the sample plots is much higher (45.0% vs 16.1% in substratum I; 35.6% vs 14.7% in substratum II; 32.8% vs 12.3% in substratum III) and it is also more abundant in terms of number of stems per plot (2.47 vs 1.96). These species are usually not considered as browse, usually being eaten in appreciable amount only in advanced cases of starvation. Therefore, they were excluded for a second series of computations of the relative availability of the browse species. *Abies balsamea* therefore appeared to be the most abundant species in the three substrata accounting for 69.6%, 89.6%, 97.6% of the number of twigs and 72.0%, 89.0% and 97.4% of the biomass. In substratum I, *Betula papyrifera*, *Rubus idaeus*, *Ribes triste*, *Salix spp.* and *Rhamnus alnifolius* accounted

TABLE 6. Relative importance of browse species in the units surveyed according to their frequency of occurrence, their number of twigs and the biomass of the previous years growth on upland sites of the western sector of the island

Species and substratum	N. stems/ 10 m ² plot	Twigs/stem ± s.d.	Twig weight (g)	% of all twigs in each substratum		% total biomass in each substratum	
				Including <i>Picea spp.</i>	Excluding <i>Picea spp.</i>	Including <i>Picea spp.</i>	Excluding <i>Picea spp.</i>
<i>P. glauca</i>							
I	2.47	358±188	0.31	9.9	-	27.5	-
II	1.44	492±342	0.31	36.9	-	65.7	-
III	0.99	751±287	0.31	44.5	-	71.0	-
<i>P. mariana</i>							
I	1.96	4,053±1,280	0.09	89.2	-	71.6	-
II	0.83	1,386±1,905	0.09	59.7	-	31.0	-
III	0.52	1,520±1,105	0.09	47.3	-	21.9	-
<i>A. balsamea</i>							
I	1.11	50.1± 3.2	0.17	0.6	69.6	0.9	72.0
II	0.37	154.1±17.1	0.17	3.0	89.6	2.9	89.0
III	0.41	322.8±46.0	0.17	7.9	97.6	6.9	97.4
<i>B. papyrifera</i>							
I	1.40	5.4± 0.3	0.18	0.1	9.5	0.1	10.4
II	0.41	8.3± 0.9	0.18	0.2	5.3	0.2	5.5
III	0.15	8.6± 4.1	0.18	0.1	1.0	0.1	1.0

TABLE 6 (continued)

Species and substratum	N. stems/ 10 m ² plot	Twigs/stem ± s.d.	Twig weight (g)
<i>R. idaeus</i>			
I	2.07	1.2±0.04	0.20
II	0.08	1.0± -	0.20
III	tr ¹	- -	-
<i>R. triste</i>			
I	0.54	4.7±0.2	0.05
II	0.01	3.2±0.7	0.05
<i>P. tremuloides</i>			
I	0.39	6.7±1.3	0.21
II	0.17	6.4±2.3	0.21
III	0.07	25.3±6.7	0.21
<i>Salix spp.</i>			
I	0.24	13.7±11.0	0.20
II	0.04	32.4±23.6	0.20
III	0.02	3.2± 3.5	0.20
<i>R. alnifolius</i>			
I	1.20	3.6± 0.5	0.08

¹ tr = < 0.01 or < 0.1%

% of all twigs in each substratum		% total biomass in each substratum	
Including <i>Picea spp.</i>	Excluding <i>Picea spp.</i>	Including <i>Picea spp.</i>	Excluding <i>Picea spp.</i>
tr ¹	3.1	tr	3.8
tr	0.1	tr	tr
tr	tr	tr	tr
tr	3.1	tr	1.0
tr	tr	tr	tr
tr	3.2	0.1	4.2
0.1	1.7	0.1	1.8
0.1	1.3	0.1	1.6
tr	4.1	0.1	5.0
0.1	2.0	0.1	2.4
tr	tr	tr	tr
tr	5.4	tr	2.7

TABLE 6 (continued)

Species and substratum	N. stems/ 10 m ² plot	Twigs/stem ± s.d.	Twig weight (g)
<i>Vaccinium spp.</i>			
I	0.08	3.8±0.4	0.04
<i>S. americanus</i>			
I	0.04	5.2±1.5	0.08
II	0.01	- ± -	0.08
<i>K. angustifolia</i>			
I	0.17	2.6±2.1	0.04
<i>D. lonicera</i>			
I	0.02	2.1±3.2	0.04
<i>Viburnum spp.</i>			
I	tr	2.3±1.3	0.06
II	tr	- -	-
<i>Amelanchier sp.</i>			
I	0.03	2.0± -	-
<i>Prunus sp.</i>			
I	0.01	1.0± -	-

% of all twigs in each substratum		% total biomass in each substratum	
Including <i>Picea spp.</i>	Excluding <i>Picea spp.</i>	Including <i>Picea spp.</i>	Excluding <i>Picea spp.</i>
tr	0.4	tr	0.1
tr	0.3	tr	0.2
tr	tr	tr	tr
tr	0.5	tr	0.2
tr	0.1	tr	tr
tr	tr	tr	tr
tr	0.1	tr	tr
tr	tr	tr	tr

TABLE 6 (continued)

Species and substratum	N. stems/ 10 m ² plot	Twigs/stem ± s.d.	Twig weight (g)
<i>C. stolonifera</i>			
I	0.02	1.0± -	0.12
<i>L. laricina</i>			
I	0.01	27.1± 5.9	0.18
II	tr	189.7±90.7	0.18
III	tr	- -	-
<i>L. groenlandicum</i>			
I	0.02	3.3± 2.1	-
TOTAL			
I	11.79	- -	-
II	3.36	- -	-
III	2.16	- -	-

% of all twigs in each substratum		% total biomass in each substratum	
Including <i>Picea spp.</i>	Excluding <i>Picea spp.</i>	Including <i>Picea spp.</i>	Excluding <i>Picea spp.</i>
tr	tr	tr	tr
tr	0.3	tr	0.4
tr	0.1	tr	1.2
tr	tr	tr	tr
tr	0.9	tr	tr
8,908/10 m ²	79.9/10 m ²	998/10 m ²	13.1 g/10 m ²
1,927/10 m ²	63.6/10 m ²	334/10 m ²	10.0 g/10 m ²
1,671/10 m ²	135.6/10 m ²	325/10 m ²	23.1 g/10 m ²

for 28.1% of the twigs and 27.1% of the biomass. The remaining species accounted for 2.0% of the twigs and 0.9% of the biomass. In substratum II, *Betula papyrifera*, *Populus tremuloides* and *Salix spp.* were the only notable species (9.0% twigs; 9.7% biomass) whereas above 1.25 m (substratum III) they accounted for 2.3% of the twigs and 2.6% of the biomass.

Table 7 presents the availability of browse according to the habitat units and types, excluding *Picea spp.* In substratum I, the peat bogs (2), because of the abundance of ericaceous shrubs, is by far the most productive habitat followed by the mixed lowland unit (35). The recent cuttings, the burns (04-08), the open black spruce (33) and the Salmon river conifer (36) units all range between 5,000 and 30,000 stems per ha, the other units offer less than 1,500 stems/ha. Moreover, *Rubus idaeus*, *Ribes triste*, *Rhamnus alnifolius* and *Ledum groenlandicum*, which are usually not included as deer browse species account for between 20% and 79% of the stems in substratum I of the upland types. Above 0.75 m only two units offer more than 5,000 stems/ha (6 year cutting (14) with 6,700 stems/ha and 20 year cutting (01) with 5,500 stems/ha) and in the former *Rubus idaeus* accounts for 22% of the stems. Finally in substratum III only 4 units offer more than 1,000 stems/ha. For all the upland units surveyed in the western sector the mean number of stems/ha for the three substrata are: 7,377, 1,129 and 667. These figures indicate that browse is very limited in the area surveyed. If we try to estimate approximately the abundance of browse in the western sector of the island by weighing the mean for each habitat type according to the area covered by these types (Table 5) the following figures are obtained:

TABLE 7. Availability of browse species in the habitat units surveyed ¹

Habitat type and unit	Substratum	Stems/ha ² ± s.e. x 1,000	Main species
Mixed regeneration - Logging			
6 year cutting (14) ³	I	25,100 ±4,870	<i>R. idaeus</i> 46% <i>B. papyrifera</i> 38% <i>P. tremuloides</i> 8%
	II	6,700 ±2,970	<i>B. papyrifera</i> 57% <i>R. idaeus</i> 22% <i>P. tremuloides</i> 19%
	III	2,100 ±1,430	<i>B. papyrifera</i> 68% <i>P. tremuloides</i> 29% <i>R. idaeus</i> 1%
15 year cutting (17)	I	20,070 ±3,430	<i>R. idaeus</i> 54% <i>R. triste</i> 25% <i>Salix sp.</i> 12%
	II	830 ±160	<i>R. idaeus</i> 82% <i>P. tremuloides</i> 9% <i>B. papyrifera</i> 9%
	III	0	
20 year cutting (01)	I	16,100 ±1,380	<i>R. idaeus</i> 45% <i>A. balsamea</i> 33% <i>B. papyrifera</i> 20%
	II	5,500 ±1,280	<i>A. balsamea</i> 71% <i>B. papyrifera</i> 26% <i>L. laricina</i> 1%
	III	4,370 ±1,160	<i>A. balsamea</i> 73% <i>B. papyrifera</i> 26% <i>L. laricina</i> 1%

TABLE 7 (continued)

Habitat type and unit	Substratum	Stems/ha ² ± s.e. x 1,000	Main species	
20 year cutting (07)	I	12,800 ±2,750	<i>B. papyrifera</i>	50%
			<i>R. idaeus</i>	28%
			<i>A. balsamea</i>	21%
	II	2,000 ±960	<i>B. papyrifera</i>	86%
			<i>A. balsamea</i>	14%
	III	730 ±260	<i>A. balsamea</i>	59%
			<i>B. papyrifera</i>	41%
20 year cutting (12)	I	5,530 ±1,165	<i>A. balsamea</i>	27%
			<i>B. papyrifera</i>	27%
			<i>R. idaeus</i>	20%
	II	400 ±141	<i>A. balsamea</i>	75%
			<i>B. papyrifera</i>	25%
	III	270 ±95	<i>A. balsamea</i>	100%
25 year cutting (31)	I	6,570 ±1,510	<i>A. balsamea</i>	35%
			<i>R. triste</i>	34%
			<i>B. papyrifera</i>	16%
	II	230 ±90	<i>B. papyrifera</i>	43%
			<i>A. balsamea</i>	29%
			<i>R. triste</i>	29%
	III	200 ±88	<i>A. balsamea</i>	85%
			<i>R. idaeus</i>	15%
Second growth - Conifer				
35 year white spruce (03)	I	1,370 ±490	<i>R. idaeus</i>	56%
			<i>R. triste</i>	24%
			<i>A. balsamea</i>	7%
	II	30 ±33	<i>R. triste</i>	100%
	III	70 ±46	<i>A. balsamea</i>	100%

TABLE 7 (continued)

Habitat type and unit	Substratum	Stems/ha ² ± s.e. x 1,000	Main species	
50 year white spruce (10)	I	100 ±100	<i>R. triste</i>	100%
	II	0		
	III	0		
Uneven aged conifer - Logging				
40 year partial cut- ting (13)	I	870 ±732	<i>A. balsamea</i> <i>R. triste</i>	95% 3%
	II	0		
	III	0		
Open hardwood conifer				
Paper birch conifer (30)	I	530 ±208	<i>R. idaeus</i> <i>R. triste</i>	62% 38%
	II	170 ±166	<i>R. triste</i>	100%
	III	100 ±57	<i>A. balsamea</i>	100%
Mixed regeneration - Fire				
1959 Burn N. (04)	I	5,780	<i>B. papyrifera</i> <i>R. idaeus</i> <i>K. angustifolia</i>	46% 35% 6%
	II	440	<i>B. papyrifera</i>	100%
	III	0		
1959 Burn S. (08)	I	28,270 ±22,325	<i>R. alnifolius</i> <i>P. tremuloides</i> <i>Salix sp.</i>	79% 9% 6%

TABLE 7 (continued)

Habitat type and unit	Substratum	Stems/ha ² ± s.e. x 1,000	Main species
	II	2,200 ± 833	<i>P. tremuloides</i> 47% <i>Salix sp.</i> 36% <i>B. papyrifera</i> 15%
	III	1,030 ±444	<i>P. tremuloides</i> 49% <i>Salix sp.</i> 42% <i>A. balsamea</i> 7%
Mature irregular Balsam - Insect			
1929 - Insect outbreak Moderate (16)	I	970 ±330	<i>A. balsamea</i> 82% <i>R. triste</i> 13% <i>Vaccinium sp.</i> 3%
	II	230 ±141	<i>A. balsamea</i> 100%
	III	570 ±217	<i>A. balsamea</i> 100%
1929 - Insect outbreak Light (06)	I	60 ±15	<i>A. balsamea</i> 100%
	II	120 ±119	<i>A. balsamea</i> 100%
	III	470 ±260	<i>A. balsamea</i> 100%
1969-1972 Insect outbreak			
1969-1972 Insect outbreak-light- moderate (20)	I	4 550 ±1 594	<i>P. tremuloides</i> 59% <i>Vaccinium sp.</i> 24% <i>A. balsamea</i> 11%
	II	900 ±523	<i>P. tremuloides</i> 89% <i>A. balsamea</i> 11%
	III	150 ±83	<i>P. tremuloides</i> 67% <i>A. balsamea</i> 33%

TABLE 7 (continued)

Habitat type and unit	Substratum	Stems/ha ² ± s.e. x 1,00	Main species
1969-1972 Insect out- break - Moderate severe (34)	I	50 ±49	<i>R. triste</i> 100%
	II	0	
	III	0	
Irregular black spruce Mature irregular black spruce (11)	I	700 ±199	<i>A. balsamea</i> 76% <i>R. triste</i> 10% <i>Amelanchier sp.</i> 10%
	II	200 ±111	<i>A. balsamea</i> 100%
	III	530 ±190	<i>A. balsamea</i> 100%
Open black spruce balsam fir (33)	I	10,270 ±3,591	<i>A. balsamea</i> 57% <i>K. angustifolia</i> 30% <i>L. groenlandicum</i> 5%
	II	1,870 ± 314	<i>A. balsamea</i> 100%
	III	1,570 ±290	<i>A. balsamea</i> 100%
Mature regular Balsam fir Mature regular balsam fir (05)	I	470 ±208	<i>A. balsamea</i> 100%
	II	130 ±64	<i>A. balsamea</i> 100%
	III	530 ±157	<i>A. balsamea</i> 100%

TABLE 7 (continued)

Habitat type and unit	Substratum	Stems/ha ² ± s.e. x 1,000	Main species
Lowlands-Bogs			
Peat bogs (2)	I	319,560 ±69,849	<i>C. maculata</i> 50% <i>K. angustifolia</i> 21% <i>L. groenlandicum</i> 11%
	II	890 ±424	<i>L. laricina</i> 75% <i>M. gale</i> 25%
	III	0	
Mixed lowlands (35)	I	42,930 ±8,636	<i>M. gale</i> 85% <i>P. fruticososa</i> 9% <i>Vaccinium sp.</i> 3%
	II	2,430 ±785	<i>M. gale</i> 84% <i>L. laricina</i> 16%
	III	230 ±115	<i>L. laricina</i> 100%
Mixed conifer East			
Salmon river conifer (36)	I	9,900 ±2,249	<i>L. groenlandicum</i> 42% <i>A. balsamea</i> 16% <i>Vaccinium sp.</i> 16%
	II	830 ±265	<i>A. balsamea</i> 69% <i>L. laricina</i> 28% <i>L. groenlandicum</i> 3%
	III	570 ±223	<i>A. balsamea</i> 70% <i>L. laricina</i> 30%
All units ¹ (Types 1-9)	I	7,377 ±340	<i>R. idaeus</i> 28% <i>B. papyrifera</i> 19% <i>A. balsamea</i> 15%

TABLE 7 (continued)

Habitat type and unit	Substratum	Stems/ha ² ± s.e. x 1,000	Main species
	II	1,129 ±50	<i>B. papyrifera</i> 36% <i>A. balsamea</i> 33% <i>P. tremuloides</i> 15%
	III	667 ±26	<i>A. balsamea</i> 62% <i>B. papyrifera</i> 23% <i>P. tremuloides</i> 10%

¹ Does not include *P. mariana* and *P. glauca*

² Based on 30 1 x 10 m sample plots in each habitat unit

³ Numbers in parentheses refer to unit numbers Figure 9

	Stems/ha		
	<u>Substratum I</u>	<u>Substratum II</u>	<u>Substratum III</u>
Upland types	6,600	1,000	700
All types	28,100	1,000	600

Estimates of browse availability based on the number of twigs per unit of area do alter appreciably these results (Table 8). The same units appear the most productive but the sharp decline in browse availability from substratum I to substratum III appears different. Despite a smaller number of stems bearing twigs in substratum III, the number of twigs per stem is higher in this substratum as most of the stems are *Abies balsamea*. Consequently the number of twigs available is still high but concentrated on a smaller number of stems and, as indicated in Table 6, 97.4% of these twigs are *Abies balsamea*. If, as done previously, we try to get a picture of the whole western sector by weighing the averages of each type according to their importance in surface area, the following pattern appears:

	Twigs/10 m ²		
	<u>Substratum I</u>	<u>Substratum II</u>	<u>Substratum III</u>
Upland types	85.5	74.2	165.3
All types	169.0	75.4	139.1

TABLE 8. Availability of woody species by substratum according to the number of twigs in each unit surveyed on Anticosti Island

Habitat type and unit	Twigs/10 m ²					
	Including <i>Picea spp.</i>			Excluding <i>Picea spp.</i>		
	I	II	III	I	II	III
Mixed regeneration - Logging						
6 year cutting (14) ¹	2,635	2,263	1,973	104	42	27
15 year cutting (17)	2,191	1,587	2,080	79	1	0
20 year cutting (01)	499	891	1,356	295	630	1,033
20 year cutting (07)	1,629	1,481	1,841	171	56	141
20 year cutting (12)	6,084	3,271	3,291	90	47	97
25 year cutting (31)	396	617	1,129	134	12	55
Second growth conifer						
35 year white spruce (03)	284	246	398	8	tr	23
50 year white spruce (10)	1,047	392	1,037	1	0	0
Uneven aged conifer logging						
40 year partial cutting (13)	375	64	203	42	0	0
Open hardwood conifer						
Paper birch conifer (30)	649	1,174	2,338	1	1	32
Mixed regeneration fire						
1959 Burn N. (04)	1,161	1	0	10	1	0
1959 Burn S. (08)	1,419	320	337	131	40	37

TABLE 8 (continued)

Habitat type and unit	Twigs/10 m ²					
	Including <i>Picea spp.</i>			Excluding <i>Picea spp.</i>		
	I	II	III	I	II	III
Mature irregular balsam - Insect outbreak						
1929 - Insect outbreak Moderate (16)	2,164	1,428	958	41	35	184
1929 - Insect outbreak Light (06)	479	303	287	3	18	152
1969-1972 Insect outbreak						
1969-1972 Insect outbreak light-moderate (20)	28,581	2,710	1,195	48	21	19
1969-1972 Insect outbreak moderate-severe (34)	1,343	98	0	0.2	0	0
Irregular black-spruce						
Mature irregular black spruce (11)	48,326	8,231	4,734	27	31	171
Open black spruce balsam fir (33)	69,500	10,759	8,327	305	288	507
Mature regular balsam fir						
Mature regular balsam fir (05)	450	132	217	24	20	171

TABLE 8 (continued)

Habitat type and unit	Twigs/10 m ²					
	Including <i>Picea spp.</i>			Excluding <i>Picea spp.</i>		
	I	II	III	I	II	III
Lowlands - bogs						
Peat bog (2)	152,425	3,512	337	1,265	129	0
Mixed lowland (35)	12,777	2,566	2,147	307	97	44
Mixed conifer - East						
Salmon river conifer (36)	150,638	10,512	6,151	272	236	217

¹ Numbers in parentheses refer to unit members Figure 8

The number of twigs is nearly twice as high in substratum III as compared to substratum I. The total availability of browse for the three substrata is 325,000 twigs/ha in upland types and 383,000 twigs/ha including all types of the western sector. Using an average of 0.17 g/twig (Table 6) the biomass of available browse can be estimated at 54.8 kg/ha in the upland types of the western sector. When the lowlands are included biomass per unit of area does not change much (54.3 kg/ha) as the mean twig weight becomes 0.14 g/twig when the bog shrubs are included.

The utilization of the browse species, excluding *Picea spp.* is summarized in Table 9 and Figure 11. *Abies balsamea* is the most important species in terms of number of twigs eaten and its importance appears to increase during winter as snow accumulates. In substratum I it accounts for 40.1% of the twigs browsed, in substratum II 52.4% and in substratum III 87.1% despite a rate of use that does not exceed 4.5%. The second most important species in terms of twigs eaten is *Betula papyrifera* which accounts for 28.7%, 40.6%, 9.7% of the twigs browsed in the three substrata. *Rubus idaeus*, *Ribes triste*, *Populus tremuloides* and *Salix spp.* contribute appreciably only in substratum I, as snow depth reaches 0.75 m more than 90% of the twigs browsed by deer are *Abies balsamea* and *Betula papyrifera*. The diet of hare appears even more simple, *Betula papyrifera* dominates in the three substrata (46%, 100%, 100%). The main associate species in the first substratum are *A. balsamea* (27.0%), *Rubus idaeus* (9.1%) and *Ribes triste* (9.1%).

TABLE 9. Intensity of browsing by deer and hare in the upland units surveyed on Anticosti Island ¹

Species	Substratum	Stems browsed (%)			Twigs browsed (%)			Relative importance (%) ²		
		Deer	Hare	Total	Deer	Hare	Total	Deer	Hare	Total
<i>A. balsamea</i>	I	26	7	27	4	0.4	4.4	40.1	27.0	38.4
	II	27	0	27	1.6	0.0	1.6	52.4	0.0	41.8
	III	24	0	24	1.1	0.0	1.1	87.1	0.0	74.9
<i>B. papyrifera</i>	I	28	11	30	21	5	26	28.7	46.0	30.9
	II	39	10	44	21	13	34	40.6	100.0	52.6
	III	24	55	66	12	21	32	9.7	100.0	22.3
<i>R. idaeus</i>	I	19	4	23	16	3	19	7.2	9.1	7.4
	II	33	0	33	33	0	33	1.2	0.0	1.0
<i>R. triste</i>	I	20	7	27	11	3	14	4.9	9.1	5.5
<i>P. tremuloides</i>	I	32	0	32	17	0	17	7.9	0.0	6.9
	II	28	0	28	7	0	7	4.3	0.0	3.5
	III	27	0	27	3	0	3	3.2	0.0	2.7
<i>Salix spp.</i>	I	32	0	32	7	0	7	4.2	0.0	3.6
	II	50	0	50	2	0	2	1.5	0.0	1.2
	III	0	0	0	0	0	0	0.0	0.0	0.0
<i>Vaccinium spp.</i>	I	43	5	45	26	1	27	2.3	0.6	2.0
<i>S. americanum</i>	I	45	11	56	21	4	25	0.9	1.2	0.9

TABLE 9 (continued)

Species	Substratum	Stems browsed (%)			Twigs browsed (%)			Relative importance (%) ²		
		Deer	Hare	Total	Deer	Hare	Total	Deer	Hare	Total
Others ³	I	21	11	32	44	12	56	3.8	7.0	4.2
	II	0	0	0	0	0	0			
	III	0	0	0	0	0	0			

¹ Excluding *Picea spp.*; upland habitats in western sector only

² $\frac{\text{Number of twigs of a given species browsed in a substratum}}{\text{Total number of twigs browsed in the same substratum}}$

³ *D. lonicera*, *L. laricina*, *Amelanchier spp.*, *P. balsamifera*

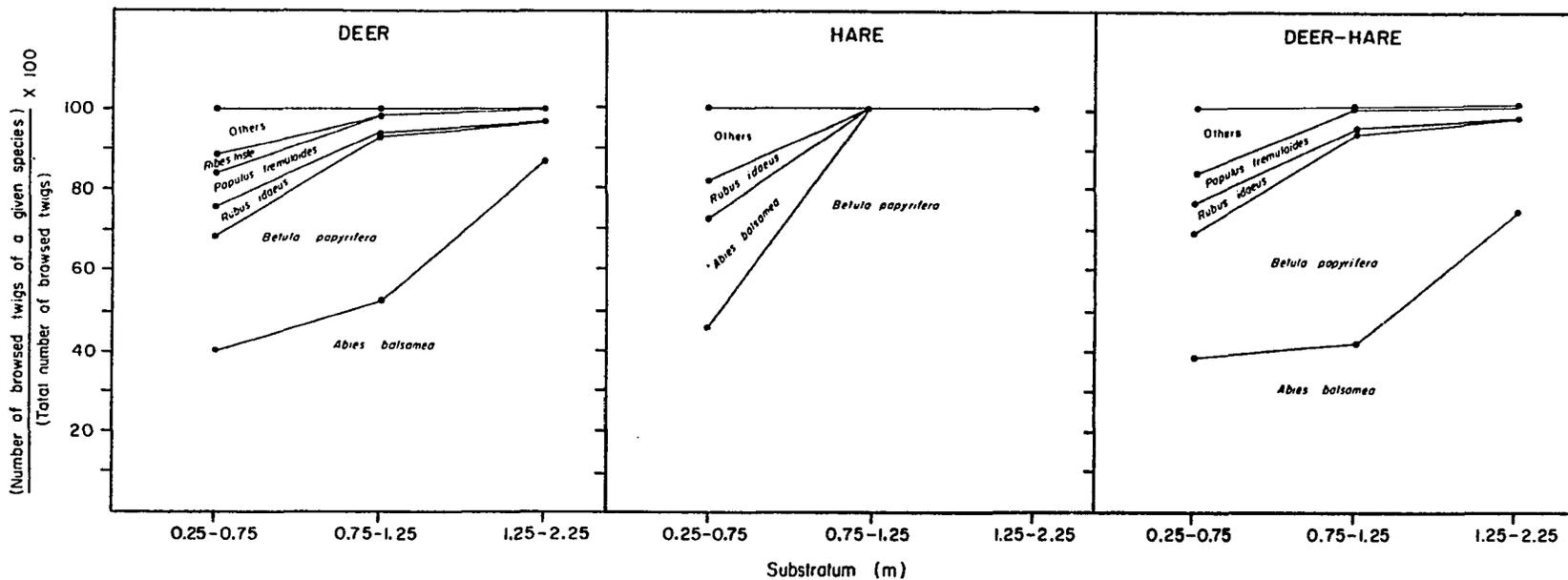


Figure 11. Relative importance (number of twigs of a given species browsed in a substratum / total number of twigs browsed in that substratum) of the browse species in the diets of deer and hare as determined by the vegetation survey (*Picea spp.* excluded)

For most species and in the three substrata between 20% and 40% of the stems had been browsed by deer the winter before the survey, when the browsing by hare is added *Betula papyrifera* shows the highest proportion of stems browsed, 30%, 44% and 66% depending on the substrata. This species is probably the one that is most browsed as the percentage of twigs browsed is also high in the three substrata (26%, 34% and 32% respectively). When considering the number of stems browsed, the intensity of browsing on *Betula papyrifera* reaches 65%, 70% and 73%. As in these cases a certain proportion of twigs that are counted as available in the browse survey are not actually accessible in winter because they are buried under the snow or are too far from cover, it appears that probably close to 100% of the easily accessible twigs of *Betula papyrifera* are browsed. The browsing on *Abies balsamea* on the contrary appears rather light (4.4%, 1.6% and 1.1% of the twigs) and this does not explain the stunted shape of a large proportion of the small trees which do not exceed 50 cm in height at 20 years of age. It is probable that this effect is due to higher deer densities in the past and also to browsing in other seasons than in winter.

In this part of the analysis *Picea glauca* and *Picea mariana* were not considered as browsed. *Picea mariana* was only very rarely browsed but we noted that close to 5% of the stems of *Picea glauca* had been browsed by deer and probably a higher percentage were browsed by hare. Browsing on *Picea glauca* is usually very light on each stem but, because of its high abundance, this species may account for an appreciable part of the diet of deer and hare of Anticosti. Actually 9.9%, 36.9% and 44.5% of the twigs, according to the substrata, belong to this species as compared to 0.6%, 3.0% and 7.9% for *Abies balsamea*.

Despite the problem inherent to the methods used to estimate the quantity of food available in winter the results of the browse survey clearly indicate that winter food resources are very low in quantity and diversity. When snow conditions are considered it becomes apparent that deer have a limited choice of browse species during at least four months of the winter. As examples we may utilize the snow accumulation recorded during winters preceding the browse surveys (Table 10).

TABLE 10. Snow depths recorded during the winters of the study near Port Menier. (From Fisheries and Environment Canada, Atmospheric Environment Monthly Record-Meteorological observations in eastern Canada)

	Snow accumulation at the end of the month (m)							
	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May
1975-1976	0.00	0.15	0.69	1.12	1.27	1.22	0.84	0.00
1976-1977	tr	0.41	1.29	1.66	1.83	1.35	0.87	tr

These figures of snow accumulation can be used in combination with the results on the availability of browse by substratum presented in Table 6. From this, it appears that in January, February, March and April 1976 approximately 90% of the biomass of browse available (excluding *Picea spp.*) was *Abies balsamea* and this proportion probably approached 95% in February and March. In 1977, 95% of the browse was *Abies balsamea* from December to late March while 90% was the same

species in April. Under these conditions only 1,010 stems/ha (0.75-1.25 m) or 570 stems/ha (1.25-2.25 m) offered twigs to deer.

The results of browse surveys conducted in other deer and moose habitats in Quebec and Alaska are summarized in Table 11. In most studies the food availability according to the number of stems/ha was much higher than on Anticosti Island. In deer habitats the number of stems approached 10,000 stems/ha and appeared to be higher in moose habitats. In the upland stands of the western sector of Anticosti the number of stems offering twigs between 0.25 and 2.25 m averaged only 7,000 (excluding *Picea spp.*). However this figure included 2,000 stems of *Rubus idaeus* which are not included in the other studies; the availability also declines very rapidly above 0.75 m. When considering only the number of twigs or the biomass of browse, Anticosti appears to be nearly equal to the other areas as *Abies balsamea* is a species which offers a large number of twigs/stem. It then appears that the availability of browse is largely dominated by *Abies balsamea* and is concentrated on a small number of stems. According to our field observations, this is even more apparent in coniferous stands where deer seem to concentrate as snow accumulates.

The dominance of *Abies balsamea* in the availability of browse is reflected in its abundance in the browse diet of deer according to the vegetation surveys. According to these surveys, between 0.75 and 1.25 m, 52.4% of the browse eaten is *Abies balsamea* and between 1.25 and 2.25 m this species accounts for 87.1% of the browse eaten. *Betula papyrifera* is important in the diet of deer only between 0.75 and 1.25 m (Table 9). These results do not include the contribution of *Picea spp.*

TABLE 11. Browse availability on Anticosti Island as compared to other deer and moose habitats

Area	Habitat	Stratum covered (m)	Stems/ha	Twigs/ha	kg/ha	Source
Thirty-one Mile Lake, Que.	Deer (good to very good)	0.46-2.13	7,300-19,800 Average 16,300	-	-	Huot, 1974
Cherry River, Que.	Deer (poor)	0.46-2.13	2,700	-	-	Juniper, 1971
	Deer (managed area)	0.50-2.25	-	392,000	315	Potvin and Huot, 1979
Lac Tremblant, Que.	Deer (good)	0.46-2.13	10,000	-	-	Stephenson, 1973
Duhamel, Que.	Deer (good)	0.46-2.13	10,500	-	-	Stephenson, 1973
Lac David, Que.	Deer (good)	0.46-2.13	11,400	-	-	Stephenson, 1973
Eagle Depot, Que.	Deer (good)	0.46-2.13	10,400	-	-	Stephenson, 1973
Kiamika, Que.	Deer (good)	0.46-2.13	9,040	-	-	Goudreault et Bédard, 1972
Pohénégamook, Que.	Deer (good) 1972-1977	0.46-2.13	8,700-11,100	-	-	Potvin et al., 1978
Hill Head, Que.	Deer (good)	0.76-2.00	5,100	-	-	Potvin, 1979
	Deer (good)	0.51-2.00	-	304,700	37±6.5	Potvin, 1979
Tanana River, Ak.	Moose	Above minimum browsed height	28,400	-	20.4	LeResche et al., 1974b. Modified from Vierek, 1970

TABLE 11 (continued)

Area	Habitat	Stratum covered (m)
Chena River, Ak.	Moose	Above minimum browsed height
Kenai 1947 burn	Moose (20 year burn)	-
Laurentide Park, Que.	Moose (poor-good)	-
Matane Reserve, Que.	Moose	-
La Mauricie Park, Que.	Moose	-
Anticosti Island	Deer All types	0.25-0.75 0.75-1.25 1.25-2.25

Stems/ha	Twigs/ha	kg/ha	Source
20,700	-	-	LeResche et al., 1974b. Modified from Vierek, 1970
16,400-82,000	-	46.5- 488.9	LeResche et al., 1974b. Modified from Seemel, 1969
2,000-31,100	-	-	DesMeules, 1965
10,200-23,300	-	-	Crête et Bédard, 1975
15,200-18,500	-	-	Audy, 1974
28,130	169,000	28.7	Present study
1,010	75,400	12.8	
510	139,100	23.6	

Lichen availability

Arboreal lichens can also contribute appreciably to the diet of deer in winter. Those that grow on the lower part of the tree, up to the height that deer can reach (here 2.25 m), are constantly available and their biomass can be estimated. However a certain proportion of the lichens that are consumed are obtained from twigs and branches that fall accidentally on the ground during winter, mainly during periods of high winds; the importance of this source is probably more variable and could not be estimated during the present study. Finally in all mature and overmature stands, but most particularly in stands where trees were killed by the insect outbreak, entire trees often fall down with their load of lichens. This source is also hard to estimate as the biomass of lichens on individual trees is not easily obtainable and the number of trees falling during one winter is probably highly variable. In this case we only attempted to estimate if this could be a significant source of food as compared to browse in the areas affected by the insect outbreak.

The estimates of the mean biomass of lichens per tree available between 0.25 and 2.25 m from the ground per conifer in mature stands surveyed are given in Table 12. Only the mature stands (> 60 year old) have been included as no significant amount of lichens could be collected in younger stands and no lichens were available on the deciduous species. These results were used in relation to the estimates of the number of trees (> 4 cm DBH) per ha to obtain an estimate of the biomass of lichens in the feeding stratum of the mature units surveyed in the western sector

TABLE 12. Biomass of arboreal lichens available to deer on coniferous trees in mature stands (> 60 year old) of the western sector of Anticosti Island

Tree species	Substratum	Biomass (g \pm s.d.) dry weight/tree
<i>A. balsamea</i> n = 53	I (0.25-0.75 m)	0 \pm -
	II (0.75-1.25 m)	0.04 \pm 0.11
	III (1.25-2.25 m)	0.97 \pm 1.56
	TOTAL	1.01 \pm 1.61
<i>P. glauca</i> n = 12	I (0.25-0.75 m)	0.05 \pm 0.09
	II (0.75-1.25 m)	0.34 \pm 0.66
	III (1.25-2.25 m)	1.67 \pm 1.24
	TOTAL	2.06 \pm 1.92
<i>P. mariana</i> n = 14	I (0.25-0.75 m)	0.21 \pm 0.35
	II (0.75-1.25 m)	0.85 \pm 1.10
	III (1.25-2.25 m)	4.48 \pm 4.27
	TOTAL	5.54 \pm 8.93

(Table 13). The only lichens considered were fructicose lichens and belonging mainly to the genus *Bryoria*, *Alectoria*, *Ramalina* and *Usnea*.

The availability of lichens in substratum I is very low, averaging 77 g/ha in general and never exceeding 290 g/ha. In the other substrata, above 0.75 m, *Abies balsamea* is the only browse species recorded except in unit 30 where *Ribes triste* is present, in substratum II and in unit 20 where *Populus tremuloides* is present in substrata II and III. However lichens are also not very abundant in these substrata, the highest quantities were recorded in the two black spruce stands, unit 11 with a total of 4,702 g/ha and unit 33 with a total of 3,298 g/ha. In view of

TABLE 13. Dry weight of lichens available in the feeding stratum of the mature units surveyed on Anticosti Island as compared to the dry weight of browse

Unit	Tree density n/ha (> 4 cm DBH)	Biomass of lichens g/ha	Biomass of browse g/ha	
40 year partial cutting (13) ¹	<i>A. balsamea</i> 222	I	0	
		II	24	
		III	346	
		Total	370	
	<i>P. glauca</i> 207	I	19	
		II	137	
		III	257	
		Total	413	
	TOTAL	I	19	7,031
		II	161	0
III		603	0	
Total		783	7,031	
Paper birch conifer (30)	<i>A. balsamea</i> 36	I	0	
		II	4	
		III	56	
		Total	60	
	<i>P. glauca</i> 973	I	88	
		II	642	
		III	1,206	
		Total	1,936	
	TOTAL	I	88	126
		II	646	27
III		1,262	5,488	
Total		1,996	5,640	
1929 - Insect outbreak moderate (16)	<i>A. balsamea</i> 420	I	0	
		II	46	
		III	655	
		Total	701	

TABLE 13 (continued)

Unit	Tree density n/ha (> 4 cm DBH)	Biomass of lichens g/ha	Biomass of browse g/ha
	<i>P. glauca</i> 149	I II III Total	13 98 185 296
	TOTAL	I II III Total	13 144 840 997
			6,811 6,025 31,279 44,115
1929 - Insect outbreak light (06)	<i>A. balsamea</i> 660	I II III Total	0 73 1,030 1,103
	<i>P. glauca</i> 54	I II III Total	5 36 67 108
	<i>P. mariana</i> 1	I II III Total	tr 1 4 5
	TOTAL	I II III Total	5 110 1,101 1,216
			511 3,144 25,792 29,447
1969-1972 - Insect outbreak light moderate (20)	<i>A. balsamea</i> 268	I II III Total	0 29 418 447

TABLE 13 (continued)

Unit	Tree density n/ha (> 4 cm DBH)	Biomass of lichens g/ha	Biomass of browse g/ha
	<i>P. glauca</i> 36	I	3
		II	24
		III	45
		Total	72
		<i>P. mariana</i> 156	I
II	172		
III	666		
Total	893		
TOTAL	I		58
	II	225	3,670
	III	1,129	3,250
	Total	1,412	15,174
	1969-1972 - Insect outbreak moderate-severe (34)	<i>A. balsamea</i> 354	I
II			39
III			552
Total			591
<i>P. glauca</i> 40			I
	II	26	
	III	50	
	Total	80	
	TOTAL	I	4
II		65	0
III		602	0
Total		671	12
Mature irregular black spruce (11)		<i>A. balsamea</i> 299	I
	II		33
	III		466
	Total		499

TABLE 13 (continued)

Unit	Tree density n/ha (> 4 cm DBH)	Biomass of lichens g/ha	Biomass of browse g/ha
	<i>P. glauca</i> 75	I	7
		II	49
		III	93
		Total	149
		<i>P. mariana</i>	I
II	312		
III	3,459		
Total	4,053		
TOTAL	I		290
	II	394	5,239
	III	4,018	29,084
	Total	4,702	38,992
	Open black spruce balsam fir (33)	<i>A. balsamea</i> 285	I
II			31
III			445
Total			476
<i>P. glauca</i> 15			I
	II	10	
	III	19	
	Total	30	
	<i>P. mariana</i> 488	I	171
II		537	
III		2,084	
Total		2,792	
TOTAL		I	172
	II	578	48,988
	III	2,548	86,155
	Total	3,298	185,547

TABLE 13 (continued)

Unit	Tree density n/ha (> 4 cm DBH)	Biomass of lichens g/ha	Biomass of browse g/ha
Mature regular balsam fir (05)	<i>A. balsamea</i> 1,252	I	0
		II	138
		III	1,953
		Total	2,091
	<i>P. glauca</i> 61	I	5
		II	40
		III	76
		Total	121
	<i>P. mariana</i> 99	I	35
		II	109
		III	423
		Total	566
TOTAL	I	40	4,003
	II	287	3,406
	III	2,452	29,084
	Total	2,779	36,493
All units	I	77	9,091
	II	290	7,833
	III	1,617	23,348
	Total	1,984	40,272

¹ Numbers in parentheses refer to unit numbers Figure 9

the fact that this constitutes the standing biomass and as the annual production is much lower than that, lichens are probably only important in providing some diversity in the diet when *Abies balsamea* is the only browse species available but they cannot be considered as reliable sources of food. It is even possible that lichens falling on the ground from the upper limbs might supply more forage than the lichens present in the feeding stratum.

The estimation of the lichen biomass of entire balsam fir killed during the recent insect outbreak is based on collections of lichens on two specimens on the island and these results were combined with a similar study conducted on the south shore of the St. Lawrence for similar purposes by Potvin and Lépine (1979). I used their results for seven trees (10-25 cm DBH) and my results for two trees (20 and 27 cm DBH). As the amount of lichen per tree increases with the size of the tree a regression equation was calculated for that relation and the results are given in Figure 12.

This relation and the results of the vegetation surveys conducted in two forest stands affected by the insect outbreak were used to estimate the biomass of lichen on the dying and dead *Abies balsamea*. During the survey each tree was considered as dead (no green foliage) or dying (25% of its normal foliage estimated visually). Knowing for each diameter class the number of stems per ha and its estimated lichen biomass from the regression equation an estimate of the potential lichen fall can be obtained. The results are given in Table 14.

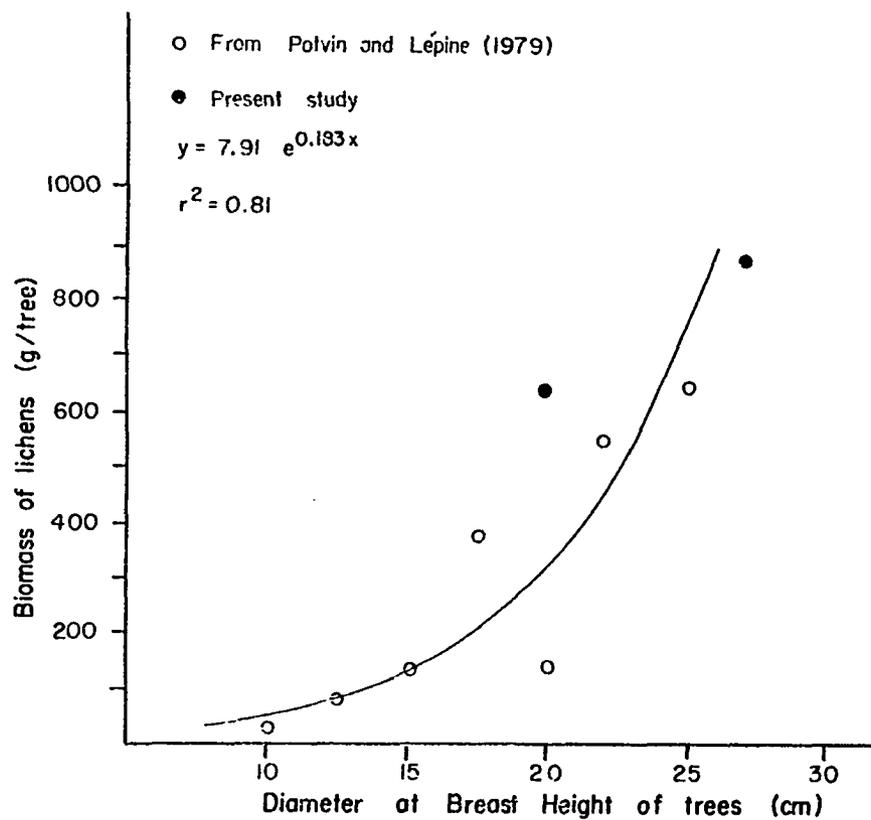


Figure 12. Relation between the diameter (DBH) of dead balsam firs and the biomass (dry weight) of lichens present on those trees

TABLE 14. Estimated biomass of lichens on dying and dead *A. balsamea* in two units affected by the hemlock looper outbreak

Unit	N stems/ha (> 10 cm)		Biomass of lichen (dry weight)	
			kg/tree	kg/ha
1969-1972 Insect outbreak light-moderate (20)	Dying	44	0.38	16.7
	Dead	141	0.47	65.6
	TOTAL	185	0.44	82.3
1969-1972 Insect outbreak moderate-severe (34)	Dying	47	0.95	44.8
	Dead	220	0.64	141.4
	TOTAL	267	0.70	186.2

The biomass of lichens on the dying and dead trees is 82.3 kg/ha in the area of light to moderate outbreak and 186.2 in the area of moderate to severe outbreak. Although it is hard to estimate the rate at which the trees will be falling in the years following their mortality we observed that deer usually used most of these fallen trees and in stands where other sources of food are not abundant this resource can probably be significant during the 5 to 10 years following the outbreak. In the stands where the mortality was not heavy the residual cover may be sufficient to retain deer in winter and lichens may then replace the loss of browse due to the mortality of *Abies balsamea*. In the areas where the mortality was more severe it is doubtful that deer can use these stands in the critical period of the winter and lichens should then be used only in early winter when browse is also available. For these

reasons the main impact of the insect outbreak in the areas of moderate to severe mortality is probably not a temporary increase in forage but the loss of cover and the potential for browse regeneration. These factors will probably be more beneficial to moose than to deer in the coming years.

Nutritive quality of browse and lichens

The results of the chemical analyses and the digestion trials are presented in Table 15. As expected, the protein content is low, in all cases, the lowest value is in lichens with 6.12%. *Abies balsamea* presents values lightly above the other browse species with 8.92% for the current season growth and 7.63% when older parts are included. The phosphorus content averages 0.10% being lowest in *Picea glauca* (0.06%) and highest in lichens *spp.*, 0.14%. The calcium content is more variable ranging from 0.21% to 1.09%, the lowest concentration being in *Larix laricina* and the highest in *Abies balsamea*. The Ca/P ratio follows the same trend, varying from 1.9 in *Larix laricina* to 9.9 in *Abies balsamea*.

In general the two digestibility estimates were consistent, the means for the six forages tested were:

1. 64.1% from the predictive equation;
2. 64.1% from 48 hours *in vitro* digestion.

There exists a good correlation between the two methods (48 hours *in vitro* and detergents-predictive equation) when comparing the

TABLE 15. Quality of the main winter forages available to deer on Anticosti Island

Forage	Composition (%)								True digestibility (%)	
	CP ¹	Ca	P	NDF ²	ADF	ADL	HEMI	CELL	From equation	In vitro 48 hrs
<i>A. balsamea</i> I ³	8.50	1.09	0.11	34.1	30.3	17.9	3.8	12.4	67.1	71.8
<i>A. balsamea</i> II ³	7.63	1.08	0.11	42.6	40.3	22.3	2.3	18.0	60.4	60.6
<i>P. glauca</i>	6.56	0.66	0.06	45.6	34.8	15.5	10.8	19.3	61.2	59.2
<i>P. mariana</i>	6.31	0.37	0.10	46.8	35.8	16.5	11.1	19.3	59.6	59.3
<i>L. laricina</i>	6.50	0.21	0.11	48.9	42.6	22.8	6.3	19.7	55.4	57.3
Lichens spp.	6.12	0.54	0.14	21.3	6.9	3.0	14.4	3.9	80.9	76.3
<i>B. papyrifera</i>	7.75	0.44	0.10	53.4	44.0	19.6	9.4	24.4	54.9	-

¹ Crude protein = N x 6.25

² NDF: neutral detergent fiber; ADF: acid detergent fiber; ADL: lignin; HEMI: hemicellulose; CELL: cellulose

³ *A. balsamea* I is previous year growth only; *A. balsamea* II contains 2 and 3 year old growth

results obtained for each forage. The regression equation between the two series of results is the following:

$$y = -4.77 + 1.08x \quad r^2 = 0.88 \quad n = 6$$

y = TDMD from detergents-summation equation

x = TDMD from *in vitro* fermentation + neutral detergent extraction

For unknown reasons *Abies balsamea* of the previous years appeared to be more digestible by the *in vitro* fermentation than according to the summation equation (71.8% as compared to 67.1%). On the contrary the *in vitro* digestion estimates for lichens was lower than the digestibility predicted by the summation equation (76.3% vs 81.0%). We believe that the *in vitro* results are probably more realistic especially when they are lower for conifers and lichens. As suggested above the presence of resins in conifers or complex organic substances in lichens may interfere with the action of the rumen microorganisms. However despite these problems the lichens appear to be more digestible than all the browse species analysed. *Abies balsamea* of the previous year follows at 71.8% according to the *in vitro* method and is 11.2 points higher in digestibility than *Abies balsamea* including older parts. The digestibility of this material and of the other species analysed ranged between 57.3% and 60.6%.

Forage Quality During the Snow-free Period

For most forages analysed for their content in protein, calcium and phosphorus, the change in the concentration of these nutrients could

be described by regression equations. The equation obtained when all the habitats sampled were pooled together are presented in Table 16.

Equations of the form: $CP = a \times (\text{Julian day})^b$ described best the change in protein concentration. Only two species differed from this trend, *Taraxacum officinale* in which the protein content decreased from mid-June to mid-July then increased till the last period in October; in *Vicia cracca*, the CP content also increased from August to September, although not significantly.

The phosphorus content followed the same trend as the CP content and could be described by equations of the same form, for this element *Taraxacum officinale* also differed from the other species.

The calcium content increased during the snow-free period and in some cases this increase could be described with an equation of the form:

$$Ca = a \log_{10} (\text{Julian day}) + b$$

The digestibility also follows a rather regular pattern and decreases as summer progresses (Table 16).

Seasonal Food Habits of Deer

The examination of the rumen contents of wild ungulates for determination of diets has been widely used during the last fifty years but some problems and limitations are associated with this method and must be taken into consideration before presenting the results. Norris (1943) working with sheep threw doubt upon the accuracy of the method

TABLE 16. Changes in the crude protein (CP), calcium (Ca), and phosphorus (P) content and digestibility of the main summer forages of deer on Anticosti Island ¹

Forage	Nutrient content (%)	TDMD ²	
		Mid-June	Early October
<i>Cornus canadensis</i>	$CP = 5.25 \times 10^5 \text{Jul}^{-2.015}$ $r^2 = 0.84 \quad n = 36$ $P = 1.66 \times 10^4 \text{Jul}^{-2.048}$ $r^2 = 0.63 \quad n = 36$ $Ca = 7.58 \times \log_{10} \text{Jul} - 15.38$ $r^2 = 0.90 \quad n = 36$	90	86
<i>Hieracium spp.</i>	$CP = 1.73 \times 10^6 \text{Jul}^{-2.292}$ $r^2 = 0.87 \quad n = 33$ $P = 1.60 \times 10^4 \text{Jul}^{-2.102}$ $r^2 = 0.57 \quad n = 33$ Ca = irregular increase	85	75
<i>Graminae</i>	$CP = 3.14 \times 10^7 \text{Jul}^{-2.803}$ $r^2 = 0.82 \quad n = 51$ $P = 1.12 \times 10^6 \text{Jul}^{-2.929}$ $r^2 = 0.85 \quad n = 51$ Ca = slight increase	84	72
<i>Anaphalis margaritacea</i>	$CP = 4.42 \times 10^6 \text{Jul}^{-2.440}$ $r^2 = 0.99 \quad n = 7$ $P = 2.72 \times 10^5 \text{Jul}^{-2.634}$ $r^2 = 0.87 \quad n = 7$ Ca = irregular increase	94	66

TABLE 16 (continued)

Forage	Nutrient content (%)	TDMD ²	
		Mid-June	Early October
<i>Fragaria virginiana</i>	CP = $1.01 \times 10 \text{ Jul}^{-1.731}$ $r^2 = 0.79$ n = 6	91	86
	P = $3.32 \times 10^3 \text{ Jul}^{-1.799}$ $r^2 = 0.95$ n = 6		
	Ca = $3.57 \times \log_{10} \text{Jul} - 6.85$ $r^2 = 0.95$ n = 6		
<i>Rubus pubescens</i>	CP = $1.02 \times 10 \text{ Jul}^{-2.587}$ $r^2 = 0.95$ n = 7	86	67
	P = $1.83 \times 10^3 \text{ Jul}^{-2.504}$ $r^2 = 0.98$ n = 7		
	Ca = $3.20 \times \log_{10} \text{Jul} - 6.31$ $r^2 = 0.83$ n = 6		
<i>Taraxacum officinale</i>	- -	85	91 ³
	P = irregular decrease Ca = irregular increase		

¹ From Tremblay and Huot in prep. a and b² True dry matter digestibility from summation equation (Goering and Van Soest 1970)³ Mid-September value

mainly due to the differential rate of digestion of the plant tissues and species of the diet. However only the readily identifiable particles were isolated contrary to the methods suggested more recently by Dirschl (1962), Bergerud and Russell (1964) and Scotter (1966). These authors attempted to identify all the particles retained in sieves with meshes of different sizes. Dirschl (1962), suggested that the 5.66 mm mesh size was more efficient and as accurate as the 2.66 and 4.00 mm mesh size for the determination of November diets of *Antilocapra americana*, McCaffery et al. (1974) used only the 6.35 mm mesh when the material from the smaller meshes (2.11 mm and 4.00 mm) appeared similar and Puglisi et al. (1978) recommended the same size of mesh. Consequently, it appears that the mesh size utilized in the present study (5.66 mm) is probably adequate for the determination of the diet for the periods when deer eat the same type of food (browse, forbs, grasses) as in the above studies. However, Bergerud and Russell (1964) indicated that thin lichen filaments of *Alectoria sarmentosa* could disappear from the rumen as soon as 4.5 hours after ingestion and that lichens are generally underestimated when only larger particles are retained for examination. Gaare et al. (1977) also discussed the effect of turnover time of botanical constituents on their relative abundance in the rumen. They suggested for instance that in a typical winter analysis of caribou rumen contents the importance of lichens might be underestimated (56% as compared to true contribution 70%) while less digestible material would be overestimated. In the present study the contribution of lichen in the diet is probably underestimated as it is present with undigestible and fibrous material such as *Abies balsamea* and *Picea spp.* (*in vitro* TDMD 76% as compared to 57 to 61%).

The higher digestibility of lichens probably increases their rate of passage through the rumen while the friability probably results in a greater loss through 5.66 mm meshes, both factors resulting in an under-estimation of lichens in the diet. The same problems may also affect the interpretation of the relative abundance of the seaweeds.

In early summer when forage is highly digestible the differences in retention time between highly digestible and less digestible fractions of the feed may also be increased if, as suggested by Hungate (1966: 240), the rumen retains undigested residue for a larger time to maintain the total minimal dry matter content approximately constant. However it is probable that this does not appreciably affect our results as these undigested fragments are probably too small to be retained in the sieve.

The results of the examination of 110 rumen samples obtained during the snow-free period are summarized in Tables 17 and 18 and in Figure 13. Two items appear particularly important, accounting together for more than 25% of the diet in every period, these are *Cornus canadensis* and *Graminae*. The former increases in importance as the season progresses and the latter is most important in early spring and ranges between 7% and 15% for the rest of the season. The other items are present only during short periods. *Taraxacum officinale* can be considered important only between mid-May and mid-August while the deciduous browse species appears in appreciable amounts between late-May and early-November. In May and June the diet is mainly composed of the first green plants to appear in abundance (*Equisetum spp.*, *Graminae spp.* and *Taraxacum*

TABLE 17. Relative abundance (%) ¹ of the main groups of plants in the rumen samples of deer of Anticosti Island according to the period of the year

Period	Relative percentage by period ¹								
	Forbs	Graminoids	Browse ²	Lichens	Mushrooms	Horsetails	Ferns	Mosses	Seaweed
Feb 03-Mar 08	0.0	0.0	86.6	12.5	0.2	0.0	0.0	0.0	0.7
Apr 13-18 (ID) ³	2.9	1.6	89.9	4.6	0.3	0.0	0.0	0.0	0.7
Apr 13-18 (CD) ³	0.3	9.0	49.5	1.7	0.2	0.0	0.0	0.0	39.3
May 15-Jun 14	30.2	54.2	9.0	0.7	0.1	5.1	0.4	0.3	0.0
Jun 18-Jul 13	71.9	6.7	19.6	0.0	0.3	0.8	0.7	0.0	0.0
Jul 14-Aug 26	72.1	7.5	18.3	0.0	1.6	0.2	0.3	0.0	0.0
Sep 02-Nov 04	69.4	6.2	20.4	0.1	2.7	0.2	0.5	0.5	0.0
Nov 05-Dec 12	67.4	14.5	13.3	0.8	0.6	3.4	0.0	0.0	0.0

¹ Percentages according to the point sampling method for the snow-free periods, for Feb-April periods according to the dry weight

² Leaves, needles and twigs of trees and shrubs

³ ID: interior deer; CD: coastal deer, feeding on seaweed

TABLE 18. Relative abundance (%) ¹ of the parts of plants in the rumen samples of deer of Anticosti Island according to the period of the year

Period	Stems ²	Leaves	Twigs- needles	Flowers	Fruits	Roots	Thallus	Unknown
Feb 03-Mar 08	tr ³	tr	86.6	0.0	0.0	0.0	13.2	0.2
Apr 13-18 (ID) ⁴	0.5	4.0	89.9	0.0	0.0	0.0	5.6	0.0
Apr 13-18 (CD) ⁴	2.0	4.1	49.5	0.0	0.0	3.2	41.2	0.0
May 15-Jun 14	7.7	82.0	6.1	0.3	0.0	0.6	1.1	0.0
Jun 18-Jul 13	6.6	86.9	3.6	2.5	0.1	0.0	0.3	0.0
Jul 14-Aug 26	8.4	85.5	2.5	0.4	1.7	0.0	1.6	0.1
Sep 02-Nov 04	9.9	80.4	3.9	0.1	0.9	0.8	3.3	0.0
Nov 05-Dec 12	10.8	82.7	5.1	0.0	0.0	0.0	1.4	0.0

¹ Percentages according to the point sampling method for the snow-free periods, according to dry weight for Feb-April periods

² Stems of graminoids and forbs only

³ Less than 0.1%

⁴ ID: deer collected in the interior of the Island; CD: coastal deer feeding on seaweed

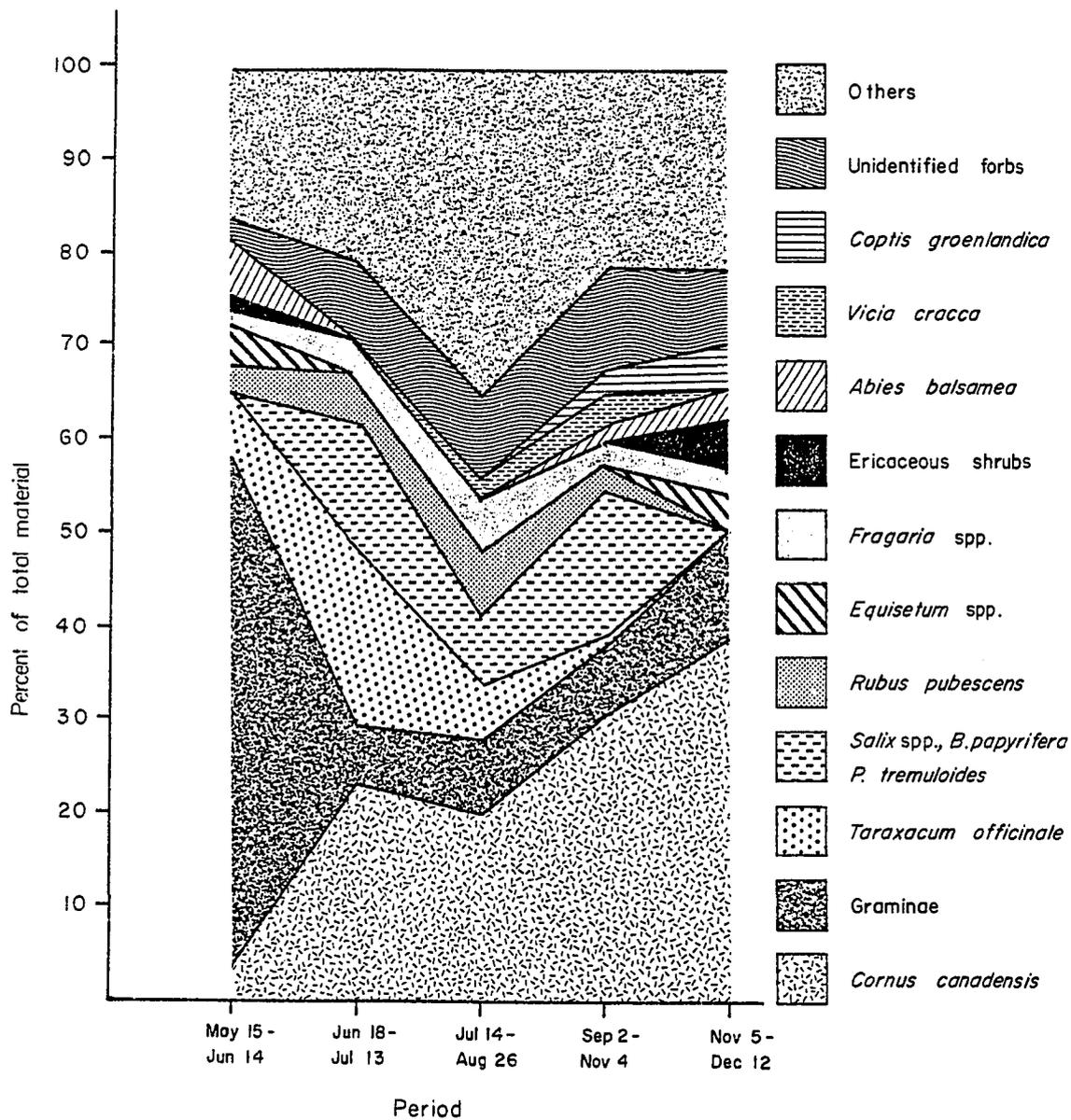


Figure 13. Diet of deer of Anticosti Island during the snow-free periods according to the rumen content analyses

officinale) and of plants retaining green leaves (Ericaceous shrubs and *Abies balsamea*). In mid-summer the diet is much more diversified (47 items identified) and in late fall the plants that retain green leaves and are protected in the understory (*Coptis groenlandica*, *Mitella nuda*, *Linnea borealis*, *Equisetum spp.* and *Cornus canadensis*) account for 54% of the diet. As a group the forbs dominate the diet from mid-June to mid-December, averaging 70.5% for all the rumen samples collected during this period while the contribution of browse ranges from 13.3% to 20.4% during the same period (Table 17). The gramineae are important in spring (May 15 - June 14) representing 54.2% of the rumen contents as compared to 30.2% for the forbs and 9.0% for browse. After leaf fall gramineae appear to increase in importance (14.5%, November 05 - December 12) while browse decreases to 13.3% as compared to an average of 19.4% for the three preceding periods.

The relative importance of the plant parts is given in Table 18. During the snow-free period leaves dominate the diet, ranging from 80.4% to 86.9%. Fruits and flowers are only of minor importance in the diet.

The contents of the rumens of 33 deer collected in winter were examined and the results are presented in Figures 14 and 15 and Tables 17 and 18. Figure 14 includes all deer while Figure 15 includes only deer killed more than 1.5 km away from the shore and represents conditions more typical of the interior of the island. Among deer from the interior of the island, *Abies balsamea* dominates the diet, increasing from 70.4% in February-March to 76.2% in April. Lichens decrease from 14.4% to

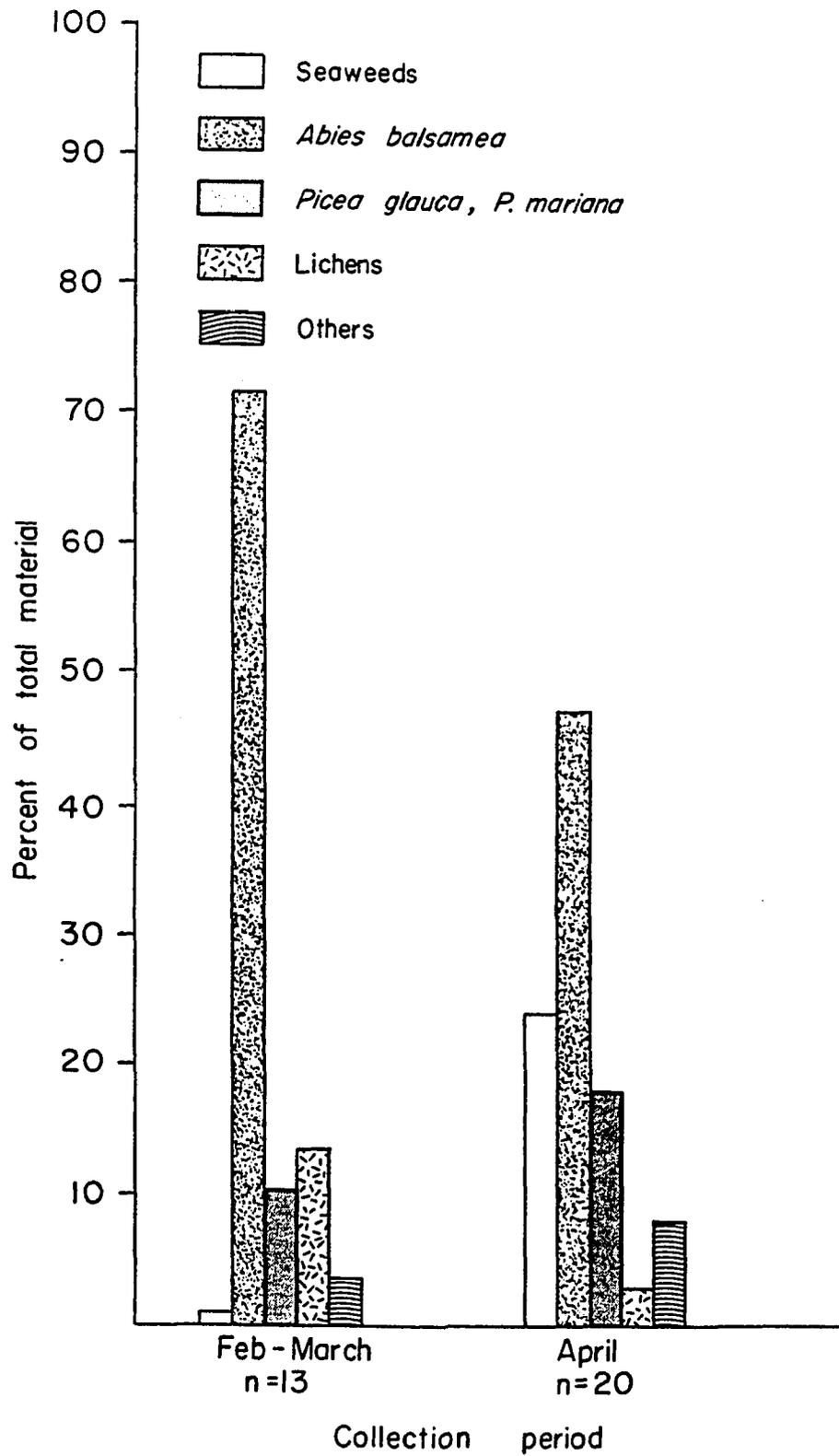


Figure 14. Composition of the rumen contents of deer collected in winter on Anticosti Island

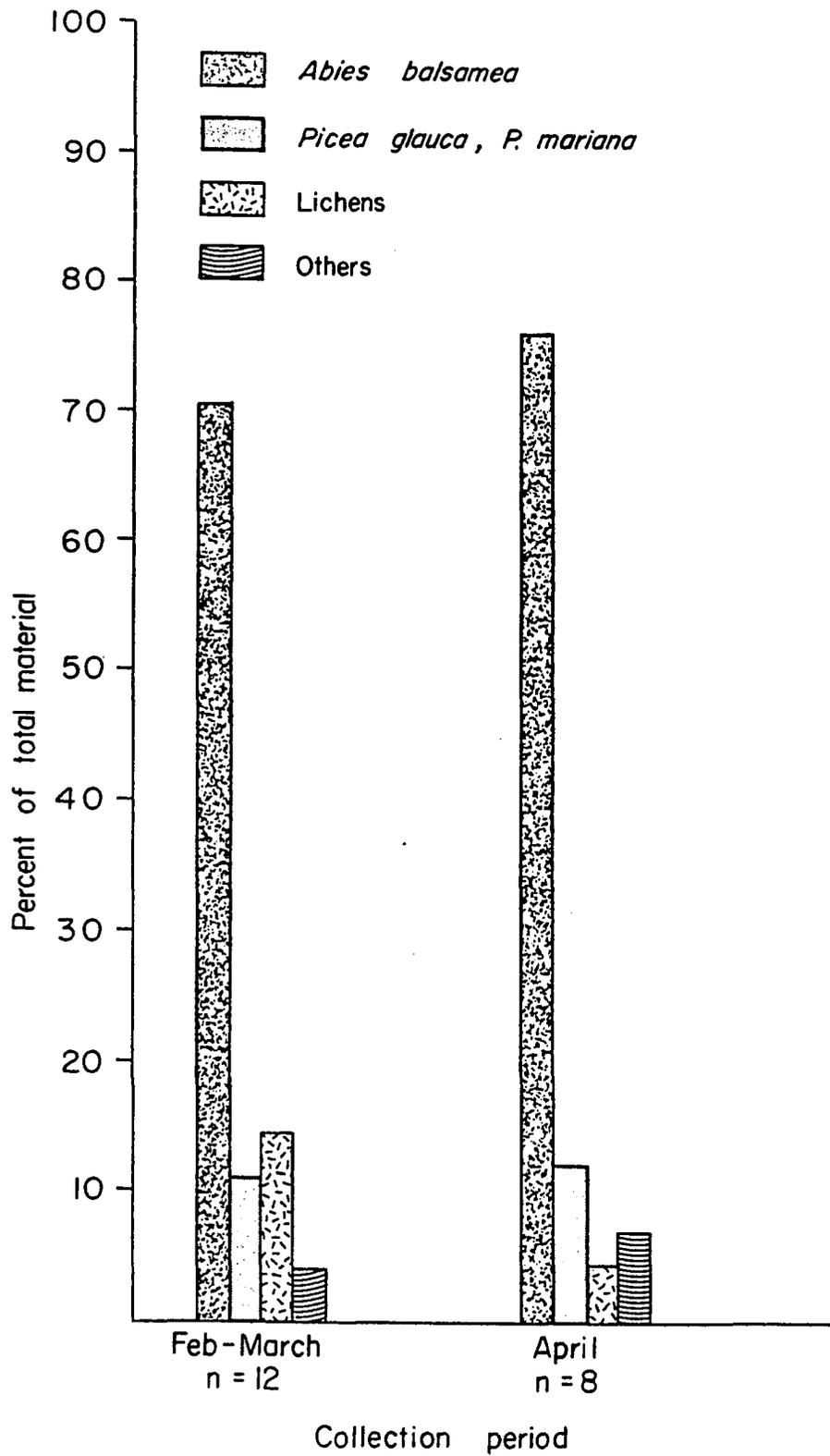


Figure 15. Composition of the rumen contents of deer collected in the interior of Anticosti Island during winter

4.6% during these months, while *Picea glauca* and *P. mariana* average 11.5%. Seaweeds constitute 39.3% (6.0% to 59.6%) of the rumen contents of deer collected near the coast and are followed by *Abies balsamea* which makes up 24.2%. Three deer found dead or dying are not included in this sample. *Picea glauca* made up 75%, 95% and 100% of their rumen contents respectively.

Analysis of the rumen samples shows that *A. balsamea* represents 98.5% of the browse eaten by inland deer in February, March and April 1977 (excluding *Picea spp.*), when the snow depth exceeded 1.25 m. According to the browse survey this species accounted at that time for 97.4% of browse biomass available and should have accounted for 87.1% of the twigs eaten (85% of the biomass). This difference in the results (85% vs 98.5%) seems reasonable when one considers the problems associated with the random sampling of deer in the wild and those associated with vegetation surveys.

Analysis of the winter rumen contents gives results on a more restricted area than the browse surveys but includes informations on items that could not be reflected in browse surveys. The presence of *Picea spp.* in the diet was confirmed and the importance of lichen could be assessed for inland deer. Ninety percent of the deer collected in winter had *Picea spp.* in their rumens but these species accounted for only 10.6% of the rumen material identified. Lichens were present in 96% of the rumens of inland deer but accounted for only 9.5% (0%–59%) of the dry weight of the rumen content. All the coastal deer collected in April had eaten seaweed which accounted for 39.3% of the diet (6.0%

to 86.4%). However, it seems that seaweed is not accessible before late winter (mid-March), before this date the coast is covered with ice and snow. Even then, only a small proportion of the total population concentrated on the south shore will include seaweeds in their diet.

The results of the browse surveys and the rumen contents analyses clearly show that deer have to rely mainly on *Abies balsamea*, *Picea spp.* and arboreal lichens in winter on Anticosti Island. *Abies balsamea* is a common species in the deer habitat of the northeast and is reported to be an important browse species in some areas (Dahlberg and Guettinger 1956: 63-76; Silver 1968; Huot 1973). However its nutritive value is generally reported to be low and it was considered to be a *starvation species* by Dahlberg and Guettinger (1956: 67) or even *worthless* by Maynard et al. (1935). Ullrey et al. (1968) concluded that this species was poorly accepted and that its digestibility was very low in digestion trials. Mautz et al. (1976) found a low apparent digestibility of the crude protein (11.3%) of *Abies balsamea*, a rather high apparent digestibility of the energy (49.6%), a high calorigenic effect (1.20 kcal/g dry weight). The value of *Abies balsamea* is probably even lower on Anticosti where deer consume more than the current year growth. *Picea glauca* and *Picea mariana* are usually not considered as browse species and there exists no published report on digestion trials conducted for these species with white-tailed deer. The chemical analysis and *in vitro* digestion trials conducted for the present study indicate that the current annual growth of these species is less digestible (12 units) than equivalent portions of *Abies balsamea*. These species also appear to be negatively selected as they are much more

available than *Abies balsamea* but account for only 10.6% of the rumen contents. Arboreal lichens are the only forages that could improve the value of the winter diet of the inland deer. This group of plants is not reported as a significant forage source for white-tailed deer, and attempts to conduct *in vivo* digestion trials with *Usnea barbata* by Silver and Colovos (1957) failed as this species was not accepted by the deer. However Cowan (1945) reported that this arboreal lichen (*Usnea barbata*) comprised 36% of the stomach contents of black-tailed deer killed in winter on the coast of Vancouver Island. Arboreal lichens are also reported to be the main winter food of musk deer (*Moschus moschiferus*) in USSR accounting for 70-90% of the stomach content by weight (Bannikov et al. 1978). The true *in vitro* dry matter digestibility of the lichens estimated in the present study (48 hours: 76.3%) is 15.3 units higher than for *Abies balsamea* and this could be sufficient to increase significantly the availability of digestible energy in the winter diet.

The Quality of the Rumen Contents

A total of 79 washed fractions and 105 unwashed fractions of rumen contents were analysed. The results are presented in Table 19 and Figures 16, 17 and 18. The four characteristics (dry matter, calcium, phosphorus and protein contents) show a regular pattern of seasonal variation. The dry matter content of the unwashed fraction is highest in winter (19.2% in February-March) and reaches its lowest value (10.2%) in June-July. Nitrogen content also shows a regular pattern with the

TABLE 19. Composition of the unwashed and the washed fractions of the rumen contents of deer collected on Anticosti Island

Period	Treatment	n	Dry matter content % ± s.d.	Composition of dry matter (% ± s.d.)		
				N	Ca	P
Feb 03-Mar 08	U ¹	13	19.2 ± 2.63	1.99 ± 0.16	0.91 ± 0.26	1.12 ± 0.14
	W ¹	13	- -	1.00 ± 0.11	0.80 ± 0.18	0.10 ± 0.04
Apr 13-18 (ID) ²	U	8	18.6 ± 1.27	1.87 ± 0.20	0.97 ± 0.18	1.14 ± 0.18
	W	8	- -	0.99 ± 0.12	0.79 ± 0.16	0.11 ± 0.07
Apr 13-18 (CD) ²	U	11	17.3 ± 1.54	2.33 ± 0.21	1.00 ± 0.16	1.09 ± 0.10
	W	10	- -	1.86 ± 0.54	0.97 ± 0.35	0.14 ± 0.04
May 15-Jun 14	U	9	13.6 ± 1.74	3.85 ± 0.86	1.31 ± 0.42	1.59 ± 0.31
	W	8	- -	2.25 ± 0.50	0.81 ± 0.22	0.16 ± 0.03
Jun 18-Jul 13	U	6	10.2 ± 0.75	5.17 ± 0.48	1.46 ± 0.15	2.14 ± 0.23
	W	10	- -	2.79 ± 0.40	1.11 ± 0.20	0.39 ± 0.12
Jul 14-Aug 26	U	22	11.9 ± 1.63	4.05 ± 0.45	1.68 ± 0.42	1.92 ± 0.31
	W	16	- -	2.28 ± 0.36	1.06 ± 0.23	0.26 ± 0.11
Sep 02-Nov 04	U	28	12.4 ± 2.64	3.90 ± 0.67	1.89 ± 0.48	1.90 ± 0.29
	W	8	- -	1.80 ± 0.43	1.06 ± 0.23	0.17 ± 0.03
Nov 05-Dec 12	U	8	17.2 ± 1.65	2.97 ± 0.75	1.87 ± 0.60	1.97 ± 0.38
	W	6	- -	1.25 ± 0.11	1.21 ± 0.21	0.15 ± 0.08

¹ U: unwashed; W: washed

² ID: deer killed in the interior of the Island; CD: coastal deer eating seaweed. Differences between ID and CD non significant ($p < 0.05$) except for N contents for which the differences are significant ($p < 0.01$)

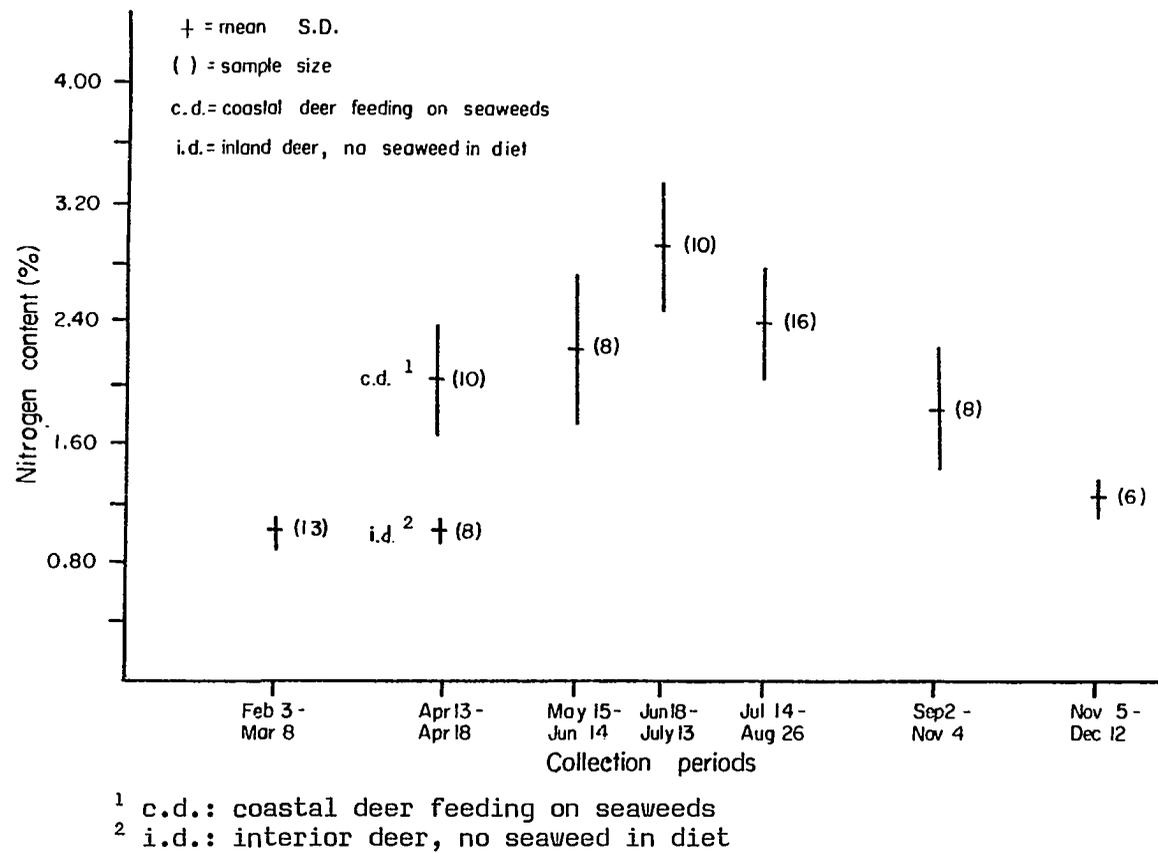
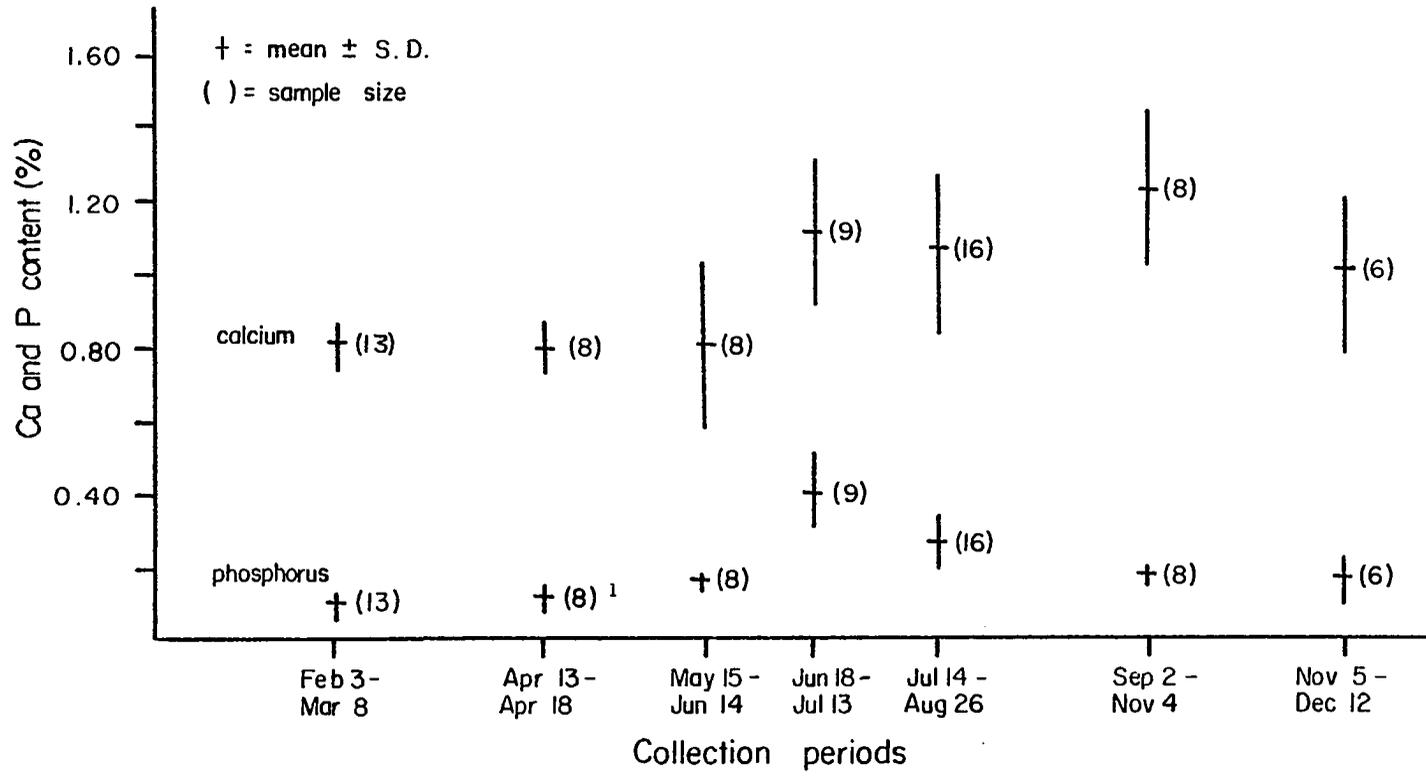


Figure 16. Variation in the nitrogen content of the washed fraction of the rumen contents according to the periods of the year



¹ Interior deer only, for coastal deer P content = 0.14

Figure 17. Variation in the calcium and phosphorus content of the washed fraction of the rumen contents of Anticosti deer according to the period of the year

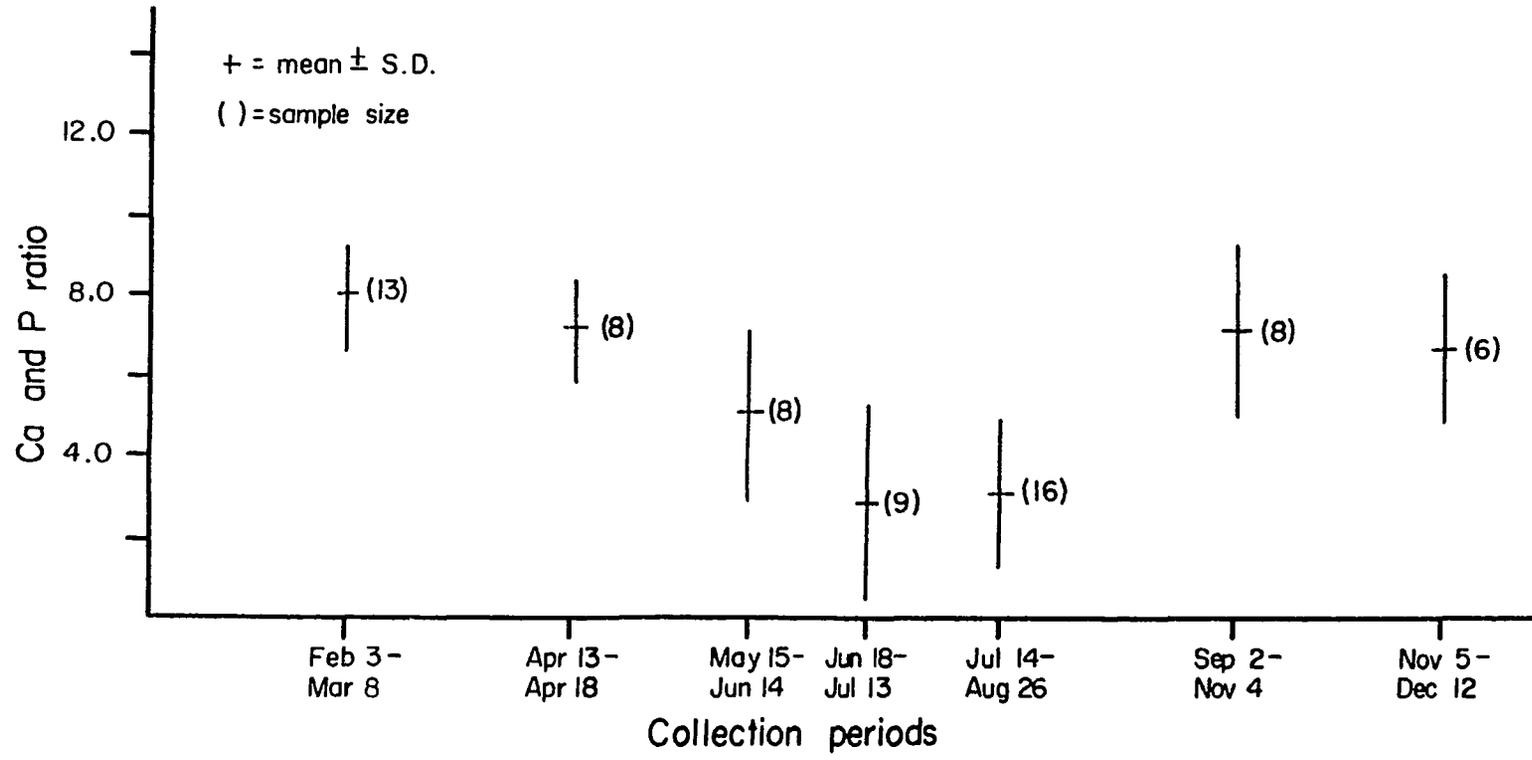


Figure 18. Variation in the calcium-phosphorus ratio of the washed fraction of the rumen contents according to the period of the year

highest concentration of 5.17% reached in June-July, while there is a steady decline after that until late winter (1.87% in April). At that time animals feeding on seaweed have a significantly ($P < 0.005$) higher concentration of nitrogen in their rumens. The calcium content is also lowest in February and March and increases until late summer, the highest concentrations are reached after late August. Finally, the phosphorus content increases from February to June-July (1.12% to 2.14%) then it appears to decline slightly or stabilize until the end of the summer.

In order to determine if the washed fraction was similar to the diet established by the identification of the species present in the rumen, and if both results were consistent, we compared the nitrogen content of the washed fraction to the nitrogen content of the vegetation identified in the rumen. For each deer we combined the results of the rumen content identification with the predicted nitrogen content of the major items according to the vegetation analyses and the prediction equations. We retained only the specimens for which we could estimate protein concentration values for at least 80% of the content, the remaining part (0 - 20%) was estimated using the average nitrogen content of similar type of plants for that time of the year.

Thirty-five specimens were analysed for the snow-free period and 32 for the winter (Figure 19). In a first attempt we had grouped all deer but a second analysis separating the two seasons greatly improved the determination coefficients. The individuals of the May-June period were omitted because they contained too high a percentage of

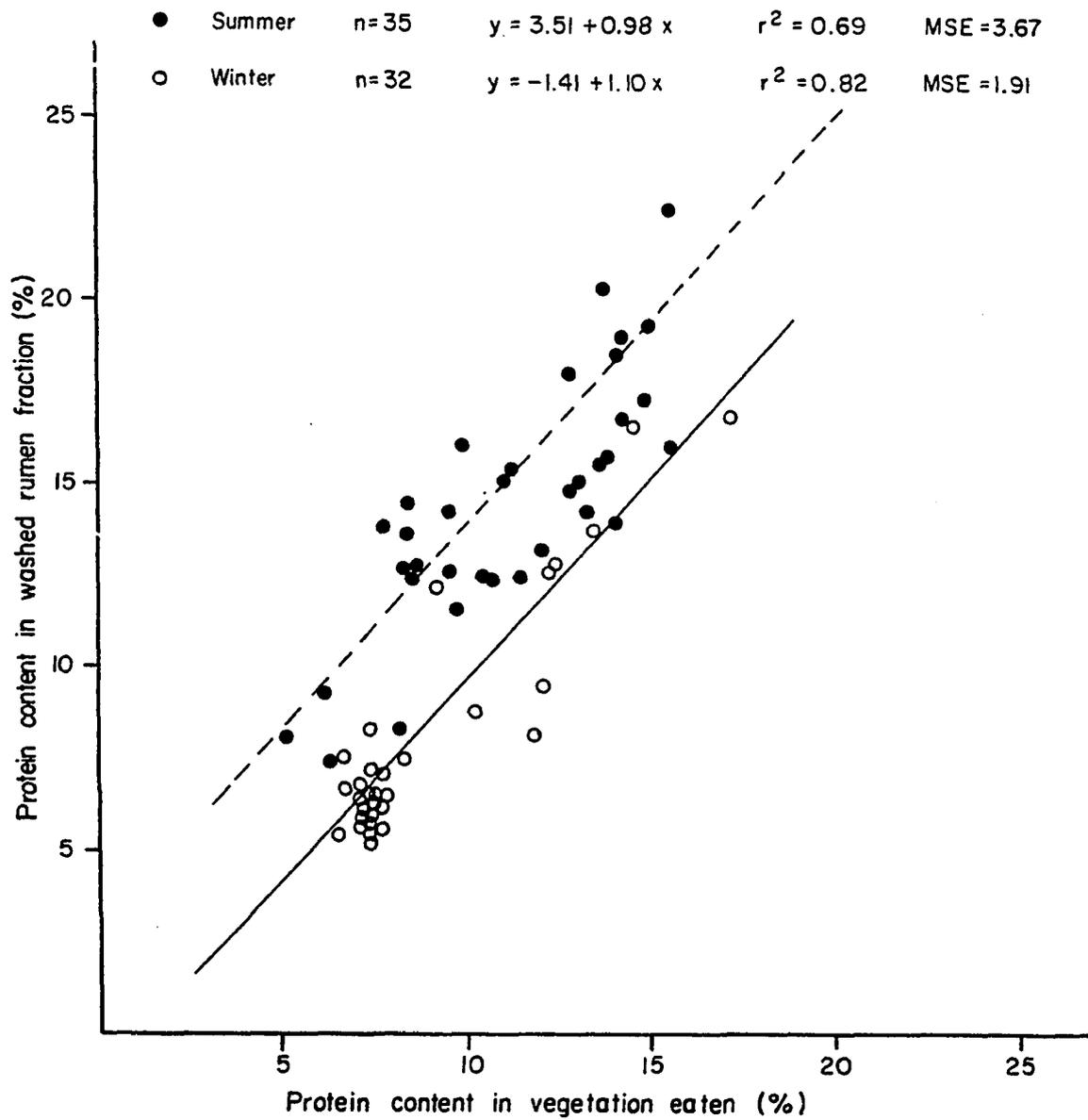


Figure 19. Relation between the protein content in the washed fraction of the rumen content and the vegetation eaten by deer

graminoids that could not be identified as young or old. As the predicted contents in the two groups are very different, 25% as compared to 4%, a small error of identification would have resulted in a large error in the prediction of the protein content. The coefficients of determination between the protein content of the washed fraction of the rumen contents and the protein content in the vegetation eaten when the winter sample and the summer samples are considered separately are relatively high (r^2 (summer) = 0.69, r^2 (winter) = 0.82). In both cases the slope (b) was not different from 1.00 ($P < 0.10$), but the average difference between the value of the washed fraction and the value of the vegetation was different from 0 ($P < 0.001$, $\bar{x} = 3.34$ in summer and $P < 0.05$, $\bar{x} = -0.54$ in winter). In summer the nitrogen content of the rumen contents is slightly higher than predicted by the analysis of the vegetation and might be due to selectivity by deer, however in winter the reverse was observed. This may be due to the loss of conifer needles through the sieves while the twigs were larger and did not pass through as easily, resulting in a bias against the needles which probably contain a higher concentration of nitrogen than the main part of the twig. Although the interpretation of the nitrogen content of gross samples of rumen contents as reported by Bissel (1959) and Kirkpatrick et al. (1969) poses problems due to the presence of non-protein nitrogen or protein nitrogen originating from the saliva and recycling of urea (Wood et al. 1960), Klein (1962, 1968) suggested that the nitrogen content of washed rumen samples are representative of the forage eaten by deer. More recently Yalden (1978) working on red deer in captivity did not find any effect of the time-after-feeding on the close relationship between the

nitrogen content of the food eaten and the rumen contents and calculated that time-after-feeding would not be an important source of variation in field studies. We also consider the washed fraction of rumen contents to be representative of the material eaten by deer. The nitrogen content of the washed fraction is lowest in winter, averaging 1.00% for inland deer during this period; it increases rapidly in spring and early summer to reach a maximum of 2.79% in June-July. The calcium content increases from a mid-winter minimum of 0.80% to a mid-fall maximum of 1.21% while the phosphorus content increases from a mid-winter minimum of 0.10% to a mid-summer maximum of 0.40%. The Ca/P ratio is minimal in summer (June-July, 2.85: 1) and reaches a maximum of 8.00:1 in February-March.

These changes appear to follow the changes in the nutrient content of the vegetation sampled during these periods. The decline in N content from the June-July period to winter parallels the decline described by the equation of Table 16. The lower value of the May-June period is due to the low availability of new forage so that the dietary requirements cannot be met without heavy use of *Graminae* of the previous year. The decline in phosphorus levels is also similar to those described by the equation of Table 14. For the same reasons as above the May-June value is lower than expected. The increase in Ca is less regular but also less predictable in the vegetation, the lower value of the November-December period is probably due to the increase in *Graminae* in the diet during this period.

Annual Cycle of Food Quality in Relation to Estimated Deer Maintenance Requirements

During recent years it has become evident that estimation of the quality of the diet of wild ungulates has to be based on its adequacy to meet the seasonal needs of the different categories of individuals in the population (fawns, adult males, adult females, ...) for their maintenance and their type and rate of production (milk, growth, hair, foetus, ...).

Numerous studies on the energy expenditure or requirements of white-tailed deer have been conducted during recent years (Silver et al. 1969, 1971; Ullrey et al. 1969, 1970; Stevens 1972; Jacobsen 1973; Thompson et al. 1973; Robbins 1973; Mattfeld 1974; Holter and Hayes 1977; Holter et al. 1977, 1979b; Fair 1978; Moen 1978; Verme and Ozoga 1980a, 1980b). Protein requirements have also received increased attention (Ullrey et al. 1975; Robbins et al. 1974a, 1974b; Smith et al. 1975; Holter et al. 1977, 1979a, 1979b; Verme and Ozoga 1980a, 1980b) but mineral needs are still largely unknown although research has been conducted on phosphorus and calcium requirements (French et al. 1955, 1956; Magruder et al. 1957; Ullrey et al. 1973, 1975).

Energy and protein requirements estimates for white-tailed deer are available mainly for young individuals and adult does. These parameters and the concentration of metabolizable energy and protein in the diet will be considered as predetermined and known values in the following attempts to balance the protein and energy budget of deer at

maintenance. The intake will be considered the variable that must be adjusted to meet the requirements with a given quality of food. Based on published data on food intakes it will be possible to assess the resulting energy and protein balances. The categories of individuals were chosen according to the availability of the published estimations of needs (weaned young 4-16 months and adult does).

Based on those reports it is possible to compare the nutritive characteristics of the diet of the Anticosti deer population to the needs of the same category of animals for maintenance. Three parameters are determinant in this examination:

1. the nutrient content of food (kcal M.E./g, g protein/100 g, gP/100 g, gCa/100 g) (1 kcal = 4.184 J);
2. the daily requirements of the animal (kcal M.E., g protein or N), and for minerals the concentration suggested (g/100 g);
3. the voluntary intake (g dry matter/day).

Calcium and phosphorus

Calcium and phosphorus requirements are maximum during growth for the formation of bones in most animals, milk production also requires appreciable amounts of those elements. In cervids, the formation of antlers adds to the requirements of calcium and phosphorus. Maynard and Loosli (1969: 158) stated that an adequate calcium and phosphorus nutrition is dependent upon three factors: a sufficient supply of each

element, a suitable ratio between them, and the presence of vitamin D. French et al. (1956) concluded that the quantitative requirements for calcium and phosphorus by white-tailed deer although not definitely ascertained were in excess of 0.09% calcium and 0.25% phosphorus. Workers of the same team reported later (Magruder et al. 1957) that a 16.9% protein diet containing 0.59% calcium and 0.54% phosphorus resulted in the *best antler growth*. However it is not possible to determine which elements or if protein were limiting in the other diets. More recently workers at Michigan State University (Ullrey et al. 1973) reported that 0.40% dietary calcium in the presence of 0.25% to 0.27% phosphorus was adequate for normal development of the fawn after weaning. The same workers (Ullrey et al. 1975) concluded that fawns do not require more than 0.26% dietary phosphorus (0.28% on a dry basis) for optimum development when calcium levels vary between 0.46% and 0.51%. The recommended levels for sheep (NBC 1975) range between 0.1% and 0.37% phosphorus and 0.21% and 0.52% calcium for maintenance to high production levels.

It is generally accepted that the desirable calcium:phosphorus ratio lies between 1:1 and 2:1, however ratios between 1:1 and 7:1 are generally satisfactory when the supply of phosphorus is adequate.

According to the analysis of the washed fraction of the rumen contents the calcium (Figure 16) content of the diet appears to be more than adequate in all periods. However phosphorus levels are above 0.25% only between mid-June and late August and vary between 0.15 and 0.17 for the rest of the spring to the fall periods. These levels are probably

inadequate for maximum growth, and the winter levels (0.10-0.14) are 0.03% to 0.06% lower than the lowest recommended levels for the maintenance of sheep. The Ca:P ratio of the unwashed fraction varies between 2.81:1 and 8.5:1 which is probably adequate. Adequate phosphorus levels in the rumen are probably maintained by the considerable amounts of phosphorus that can be recycled through the salivary glands as the phosphorus levels of the unwashed fraction of the rumen contents are at least ten times higher than the levels measured in the washed fraction between late-August and mid-June. During the year, the resulting Ca:P ratios in the rumen vary only slightly between 1.0:1 and 1.5:1.

Energy

The parameters used for the estimation of the metabolizable energy required for maintenance of an adult doe are summarized in Table 20. Their estimation follows the procedure described below.

1. True digestible energy estimation (TDE). The gross energy content of the main food items of the summer diet and the digestibility of the dry matter (TDMD) were based on the estimates of Tremblay and Huot (in prep. b). The digestibility of the energy was considered to be equal to the digestibility of the dry matter. For the winter periods, the values obtained from the *in vitro* digestion trials (Table 15) were used as estimates of the true digestibility of the energy and were applied to the composite diet of Figure 15. The procedure for the estimation of the TDE content of the composite winter diet is given in Appendix 1, the same procedure was followed for the summer diet.

TABLE 20. Estimates of the dietary energy values and of the maintenance metabolizable energy requirements (MMER) of an adult doe (see text for explanations)

Period	Energy values of the composite diet						Daily Maintenance requirements FHP x (net energy efficiency) ⁻¹ (kcal / kgW ^{0.75})
	TDE ¹		ADE		ME		
	(%) ²	kcal/g	(%)	kcal/g	(%)	kcal/g	
Feb 03 - Mar 07	62.8	3.03	45.4	2.19	33.9	1.62	97.5 x 1.55 = 151.1
Apr 13-18	61.2	3.03	41.5	2.05	30.7	1.52	97.5 x 1.57 = 152.8
May 15 - Jun 14	72.6	3.46	56.0	2.67	45.9	2.19	146.3 x 1.46 = 214.0
Jun 18 - Jul 13	86.8	3.76	74.1	3.21	60.8	2.63	146.3 x 1.37 = 200.8
Jul 14 - Aug 30	85.8	3.66	72.8	3.11	59.7	2.55	146.3 x 1.38 = 201.8
Sep 02 - Nov 04	85.4	3.69	72.3	3.12	59.3	2.56	146.3 x 1.38 = 201.8
Nov 05 - Dec 12	83.8	3.57	70.3	2.99	57.6	2.45	97.5 x 1.39 = 135.5

¹ Abbreviations: TDE: true digestible energy; ADE: apparent digestible energy; ME: metabolizable energy; FHP: fasting heat production

² As a percentage of GE (gross energy)

2. Estimation of the apparent digestible energy (ADE). As the winter diet is mainly composed of browse, the estimation of the ADE was based on the difference of 19.1 units of digestibility between ADE and TDE for browse rations reported by Robbins et al. (1975a). For the other periods we used the equation suggested for cattle (Goering and Van Soest 1970):

$$M = 36.57 - 0.275X$$

M: estimated metabolic fecal losses
X: estimated true digestibility

This equation seems more appropriate than the (12.9 units) constant normally used for sheep as in feeding trials conducted with deer by Robbins et al. (1975a) the metabolic fecal excretion varied from 14.0 to 20.5 for corresponding digestibilities of 74.0% and 61.9%.

3. Estimation of the metabolizable energy (ME). This parameter was estimated for the first two periods (diet mainly composed of *A. balsamea*) using the ME/ADE ratio reported by Mautz et al. (1976) for this browse species (0.74). For the snow-free periods the 0.82 ratio suggested by ARC (1965) and NRC (1976) was used.

4. Net energy efficiency. The equation suggested by Blaxter (1962: 233-235) to describe the relationship between the efficiency of the metabolizable energy to meet maintenance needs and the concentration of metabolizable energy in the diet as a percentage of the gross energy was used to estimate the net energy efficiency factor.

$$E = 54.6 + 0.30 Q$$

Q: metabolizable energy as a percentage of the gross energy
E: metabolizable energy efficiency to meet maintenance needs
(net energy efficiency)

The fasting heat production (FHP) values used are those estimated by Silver et al. (1969) as recalculated by sex and age classes by Moen (1973). For the young individuals (Table 21) similar procedures were used for the periods between February and July as the FHP values of Silver et al. (1969) from Moen (1973) are available. Other estimates are based on the feeding trial results reported by Thompson et al. (1973) and Holter et al. (1979b). We used the January-March estimate of Thompson et al. (1973) for our November-April periods, their May-August average for yearlings for our May-August periods and their October estimate for our September-November period.

For the adult doe the only other maintenance metabolizable energy requirement estimate available was 131 kcal/kgW^{0.75}/day given by Ullrey et al. (1970). This estimate based on feeding trials in winter is lower than the 151.1 to 152.8 estimate suggested in Table 20 but the feed utilized in the Michigan trials was much more digestible (ADE: 65.4%) than the natural winter forages of Anticosti Island and their expected net energy efficiency would be 74% as compared to 64% using the equation of Blaxter (1962: 235). For the same reasons the winter MMER of the fawn (Table 20) are higher when estimated from the FHP of animals on diets with low net energy efficiencies than when estimated from feeding trials using highly digestible pelleted ratios. According

TABLE 21. Estimates of the maintenance metabolizable energy requirements (MMER) of young deer (TDE, ADE, and ME as in Table 18)

Period	FHP x (net energy efficiency) ⁻¹ (kcal/kgW ^{0.75} /24 hrs)	From feeding trials ¹		Ranges and Medians
		Thompson et al., 1973	Holter et al., 1979b	
Feb 03-Mar 07	90.1 x 1.55 = 139.7 (F) ²	125 (F)	116-127 (F)	116-140 (130-F) ³
April 13-18	90.1 x 1.57 = 141.5 (F)	125 (F)	116-127 (F)	116-141 (130-F)
May 15-Jun 14	130.6 x 1.46 = 190.7 (FY)	173 (FY)	182 (FY)	173-191 (180-FY)
Jun 18-Jul 13	130.6 x 1.37 = 178.9 (Y)	173 (Y)	182 (Y)	173-182 (180-Y)
Jul 14-Aug 26	-	173 (Y)	182 (Y)	173-182 (180-Y)
Sep 02-Nov 04	-	166 (F)	182(Y) - 156(F)	155-166 (160F) (180Y)
Nov 05-Dec 12	-	125 (F)	116-127 (F)	116-127 (120-F)

¹ Modified (see text)

² (F): fawn; (Y): yearling; (FY): 11-12 months

³ Medians to nearest 5 units

to the prediction equations of Moen (1978), the metabolizable energy requirements of a deer would be at a minimum on Julian day 31 and would average $123 \text{ kcal/kgW}^{0.75}$ (snow depth: 0 cm); however, his estimates were also obtained with animals fed pelleted rations, probably with a high net energy efficiency.

Protein

The protein requirements for maintenance can be estimated factorially by adding the minimal losses of nitrogen or protein represented by:

1. endogenous urinary nitrogen (EUN);
2. metabolic fecal nitrogen (MFN), and
3. skin and hair losses (SL)

or can also be estimated from protein balances in feeding trials. Several recent publications give estimates of nitrogen losses of deer or maintenance requirements, the estimated values are given in Table 22. Based mainly on these published values we used the following formula to predict the maintenance crude protein requirements (MCPR) for deer of Anticosti Island.

$$\text{MCPR (g/day)} = \frac{(\text{EUN}) + (\text{MFN}) + (\text{SL}) \times 6.25}{(\text{TCPD}) (\text{BV})}$$

- EUN (endogenous urinary nitrogen): the $0.115 \text{ g/kgW}^{0.75}$ value for deer was retained
- MFN (metabolic fecal nitrogen): this value varies with the digestibility of the dry matter. For that reason the equation suggested by Swanson (1977) was retained: $(9.71 - 0.088\text{DDM/kg DMI})$

TABLE 22. Selected published values related to the nitrogen metabolism of deer and cattle

Animal	Diet type and CP content (%)	Protein digestibility		MFN (g/kg DMI)	EUN ¹	DMI ¹	Reference
		True (%)	Apparent (%)				
Two fawns W.t. deer	Concentrate 5-12-19-26	-	-	-	0.115	-	Robbins et al. 1974b
Published values Mule and W.t. deer	Browse Alfalfa 5 to 20	93.7	$\frac{(-4.719 + 0.397CP) 100}{CP}$	7.55 ± 3.37	-	-	Robbins et al. 1974b
Eight fawns W.t. deer	Concentrate 11-15-20-25	80-82 87-85	59.3-67.3-75.1-75.7	3.7	-	87-102	Smith et al. 1975
Five fawns- yearlings W.t. deer	Concentrate 12 to 24	74	70	1.0	-	71.9	Holter et al. 1977
Six yearlings W.t. deer	Concentrate 8 to 24	89.4	42 to 78	5.3	0.766	82.8	Holter et al. 1979a
Published values cattle	Various types	-	$\frac{(-3.16 + 0.898CP) 100}{CP}$	9.71 - 0.088DDM	0.44	-	Swanson 1977

¹ EUN: endogenous urinary nitrogen (g/kgW^{0.75}); DMI: dry matter intake (g/kgW^{0.75})

² Holter et al. (1979a) also suggested a 5.8% minimum concentration of CP in diet to meet maintenance requirements, and estimated nitrogen maintenance requirements at 0.766 g/kgW^{0.75}

- SL (skin losses): as no value exists for deer the 0.035 gN/kgW^{0.6} suggested by Swanson (1977) was retained
- TCPD (true crude protein digestibility): this value varies between 74% and 93.7% in Table 20. This variation is probably due to the digestibility of the dry matter, the less digestible material being retained a longer time in the rumen, the digestion of protein can be more complete. For that reason, the 93.7% value suggested by Robbins et al. (1974b) was used for winter conditions and an arbitrary value of 85% (based on the estimates of Table 20) was used for the snow-free period
- BV (biological value): the biological value of the protein is based on the estimate of Robbins et al. (1974b):
 $\text{Log}_e \text{BV} = 4.9825 - 0.3096 \ln \text{CP}\%$

Incorporating these estimates in the formula gives the following estimator for the maintenance requirements of dietary crude protein in g/day (MCPR).

$$\text{MCPR} = \frac{|0.115(W_{\text{kg}}^{0.75}) + (9.71 - 0.088\text{DDM}_{\%})(\text{DMI}_{\text{kg}}) + 0.035 (W_{\text{kg}}^{0.60})| \times 6.25}{(\text{TCPD}) - \chi (e^{(4.9829 - 0.3096 \ln \text{CP})})}$$

Food intake

From the estimates of energy needs for maintenance (Tables 20 and 21) and forage digestibility (Table 20) it is possible to determine the required food intake (DMI) to meet those needs. From these DMI and the level of CP in forage it is also possible to determine if maintenance protein requirements will be met. Finally the comparison of those DMI estimates to the published values of DMI for deer can be used to assess the energy and protein balances. The dry matter intakes required to meet the energy demands given in Tables 20 and 21 are presented in Table 23 with the resulting crude protein intakes and requirements and the daily predicted protein balances.

TABLE 23. Dry matter intake (DMI) required to meet maintenance energy requirements of white-tailed deer on Anticosti and the resulting effects on protein balance

Period	DMI required ¹ g/kgW ^{0.75}		CP required ² (g/day)		CP intake ³ (g/day)		CP balance (g/day)	
	Adult doe	Young	Adult doe	Young	Adult doe	Young	Adult doe	Young
Feb 03-Mar 08	93.3	80.2 (F) ⁴	101	61 (F)	110	64	+ 9	+ 3 (F)
April 13-18	100.5	85.5 (F)	112	67 (F)	117	68	+ 5	+ 1 (F)
May 15-Jun 14	97.7	82.2 (Y)	129	96 (Y)	256	182	+127	+ 86 (Y)
Jun 18-Jul 13	76.3	68.4 (Y)	87	69 (Y)	250	190	+163	+121 (Y)
Jul 14-Aug 26	79.4	70.6 (Y)	86	67 (Y)	213	160	+127	+ 93 (Y)
Sep 02-Nov 04	78.8	62.5 (F) 70.3 (Y)	80	47 (F) 63 (Y)	167	90 126	+ 87	+ 43 (F) + 63 (Y)
Nov 05-Dec 12	55.3	49.0 (F)	59	38 (F)	81	49	+ 22	+ 11 (F)

¹ From MMER (Tables 18-19) / (ME/g) (Table 18)

² From equation page 130

³ From estimated CP content of washed fraction of rumen content x DMI

⁴ Fawn: (F); Yearling: (Y)

For the categories of animals used in the analyses the protein balance will always be positive when the intake is adjusted to the maintenance energy requirements. The balance is highly positive and will probably correspond to the maximum of protein deposition between mid-May and early November when the CP content of the forage varies between 11.25% and 17.44%. In November the relatively high ME content of the forage (2.45 kcal/g) and the low metabolic rates predicted result in a low DMI. At that time the CP content of the ingested material is low (7.81%) and this period appears to be more favorable to fat deposition than to growth.

To our knowledge no estimates of dry matter intake have been published for free ranging white-tailed deer and most estimates on penned animals are for pelleted concentrated diets, short trials on a few browse species. Alldredge et al. (1974) estimated the forage intake rate of free ranging mule deer with fallout Cesium-137, while Holleman et al. (1979) used the same technique on free ranging caribou. In the latter study it was estimated that the dry matter intake (lichen) of free ranging caribou was close to four times as high as the intake of penned reindeer also fed lichens. Short (1975) estimated the digestible dry matter intake for white-tailed deer based on the reticulo-rumen dry matter content of deer killed in the wild and turnover rates estimated with captive deer. His intake figures range from a minimum of $42 \text{ g/kgW}^{0.75}$ in December to a maximum of $60 \text{ g/kgW}^{0.75}$ in May, the corresponding turnover rates of the rumino-reticulum content were 1.30 and 2.53 times per 24 hours.

Deer in captivity appear to follow the principles of food intake regulation described by Montgomery and Baumgardt (1965). Ammann et al. (1973) concluded in a study of food intake by penned fawns in winter that the intake increased as digestibility decreased from a high of 3.44 kcal DE/g to 2.17 kcal DE/g, below this point the intake decreased. In this control system of food intake, energy balance is the regulated component. The animal will ingest as much food as the gut capacity permits or until the energy intake corresponds to a fixed threshold value under given circumstances of energy needs. The increase in intake with digestibility is associated with a shorter retention time for more digestible food (Mautz and Petrides 1971; Thornton and Minson 1973). There is also an adaptation of the threshold when the energy requirements increase as shown for lactating rats by Baumgardt (1970) and lactating ewes by Clancy et al. (1976) and Owen et al. (1980).

In deer many stimuli (*sensu* McClymont 1967) can be suspected to influence the foraging behavior and result in a high food intake in summer and low food intake in winter:

1. Total energy demand. This variable reaches a maximum during the snow-free period due to accelerated growth, lactation, recovery from winter losses, and accumulation of fat reserves. The minimum energy expenditure should be reached in late January according to the model proposed by Moen (1978) ($1.7 \times 70 W_{\text{kg}}^{0.75}$ as compared to an early August value of $3.7 \times 70 W_{\text{kg}}^{0.75}$).

2. Palatability. Although this factor is not clearly understood, it is obvious that deer have a greater choice of forage in summer, including all species available in winter. Browse species available on Anticosti Island in winter are usually rated as *second choice* or even *starvation* species. In feeding trials reported by Ullrey et al. (1968) the voluntary food intake of adult does averaged 0.12 kg/deer/day for balsam fir as compared to 1.24 kg/deer/day for white cedar. However, on Anticosti Island, in attempts to capture deer, balsam fir appeared to be much more effective bait than white cedar and alfalfa hay. Balsam fir is then probably much more readily accepted by these deer than what is normally reported in the literature.

3. Gastro intestinal or ruminal distention. In winter it is most probable that this factor will limit the intake of food on Anticosti Island where the apparent digestibility of the composite diet which averages 43% should result in a slow passage rate. In summer the high digestibility of forage (56% to 73%) should result in an increased passage rate and intake. The high proportion of leaves in the diet (80% to 87%, Table 18) should also favor short retention times as found by Laredo and Minson (1973). These authors concluded that the 46% higher intake of grass leaves as compared to stems of equal digestibility was associated with a shorter retention time of the leaves in the rumen. This was apparently caused by the larger surface initially available to bacterial degradation.

4. Energy intake. In winter the energy concentration of the composite diet averages 2.10 kcal ADE/g, a value close to but lower than the threshold value of Ammann et al. (1973) (2.17 kcal ADE/g). The threshold values for summer conditions are not known but are probably much higher as energy demands are higher. Moreover, it is now generally accepted that for a given diet the voluntary intake will be lower in winter than in summer and that the intake level will probably be under maintenance level even for nutritious food. It is then probable that even this low threshold fixed below maintenance cannot be attained due to the poor quality of Anticosti Island winter forage.

5. Meteorological stress. Winter food intake may also be periodically reduced by adverse conditions according to Siegler (1968: 53), Ozoga and Verme (1970) and Mautz (1978b: 342). Siegler (1968: 53) reported that deer were observed to stay bedded for two or three successive days during stormy weather.

Selected published values of food intake by cervids are presented in Table 24. In cases where summer and winter values are available, winter values are lower by 20% to 30% and in most cases animals lost weight. Estimates of dry matter intake for deer in winter usually range between 40 and 55 g/kgW^{0.75} except for feeding trials with browse where intakes are usually lower but quite variable. In summer the estimates range between 50 and 83 g/kgW^{0.75}. The winter intake values for concentrates agree with the prediction equation suggested by Ammann et al. (1973), these diets containing usually between 3.0 and 3.6 kcal DE/g should be consumed at daily rates varying

TABLE 24. Published values of voluntary food intake by some northern cervids

Animal	Condition and diet	Dry matter intake/day	Reference
W. tailed deer Adult doe	In captivity-browse Jan-Mar	Balsam fir: 0.06 kg/deer w. cedar: 0.57 kg/deer	Ullrey et al., 1968
W. tailed deer	In captivity-browse Winter	30.4 -44.6 g/kgW ^{0.75}	Mautz et al., 1976
W. tailed deer Fawn	In captivity-concentrate 70%-83% DDM	Oct: 74.2 g/kgW ^{0.75} Jan: 45.4 g/kgW ^{0.75} Mar: 40.2 g/kgW ^{0.75} May: 58.8 g/kgW ^{0.75} Aug: 49.5 g/kgW ^{0.75}	Thompson et al., 1973
W. tailed deer yearlings (May-Oct) Fawns (Sep.Apr)	In captivity-concentrate 64%-67% DDM	Sep-Nov: 93.5 g/kgW ^{0.75} Dec-Apr: 54.4 g/kgW ^{0.75} May-Oct: 75.1 g/kgW ^{0.75}	Holter et al., 1979b
Mule deer	Free ranging	Summer: 25.7 g/kgW Winter: 20.1 g/kgW (Approximately 70 and 55 g/kgW ^{0.75}) ¹	Allredge et al., 1974
Caribou-reindeer	In captivity-lichens In captivity-lichens+forage Free ranging-lichens	Nov-Mar: 16.4 g/kgW Nov-Mar: 36.3 g/kgW Nov-Mar: 61.3 g/kgW (Approximately 50, 110 and 180 g/kgW ^{0.75})	Holleman et al., 1979
Roe deer	In captivity Mainly browse	Spring: 65-75 g/kgW ^{0.75} Summer: 60-70 g/kgW ^{0.75} Winter: 40-50 g/kgW ^{0.75}	Drozdz et al., 1975

¹ Our estimation

between 37 and 50 g/kgW^{0.75}. Under these conditions the energy intake would average 155 kcal DE/kgW^{0.75}. Some browse species may be unpalatable for deer normally fed concentrates and intake rates may not be representative of natural conditions, balsam fir appears to be one of these species. Robbins et al. (1975) reported intake of 35.2 g/kgW^{0.75} for a ration containing 55% of this species and according to the predicted equation of Ammann et al. the intake should be the maximum (70 g/kgW^{0.75}) permissible for the size of the digestive tract.

All these winter intake estimates, even at maximum energy intake of 155 kcal DE/kgW^{0.75}, are under the estimated maintenance requirements (Tables 20, 21). The energy and protein deficits or surpluses predicted according to different possible intakes are presented in Figure 20. This figure also shows the levels of intake at which 30% and 35% of the body weight will be lost after 120 days on a winter diet. In these predictions each g of body weight loss supplies 6 kcal of energy as assumed by Mautz (1978b).

The protein balance will be positive only for intakes close to or above 70 g/kgW^{0.75} and consequently it is most probable that protein will be lost and growth will cease under these conditions.

In summer, it is not before mid-June that the intake required for energy maintenance decreases significantly and probably permits some recovery from winter body depletion or new tissue production. Unless the pregnant does very actively select the young vegetation, increase significantly their intake or can use fat reserves at this time, their chances of producing a viable fawn are probably very small. The protein

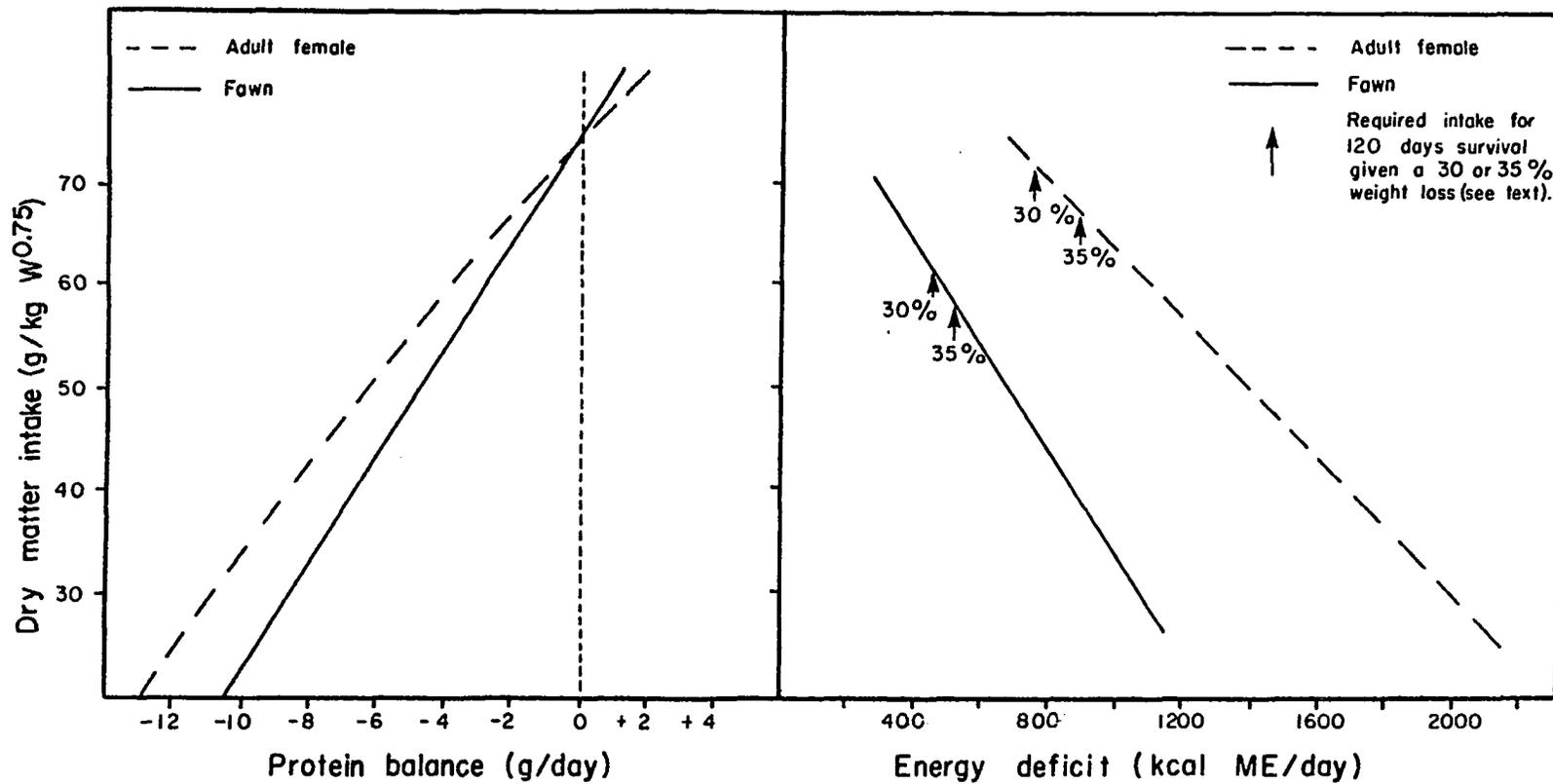


Figure 20. Winter protein and energy balances predicted for a young deer and an adult female on Anticosti Island

needs however appear to be satisfied before the energy needs because in the May-June period at energy maintenance intake the protein balance is highly positive. These aspects will be discussed in more detail after considering the estimated seasonal weight changes. It appears however that deer on Anticosti Island will be in negative energy balance from late December or when snow accumulation reaches 0.75 m until late April. Their protein balance will probably also be negative during these four months. Some individual animals that have access to seaweed may improve on this pattern, especially if they can metabolize a large proportion of the nitrogen contained in these plants. The selection of habitat in spring is also probably critical at a time when the energy demand rapidly increases. It is doubtful however that the energy balance becomes significantly positive for most deer before mid-June. The energy and protein balances probably remain positive until late November and depending on the snowfall in December both can probably be maintained positive or neutral.

PART II - The Annual Cycle of Body Condition

Introduction

The importance of the contribution of the body reserves to the winter energy budget of northern ungulates is now generally accepted by wildlife ecologists and most energy balance models include an estimate of energy supplied by these reserves (Gasaway and Coady 1974; Wallmo et al. 1977; Mautz 1978a, 1978b; Swift et al. 1980). However, little is known about the relative importance of the body chemical components in relation to total weight loss and of the importance of the contribution by the viscera, the muscles, and the subcutaneous tissue to the energy and protein balance of these ungulates.

This section deals with these aspects and describes the effects of the winter energy deficit on the body weight and composition of Anticosti deer. The importance of the summer nutrition in recovering from winter weight losses and in achieving normal body growth and reproductive output is also discussed.

Body Composition of the Deer Collected

Variations in the (C)IFBW composition of deer analysed are illustrated in Figure 21 and detailed in Appendices 2 to 8. Water and fat are the most variable components of the fresh (C)IFBW and are negatively correlated. The highest fat concentrations are reached in autumn (13.88% between Nov 05 and Dec 12 and 14.34% between Sep 02 and Nov 04), while water contents average 59.79% and 59.84% for the corresponding periods. The highest water contents are reached in spring (71.54% between April 13 and 18 and 71.21% between May 15 and June 14), while the fat contents average 0.93% and 0.83% for the same periods.

The relationship between fat and water contents based on all the animals sampled is described by the following regression:

$$y = 81.47 - 1.13x \quad r = 0.983 \quad N = 119$$

y = fat content (%)
x = water content (%)

The caloric content of the (C)IFBW (Table 25) follows a pattern similar to that for fat concentration. It varies from a low value of 1.27 kcal/g in deer collected in April to a high of 2.51 kcal/g for deer collected between Sep 02 and Nov 04.

Seasonal variations in the fat reserves are detailed in Table 25 according to the collection period and the sex and age class of the deer. The loss of fat reserves is already apparent in February-March when the fat level averages $8.39 \pm 4.77\%$ for adults and is as low as

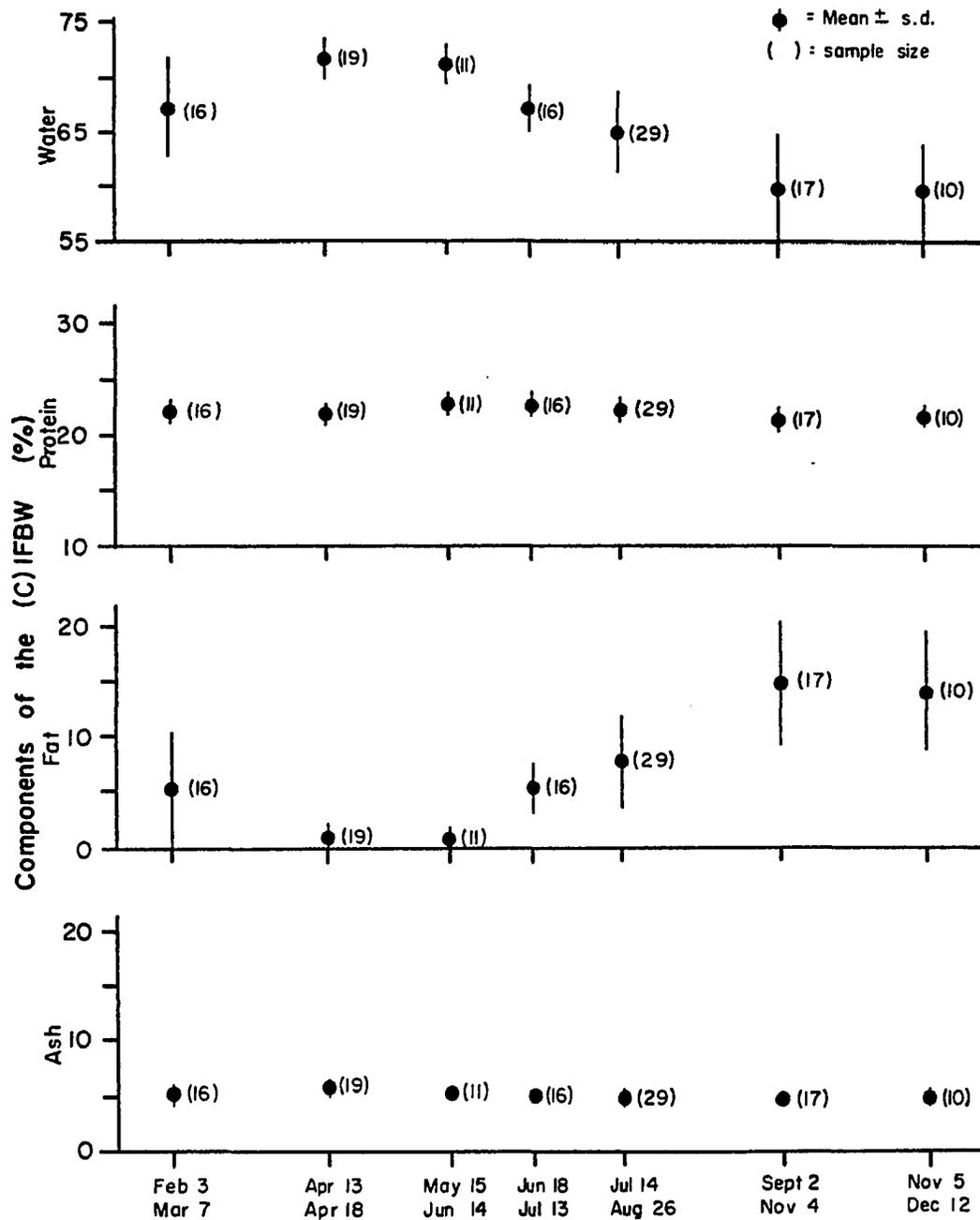


Figure 21. Water, protein, fat and ash content of the (C)IFBW of Anticosti Island deer (2-month-old and older) according to period of the year

TABLE 25. Fat and caloric content of the (C)IFBW of deer collected on Anticosti Island according to collection period and age and sex of the animal

Period Age and sex	N	Fat content %		Caloric content kcal/g \pm s.d.
		Mean \pm s.d.	Range	
Feb 03 - Mar 08				
Females (Y ⁺) ¹	8	8.23 \pm 5.08	0.23 - 15.58	1.95 \pm 0.44
Males (Y ⁺)	1	9.62 -	- -	2.06 -
Total (Y ⁺)	9	8.39 \pm 4.77	0.23 - 15.58	1.96 \pm 0.41
Fawns ²	7	1.12 \pm 1.58	0.25 - 4.46	1.32 \pm 0.16
Total	16	5.21 \pm 5.20	0.23 - 15.58	1.68 \pm 0.46
Apr 13 - 18				
Females (Y ⁺)	10	1.32 \pm 1.33	0.01 - 4.16	1.32 \pm 0.13
Males (Y ⁺)	4	0.89 \pm 0.97	0.17 - 2.25	1.31 \pm 0.11
Total (Y ⁺)	14	1.19 \pm 1.22	0.10 - 4.16	1.28 \pm 0.05
Fawns	5	0.18 \pm 0.05	0.10 - 0.24	1.14 \pm 0.06
Total	19	0.93 \pm 1.14	0.10 - 4.16	1.27 \pm 0.13
May 15 - Jun 14				
Females (Y ⁺)	5	0.62 \pm 0.63	0.17 - 1.63	1.30 \pm 0.10
Males (Y ⁺)	4	1.40 \pm 1.55	0.31 - 3.47	1.38 \pm 0.14
Total (Y ⁺)	9	0.97 \pm 1.13	0.17 - 3.47	1.34 \pm 0.11
Fawns	2	0.22 \pm 0.03	0.20 - 0.24	1.19 \pm 0.03
Total	11	0.83 \pm 1.05	0.17 - 3.47	1.31 \pm 0.12
Jun 18 - Jul 13				
Females (Ad) ³	4	6.00 \pm 2.85	2.25 - 9.09	1.81 \pm 0.21
Males (Ad)	5	7.01 \pm 1.83	4.02 - 8.46	1.86 \pm 0.15
Total (Ad)	9	6.56 \pm 2.23	2.25 - 9.09	1.84 \pm 0.17
Yearlings ⁴	7	3.67 \pm 1.70	2.14 - 6.88	1.57 \pm 0.10
Total	16	5.30 \pm 2.45	2.14 - 9.09	1.72 \pm 0.19
Jul 14 - Aug 26				
Females (Ad)	11	8.68 \pm 5.16	1.77 - 16.52	2.00 \pm 0.47
Males (Ad)	3	10.03 \pm 5.14	4.00 - 13.89	2.14 \pm 0.50
Total (Ad)	14	8.97 \pm 4.98	1.77 - 16.52	2.03 \pm 0.46
Fawns	4	4.38 \pm 2.10	1.96 - 6.83	1.70 \pm 0.23
Yearlings	11	7.47 \pm 3.10	3.48 - 13.42	1.92 \pm 0.27
Total	29	7.77 \pm 4.22	1.77 - 16.52	1.94 \pm 0.38

TABLE 25 (continued)

Period Age and sex		Fat content %		Caloric content kcal/g \pm s.d.
		Mean \pm s.d.	Range	
Sep 02 - Nov 04				
Females (Ad)	4	18.38 \pm 8.81	10.07 - 30.55	2.82 \pm 0.77
Males (Ad)	2	18.17 \pm 0.70	17.67 - 18.66	2.81 \pm 0.08
Total (Ad)	6	18.31 \pm 6.83	10.07 - 30.55	2.85 \pm 0.59
Fawns	7	11.53 \pm 4.63	6.28 - 17.75	2.44 \pm 0.33
Yearlings	4	13.31 \pm 4.13	8.79 - 18.79	2.28 \pm 0.41
Total	17	14.34 \pm 5.95	6.28 - 30.55	2.51 \pm 0.52
Nov 05 - Dec 12				
Females (Ad)	5	13.03 \pm 6.36	6.31 - 22.89	2.42 \pm 0.56
Males (Ad)	2	13.90 \pm 7.69	8.46 - 19.33	2.49 \pm 0.64
Total (Ad)	7	13.27 \pm 6.08	6.31 - 22.89	2.44 \pm 0.53
Fawns	3	15.28 \pm 4.48	10.50 - 19.39	2.63 \pm 0.37
Yearlings	0	-	-	-
Total	10	13.88 \pm 5.48	6.31 - 22.89	2.49 \pm 0.48

¹ Y+: 11.5-month-old and older (date of birth, June 30)

² Fawns: < 11.5-month-old

³ Ad: > 23.5-month-old

⁴ Yearlings: 11.5-23.5-month-old

1.12 ± 1.58% for fawns. At this time several fawns (not included in these results) had already been found dead or incapable of standing. From mid-April to mid-June the fat reserves remain low; none of the fawns collected during this period had more than 0.24% fat. These deer therefore can and often do utilize almost all of their ether extractable fat and still manage to survive. In experiments involving food deprivation and weight losses in sheep the animals are usually allowed to recover before they reach this low level of body condition but Panaretto (1964) reported that in an experiment with moderately fat sheep (< 25% fat) fat reserves could be almost completely used after 200 days and that in two animals water accounted for 75% of body weight under these conditions. Searle et al. (1979) also reported fat levels under 1% (75.5% water) in two young sheep after a period of experimental undernutrition. In the present study we believe that the observed levels of ether extract are realistic and are not due to methodological errors. Although some forms of lipids are not extracted by petroleum ether, it is doubtful that these can be used as a source of energy or that their contribution would appreciably increase the fat reserves. We are also confident that all the ether extractable lipids were removed as a second extraction run on several samples failed to show any measurable amount of fat. Moreover similar extractions conducted on foetuses of different weights containing between 0.30% and 2.8% fat (weights 164 - 4,662 g) gave results in very close agreement with those published by Robbins and Moen (1975). Finally in the five fawns collected in April no fat could be extracted from the femur bone marrow which is usually considered the last reserve to be used; the average water content of the femur marrow at that time was 97.3 ± 0.61%.

In late June and early July recovery is apparent in all age classes and both sexes, although yearlings appear to lag, showing fat content levels slightly higher than 50% of the levels found in the adults. The increase is also apparent in late July and August but the inter-individual variations, especially in females, is very high. Although the sample size is too small to allow analysis of these results statistically it is interesting to consider fat reserves in relation to age and reproductive status of females on an individual basis:

<u>Fat level %</u>	<u>Age</u>	<u>Status and collection area</u>
4.52, 3.96	> 5-year	Lactating-eastern sector
8.85, 8.85 3.52, 8.45 9.42	> 2-year	Lactating-western sector
1.77	2-year	Lactating-western sector
16.52	2-year	Non lactating-eastern sector
15.88, 14.78	> 2-year	Non lactating-western sector

It appears that lactation is retarding the accumulation of fat and in a young individual (2 years of age) may keep the reserves at a very low level (1.77%). The 2 lactating females collected on August 12 in the eastern sector, which is covered mainly by black spruce stands and bogs, also appear to have lower fat reserves than the ones collected in the western sector during the same period. None of the 11 yearlings collected was lactating but they had fat reserves similar to the older

lactating does: 7.77% for the former as compared to 7.82% for the latter.

During the following period (Sep 02–Nov 04) only 4 adult does were collected. Of these, 3 were lactating and they averaged $14.32 \pm 4.20\%$ fat content. The other was a 6-year-old doe which had apparently never reproduced, according to an histological examination of the ovaries, and its fat content was 30.55%.

In the Nov 05–Dec 12 period all females still had milk in the udder and their fat content was very variable (6.31% to 22.89%). The 3 fawns collected in that period were in very good condition ($15.25 \pm 4.48\%$ fat). One of the 2 adult males was a 3-year-old individual collected on Nov 17, probably before the peak of rutting, and it had a high fat content (19.33%). The other one was a 5-year-old individual collected on Dec 04 at or shortly after the peak of rutting. It had very large 8 point antlers and showed many bruises on the carcass indicating an active participation in rutting activity. Its fat reserves (8.46%) were less than half of the fat reserves of the adult bucks collected between Sep 02 and Nov 17. Antlers were not included in any of the analyses.

These results indicate that although many factors (e.g. milk production, age at least up to two years, rutting activity, and range condition) may influence the level of fat reserves that will be available to free-ranging deer in fall, the deer of Anticosti Island can accumulate fat reserves comparable to and possibly exceeding levels reported for other free-living or even captive wild ungulates. This is achieved without

the availability of highly energetic and digestible foods such as acorns and fruits common to other deer ranges.

The highest fall fat levels for wild ungulates have been reported for three Svalbard reindeer (29.0, 32.4 and 40.8%) by Ringberg et al. (1980a). Fat reserves in spring were also very high (10.5, 21.6 and 20.3%) as compared to our present estimates.

Concentrations of protein and ash are much more stable (Figure 21). Protein values are highest in spring (22.73%, May 15–Jun 14) and lowest in the Sep 02–Nov 04 period (21.35%) while the ash content varies from a low of 4.47% in the Sep 02–Nov 04 period to a high of 5.73% in April (Appendices 2 to 8).

The concentration of the main chemical components of the (C)IFBW of the deer collected in autumn (Sep 02–Dec 12) and in spring (Apr 13–Jun 14) are compared on a fat-free fresh weight basis and a fat-free dry weight basis in Table 26. It appears that for every class of individuals both the water content ($P < 0.001$) and the protein content are higher ($P < 0.001$) in spring as compared to fall values, whereas the ash values do not differ significantly. When only protein and ash are considered (fat-free dry mass), in all cases the protein concentrations are significantly higher in fall while the ash concentrations are correspondingly lower ($P < 0.05$ to $P < 0.001$).

The composition of the fat-free (C)IFBW of Anticosti yearling and adult deer in fall is similar to the composition of captive deer (> 25 kg) in late October reported by Robbins (1973: 37). Composition

TABLE 26. Composition of the fresh fat-free ingesta-free body and dry fat-free ingesta-free body of deer collected in spring and fall on Anticosti Island

Date	Condition Sex and age	N	Water % ± s.d.	Protein % ± s.d.	Ash % ± s.d.	
Apr 13-Jun 14	Fresh body					
	Females (Y ⁺) ¹	15	71.68 ± 1.41*** ²	22.66 ± 1.14***	5.66 ± 0.65 ^{n.s.}	
	Males (Y ⁺)	8	71.42 ± 0.55**	22.81 ± 0.83***	5.80 ± 0.79 ^{n.s.}	
	Total (Y ⁺)	23	71.59 ± 1.17***	22.71 ± 1.02***	5.71 ± 0.69 ^{n.s.}	
	Fawns ³	7	73.58 ± 1.06***	21.12 ± 0.99***	5.28 ± 0.54 ^{n.s.}	
	Total	30	72.06 ± 1.42***	22.34 ± 1.21***	5.61 ± 0.67 ^{n.s.}	
	Dry body					
	Females (Y ⁺)	15		80.00 ± 1.83***	20.00 ± 1.83***	
	Males (Y ⁺)	8		80.08 ± 3.05*	19.92 ± 3.05*	
	Total (Y ⁺)	23		80.03 ± 2.25***	19.97 ± 2.25***	
	Fawns	7		79.96 ± 1.88**	20.04 ± 1.88**	
	Total	30		80.01 ± 2.14***	19.99 ± 2.14***	
	Sep 02-Dec 12	Fresh body				
		Females (Y ⁺)	12	69.51 ± 1.17	25.21 ± 1.17	5.30 ± 0.64
Males (Y ⁺)		5	69.92 ± 0.90	24.82 ± 0.48	5.24 ± 0.63	
Total (Y ⁺)		17	69.63 ± 1.09	25.09 ± 1.01	5.28 ± 0.61	
Fawns		10	69.67 ± 0.87	25.05 ± 0.92	5.27 ± 0.56	
Total		27	69.64 ± 0.99	25.08 ± 0.96	5.28 ± 0.58	
Dry body						
Females (Y ⁺)		12		82.65 ± 2.01	17.33 ± 2.01	
Males (Y ⁺)		5		82.53 ± 1.65	17.47 ± 1.65	
Total (Y ⁺)		17		82.62 ± 1.86	17.38 ± 1.86	
Fawns		10		82.68 ± 1.77	17.32 ± 1.77	
Total		27		82.65 ± 1.79	17.35 ± 1.79	

¹ Y⁺ = 11.5-month-old and older

² Less than 11.5-month-old

³ Differences between fall and spring values (Student's "t" tests), *** P < 0.001; ** P < 0.01; * P < 0.05

of the Anticosti deer given in Table 25 is: 71.59% water, 22.71% protein and 5.71% ash as compared to 71.73% water, 23.25% protein and 5.02% ash for the captive New-York deer.

The composition of the dry fat-free ingesta-free body of domestic animals was discussed in detail by Reid et al. (1968). They concluded that the protein/ash ratio was very constant and unaffected by underfeeding and realimentation. After an extensive review of the literature on body composition they established the protein content of the dry fat-free body of pigs, sheep and cattle at 83.42%, 81.09% and 80.26% respectively, with corresponding ash percentages of 17.01%, 18.91% and 19.71%. For captive white-tailed deer (> 25 kg) Robbins (1973) reported a composition of $82.65 \pm 1.03\%$ protein and $17.35 \pm 1.03\%$ ash. In the present study the protein content of the fat-free dry body of yearlings and adults in fall was $82.62 \pm 1.86\%$ while the ash content was $17.38 \pm 1.86\%$.

The fact that the Anticosti deer population and the deer studied by Robbins (1973) had very different nutritional regimes and environmental conditions but similar body composition in fall is in agreement with the conclusion of Reid et al. (1968) suggesting that the dry fat-free body composition is very stable. However, the fact that there is a significant difference in the content of protein in the fresh and in the dry fat-free ingesta-free body between spring and fall (Table 26) is an indication of the severity of the nutritional stress imposed on these animals. The difference is most pronounced in fawns: 3.93% (fresh weight basis) and 2.72% (dry weight basis). A similar difference in the

protein and water content of the fat-free fasted body of sheep was reported by Farrell and Reardon (1972) for *well-nourished* and *under-nourished* animals.

Analysis of the Total Body Reserves Dynamics

In order to understand the relationship between food resources and body condition at the population level, the analysis of total body reserves must take into account the body weight cycle as well as the variations in the chemical composition of the animal. The relationship between the weight of the main chemical components of the body (water, protein, fat and ash) and the ingesta-free body weight has been a very useful tool for the study of body composition in relation to growth (Tulloh 1963; Reid et al. 1968; Drew 1971; Burton et al. 1974; Robbins et al. 1974a) and the following section is based on this scheme of analysis.

According to this method the weight of the body components can be estimated from the ingesta-free body weight (IFBW)¹ according to the following equation:

$$\ln (\text{component weight}) = a + b \ln (C)\text{IFBW}^1$$

Although in some cases linear regressions are sufficient to describe the relationship, a better fit was generally obtained with a

¹ When pregnant does are included, the weight of the uterus and its content is subtracted, this is the corrected ingesta-free body weight CIFBW. When a group of deer includes pregnant and non-pregnant animals the abbreviation (C)IFBW is used to indicate that the weight of the pregnant individuals was corrected.

In equation as used by Burton et al. (1974), Robbins et al. (1974a) and Thornton et al. (1979).

A sample of total body weights taken in late winter (TBW) available from files of the Consolidated Bathurst Co. was combined with our sample to obtain estimates of IFBW of deer by sex and age class. The relationship between IFBW and TBW for the deer collected during the present study was as follows:

$$\begin{array}{l}
 \text{Males (Y}^+) \text{ : } \ln \text{ IFBW} = -0.4464 + 1.0576 \ln \text{ TBW} \\
 \qquad \qquad \qquad s_{yx} = 0.0351 \quad r = 0.994 \quad N = 7 \\
 \text{Females (Y}^+) \text{ : } \ln \text{ IFBW} = -0.0166 + 0.9741 \ln \text{ TBW} \\
 \qquad \qquad \qquad s_{yx} = 0.0513 \quad r = 0.974 \quad N = 18 \\
 \text{Fawns} \qquad \qquad \text{ : } \ln \text{ IFBW} = -0.4205 + 1.0382 \ln \text{ TBW} \\
 \qquad \qquad \qquad s_{yx} = 0.0683 \quad r = 0.954 \quad N = 14 \\
 \text{Total} \qquad \qquad \text{ : } \ln \text{ IFBW} = -0.4252 + 1.0418 \ln \text{ TBW} \\
 \qquad \qquad \qquad s_{yx} = 0.0748 \quad r = 0.993 \quad N = 39
 \end{array}$$

In fall a sample of weights of dressed deer killed by hunters after October 15 was used to estimate weight of the ingesta-free body components of the population. The relationship between dressed weight and IFBW and dressed weight and the weight of the body components will be given in a following section.

Relationship between weight of the body components and (C)IFBW

The equations describing the relationship between the weight of the chemical components and the (C)IFBW in spring and fall are given in Tables 27 and 28. The relationship is highly significant ($P < 0.01$)

TABLE 27. Relationships between ingesta-free body weight (kg) and weight of body components (kg) of Anticosti deer in fall

Sex and age	N	Component	Equation
Males (Y ⁺) ¹	5	Water** ²	$\ln \text{Wat.} = -0.1245 + 0.9048 \ln \text{IFBW}$ $r^2 = 0.974; s_{yx} = 0.0637; s_b = 0.0069$
		Protein**	$\ln \text{Prot.} = -1.0040 + 0.8669 \ln \text{IFBW}$ $r^2 = 0.980; s_{yx} = 0.1984; s_b = 0.0214$
		Fat ^{n.s.}	$\ln \text{Fat} = -4.8507 + 1.6932 \ln \text{IFBW}$ $r^2 = 0.769; s_{yx} = 0.3932; s_b = 0.0425$
		Ash*	$\ln \text{Ash} = -2.7599 + 0.9141 \ln \text{IFBW}$ $r^2 = 0.857; s_{yx} = 0.3208; s_b = 0.0347$
Females (Y ⁺)	10	Water**	$\ln \text{Wat.} = 0.8122 + 0.6480 \ln \text{IFBW}$ $r^2 = 0.898; s_{yx} = 0.0792; s_b = 0.0065$
		Protein**	$\ln \text{Prot.} = -0.9221 + 0.8378 \ln \text{IFBW}$ $r^2 = 0.942; s_{yx} = 0.0830; s_b = 0.0068$
		Fat**	$\ln \text{Fat} = -7.2109 + 2.3706 \ln \text{IFBW}$ $r^2 = 0.786; s_{yx} = 0.5859; s_b = 0.0480$
		Ash**	$\ln \text{Ash} = -2.7008 + 0.8930 \ln \text{IFBW}$ $r^2 = 0.750; s_{yx} = 0.2273; s_b = 0.0186$
Total (Y ⁺)	15	Water**	$\ln \text{Wat.} = 0.1176 + 0.8346 \ln \text{IFBW}$ $r^2 = 0.924; s_{yx} = 0.0772; s_b = 0.0050$
		Protein**	$\ln \text{Prot.} = -1.0593 + 0.8758 \ln \text{IFBW}$ $r^2 = 0.966; s_{yx} = 0.1002; s_b = 0.0065$
		Fat**	$\ln \text{Fat} = -5.1138 + 1.8020 \ln \text{IFBW}$ $r^2 = 0.713; s_{yx} = 0.4142; s_b = 0.0270$
		Ash**	$\ln \text{Ash} = -2.8007 + 0.9207 \ln \text{IFBW}$ $r^2 = 0.836; s_{yx} = 0.2609; s_b = 0.0170$

TABLE 27 (continued)

Sex and age	N	Component	Equation
Fawns	10	Water**	$\ln \text{Wat.} = 0.2169 + 0.7789 \ln \text{IFBW}$ $r^2 = 0.953; s_{yx} = 0.0462; s_b = 0.0045$
		Protein**	$\ln \text{Prot.} = -1.2387 + 0.9125 \ln \text{IFBW}$ $r^2 = 0.981; s_{yx} = 0.0983; s_b = 0.0096$
		Fat**	$\ln \text{Fat} = -6.4859 + 2.3458 \ln \text{IFBW}$ $r^2 = 0.833; s_{yx} = 0.5517; s_b = 0.0538$
		Ash**	$\ln \text{Ash} = -2.8238 + 0.9189 \ln \text{IFBW}$ $r^2 = 0.776; s_{yx} = 0.2444; s_b = 0.0238$
Total	25	Water**	$\ln \text{Wat.} = -0.1552 + 0.9003 \ln \text{IFBW}$ $r^2 = 0.972; s_{yx} = 0.0721; s_b = 0.0039$
		Protein**	$\ln \text{Prot.} = -1.2934 + 0.9332 \ln \text{IFBW}$ $r^2 = 0.988; s_{yx} = 0.1673; s_b = 0.0091$
		Fat**	$\ln \text{Fat} = -3.9071 + 1.5145 \ln \text{IFBW}$ $r^2 = 0.792; s_{yx} = 0.5765; s_b = 0.0313$
		Ash**	$\ln \text{Ash} = -2.9047 + 0.9459 \ln \text{IFBW}$ $r^2 = 0.927; s_{yx} = 0.3805; s_b = 0.0207$

¹ (Y⁺): yearling and older

² Correlation coefficient: ** P < 0.01
* P < 0.05

TABLE 28. Relationships between ingesta-free body weight (kg) and weight of body components (kg) of Anticosti deer in spring

Sex and age	N	Component	Equation
Males (Y ⁺) ¹	8	Water** ²	$\ln \text{Wat.} = -0.1917 + 0.9557 \ln \text{IFBW}$ $r^2 = 0.991; s_{yx} = 0.0210; s_b = 0.0021$
		Protein**	$\ln \text{Prot.} = -1.7466 + 1.0726 \ln \text{IFBW}$ $r^2 = 0.964; s_{yx} = 0.1037; s_b = 0.0104$
		Fat ^{n.s.}	$\ln \text{Fat} = -10.9583 + 2.6553 \ln \text{IFBW}$ $r^2 = 0.127; s_{yx} = 1.4759; s_b = 0.1475$
		Ash*	$\ln \text{Ash} = -2.8526 + 0.9939 \ln \text{IFBW}$ $r^2 = 0.658; s_{yx} = 0.2091; s_b = 0.0209$
Females (Y ⁺)	15	Water**	$\ln \text{Wat.} = -0.0257 + 0.9060 \ln \text{IFBW}$ $r^2 = 0.986; s_{yx} = 0.0210; s_b = 0.0016$
		Protein**	$\ln \text{Prot.} = -1.6149 + 1.0347 \ln \text{IFBW}$ $r^2 = 0.932; s_{yx} = 0.1082; s_b = 0.0082$
		Fat**	$\ln \text{Fat} = -18.6707 + 4.9805 \ln \text{IFBW}$ $r^2 = 0.508; s_{yx} = 1.4459; s_b = 0.1096$
		Ash**	$\ln \text{Ash} = -4.1411 + 1.3682 \ln \text{IFBW}$ $r^2 = 0.916; s_{yx} = 0.2526; s_b = 0.0192$
Total (Y ⁺)	23	Water**	$\ln \text{Wat.} = -0.0936 + 0.9269 \ln \text{IFBW}$ $r^2 = 0.988; s_{yx} = 0.0206; s_b = 0.0012$
		Protein**	$\ln \text{Prot.} = -1.6563 + 1.0470 \ln \text{IFBW}$ $r^2 = 0.948; s_{yx} = 0.1064; s_b = 0.0064$
		Fat**	$\ln \text{Fat} = -15.1814 + 3.9174 \ln \text{IFBW}$ $r^2 = 0.338; s_{yx} = 1.3876; s_b = 0.0838$
		Ash**	$\ln \text{Ash} = -3.6994 + 1.2366 \ln \text{IFBW}$ $r^2 = 0.847; s_{yx} = 0.2357; s_b = 0.0142$

TABLE 28 (continued)

Sex and age	N	Component	Equation
Fawns	7	Water**	$\ln \text{Wat.} = -0.2942 + 0.9946 \ln \text{IFBW}$ $r^2 = 0.994; s_{yx} = 0.0286; s_b = 0.0040$
		Protein**	$\ln \text{Prot.} = -1.7748 + 1.0810 \ln \text{IFBW}$ $r^2 = 0.957; s_{yx} = 0.1505; s_b = 0.0212$
		Fat ^{n.s.}	$\ln \text{Fat} = -6.895 + 1.2226 \ln \text{IFBW}$ $r^2 = 0.397; s_{yx} = 0.6404; s_b = 0.0901$
		Ash*	$\ln \text{Ash} = -2.2472 + 0.7388 \ln \text{IFBW}$ $r^2 = 0.710; s_{yx} = 0.3041; s_b = 0.0428$
Total	30	Water**	$\ln \text{Wat.} = 0.1715 + 0.9494 \ln \text{IFBW}$ $r^2 = 0.997; s_{yx} = 0.0280; s_b = 0.0016$
		Protein**	$\ln \text{Prot.} = 1.7560 + 1.0755 \ln \text{IFBW}$ $r^2 = 0.987; s_{yx} = 0.2120; s_b = 0.0118$
		Fat**	$\ln \text{Fat} = -11.0501 + 2.7291 \ln \text{IFBW}$ $r^2 = 0.537; s_{yx} = 2.0719; s_b = 0.1150$
		Ash**	$\ln \text{Ash} = -3.2063 + 1.0941 \ln \text{IFBW}$ $r^2 = 0.940; s_{yx} = 0.3925; s_b = 0.0218$

¹ (Y⁺): yearling and older

² Correlation significant: ** P < 0.01
* P < 0.05

in fall except for ash and fat in yearling and older males for which the sample size is small ($n = 5$). In spring the relationship is not significant for fat in yearling and older males and in fawns and in the same categories of animals for ash it is only significant at $P < 0.5$.

The high correlations between water weight and (C)IFBW and between protein weight and (C)IFBW can be used as a basis for estimation of total body composition as variability of the ash content in percent cannot affect the resulting estimate of fat. So in all cases fat has been estimated as the difference between the (C)IFBW and the weight of the water, protein and ash fractions as predicted by regression equations.

Similar equations can be used to estimate the total caloric content of deer in spring and fall (Table 29). The correlation coefficients are also relatively high in most cases but in order to obtain a more consistent composition and energetic picture of the animals the caloric content has also been estimated in each case directly from the body composition.

Body composition estimates based on dressed weights

An adequate sample of dressed body weight (DBW) can easily be obtained during the hunting season and can be a useful tool for body composition studies. This presupposes, however, that the IFBW can be estimated accurately from the sample or that there is a strong relationship between the weight of the components of the IFBW and the DBW. The

TABLE 29. Relationships between ingesta-free body weight (kg) and total caloric content (Mcal) of Anticosti deer in fall (Sep 02-Dec 12) and spring (Apr 13-Jun 14)

Season	Sex and age	N	Equation
Fall	Males (Y+) ¹ * ²	5	$\ln \text{Mcal} = -0.2708 + 1.2879 \ln \text{IFBW}$ $r^2 = 0.905; s_{yx} = 0.1768; s_b = 0.0191$
	Females (Y+)**	10	$\ln \text{Mcal} = -1.8204 + 1.7207 \ln \text{IFBW}$ $r^2 = 0.904; s_{yx} = 0.1916; s_b = 0.0157$
	Total (Y+)**	15	$\ln \text{Mcal} = -0.5774 + 1.3854 \ln \text{IFBW}$ $r^2 = 0.864; s_{yx} = 0.1812; s_b = 0.0118$
	Fawns**	10	$\ln \text{Mcal} = -1.0742 + 1.5964 \ln \text{IFBW}$ $r^2 = 0.914; s_{yx} = 0.1445; s_b = 0.0141$
	Total**	25	$\ln \text{Mcal} = 0.0210 + 1.2422 \ln \text{IFBW}$ $r^2 = 0.920; s_{yx} = 0.1603; s_b = 0.0087$
Spring	Males (Y+)**	8	$\ln \text{Mcal} = -0.3333 + 1.1741 \ln \text{IFBW}$ $r^2 = 0.894; s_{yx} = 0.0805; s_b = 0.0080$
	Females (Y+)**	15	$\ln \text{Mcal} = -0.8196 + 1.3207 \ln \text{IFBW}$ $r^2 = 0.928; s_{yx} = 0.0864; s_b = 0.0066$
	Total (Y+)**	23	$\ln \text{Mcal} = -0.5999 + 1.2538 \ln \text{IFBW}$ $r^2 = 0.921; s_{yx} = 0.0805; s_b = 0.0049$
	Fawns**	7	$\ln \text{Mcal} = -0.0746 + 1.0824 \ln \text{IFBW}$ $r^2 = 0.952; s_{yx} = 0.0524; s_b = 0.0074$
	Total**	30	$\ln \text{Mcal} = -0.3424 + 1.1796 \ln \text{IFBW}$ $r^2 = 0.978; s_{yx} = 0.0796; s_b = 0.0044$

¹ (Y+): yearling and older

² ** P < 0.01

* P < 0.05

equations describing these relationships are presented in Tables 30 and 31. In Table 30, the " r^2 " values of the relationships between the total weight of each component of the IFBW and the independent variable DBW are close to the " r^2 " for the same type of relationships with the IFBW as the independent variable (Table 27). The relationships between the total caloric content of the IFBW and the DBW (Table 31) are also as strong as the one given in Table 29 for the same animals.

The correlation between the DBW and the IFBW in fall is also very high:

$$\text{IFBW} = 0.901 + 1.130 \text{ DBW}$$

$$N = 27; \quad r^2 = 0.996; \quad s_{yx} = 1.21$$

In the following analyses the fall IFBW values were estimated using this regression equation for a sample of 381 deer killed during the hunting season.

Total body reserves in spring and fall

The average fall and spring weights of deer were obtained by the regression equations; the estimates are given in Table 32. Based on these weights, on the regression equations presented in Tables 27 and 28 and on caloric values of 9.490 kcal/g for fat and 5.413 kcal/g for protein (Robbins et al. 1974a), the composition and the caloric content of the IFBW can be calculated (Tables 33 and 34). These results are consistent with the composition estimates based on the mean of the

TABLE 30. Relationships between dressed body weight (DBW) in kg and weight of the main chemical components of the ingesta-free body weight (IFBW) of deer killed for research between Sep 02 and Dec 12 on Anticosti Island

Sex and age	N	Component	Equation
Males (Y ⁺) ¹	5	Water** ²	$\ln \text{Wat.} = 0.3419 + 0.8116 \ln \text{DBW}$ $r^2 = 0.937; s_{yx} = 0.1041; s_b = 0.0115$
		Protein**	$\ln \text{Prot.} = -0.7003 + 0.8197 \ln \text{DBW}$ $r^2 = 0.992; s_{yx} = 0.0848; s_b = 0.0095$
		Fat*	$\ln \text{Fat} = -4.3887 + 1.6903 \ln \text{DBW}$ $r^2 = 0.877; s_{yx} = 0.5600; s_b = 0.0629$
		Ash*	$\ln \text{Ash} = -2.4392 + 0.8642 \ln \text{DBW}$ $r^2 = 0.867; s_{yx} = 0.3109; s_b = 0.0347$
Females (Y ⁺)	10	Water**	$\ln \text{Wat.} = 0.8690 + 0.6582 \ln \text{DBW}$ $r^2 = 0.903; s_{yx} = 0.0821; s_b = 0.0070$
		Protein**	$\ln \text{Prot.} = -0.8177 + 0.8425 \ln \text{DBW}$ $r^2 = 0.928; s_{yx} = 0.0831; s_b = 0.0071$
		Fat**	$\ln \text{Fat} = -6.8423 + 2.3642 \ln \text{DBW}$ $r^2 = 0.762; s_{yx} = 0.5853; s_b = 0.0498$
		Ash**	$\ln \text{Ash} = -2.7224 + 0.9339 \ln \text{DBW}$ $r^2 = 0.800; s_{yx} = 0.2245; s_b = 0.0191$
Total (Y ⁺)	15	Water**	$\ln \text{Wat.} = 0.2990 + 0.8178 \ln \text{DBW}$ $r^2 = 0.940; s_{yx} = 0.0724; s_b = 0.0049$
		Protein**	$\ln \text{Prot.} = -0.8402 + 0.8507 \ln \text{DBW}$ $r^2 = 0.966; s_{yx} = 0.0891; s_b = 0.0060$
		Fat**	$\ln \text{Fat} = -4.4684 + 1.6992 \ln \text{DBW}$ $r^2 = 0.672; s_{yx} = 0.5481; s_b = 0.0371$
		Ash**	$\ln \text{Ash} = -2.6209 + 0.9076 \ln \text{DBW}$ $r^2 = 0.861; s_{yx} = 0.2557; s_b = 0.0173$

TABLE 30 (continued)

Sex and age	N	Component	Equation
Fawns	10	Water**	$\ln \text{Wat.} = 0.3675 + 0.7671 \ln \text{DBW}$ $r^2 = 0.939; s_{yx} = 0.0562; s_b = 0.0057$
		Protein**	$\ln \text{Prot.} = -1.0633 + 0.8990 \ln \text{DBW}$ $r^2 = 0.970; s_{yx} = 0.0932; s_b = 0.0095$
		Fat**	$\ln \text{Fat} = -6.0873 + 2.3279 \ln \text{DBW}$ $r^2 = 0.835; s_{yx} = 0.5472; s_b = 0.0559$
		Ash**	$\ln \text{Ash} = -2.7049 + 0.9240 \ln \text{DBW}$ $r^2 = 0.799; s_{yx} = 0.2436; s_b = 0.0249$
Total	25	Water**	$\ln \text{Wat.} = 0.0125 + 0.8893 \ln \text{DBW}$ $r^2 = 0.975; s_{yx} = 0.0662; s_b = 0.0037$
		Protein**	$\ln \text{Prot.} = -1.1124 + 0.9197 \ln \text{DBW}$ $r^2 = 0.986; s_{yx} = 0.1540; s_b = 0.0087$
		Fat**	$\ln \text{Fat} = -3.5749 + 1.4818 \ln \text{DBW}$ $r^2 = 0.779; s_{yx} = 0.5939; s_b = 0.0335$
		Ash**	$\ln \text{Ash} = -2.7415 + 0.9381 \ln \text{DBW}$ $r^2 = 0.937; s_{yx} = 0.3762; s_b = 0.0212$

¹ (Y⁺): yearling and older

² Correlation significant: ** P < 0.01

* P < 0.05

TABLE 31. Relationships between dressed body weight (DBW) in kg and caloric content (Mcal) on an ingesta-free body weight basis (IFBW) of deer killed for research between Sep 02 and Dec 12

Sex and age	N	Equation
Fawns	10** ¹	$\ln \text{Mcal} = -0.7931 + 1.5811 \ln \text{DBW}$ $r^2 = 0.913; s_{yx} = 0.1358; s_b = 0.0139$
Females (Y ⁺) ²	10**	$\ln \text{Mcal} = -1.5815 + 1.7237 \ln \text{DBW}$ $r^2 = 0.884; s_{yx} = 0.1949; s_b = 0.0166$
Males (Y ⁺)	5*	$\ln \text{Mcal} = 0.3057 + 1.1861 \ln \text{DBW}$ $r^2 = 0.872; s_{yx} = 0.2060; s_b = 0.0230$
Total (Y ⁺)	15**	$\ln \text{Mcal} = 0.1292 + 1.3190 \ln \text{DBW}$ $r^2 = 0.830; s_{yx} = 0.1959; s_b = 0.0133$
Total	25**	$\ln \text{Mcal} = 0.2169 + 1.2351 \ln \text{DBW}$ $r^2 = 0.905; s_{yx} = 0.1844; s_b = 0.0104$

¹ ** P < 0.01

* P < 0.05

² (Y⁺): yearling and older

TABLE 32. Fall and spring total body weights and ingesta-free body weights on Anticosti deer ¹

Sex and age (years)	(Corrected) total body weight (kg)				(Corrected) ingesta-free body weight (kg)			
	Fall		Spring		Fall		Spring	
	N	Weight ± s.d.	N	Weight ± s.d.	N	Weight ± s.d.	N	Weight ± s.d.
Males								
0.3-0.8	30	32.2 ± 3.10	5	21.0 ± 3.33	30	26.6 ± 2.59	5	15.5 ± 2.92
1.3-1.8	37	50.9 ± 6.38	4	39.7 ± 5.45	37	42.2 ± 5.33	4	32.2 ± 4.46
2.3-2.8	57	59.9 ± 12.70	5	42.7 ± 5.83	57	48.4 ± 9.74	5	34.7 ± 4.72
3.3-3.8	38	67.1 ± 13.08	6	39.5 ± 4.74	38	55.8 ± 10.93	6	31.2 ± 3.88
(4.3-4.8) ⁺	32	86.2 ± 18.21	9	50.9 ± 8.25	32	71.8 ± 15.21	9	41.4 ± 6.78
Females								
0.3-0.8	32	30.1 ± 3.46	12	20.8 ± 2.43	32	25.4 ± 2.68	12	15.3 ± 2.92
1.3-1.8	33	47.5 ± 7.52	24	35.2 ± 6.15	33	38.6 ± 5.68	24	28.1 ± 4.63
2.3-2.8	38	57.9 ± 6.80	9	44.5 ± 2.84	38	46.4 ± 5.15	9	35.0 ± 2.09
3.3-3.8	19	58.0 ± 7.51	6	43.9 ± 6.19	19	46.5 ± 5.69	6	34.6 ± 4.56
(4.3-4.8) ⁺	65	60.3 ± 9.03	24	44.2 ± 6.95	65	48.2 ± 6.79	24	34.8 ± 5.12

¹ Spring total body weights were obtained by combining weight data from Consolidated Bathurst Co. files and deer weights obtained during the present study (April 1 - June 14). Ingesta-free weights were estimated using the regression equation given page 159. Fall total and ingesta-free weights were obtained from a sample of deer killed during the regular hunting seasons of 1975 and 1976. The regression equations given previously were used to obtain the ingesta-free weight from the eviscerated body weight.

TABLE 33. Composition and caloric content of Anticosti deer in fall as predicted by regression equations and their mean ingesta-free body weight ¹

Sex and age (years)	Ingesta-free weight (kg)	Composition								Caloric value	
		Water		Protein		Ash		Fat		Mcal	(Kcal/g)
		kg	(%)	kg	(%)	kg	(%)	kg	(%)		
Males											
0.3	26.6	16.00	(60.1)	5.78	(21.7)	1.33	(5.0)	3.49	(13.1)	64.41	(2.42)
1.3	42.2	26.09	(61.8)	9.36	(22.2)	1.94	(4.6)	4.81	(11.4)	96.31	(2.28)
2.3	48.4	29.54	(61.0)	10.58	(21.9)	2.20	(4.5)	6.08	(12.6)	114.97	(2.37)
3.3	55.8	33.60	(60.2)	11.97	(21.5)	2.50	(4.5)	7.73	(13.9)	138.34	(2.48)
4.3	71.8	42.20	(58.8)	14.90	(20.8)	3.15	(4.4)	11.55	(16.1)	190.26	(2.65)
Females											
0.3	25.4	15.43	(60.8)	5.55	(21.9)	1.27	(5.0)	3.15	(12.4)	59.73	(2.36)
1.3	38.6	24.03	(62.3)	8.49	(22.0)	1.75	(4.5)	4.33	(11.2)	87.05	(2.26)
2.3	46.4	27.08	(58.4)	9.90	(21.3)	2.06	(4.4)	7.36	(15.9)	123.44	(2.66)
3.3	46.5	27.12	(58.3)	9.92	(21.3)	2.07	(4.5)	7.39	(15.9)	123.83	(2.66)
4.3	48.2	27.76	(57.6)	10.22	(21.2)	2.14	(4.4)	8.08	(16.8)	132.00	(2.74)

¹ Water, protein and ash weights were estimated from the regression equations presented in Table 27. Fat weights were obtained by difference (see text for details) and the caloric value was estimated using the composition data and the caloric value of protein and fat given by Robbins et al. (1974).

TABLE 34. Composition and caloric content of Anticosti deer in spring as predicted by regression equations and their mean ingesta-free weight for each sex and age category ¹

Sex and age (years)	(C)IFBW (kg)	Composition								Caloric value	
		Water		Protein		Ash		Fat		Mcal	(kcal/g)
		kg	(%)	kg	(%)	kg	(%)	kg	(%)		
Males											
0.8	15.5	11.37	(73.4)	3.28	(21.1)	0.80	(5.2)	0.05	(0.3)	18.23	(1.18)
1.8	32.2	22.79	(70.8)	7.22	(22.4)	1.81	(5.7)	0.38	(1.2)	42.69	(1.33)
2.8	34.7	24.48	(70.8)	7.83	(22.6)	1.76	(5.7)	0.43	(1.2)	46.46	(1.34)
3.8	31.2	22.12	(70.9)	6.98	(22.4)	1.76	(5.7)	0.34	(1.1)	41.01	(1.31)
4.8 ⁺	41.4	29.25	(67.8)	9.46	(22.8)	2.33	(5.6)	0.36	(0.9)	54.62	(1.32)
Females											
0.8	15.3	11.23	(73.4)	3.23	(21.1)	0.79	(5.2)	0.05	(0.3)	17.98	(1.18)
1.8	28.1	20.01	(71.2)	6.27	(23.3)	1.53	(5.4)	0.29	(1.0)	36.69	(1.31)
2.8	35.0	24.42	(69.8)	7.88	(22.5)	2.06	(5.9)	0.64	(1.8)	48.73	(1.39)
3.8	34.6	24.17	(69.8)	7.78	(22.5)	2.03	(5.9)	0.62	(1.8)	48.00	(1.39)
4.8 ⁺	34.8	24.29	(69.8)	7.83	(22.5)	2.04	(5.9)	0.64	(1.8)	48.46	(1.39)

¹ Water, protein and ash weights were estimated from the regression equations presented in Table 28. Fat weights were obtained by difference (see text for details) and the caloric value was estimated using the present composition data and the caloric value of protein and fat given by Robbins et al. (1974).

smaller sample of deer collected and analysed for body composition (Table 25 and Appendices 2 to 8).

This new set of data can be used to obtain estimates of the loss of body weight and of body components from fall to spring (Table 35). It can be seen that appreciable amounts of water, protein and fat are lost during winter. Between 91.3% and 98.6% of the fat reserves are used whereas the proportion of the protein which is lost varies between 20.4% and 43.3%. Fawns are severely affected by winter as they lose some 40% of their protein. Although these estimated losses appear to be high they are probably not unrealistic as two fawns captured, marked and released on Anticosti Island in mid-December, were followed till their death in mid-April. By then, they had lost 35 to 46% of their TBW (Boulet et al., unpubl.). An adult female in the same study lost 43% of its weight between early January and the time of its death in mid-April. Verme (1970) reported similarly that a *winter-killed* bull moose had lost 33% of its pre-winter weight.

The weight loss figures presented in Table 35 may be underestimated as some of the animals included in the sample were probably not at their highest or lowest weight of the annual cycle. Moreover, especially in fawns, some of the animals included in the fall sample, probably the smaller ones, do not survive until spring so that the spring sample might be biased in favor of the animals that were heavier than average in fall.

In a study of starvation on mule deer in captivity, De Calesta et al. (1975) concluded that deer could recover if their weight loss was

TABLE 35. Loss of body weight, body components and caloric content in Anticosti deer between fall and spring ¹

Sex and age (years)	(C)IFBW loss		Loss of components (C)IFBW								Caloric content		
			Water		Protein		Ash		Fat		Mcal	kcal/g	
	kg	(%)	kg	(%)	kg	(%)	kg	(%)	kg	(%)		(C)IFBW	(C)TBW
Males													
0.3-0.8	11.1	(41.7)	4.63	(28.9)	2.50	(43.3)	0.53	(39.8)	3.44	(98.6)	46.18	4.16	4.12
1.3-1.8	10.0	(23.7)	3.30	(12.6)	2.14	(22.9)	0.13	(6.7)	4.43	(92.1)	53.63	5.36	4.79
2.3-2.8	13.7	(28.3)	5.06	(17.1)	2.75	(26.0)	0.24	(10.9)	5.65	(92.9)	68.50	5.00	4.15
3.3-3.8	24.6	(44.1)	11.48	(34.2)	4.99	(41.7)	0.74	(29.6)	7.39	(95.6)	97.14	3.95	3.52
(4.3-4.8) ⁺	30.4	(42.3)	12.95	(30.6)	5.44	(36.5)	0.82	(26.0)	11.19	(96.9)	135.64	4.46	3.84
Females													
0.3-0.8	10.1	(39.8)	4.20	(27.2)	2.32	(41.8)	0.48	(37.8)	3.10	(98.4)	41.98	4.16	4.51
1.3-1.8	10.5	(27.2)	4.02	(16.7)	2.22	(26.1)	0.22	(12.6)	4.04	(93.3)	50.36	4.80	4.09
2.3-2.8	11.4	(24.6)	2.66	(9.8)	2.02	(20.4)	0.00	(0.0)	6.72	(91.3)	78.17	6.86	5.83
3.3-3.8	11.9	(25.6)	2.95	(10.9)	2.14	(21.6)	0.04	(2.0)	6.77	(91.6)	75.83	6.37	5.38
(4.3-4.8) ⁺	13.4	(27.8)	3.47	(12.5)	2.39	(23.4)	0.10	(4.7)	7.44	(92.1)	89.39	6.67	5.55

¹ Estimates obtained by subtracting spring values from values of previous fall for each parameter (Tables 32, 33 and 34).

Percentages expressed as: $\frac{\text{Loss estimated} \times 100}{\text{Fall value}}$

less than 30% of their pre-starvation weight. Three of their 13 fawns died after losing an average of 30% of their initial live weight while one doe died after losing 37% of its body weight. Although they mention that their animals were in good condition at the beginning of the experiment it is probable that at that time of the year (February 29) they had already lost some weight. Gasaway and Coady (1974) estimated that the overwinter weight loss (live weight) of an adult breeding cow moose in Alaska averages 24%, which is very similar to our estimates for adult does. Young domestic sheep can also recover easily from an experimental weight loss of 25% (IFBW) (Drew 1971; Thornton et al. 1979) or 30% (IFBW) Burton et al. (1974) and reach their normal adult weight through a more rapid growth rate after refeeding. In an experiment with moderately fat ewes (< 25% fat), Panaretto (1964) reported weight losses of approximately 50% for two animals. He suggested that one third of the protein reserves and entire body fat stores can be utilized, and concluded that the critical point beyond which recovery is unlikely is when total body water reaches 73 to 75% of the wool-free total body weight.

In the present study water content of fawns is predicted to reach 73.4% (Table 34) in spring with slightly more than 40% of the protein and 98% of the fat reserves utilized (Table 35). In older females, 20.4% to 26.1% of body protein is utilized while in males water appears to account for a larger proportion of the over winter weight loss as they reach sexual maturity. This is probably the result of the loss of fat reserves during the rut as discussed before. In yearling and older animals protein accounts for 16.0% to 19.1% of the IFBW loss depending on age and sex, these figures are all within the range of

protein losses of deer involved in feeding trials on browse. According to a review by Robbins (1973), protein accounts for between 14.37% and 22.22% of the live-weight losses of deer based on nitrogen balance estimates.

Caloric values of body weight losses are given in Table 35. On a TBW basis caloric values vary between 3.52 and 5.83 kcal/g depending on the sex and the age of the individual (3.95 to 6.86 kcal/g on an IFBW basis). In adult females (2.5 years of age and older) caloric values are highest and vary little (5.38 to 5.83 kcal/g TBW). The lowest values are found in adult males (3.52–3.84 kcal/g) and are due to the high proportion of water in the loss.

Reviews of the energetics of body tissue mobilization in dairy cows by Moe et al. (1970) and Reid and Robb (1970) have been generally used as a reference for the estimation of the caloric values of the body weight loss of wild ungulates in winter. The former suggested caloric values between 5 and 7 Mcal/kg live weight loss corrected for variations in rumen fill while the latter concluded that although the loss may vary from 90% fat to 100% water the energy equivalence was usually between 6.3 and 7.9 Mcal/kg. From this Mautz et al. (1976) decided to use 6 kcal/g of live body weight loss in white-tailed deer and Wallmo et al. (1977) used the same figure for mule deer. In a review of energy requirements by moose in winter Gasaway and Coady (1974), also based their estimate on reports of research on milk cows and suggested that the live weight loss of an adult moose was composed of 20% protein and 80% fat, giving a caloric value of 8.6 kcal/g.

Research on sheep indicates that the caloric value of the weight loss is variable. Searle et al. (1979) reported weight losses of 30% (fasted and shorn) with an energetic value increasing from 2.63 kcal/g for the first 4 kg to 3.82 kcal/g for the following 6 kg of weight loss. In grazing ewes, Farrell et al. (1972) reported weight losses varying from 13% to 28% for which the corresponding caloric values were 6.43 kcal/g and 5.52 kcal/g (fasted and fleece-free) live weight. Burton (1970: 49), working with ewes, estimated the loss of energy per unit of *empty body weight* at 7.586 kcal/g. This was estimated for a weight loss between 64 and 50 kg after the animal had already lost 7 kg from an initial weight of 71 kg, and the fat content of the *empty body* at the end of the loss was still high (35.01%). Our results are within these limits but lower than the value generally used for wild ungulates, especially for males and if the *live weight* is used instead of the IFBW. The higher proportion of water in the weight loss of male deer is probably responsible for the low caloric value in both sexes, however when taken on a *live weight* basis, part of the weight loss in both sexes is due to a reduction in the weight of ingesta; that component may comprise 13.9% of the TBW loss in full grown males and 16.8% in does. In male fawns almost no reduction in the weight of ingesta occurs and in female fawns a slight increase exists. For that reason, the caloric value of the weight loss is higher on a TBW than on an IFBW basis.

TABLE 36. Relationships between ingesta-free body weight (IFBW, kg) and the weight of the chemical components (kg) for fawns collected between Sep 02 and Jun 14 on Anticosti Island

Component	N	Equation
Water** ¹	24	$\ln \text{Wat.} = 0.3321 + 0.7506 \ln \text{IFBW}$ $r^2 = 0.962; s_{yx} = 0.0647; s_b = 0.0045$
Protein**	24	$\ln \text{Prot.} = -1.5747 + 1.0166 \ln \text{IFBW}$ $r^2 = 0.980; s_{yx} = 0.1922; s_b = 0.0082$
Ash**	24	$\ln \text{Ash} = -2.2894 + 0.7594 \ln \text{IFBW}$ $r^2 = 0.869; s_{yx} = 0.2883; s_b = 0.0200$
Fat**	24	$\ln \text{Fat} = -18.0337 + 5.7170 \ln \text{IFBW}$ $r^2 = 0.732; s_{yx} = 2.0259; s_b = 0.1691$

¹ ** P < 0.01

The loss of body substance by fawns in winter

In order to assess the change in the proportion of the main body components from the peak condition in fall to the minimum in spring, a series of regression equations relating the weight of the components to the IFBW were computed using all the fawns sampled between Sep 02 and Jun 14 (Table 36). All the correlations are highly significant (P < 0.01), although as in the other cases the "r²" for fat is lower than for the other substances. For this reason in the following analysis the fat content will be determined by difference, a procedure used in the previous section.

By differentiating these equations it is possible to estimate the amount of each component per unit (kg) of body weight loss at a given weight (Figure 22). From this figure it can be seen that the proportions of protein and ash in the loss are almost constant at 22% and 3-4% respectively.

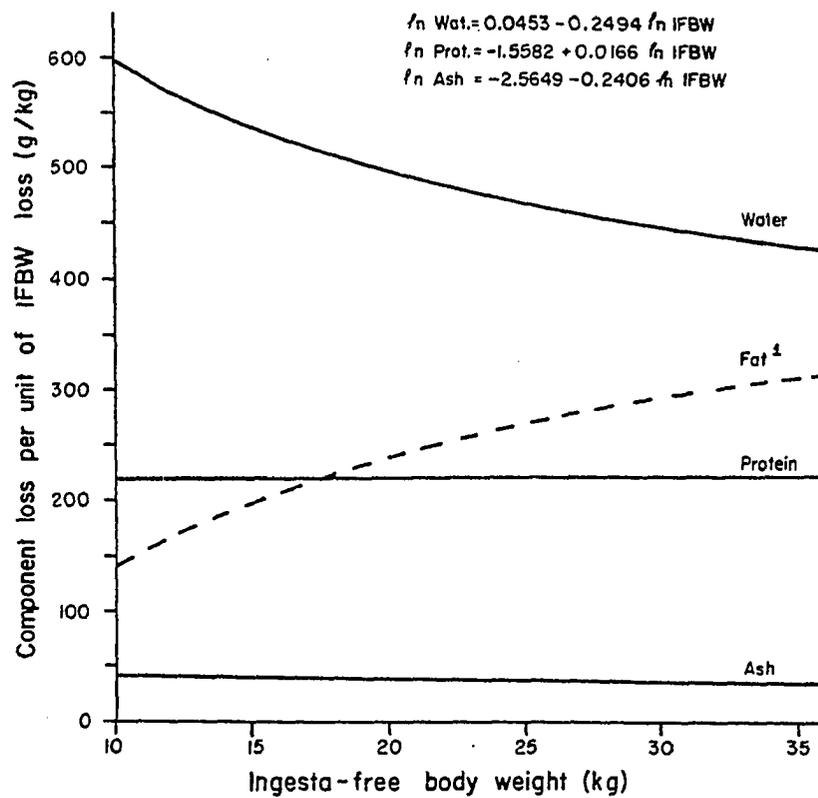
However the proportion of fat decreases from 30% to 15% as the proportion of water increases in the loss. As a consequence, the caloric value (kcal/g) of the substance lost also decreases as winter progresses.

Gain of weight and body reserves in summer

The difference between the fall weight and the weight estimated in the previous spring for the (C)TBW, the (C)IFBW and the weight of each component is interpreted as the summer gain for each age class (Table 37).

The proportion of protein in the IFBW gain in a given summer is very similar to the loss of the previous winter: yearlings: 23%; 2-year-old: 21% in males, 20% in females; older males: 18% to 20%; older females: 18%. Fat constituted only 18% of the IFBW gains in yearlings but increased to over 35% in older males and to 50 to 59% of the gain in females older than 3 years.

Most of the growth must occur during the 120 day period between mid-June and mid-October when the ME of the diet is between 2.55 and 2.63 kcal/g (Table 20) and the protein content between 11 and 18%. Therefore the rate of gain must be high both in absolute value (g/day) and percentage of spring body weight for the period (Table 38). Yearlings of



¹ Fat estimated by difference

Figure 22. Changes in the composition of the IFBW loss of fawns according to their residual IFBW. The equations were obtained by differentiation of the equations presented in Table 36

TABLE 37. Gain in body weight, body components and caloric content of Anticosti deer between spring and fall ¹

Sex and age (years)	(C)TBW gain (kg)	(C)IFBW gain (kg)	Gain of components (kg)				Caloric value		
			Water	Protein	Ash	Fat	Mcal	kcal/g	
								(C)IFBW	(C)TBW
Males									
0.8-1.3	29.9	26.7	14.72	6.08	1.14	4.76	78.08	2.92	2.61
1.8-2.3	20.2	16.2	6.75	3.36	0.39	5.70	72.28	4.46	3.58
2.8-3.3	24.4	21.1	9.12	4.14	0.54	7.30	91.69	4.26	3.76
3.8-4.3	46.7	40.6	20.08	7.92	1.39	11.21	149.25	3.68	3.20
(4.8-5.3) ⁺	35.3	30.4	12.95	5.44	0.82	11.19	135.64	4.46	3.84
Females									
0.8-1.3	26.7	23.3	12.80	5.26	0.96	4.28	69.09	2.97	2.59
1.8-2.3	22.7	18.3	7.07	3.63	0.53	7.07	86.74	4.74	3.82
2.8-3.3	13.5	11.5	2.70	2.04	0.01	6.75	75.10	6.53	5.56
3.8-4.3	16.4	13.6	3.59	2.44	0.11	7.46	84.00	6.18	5.12
(4.8-5.3) ⁺	16.1	13.4	3.47	2.39	0.10	7.44	83.54	6.14	5.19

¹ Estimates obtained by subtracting spring values from the following fall values (Tables 32, 33 and 34)

TABLE 38. Daily gains in body components and energy and seasonal gains in relation to initial (C)IFBW in spring for Anticosti deer

Sex and age (years)	Relative gain ¹ (g)	Daily gain ²					
		(C)IFBW (g)	Protein (g)	Fat (g)	Energy (kcal)		
					Protein	Fat	Total
Males							
0.8-1.3	172	222.5	50.7	39.7	274.3	376.4	650.7
1.8-2.3	50	135.0	28.0	47.5	151.6	450.8	602.4
2.8-3.3	61	179.0	34.5	60.8	186.7	577.0	763.7
3.8-4.3	130	338.3	66.0	93.4	357.3	886.5	1,243.8
(4.3-5.8)+	73	253.3	45.3	93.3	245.4	884.9	1,130.3
Females							
0.8-1.3	152	194.2	43.8	35.7	237.3	338.5	575.8
1.8-2.3	65	152.5	30.3	58.9	163.7	559.1	722.8
2.8-3.3	52	95.8	17.0	56.3	92.0	533.8	625.8
3.8-4.3	39	113.3	20.3	62.2	110.0	590.0	700.0
(4.8-5.3)+	39	111.7	19.9	62.0	107.8	588.4	696.2

¹ |(C)IFBW gain / spring (C)IFBW| x 100

² Growth period: 120 days, mid-June to mid-October

both sexes show the greatest gains in relation to their initial size 172% (males) and 152% (females) and they also have higher protein deposition rates per day (males 50.7 g/day and females 43.8 g/day) than all other age classes except males in their last summer of growth (66.0 g/day). Adult males 3.8 years of age and older also show the highest rate of energy retention per day 1,130.3-1,243.8 kcal per day; adult females have a rate of approximately 700 kcal/day. The cost of lactation is probably sufficient to explain why the deposition of energy in females does not increase with age after the second season of growth.

The data available do not allow a more detailed analysis of the growth process in summer but it is highly probable that the rates are not constant and that the fat: protein ratio of the gain also increases with time as reported for domestic ruminants and for deer (Robbins 1973). Based on the analysis of dietary quality (Part I), the peak of growth for non-lactating animals should probably occur during the 60 day period between mid-June and mid-August when the diet's protein content is above 12% and its ME is above 2.50 kcal/g.

If we assume a protein deposition rate three times as high for this short period as compared to the rest of the summer, it means the deposition rate should reach 75 g/day for a yearling male.

Taking into account the gain in protein and the maintenance equations in section: Protein (p. 128), one can estimate the CP content and DMI required to meet the needs of a 35 kg yearling male. On a 16% CP diet a yearling will need an intake of 168 g of CP or 1,050 g DM ($73.0 \text{ g DMI/kgW}^{0.75}$).

Based on the review of Moe and Tyrrell (1976) and on the estimate of Burton (1970) for normally growing sheep we used an efficiency of 60% for the retention of net energy from ME estimates in order to assess the necessary food intake to meet energy gain in summer. During the period of maximum protein deposition, the increase in fat is probably not higher than what it will be at the end of the growing season, therefore the total energy retention can be set at: 780 kcal NE per day or 1,300 kcal ME per day. This value added to 2,590 kcal ME per day for maintenance requirements (Table 21) comes to a total of approximately 3,890 kcal ME requirement per day. The diet at that time contains 2.63 kcal ME/g and 1,479 g of DMI would be necessary to fulfill all needs ($102.8 \text{ DMI/kgW}^{0.75}$).

If the efficiency of the utilization of ME above maintenance is increased to 75.3% as estimated by Burton (1970) for sheep experiencing compensatory growth, the daily intake can be lowered to $95.8 \text{ g DM/kgW}^{0.75}$. Even in young deer the need for protein will be filled more easily than the need for energy during the mid-summer period. This agrees closely with the model suggested by Robbins (1973: 173-174).

Relationship Between Body Condition Indices and Total Fat Reserves

The level of fat reserves in wild ungulates traditionally has been considered as an index of body condition and many techniques have been suggested for its assessment (Cheatum 1949; Riney 1955; Ransom 1965; Smith 1970; Anderson et al. 1972a; Hesselton and Sauer 1973; and many others). In the present study it was possible to look at

seasonal variations of many fat indices and to relate these to total body fat reserves.

The mean values of the fat indices are given by period and age class in Table 39. All the indices follow the trend of total fat reserves (percentage of fat in the ingesta-free body). The lowest values were reached between mid-April and mid-June for all indices. The recovery was slow in early summer but appeared to be faster in late July and early August when all indices double in value, except for femur marrow fat which recovered more rapidly. The change in fat indices was much more apparent at that time (Jul-Aug) than the change in total fat reserves. Sub-cutaneous fat appeared to be deposited mainly after the end of August.

Between mid-December and late February all indices, except femur marrow fat (FMF) showed a sharp decline in values. In females the declines ranged between 66% and 95% of the fall values while the loss of total body fat reserves was of only 49%. The FMF decline was evident in fawns at that time but happened only in March in most adults and yearlings.

In order to determine the utility of each index in assessing total fat reserves of deer the correlation coefficient between each body condition index and total fat reserves was determined for the different classes of animals in fall and spring (Tables 30, 41 and 42). The correlation coefficients were high for most indices in fall; at that time FMF did not appear to be a reliable index of the level of body fat reserves in adults, especially in males. Eviscerated weight (EW) is

TABLE 39. Seasonal variations in several fat indices and in the total fat reserves of deer collected on Anticosti Island

Period Sex and age ¹	N	Fat indices (mean \pm s.d.)					Total body fat % \pm s.d.
		KFI-T ²	KFI-R	DBF	FMF	Per. W.	
Feb 03-Mar 08							
Female (Y ⁺)	8	54.3 \pm 57.0	20.8 \pm 18.6	0.7 \pm 1.2	62.7 \pm 33.2	86.3 \pm 115.7	8.2 \pm 5.1
Male (Y ⁺)	1	34.5 \pm -	11.3 \pm -	0.0 \pm -	52.3 \pm -	34.3 \pm -	9.6 \pm -
Fawns	7	5.7 \pm 4.2	3.7 \pm 2.8	0.0 \pm 0.0	11.0 \pm 14.8	2.4 \pm 0.8	1.1 \pm 1.6
Apr 13-18							
Female (Y ⁺)	10	11.0 \pm 6.3	4.9 \pm 2.5	0.0 \pm 0.0	8.0 \pm 8.3	5.3 \pm 2.3	1.3 \pm 1.3
Male (Y ⁺)	4	10.2 \pm 4.6	4.6 \pm 1.5	0.0 \pm 0.0	4.6 \pm 7.9	5.4 \pm 2.9	0.9 \pm 1.0
Fawns	5	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	1.5 \pm 0.3	0.2 \pm 0.05
May 15-Jun 14							
Female (Y ⁺)	5	6.1 \pm 2.5	6.0 \pm 2.3	0.0 \pm 0.0	11.5 \pm 13.0	3.7 \pm 1.8	0.6 \pm 0.6
Male (Y ⁺)	4	13.1 \pm 11.7	7.6 \pm 3.8	0.0 \pm 0.0	2.2 \pm 2.0	5.3 \pm 4.0	1.4 \pm 1.6
Fawns	2	5.8 \pm 1.3	5.8 \pm 1.3	0.0 \pm 0.0	4.8 \pm 5.4	1.7 \pm 0.6	0.2 \pm 0.03
Jun 18-Jul 13							
Female (Ad)	4	23.5 \pm 8.6	11.9 \pm 6.3	2.2 \pm 2.0	54.8 \pm 32.4	40.6 \pm 27.5	6.0 \pm 2.9
Male (Ad)	5	30.3 \pm 12.5	14.9 \pm 5.3	3.9 \pm 3.5	74.6 \pm 8.0	94.1 \pm 87.3	7.0 \pm 1.8
Fawns	7	15.2 \pm 10.7	8.3 \pm 4.8	0.0 \pm 0.0	34.7 \pm 22.2	11.5 \pm 8.3	3.7 \pm 1.7

TABLE 39 (continued)

Period Sex and age ¹	N	Fat indices (mean \pm s.d.)					Total body fat % \pm s.d.
		KFI-T ²	KFI-R	DBF	FMF	Per. W.	
Jul 14-Aug 26							
Female (Ad)	11	75.5 \pm 89.1	24.0 \pm 25.2	5.4 \pm 5.8	65.3 \pm 27.3	85.9 \pm 75.2	8.7 \pm 5.2
Male (Ad)	3	65.8 \pm 59.0	23.5 \pm 14.3	5.5 \pm 5.3	84.6 \pm 7.4	113.0 \pm 93.1	10.0 \pm 5.1
Yearlings	11	32.5 \pm 15.8	16.6 \pm 8.2	2.4 \pm 2.3	65.5 \pm 14.5	40.7 \pm 22.8	7.5 \pm 3.1
Fawns	4	30.6 \pm 7.0	17.4 \pm 3.4	0.0 \pm 0.0	33.9 \pm 3.0	9.3 \pm 6.2	4.4 \pm 2.1
Sep 02-Dec 12							
Female (Ad)	9	200.6 \pm 104.0	98.7 \pm 71.1	14.4 \pm 11.2	82.6 \pm 8.6	253.3 \pm 223.1	15.4 \pm 7.4
Male (Ad)	4	198.4 \pm 130.5	111.3 \pm 72.8	17.9 \pm 14.7	74.1 \pm 12.7	330.0 \pm 155.8	16.0 \pm 5.9
Yearlings	4	124.8 \pm 59.0	54.4 \pm 20.1	9.7 \pm 9.3	74.0 \pm 15.0	135.5 \pm 10.6	13.3 \pm 4.1
Fawns	9	200.9 \pm 158.3	79.5 \pm 65.4	4.8 \pm 6.6	70.7 \pm 18.2	115.6 \pm 82.1	12.7 \pm 4.4

¹ (Y+): 11.5-month-old and older; (Ad): > 23.5-month-old; Yearlings: 11.5-23.5-month-old; Fawns: < 11.5-month-old

² KFI-T: Kidney fat index (total fat); KFI-R: Kidney fat index (Riney); DBF: Depth of back fat; FMF: Femur marrow fat; Per. W.: Peritoneum weight

TABLE 40. Relationships between total fat reserves and selected indices of body condition for yearling and adult males on Anticosti Island ¹

Fat reserves expressed as	Index	Feb 03 - Jun 14		Jul 14 - Dec 12	
		N	"r"	N	"r"
ln Fat Weight (kg)	ln DW ² (kg)	9	0.245	14	0.845**
ln Fat Weight (kg)	ln IFBW (kg)	9	0.082	14	0.849**
Fat Weight (g)	Dry Per. W. (g)	9	0.937** ³	13	0.763**
Fat Weight (g)	KFW-R (g)	9	0.462	14	0.919**
Fat Weight (g)	KFW-T (g)	9	0.669*	14	0.735**
% Fat ⁴	EW/HFL ³ (kg/cm ³)	9	-0.002	14	0.803**
% Fat	KFI-R	9	0.643	14	0.817**
% Fat	KFI-T	9	0.776*	14	0.844**
% Fat	DBF (mm)	9	All DBF values equal to 0.00	14	0.832**
% Fat	FMF (%)	8	0.904**	13	0.240

¹ Relationships: Fat reserves = a + b (Index); "r" = correlation coefficient

² DW: Dressed weight; IFBW: Ingesta-free body weight; Dry Per. W.: Dry peritoneum weight; KFW-R: Kidney fat weight (Riney); KFW-T: Kidney fat weight (total); EW/HFL: Eviscerated weight / Hind foot length; KFI-R: Kidney fat index (Riney); KFI-T: Kidney fat index (total); DBF: Depth of back fat; FMF: Femur marrow fat

³ Significance level: ** P < 0.01; * P < 0.05

⁴ % Fat: (Total fat weight / IFBW) x 100

TABLE 41. Relationships between total fat reserves and selected indices of body condition for yearling and adult females on Anticosti Island¹

Fat reserves expressed as	Index	Feb 03-Jun 14		Jul 14-Dec 12	
		N	"r"	N	"r"
ln Fat Weight (kg)	ln DW ² (kg)	23	0.788** ⁴	28	0.827**
ln Fat Weight (kg)	ln IFBW (kg)	23	0.809**	28	0.822**
Fat Weight (g)	Dry Per. W. (g)	19	0.910**	26	0.855**
Fat Weight (g)	KFW-R (g)	23	0.856**	27	0.518**
Fat Weight (g)	KFW-T (g)	23	0.810**	27	0.802**
% Fat ³	EW/HFL ³ (kg/cm ³)	23	0.694**	28	0.868**
% Fat	KFI-R	23	0.792**	27	0.857**
% Fat	KFI-T	23	0.744**	27	0.801**
% Fat	DBF (mm)	23	0.589**	28	0.857**
% Fat	FMF (%)	23	0.926**	28	0.522**

¹ Relationships: Fat reserves = a + b (Index); "r" = correlation coefficient

² DW: Dressed weight; IFBW: Ingesta-free body weight; Dry Per. W.: Dry peritoneum weight; KFW-R: Kidney fat weight (Riney); KFW-T: Kidney fat weight (total); EW/HFL: Eviscerated weight / Hind foot length; KFI-R: Kidney fat index (Riney); KFI-T: Kidney fat index (total); DBF: Depth of back fat; FMF: Femur marrow fat

³ % Fat: (total fat weight / (C)IFBW) x 100

⁴ Significance levels: ** P < 0.01; * P < 0.05

TABLE 42. Relationships between total fat reserves and selected indices of body condition for fawns on Anticosti Island ¹

Fat reserves expressed as	Index	Feb 03-Jun 14		Jul 14-Dec 12	
		N	"r"	N	"r"
In Fat Weight (kg)	In DW ² (kg)	14	0.438	12	0.948** ⁴
In Fat Weight (kg)	In IFBW (kg)	14	0.426	12	0.962**
Fat Weight (g)	Dry Per. W. (g)	13	0.139	10	0.960**
Fat Weight (g)	KFW-R	14	0.530	12	0.943**
Fat Weight (g)	KGW-T	14	0.351	12	0.942**
% Fat ³	EW/HFL ³ (kg/cm ³)	14	0.146	10	0.915**
% Fat	KFI-R	14	0.451	12	0.769**
% Fat	KFI-T	14	0.294	12	0.744**
% Fat	DBF (mm)	14	All DBF values equal to 0.00	11	0.780**
% Fat	FMF (%)	14	0.766** ³	11	0.827**

¹ Relationships: Fat reserves = a + b (Index); "r" = correlation coefficient

² DW: Dressed weight; IFBW: Ingesta-free body weight; Dry Per. W.: Dry peritoneum weight; KFW-R: Kidney fat weight (Riney); KFW-T: Kidney fat weight (total); EW/HFL: Eviscerated weight / Hind foot length; KFI-R: Kidney fat index (Riney); KFI-T: Kidney fat index (total); DBF: Depth of back fat; FMF: Femur marrow fat

³ % Fat: (Total fat weight / (C)IFBW) x 100

⁴ Significance level: ** P < 0.01; * P < 0.05

probably the most easily available index for a population hunted in fall and in such cases it is probably the most appropriate index.

In spring many indices were highly correlated with fat reserves in yearling and adult females but in males and fawns the low levels of fat resulted in low values for the indices; these were not significantly correlated to body fat reserves in most cases. In the three groups however, FMF appeared to be the best index of fat reserves both because of its high correlation coefficient and because of the ease with which it can be obtained. The dry weight of the peritoneum was also highly correlated with total fat weight but it is sometimes damaged during collection and is not as easily obtainable from a frozen carcass.

Seasonal Changes in the Weight of Some Organs and Parts

The effect of nutrition on the size of the organs has been investigated in domestic and wild mammals but the results are still contradictory in many cases (Palsson 1955; Doljanski 1960; Hoffman and Robinson 1966; Peters and Boyd 1968; Burton 1970; Mitchell et al. 1976; Murray and Slezacek 1980; Verme and Ozoga 1980a, 1980b).

This study presented an opportunity to assess the relationships between the general body condition cycle in deer and the weight of organs and parts. Analysis of the data, except for the alimentary tract, has been done according to procedures used by Murray and Slezacek (1980). The analysis is based on regression equations using the \ln of the weight of the specific organ or part as the dependent variable (Y) and the \ln of the (C)IFBW as (X). When the correlation was significant the weight of an

organ or part was predicted for the average weight of a deer of a given class in fall and spring (Tables 43 and 44). The estimated relative weight (g/100 g (C)IFBW) can be used to assess the effect of the winter nutritional stress on each part or organ. For the digestive tract the ratios were not based on equations but were calculated directly from each sample; that procedure is the most frequently used in the literature.

In two groups of deer, fawns, and yearlings and older females, the skin seems to follow closely the trend of the IFBW, as the relative weights are very similar in spring and fall. The weight of the heart also follows the (C)IFBW in (Y⁺) females but does not show the same rate of decline as does the IFBW of fawns although a weight loss of this organ is also apparent. The same is true for the spleen and the liver in fawns. The brain may be one of the few parts of the body to gain weight in winter; the weight of kidneys does not appear to change in relation to the IFBW in any of the two groups.

Taking into account the small sample size and the variability among the individuals these results are consistent with most of the findings cited in the literature. However, the stability in the weight of the kidneys is different from what has been reported by Batcheler and Clarke (1980), Dauphiné (1975), Mitchell et al. (1976) and Verme and Ozoga (1980a). These researchers have all reported appreciable changes in the weight of the kidneys in relation to seasonal or experimental nutritional changes. However, Brown and Guthrie (1968) and Peters and Boyd (1968) using rats and Burton (1970) using sheep, reported that kidneys were not very affected by undernutrition and Burton (1970: 17)

TABLE 43. Regression equations and predicted weights (anti-ln y) of deer parts and organs of fawns in relation to ln IFBW in fall and spring

Date and Dependent variable	N	Equation	"r"	"sb"	Predicted weight ¹		
					g	% IFBW	% TBW
Sep 02-Dec 12							
ln Sk. W. ²	9	y = -1.6490 + 0.9353 x	0.902** ³	0.0040	2,542	9.97	8.20
ln Li. W.	7	y = -2.3034 + 0.8620 x	0.957**	0.0035	628	2.46	2.03
ln Hea. W.	7	y = -1.8878 + 0.7272 x	0.879**	0.0100	242	0.95	0.78
ln Kid. W.	10	y = -3.6724 + 0.7959 x	0.592 ^{n.s.}	0.0087	(85±31)	-	-
ln Lu. W.	7	y = -2.2842 + 0.7928 x	0.817*	0.0062	317	1.24	1.02
ln Spl. W.	7	y = -5.7154 + 0.9979 x	0.927**	0.0071	82	0.32	0.27
ln Br. W.	4	y = -0.5575 + 0.5404 x	0.969*	0.0020	138	0.54	0.44
Apr 13-Jun 14							
ln Sk. W.	8	y = -1.3697 + 0.9052 x	0.671 ^{n.s.}	0.0075	1,548	10.18	7.37
ln Li. W.	7	y = -4.9441 + 1.1434 x	0.921**	0.0061	441	2.84	2.10
ln Hea. W.	8	y = -1.4321 + 0.6887 x	0.953**	0.0020	184	1.18	0.87
ln Kid. W.	8	y = 3.7229 + 0.0692 x	0.079 ^{n.s.}	0.0071	(81±13)	-	-
ln Lu. W.	8	y = -1.8948 + 0.7858 x	0.486 ^{n.s.}	0.0122	(287±92)	-	-
ln Spl. W.	8	y = -8.9816 + 1.3318 x	0.652 ^{n.s.}	0.0135	(46±17)	-	-
ln Br. W.	8	y = 1.5765 + 0.3510 x	0.840**	0.0021	143	0.92	0.68

¹ When "r" significant P < 0.05 the weight is predicted using a mean IFBW of 25.5 kg in fall and 15.5 kg in spring (TBW: 31.0 and 21.0 kg) in the other cases the average organ weight and its s.d. are given in parentheses.

² Sk. W.: Skin weight; Li. W.: Liver weight; Hea. W.: Head weight; Kid. W.: Kidney weight; Lu. W.: Lung weight; Spl. W.: Spleen weight; Br. W.: Brain weight

³ ** P < 0.01; * P < 0.05

TABLE 44. Regression equations and predicted weights (anti-ln y) of parts and organs of yearling and adult females in relation to ln (C)IFBW (g) in fall and spring

Date and Dependent variable	N	Equation	"r"	"sb"	Predicted weight ¹		
					g	% (C)IFBW	% (C)TBW
Sep 02-Dec 12							
ln Sk. W. ²	12	y = -1.9191 + 0.9533 x	0.723** ³	0.0061	4,088	8.89	7.11
ln Li. W.	6	y = -3.5327 + 0.9881 x	0.962**	0.0081	1,183	2.57	2.06
ln Hea. W.	6	y = -0.6434 + 0.6297 x	0.951**	0.0018	454	0.99	0.79
ln Kid. W.	12	y = -0.2187 + 0.4830 x	0.614*	0.0041	144	0.31	0.25
ln Lu. W.	6	y = 5.4969 + 0.0991 x	0.010 ^{n.s.}	0.0097	(717±138)	-	-
ln Spl. W.	6	y = -24.0544 + 2.7444 x	0.857*	0.0242	224	0.49	0.39
ln Br. W.	5	y = 4.2681 + 0.0857 x	0.121 ^{n.s.}	0.0081	(181 ± 27)	-	-
Apr 13-Jun 14							
ln Sk. W.	14	y = -0.8801 + 0.8331 x	0.804**	0.0033	3,121	8.92	7.01
ln Li. W.	14	y = -0.9607 + 0.7266 x	0.640*	0.0046	766	2.19	1.72
ln Hea. W.	11	y = -3.0082 + 0.8488 x	0.751*	0.0044	355	1.01	0.80
ln Kid. W.	13	y = -3.3576 + 0.7944 x	0.736**	0.0045	149	0.43	0.33
ln Lu. W.	10	y = -1.9293 + 0.7956 x	0.869**	0.0027	599	1.71	1.35
ln Spl. W.	14	y = -4.7889 + 0.9036 x	0.662**	0.0059	106	0.30	0.24
ln Br. W.	13	y = 3.3066 + 0.1770 x	0.192 ^{n.s.}	0.0028	(170 ± 14)	-	-

¹ When "r" significant P < 0.05 the weight is predicted using a mean (C)IFBW of 46.0 kg in fall and 35.0 kg in spring [(C)TBW: 44.5 and 57.5 kg] in the other cases the average organ weight and its s.d. are given in parentheses.

² Sk. W.: Skin weight; Li. W.: Liver weight; Hea. W.: Head weight; Kid. W.: Kidney weight; Lu. W.: Lung weight; Spl. W.: Spleen weight; Br. W.: Brain weight

³ ** P < 0.01; * P < 0.05

suggested that the kidney might be a preferential site of nutrient consumption as compared to the body as a whole.

The characteristics of the digestion tract are most likely to be affected by changes in body weight and food quality as shown in Table 45. Weight of the viscera, averages 30% of TBW in fall but increases to 36% of TBW when the animal is emaciated in spring. The increase in the relative amount of the ingesta is mainly responsible for this change. The rumen volume: body weight ratio of Anticosti deer of 10.3% in fall is very similar to the 10% that has been reported for southern white-tailed deer (Short 1964) and the 10.3% for mule deer (Short et al. 1965). However this ratio increases to 15.9% for does and 18.7% for fawns in late winter and spring.

The fresh weight of the rumino-reticular content as a proportion of TBW amounts to 9.4% for Anticosti deer in summer and fall, using a dry weight basis for the content the proportion is 1.1%. These figures are within the range of the values reported for other wild cervids: roe deer 7% fresh (1.7% dry) (Prins and Greelen 1971) and 8.5% (Nagy and Regelin 1975); white-tailed deer 8% (1.4%) (Short et al. 1969); mule deer 7.4% (1.0% (Short et al. 1965); fallow deer 9-12% (1.06% (Prins and Greelen 1971) 11.6% (Nagy and Regelin 1975); and moose 8.0-11.4% (Gasaway and Coady 1974). In spring, on Anticosti Island the dry weight of the content of the rumino-reticulum accounts for 2.06% of the (C)TBW in does and 2.38% in fawns. The proportion of the physical capacity of the rumino-reticulum that is filled by the content is highly variable even within a given age and sex group and in a given season. The percentage averages 78 for all deer examined for this criterion.

TABLE 45. Relative size of the reticulo-rumen and its content [volume (cc) x 100 / (C)IFBW (g)] and relative weight of the viscera and ingesta [weight of part (g) x 100 / (C)IFBW (g)] in yearling and adult female deer and in fawns according to the period of the year

Age and sex	Body part	Period of the year		
		Apr 13-Jun 14	Jun 18-Aug 26	Sep 02-Dec 12
Y and Ad ¹ Females	Viscera W.	35.7 ± 4.90 (12) ^{a 2}	31.0 ± 3.36 (22)	31.1 ± 3.42 (11) ^a
	Ingesta W.	24.0 ± 3.24 (12) ^b	19.6 ± 3.37 (23)	20.1 ± 3.07 (11) ^b
	R.R. Vol.	15.9 ± 4.71 (10)	12.5 ± 3.49 (10)	10.3 ± 2.09 (3)
	R.R. Vol. C.	11.6 ± 2.28 (10)	9.8 ± 2.43 (16)	10.5 ± 2.32 (6)
	R.R. W. C. (Fresh)	11.3 ± 2.23 (8)	8.9 ± 2.01 (12)	12.6 ± 0.65 (2)
	R.R. W. C. (Dry)	2.06 ± 0.12 (8) ^b	1.02 ± 0.23 (12)	1.56 ± 0.06 (2) ^b
	$\frac{\text{R.R. Vol. C.}}{\text{R.R. Vol.}} \times 100$	72.1 ± 15.22 (10)	79.9 ± 12.82 (10)	90.2 ± 6.36 (3)
	Fawns	Viscera W.	36.9 ± 4.24 (8) ^b	
	Ingesta W.	26.3 ± 5.15 (8) ^b		16.5 ± 2.54 (10) ^b
	R.R. Vol.	18.7 ± 2.84 (3) ^a		10.3 ± 0.50 (2) ^a
	R.R. Vol. C.	13.6 ± 1.84 (7) ^b		7.6 ± 0.89 (4) ^b
	R.R. W. C. (Fresh)	12.8 ± 1.80 (5)		8.6 ± - (1)
	R.R. W. C. (Dry)	2.38 ± 0.27 (5)		1.20 ± - (1)
	$\frac{\text{R. R. Vol. C.}}{\text{R.R. Vol.}} \times 100$	80.3 ± 15.97 (3)		81.1 ± 3.11 (2)

¹ Pregnant females with uterus and content exceeding 1 kg not included

² Mean ± s.d. (sample size); comparisons made between spring and fall values: "a" indicates a difference P < 0.05; "b" a difference P < 0.01 (adults and fawns tested independently)

From these results it can be concluded that Anticosti deer do not differ appreciably from mule deer or white-tailed deer on different habitats in terms of the relative size of the rumen and the mass of its content in fall. The amount of ingesta, however (including intestine content) seems to be greater than the calculated value using the equation proposed by Robbins (1973: 32) (16.5-20.1% as compared to 9-10% for deer of similar weights).

The evidence for an increase in the proportion of the ingesta during winter and for changes in the volume and water content of the rumen also suggests that these factors may affect the estimates of weight losses and metabolic parameters on live animals during this season and hence must be taken into account.

GENERAL DISCUSSION AND CONCLUSIONS

The relationships found between food resources and body condition of deer on Anticosti Island clearly show that their survival is highly dependent on their ability to adapt their seasonal physiological rhythm to the seasonally cyclic availability and quality of the food resources. An understanding of the relationships between these two systems permits a more precise definition of the time of year and circumstances under which a critical point for survival will be reached and how the production of new biomass in the herd, either by reproduction or body growth, is confined within narrow limits.

One important aspect of this relationship is the weight cycle of deer which determines nutrient requirements in relation to the availability of food resources. Based on estimates of spring and fall weights and on information on body composition, a schematic representation of weight variations is given in Figures 23 and 24. The slopes of the curves are based on the interpretation of the annual cycle of the herd in relation to food availability and quality, whereas the minima and maxima are based on the data presented in Table 32. Live weights in spring and

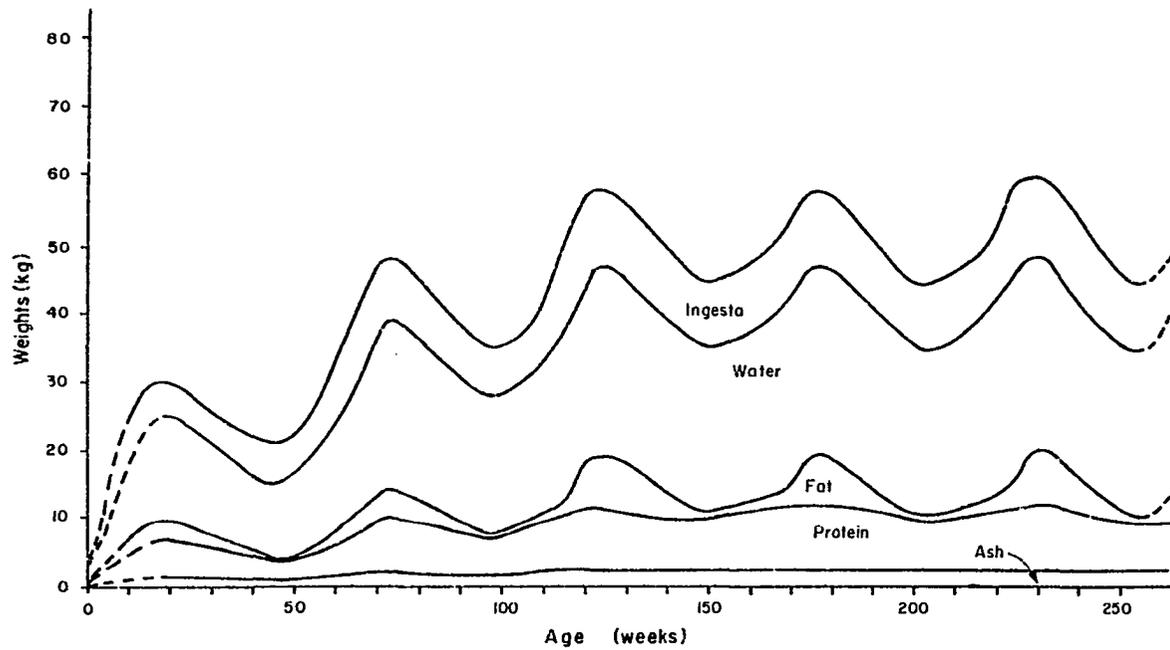


Figure 23. Seasonal variations in the body composition and weight of female deer of Anticosti Island. The maximum and minimum weights are based on the data presented in preceding tables, the slopes are approximated from the general knowledge of the annual cycle of the herd

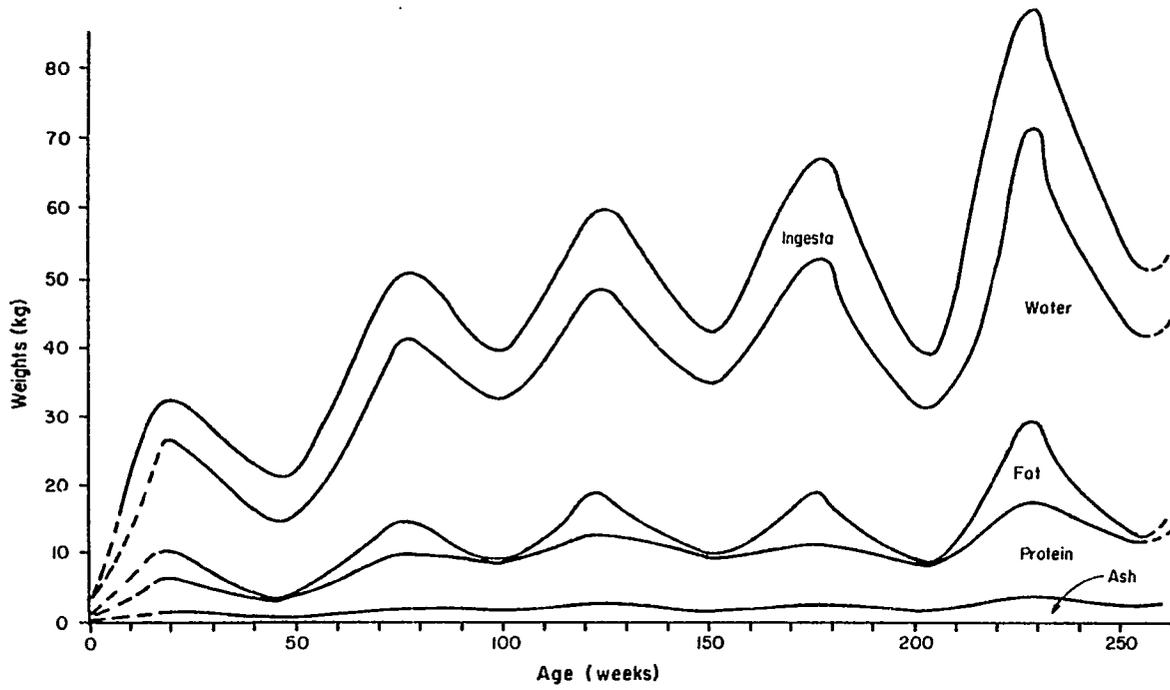


Figure 24. Seasonal variations in the body composition and weight of male deer of Anticosti Island. The maximum and minimum weights are based on the data presented in preceding pages, the slopes are approximated from the general knowledge of the annual cycle of the herd

fall are based on data presented in Tables 32, 33 and 34. Deer of both sexes and all ages, including fawns, lose a considerable amount of body substance in winter and must compensate by a rapid gain during a short period in summer. As reported by Bandy et al. (1970) for captive deer and by McEwan (1968) for caribou the loss after the first year of life is much less important in females than in males. The difference between the sexes is especially pronounced after bucks reach full sexual maturity, presumably at 3.5 years of age. In females there is no apparent increase in weight loss after the first winter. After the first fawn is produced, usually when they are 3-year-old (\approx week 156), there is no further gain in fall weight.

In relation to the seasonal rhythm of the annual cycle, factors essential for the survival, growth and productivity of deer are their capacity to find, ingest and process the required nutrients as well as the adoption of conservation strategies during critical periods. During certain periods, it can be expected that nutrients will be scarce and that intraspecific competition or searching time will be limiting. At other times, even if high quality forage is readily available, the requirements might be so high that the processing rate is insufficient to allow all the needs to be met. Finally, at other times the general quality of the forage can be so low that despite an abundance of forage the rate of passage will limit the availability of nutrients to the organism below maintenance needs. It appears that under most circumstances on Anticosti Island protein requirements will be satisfied before energy requirements. Therefore energy requirements are examined

in detail using a young male and an adult female producing a single fawn as examples (Figures 25 and 26).

These figures give a schematic representation of the energy requirements for maintenance based on estimates given in Tables 20 and 21, and of requirements for growth based on weight and body composition data presented in Table 37. Body composition changes are based on estimates presented in Table 35 and on the assumed rates of protein and fat deposition discussed previously. In the adult female energy requirements are estimated for the production of one 3.5 kg fawn born on June 30. These estimates are based on the net energy retention equation developed by Robbins and Moen (1975), using a net energy coefficient of 75%. The peak milk production ($78 \text{ kcal/kgW}^{0.75}$) was based on the value given by Sadleir (1980) for a black-tailed doe with a single fawn. The 64.4% net energy coefficient for milk production from food was reported by Moe et al. (1970) and the shape of the lactation curve was visually fitted based on the curves given by Moen (1973: 355). Utilizing these energy requirements and the metabolizable energy values of the diet of Anticosti deer (Table 20), it was possible to calculate the required dry matter intakes which are given in the upper part of Figures 25 and 26.

The cycle of energy requirements for the young male given in Figure 25 covers the period extending from the beginning of its first winter to the end of its second fall. During the first winter the body reserves supply approximately one third of the maintenance needs with the result that there is a 34.8% loss of total body weight. The rest of the maintenance needs are supplied by food consumed. For a deer with a

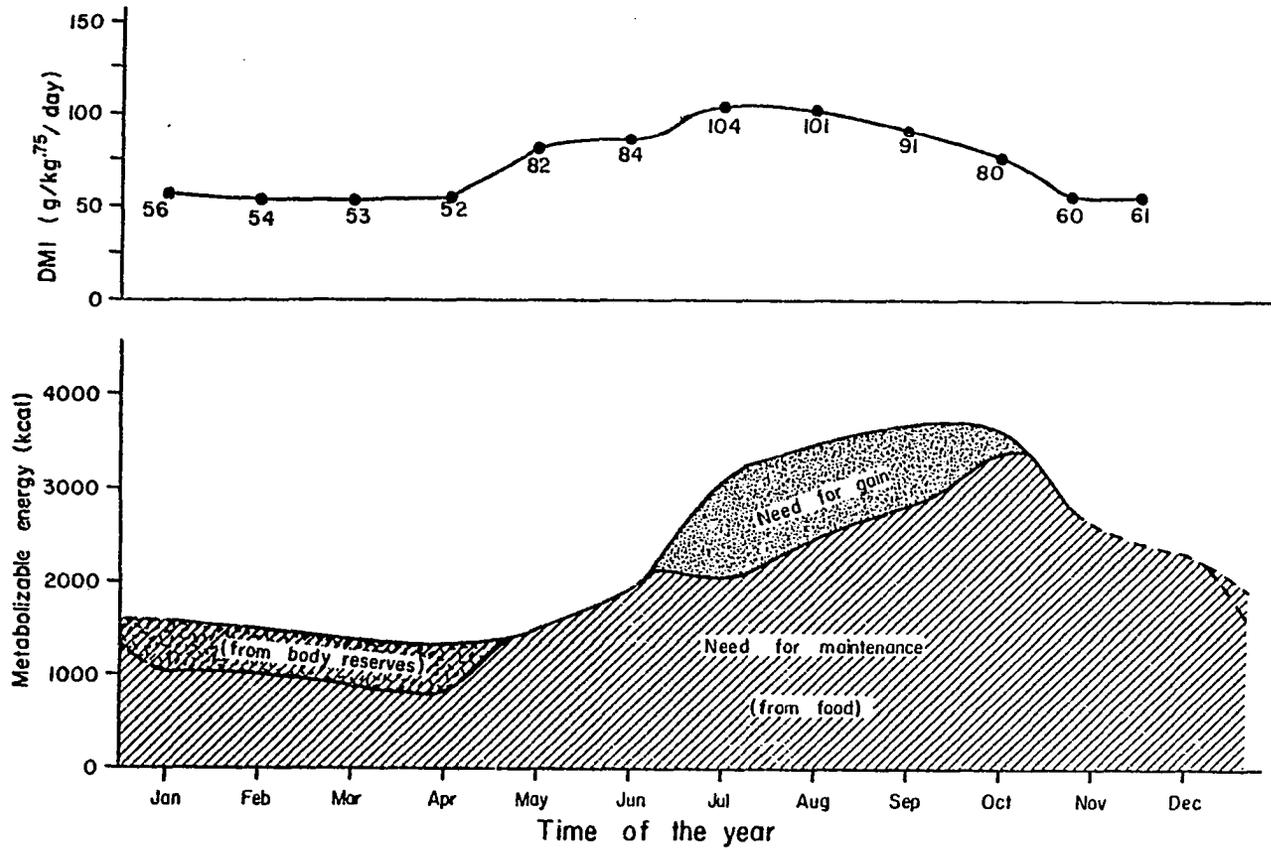


Figure 25. Schematic representation of energy requirements and sources for male deer on Anticosti Island during their first winter and the following summer

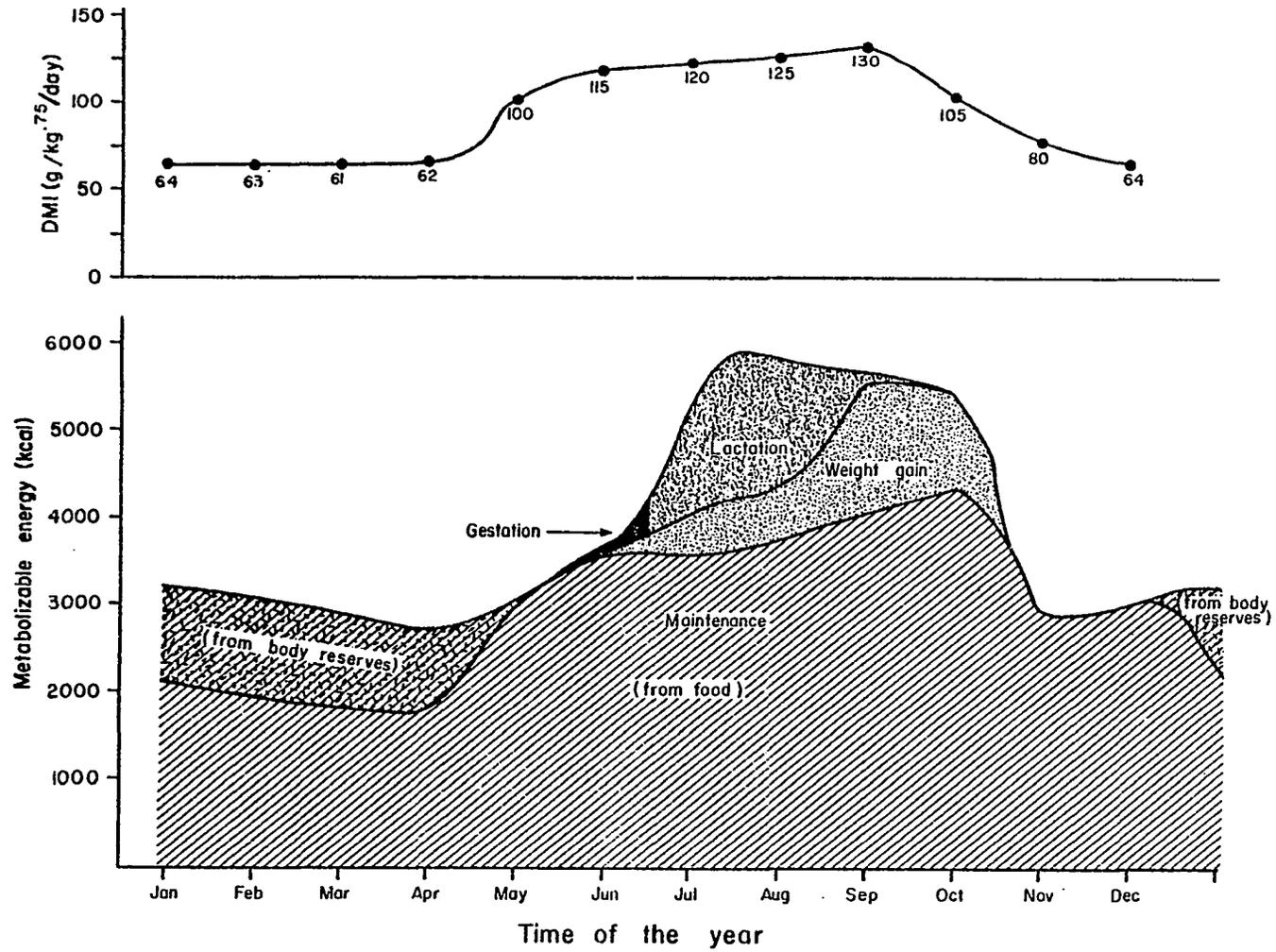


Figure 26. Schematic representation of energy requirements and sources for mature female deer on Anticosti Island producing a single fawn and reaching average fat reserves in fall

typical diet, mainly composed of *A. balsamea* and lichens, the required dry matter intake would average $54 \text{ g/kgW}^{0.75}$.

With the arrival of spring in May, highly digestible vegetation appears but it is available in very limited quantity and will be most often covered by the old grasses and forbs of the previous year. Despite a noticeable intensive selection at that time, only a small proportion of the diet is constituted of the new growth vegetation. The diet consists largely of grasses and forbs (mainly *Fragaria virginiana* and *Cornus canadensis*) of the previous year. During this period, which extends from late April to late May, deer were frequently seen in snow-free areas, especially on southern slopes, feeding on very young graminoids and forbs and digging their roots (especially *Taraxacum officinale* and *Hieracium spp.*, and *Equisetum spp.*). Concurrently there is also a necessary increase in metabolic rate and despite the presence of nutritious new plant growth it is probably impossible for a deer to digest the $82.2 \text{ g/kgW}^{0.75}$ that should be ingested daily to meet metabolic requirements. As a result some physiological processes may be delayed: molting was observed to last until mid-July in some young animals and body growth probably can be delayed until early June, but if spring is late mortality among fawns may occur as late as in May. It is probably not until mid-June that quality of the food permits intakes sufficient to allow growth to take place. The maximum deposition of energy and protein occurs in July and early-August when high quality food is abundant and can be rapidly processed in the rumen. In September and October digestibility of forage has decreased and deer presumably are more selective in feeding. Concurrently, rate of passage declines as well as

food intake and it is probable that the relative physiological dormancy period begins in late October when growth ceases, metabolic rate decreases as well as food requirements. *Cornus canadensis* is then an important component of the diet and species growing under forest cover and offering green leaves (*Coptis groenlandicum*, *Linnea borealis*) as well as ericaceous shrubs and *Equisetum spp.* increase in abundance in the rumen contents.

The energy cycle of the adult doe is also confined within the narrow limits imposed by the food quality. In winter, according to this model, the body reserves should supply 20% to 25% of the maintenance energy and the daily intake should have to be maintained at $62 \text{ g/kgW}^{0.75}$ in order to supply the rest of the energy required. In spring, a sharp rise in metabolic rate normally occurs at a time when high quality forage is still scarce and does as well as fawns will have to be very selective in order to incorporate a sufficient amount of highly digestible and rapidly passing forage in their diet which is primarily composed of green vegetation of the previous year.

In early June the added cost of gestation will raise the needs appreciably but it appears that some recovery is possible as the average fat content increases from 0.6 to 6.0% between the May 15-June 14 period and the June 18-July 13 period. However some females probably use a portion of their available fat reserves in late May and early June to compensate for their high energy requirements of late pregnancy. The end of June is the most energy demanding period, coinciding with lactation. Soon after this, body reserves must be accumulated before the decline in forage quality in late summer and fall. In domestic ruminants, although it

is usual that a substantial part of the energy requirements be supplied by body reserves during lactation (Moe et al. 1970; Reid and Robb 1970; Cowan et al. 1979), Cowan et al. (1980) working with domestic sheep reported that, given a high quality diet during lactation, ewes that had little fat reserves at the end of gestation could deposit fat during the period of peak milk production. They also observed that the yield of milk was related to the quality of the diet during lactation and not to the fat reserves, but that the contrary was the case for the fat content of milk.

Despite a capability for an early build up of fat reserves, it is probably not possible for all does to realize this as some lactating females are still very thin in mid-August. As a consequence there is a need for high forage intakes as well as high quality of forage in September and October if the average fat reserve of 15% of body weight is to be reached. In late summer and fall, there appears to be an increased selection for green vegetation, such as the leaves of herbaceous plants and shrubs growing in wet areas or under forest cover. *Cornus canadensis*, which may remain green and highly digestible in these habitats as late as early November (Tremblay and Huot, unpubl. data) accounts for 30% of the diet at that time. After that period the metabolic rate of does declines and the breeding period is relatively quiet and much less energetically demanding than for bucks. As snow begins to cover the ground deer continue to feed selectively on forest floor plants still available under large conifers, *Cornus canadensis* accounts for 41% of the diet and the remainder is primarily small plants with green leaves

(*Coptis groenlandicum*, *Mitella nuda*, *Epigaea repens*, *Linnea borealis*) and *Equisetum spp.*

The models of the energy cycles of Anticosti Island young and adult female deer (Figures 25 and 26) appear to be realistic and in accordance with what is presently known about wild ungulates living in northern environments. They need, however, to be assessed in relation to deer population dynamics and survival on Anticosti Island.

Under the environmental conditions of Anticosti Island mortality of fawns in winter can be very high and in some years only a small proportion might survive if snow remains on the ground for a long period or if inclement weather conditions prevent deer from having free access to new vegetation in spring. The body condition attained by the animal in the fall, the degree of energy conservation that can be maintained during winter, the amount of weight loss that can be tolerated before death and the date of arrival of spring, probably are the most important factors influencing fawn survival under these conditions. In other words the survival of deer will be more related to their capacity to survive starvation than their ability to feed efficiently in winter. Each kilogram of weight gained in late summer and fall can probably provide energy for an additional 5 days of survival at the end of winter in the event that forage is unavailable or spring is delayed. It also appears that on Anticosti Island the degree of emaciation that can be tolerated in fawns is extreme. The fact that they have easy access to mature coniferous forest can protect them against sudden stressful weather conditions which could be fatal for an emaciated animal. Such

short term heavy demand has been suggested as the cause of mortality of red deer still carrying fat reserves (Mitchell and Staines 1976). In a study on white-tailed mortality on the mainland in Quebec, Potvin et al. (1978) reported that 25% of the individuals that had apparently died of starvation showed femur marrow fat levels exceeding 25%. The importance of the reduction in activity as an energy conservation strategy in winter has already been reported for white-tailed deer in captivity by Ozoga and Verme (1970) and Verme and Ozoga (1980b), and for free-ranging white-tailed deer by Moen (1976) and for roe deer (Cederlund, in press).

In the present model, no supplementary requirements were added for thermoregulation and the maintenance requirements are those reported for captive animals. Despite these conservative estimates it is doubtful that the indicated intakes can be achieved by the deer on Anticosti Island because of the low digestibility of the available forage. In April, the average dry matter content of the rumen-reticulum was only 50 g/kgW^{0.75} for fawns and 53 g/kgW^{0.75} for yearling and older females and according to tracking observations (Boulet et al., unpubl.) the dry matter intake of fawns in winter averaged 32 g/kgW^{0.75}. Verme and Ozoga (1980b) reported that deer having free access to white cedar (*Thuja occidentalis*) could reach intakes exceeding 100 g/kgW^{0.75} (fresh weight) to compensate for the deer's poor fall condition. However, while white cedar is known to be a highly preferred browse species in winter for white-tailed deer in the north-eastern and Great Lakes states, *A. balsamea* is the main browse species on Anticosti Island, and this is usually considered as a starvation food (Hosley 1965; Ullrey et al. 1968). Possibly, then, the state of

chronic starvation experienced by deer during the winter may cause a lowering of the rate of metabolism to below the level usually maintained in captive animals, resulting in lower general maintenance costs. These depression in basal or resting metabolism associated with starvation have already been reported for humans (Keys et al. 1950; Grande et al. 1958; Fliederbaum et al. 1979) and rats (Montemurro and Stevenson 1960; Kham and Bender (1979).

The importance of this phenomenon has also been suggested for wild reindeer in Svalbard (Nilssen and Ringberg 1980) and Øritsland (1977, 1980) has incorporated such a decreased metabolic rate in models of energy balance under winter food deprivation conditions. In humans and rats the BMR has shown decreases ranging from 30 to 50% after a severe restriction in nutrient intake. Using the formula suggested by Øritsland (1980), by mid-winter the BMR of a fawn would be 80% of its normal value and in spring 60%. The required DMI would decrease from 52 g/kgW^{0.75} in early January to 22.5 g/kgW^{0.75} in early April which would be much closer to what has been reported for captive deer (see Table 24) and to the unpublished results of Boulet et al.

For female deer, a similar pattern probably exists during winter, but the summer period is also critical for the survival of the offspring as well as for the physical condition that will be attained in fall and the reproductive performance at that time. The condition of the doe in spring might determine the fate of the fawn in the first days following parturition (Verme 1963, 1977) and it is probable that on Anticosti Island following severe winters many newborn fawns do not survive for long. In such cases, without the need for lactation, does

will have the opportunity to build up new reserves for the coming fall and will probably be in good condition during the breeding period. If the fawn survives, however, and the amount of milk produced is sufficient for normal growth, it is highly probable that the energy requirements for both lactation and the replenishment of normal body reserves will not be met. The high intake necessary to build up body reserves in September and October probably can not be reached. Although the greatest recorded rumen fill for all deer occurred in mid-October in lactating females (8.9 and 10.2 kg fresh weight), the dry weight of the rumen content amounted to only $46 \text{ g/kgW}^{0.75}$, which is well below the estimated requirement of $105 \text{ g/kgW}^{0.75}$ (Figure 26). This may explain why some lactating females had fat levels 40 and 50% lower than the average in late October and November (16% of IFBW). Under such circumstances it is possible that many of these does will not breed every year, especially if they have raised twins. Goudreault (1980) reported that a large proportion of adult females do not reproduce in a given year on Anticosti Island and that this appeared to be inversely related to the success of the previous season or the fawn survival of the preceding summer. Those findings are consistent with reports of the effects of nutrition on the reproductive efficiency of domestic ruminants. In an extensive review of this subject, Rattray (1977) reported that lactation and low energy levels significantly delayed post-partum follicular growth and ovulation in cows and that in sheep an interaction existed between low levels of nutrition, lactation, body condition and conception. He also indicated that long-term level of nutrition (and its effect on body weight) and sudden changes in the level of nutrition at and before mating can influence ovulation rate. He also concluded that

sexual development in young ruminants is highly dependent on rate of growth and that reduced energy intakes could have adverse effects on pituitary function such as the synthesis or release of gonadotropins. This may explain why the female deer of Anticosti Island do not breed before 2 or even 3 years of age, have a tendency to produce single fawns, and do not breed every year (Goudreault and Huot, unpubl.).

Although the cycle of energy balance on Anticosti Island appears to be of utmost importance in determining the size of the animal and its reproductive performance it is also certain that these characteristics are influenced by a complex interaction of the hormonal system and natural selection for some particular traits. Energy availability in summer, as well as energy demands for reproduction will influence the rate of growth but the hormonal system is also responsible for the cessation of growth at some point which may be genetically determined. Female deer on Anticosti Island at the end of their first summer (5-6 month old) are 23% smaller than individuals of the same age on the mainland; at maturity, they are 36% smaller. Males on Anticosti Island are also 20% to 25% smaller as compared to males in the original stock from which the Anticosti Island deer came. Even though the direct effect of a very limited availability of energy can explain these differences, the smaller body size on Anticosti Island may also have survival advantages. It appears that in domestic animals, species and breeds of large *ultimate size* start to fatten at higher body weight than animals of small ultimate size. Consequently at any given body weight the latter will be fatter (Searle et al. 1972). When fat is as important for winter survival as it is on Anticosti Island small animals with a

larger proportion of fat may be at an advantage. Although for animals of larger body size the energy expenditure for BMR is lower per unit of live weight, and movement through the snow may be facilitated, smaller individuals will not be greatly disadvantaged, if the winter strategy is based on energy conservation, restricted movements and low food intakes. Moreover total food requirements are less the smaller the individual, therefore when high quality forage is scarce in spring, early summer and late fall and selective feeding may be required, foraging time may be limiting for large animals as suggested by Hanley (1980).

SUMMARY

This thesis is based upon the analysis of the relationships between the annual cycle in the food resources and body condition of deer on Anticosti Island, and discusses the importance of this cycle for the survival and productivity of the population.

A vegetation survey in several representative habitats of Anticosti Island indicated that browse is extremely limited in quantity and diversity in winter as compared with that reported in most other deer or moose range studies. When the lowlands, which supply forage almost exclusively when snow accumulation is under 0.75 m, are excluded, *Picea mariana* and *P. glauca* account for 99.1% of the twigs available in substratum I (0.25 m - 0.75 m from the ground surface), 96.6% in substratum II (0.75 m - 1.25 m) and 91.8% in substratum III (1.25 m - 2.25 m) in the western sector of the Island (71% of the surface area of the island). When these two species, which have never been reported as acceptable forage for deer, are excluded, *Abies balsamea* dominates the feeding stratum accounting for 69.6% of the twigs in substratum I, 89.6% in substratum II and 97.6% in substratum III.

Taking into account the relative area covered by each habitat type in the western sector it appears that, excluding *Picea spp.* the available browse is concentrated on an average of 6,600 stems/ha in substratum I, 1,000 stems/ha in substratum II and 700 stems/ha in substratum III. As most of the browse in substratum III is concentrated on the lower limbs of large *A. balsamea*, despite the low number of stems in this substratum, it offers almost twice as many twigs per unit of area as substratum I. So, as snow accumulates a new source of browse becomes available but it is concentrated on fewer stems and is much less varied in species composition. When snow conditions are considered for the two winters preceeding the surveys, it is estimated that 95% of the biomass available (twigs of the previous summer's growth) was *A. balsamea* in February and March 1976, and between early January and late March 1977.

The dominance of *A. balsamea* in the feeding stratum of deer is reflected by its abundance in the diet of deer as determined by the browse surveys. Excluding *Picea spp.*, this species accounts for 52.4% of the twigs eaten in substratum II and 87.1% in substratum III. *Betula papyrifera* is the second most abundant species of browse in the diet.

The only other forage that can contribute appreciably to the winter diet of deer inhabiting the interior of the island are tree lichens. Within the feeding stratum lichens are most abundant on *P. mariana* (5.54 ± 8.93 g dry weight/tree), consequently mature black spruce stands offer the greatest biomass of lichens by unit of area (4.7 kg/ha). This indicates that the lichens growing within the feeding stratum cannot account for a major part of the diet and an appreciable quantity of

lichens must almost certainly be provided by the dead twigs and branches blown down by the wind. The presence of dead branches on the ground is more apparent in areas where insects have killed a large proportion of the trees but its importance could not be assessed.

The assessment of the nutritive quality of the main browse species and of the lichens is mainly based on crude protein content estimates, gross energy determinations, IVDMD (*in vitro* dry matter digestibility) trials and detergent analyses. Apparent digestibility (IVDMD) of the composite diet decreases from 45.4% in February-March to 41.5% in April. Lichens have the lowest CP content (6.12%), and *A. balsamea* the highest (7.63%).

The nutritive quality of the forage eaten during the snow-free period is based on values estimated by co-workers and reported separately. For most forages the change in CP content can be adequately described by regression equations. In most species, the digestibility also follows a rather regular pattern of decline as summer progresses.

The seasonal diet of deer was determined by the examination of rumen contents. In winter, browse dominates the diet of deer collected in the interior of the Island. On a dry weight basis, browse accounts for 86.6% of the rumen contents in February-March and 89.9% in April. *A. balsamea* accounts for 81.3% of the browse in February-March and 84.8% in April while *P. glauca* and *P. mariana* average 13% of the browse for both periods. Lichens decrease in dry weight contribution from 14.4% in February-March to 4.1% in April.

During the snow-free sampling periods, forbs dominate the diet. According to the point sampling analysis of the rumen contents, forbs account for 67.4% to 72.1% of the diet from mid-June to mid-December. In May-June, graminoids account for 54.2% of the diet.

The composition of the diet and the results of the forage quality analyses were combined to estimate the metabolizable energy (ME) and the crude protein (CP) of the composite diet by period for a complete annual cycle. These estimates were compared to published values of maintenance requirements for deer.

The ME concentration in the diet is lowest in April (1.52 kcal/g) and increases to a peak of 2.63 kcal/g in June-July. During the same corresponding periods the daily maintenance metabolizable energy requirements (MMER) were estimated to be 152.8 kcal/kgW^{0.75} and 200.8 kcal/kgW^{0.75} for an adult doe and 130 kcal/kgW^{0.75} and 180 kcal/kgW^{0.75} for a fawn.

When the dry matter intake is set to meet these energy requirements, the predicted CP balance is positive in all periods of the year. However, in winter the required intakes appear excessive, varying between 80.2 and 85.5 g/kgW^{0.75} for a fawn and 93.5 and 100.5 g/kgW^{0.75} for the adult doe without weight loss.

A review of the published estimates of dry matter intake by deer in winter suggests that the normal intakes range between 40 and 50 g/kgW^{0.75}. This indicates that on the balsam fir diet observed on Anticosti Island the intake will be most likely lower than the estimated

required intake for maintenance. Under these conditions, a substantial amount of energy must be supplied by the body reserves.

The analysis of the body composition of a sample of deer collected at different periods of the year clearly shows that deer of both sexes and all age classes present a well defined pattern in body weight and composition. Maximum fat levels are reached between September and mid-December and minimum levels between mid-April and mid-June. In fawns, ether extractable fat reserves vary from a maximum $15.28 \pm 4.48\%$ in fall to a minimum of $0.18 \pm 0.05\%$ in spring. In adults the fat content averages $1.19 \pm 1.22\%$ in spring and peaks to $18.31 \pm 6.83\%$ in the September-November period. The lean body composition also changes significantly ($P < 0.001$) during the year. The protein content is maximum in fall ($25.05 \pm 0.92\%$ in fawns, $25.09 \pm 1.01\%$ in adults) and decreases to a minimum in April-June (21.12 ± 0.99 in fawns, $22.71 \pm 1.02\%$ in adults).

The correlation between the weight of the individual body components (fat, protein, ash and water) and the ingesta-free body weight is best described by equations of the form: $\ln(\text{component weight}) = a + b \ln \text{IFBW}$. Using this correlation, it is possible to assess the composition change of the body based on the body weights of a large sample of deer killed during the hunting season, and of a sample of deer killed in spring by the former owner of the Island. The analysis of these data suggests that the overwinter weight loss is minimum in yearling males, 23.7% of the fall IFBW, and maximum in adult males (3 years of age and older) 42.3% to 44.1%. In fawns the loss is 39.8% for females and 41.7% for males. In these animals 98.4% (females) and 98.6% (males) of the fat is catabolized

during winter. This accounts for to 31% of the loss of body weight. In female fawns 41.8% and in males 43.3% of the protein is lost and this account for 23% of the loss of body weight. Water losses of 27.2% (females) and 28.9% (males) account for 42% of the loss of body weight. On an IFBW basis the caloric content of the loss ranges between 4.16 kcal/g for fawns to 6.67 kcal for adult females (4 years of age and older).

It is suggested that the proportion of protein in the body substance lost by fawns is almost constant during winter, averaging 22% to 23%, whereas the proportion of fat decreases as the proportion of water increases.

The average daily gain in weight between mid-June and mid-October is maximum in adult males 253.3 g/day (4 years of age and older) and 338.3 g/day for 3-year-old individuals. The lowest rates of gain are shown by females: 95.8 g/day for 2-year-olds; 113.3 g/day for 3-year-olds; and 111.7 g/day for those which are 4 or more years old.

This cycle of body composition corresponds to a cycle in several fat indices currently used in wildlife studies. However, based on the linear correlation coefficient "r" between the total fat reserves and the individual indices, it appears that the efficiency of the indices for predicting fat reserves varies according to the category of individuals and the time of the year. In spring, among the indices tested, only two appear acceptable: the dry weight of the peritoneum and the percentage of fat in the femur marrow (FMF). In fall almost all the indices appear to be acceptable and are almost equally efficient in predicting the

total fat reserves. The FMF is the only index that shows a poor correlation at that time of the year, especially in adult males ($r = 0.240$). In fawns, it is an acceptable index ($r = 0.827$), but the dressed body weight shows a better correlation.

The weight of the skin including the hairs, follows a pattern of change similar to the pattern shown by the total body weight. A similar relationship was found for the liver, the spleen, and the heart while there is no apparent cycle in the weights of the kidneys and the brain. This last organ might even increase in size in fawns during winter. When considered as a whole, the viscera including the ingesta constitute a significantly larger proportion of the body weight in spring than in fall. This increase is mainly due to a change in the proportion of the ingesta in relation to the total body weight. In fawns the ingesta accounts for $16.5 \pm 2.54\%$ of the total body weight in fall as compared to $26.3 \pm 5.15\%$ in spring.

The relationship found between food resources and body condition of deer on Anticosti Island clearly shows that their survival is highly dependent on their ability to adapt their seasonal physiological rhythm to the seasonally cyclic availability and quality of the food resources. Under these conditions it is predicted that in order to accumulate the estimated average fat content of 15% a lactating doe will have to maintain a dry matter intake of $120 \text{ g/kgW}^{0.75}$ from late June to mid-September. For a yearling the intake will have to reach $100 \text{ g/kgW}^{0.75}$ in July and August.

In winter the body reserves supply approximately one third of the maintenance needs of a fawn and 20% to 25% of the maintenance needs for an adult female. The predicted dry matter intake would have to reach 54 g/kgW^{0.75} for the fawn and 62.5 g/kgW^{0.75} for the doe on a diet mainly composed of *A. balsamea* and lichens.

These intakes are higher than most intakes reported for ungulates in winter and equal or even exceed the average dry matter content of the reticulo-rumen of Anticosti deer during this period (fawns: 52 g/kgW^{0.75}, does: 53 g/kgW^{0.75}). Therefore, I suggest that winter starvation due to the poor quality of the available forage lowers the maintenance requirements of Anticosti deer, and in particular lowers the basal metabolic rate to values below those usually reported for captive animals.

Under these conditions the survival of deer through winter will be more dependent on their capacity to survive starvation than on their ability to feed efficiently. The body condition reached in fall, the degree of energy conservation that can be maintained during winter, the amount of weight loss that can be tolerated before death and the date of spring arrival will probably be the most important factors affecting the survival of deer, and especially fawns on Anticosti Island.

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APPENDIX 1. Estimation of the true digestible energy content of the winter diet of deer on Anticosti Island

Period and diet item	Gross energy content (kcal/kg)	True dry matter digestibility (%)	TDE (kcal/g)	Diet composition	
				Item (%)	Energy contribution kcal/kg diet
Feb 03-Mar 08					
<i>A. balsamea</i>	5,021	60.6	3,043	70.40	2,142
<i>P. glauca</i>	4,862	59.2	2,878	7.68	221
<i>P. mariana</i>	4,933	59.3	2,925	3.42	100
Lichens	4,063	76.3	3,100	14.40	446
Others	4,660	62.8	2,925	4.10	120
TOTAL					3,029
Apr 13-18					
<i>A. balsamea</i>	5,021	60.6	3,043	76.20	2,319
<i>P. glauca</i>	4,862	59.2	2,878	8.83	254
<i>P. mariana</i>	4,933	59.3	2,925	3.07	90
Lichens	4,063	76.3	3,100	4.60	143
Others	5,013	61.2	3,068	7.30	224
TOTAL					3,030

APPENDIX 2. Composition and caloric content of deer collected between February 03 and March 08 on Anticosti Island

Sex and age	N	Water % ± s.d.	Fat % ± s.d.	Protein % ± s.d.	Ash % ± s.d.	Caloric value kcal/g ± s.d.
Fresh ingesta-free weight basis						
Females (Y ⁺) ¹	8	64.79 ± 4.16	8.23 ± 5.08	21.54 ± 1.10	5.43 ± 0.64	1.95 ± 0.44
Males (Y ⁺)	1	63.40 ± -	9.62 ± -	21.15 ± -	5.82 ± -	2.06 ± -
Total (Y ⁺)	9	64.63 ± 3.92	8.39 ± 4.77	21.50 ± 1.04	5.47 ± 0.61	1.96 ± 0.41
Fawns ²	7	71.09 ± 2.02	1.12 ± 1.58	22.31 ± 1.29	5.49 ± 0.46	1.32 ± 0.16
Total	16	67.46 ± 4.55	5.21 ± 5.20	21.79 ± 1.36	5.48 ± 0.53	1.68 ± 0.46
Dry ingesta-free weight basis						
Females (Y ⁺)	8		22.08 ± 12.39	62.19 ± 10.30	15.80 ± 3.07	
Males (Y ⁺)	1		26.32 ± -	57.87 ± -	15.93 ± -	
Total (Y ⁺)	9		22.55 ± 11.67	61.71 ± 9.74	15.82 ± 2.87	
Fawns	7		3.60 ± 4.84	77.35 ± 4.94	19.03 ± 1.96	
Total	16		15.62 ± 15.00	68.55 ± 11.16	17.23 ± 2.94	
Fresh ingesta-free fat-free weight basis						
Females (Y ⁺)	8	70.55 ± 0.67			23.50 ± 0.86	5.99 ± 0.79
Males (Y ⁺)	1	70.20 ± -			23.41 ± -	6.44 ± -
Total (Y ⁺)	9	70.51 ± 0.64			23.49 ± 0.80	6.04 ± 0.75
Fawns	7	71.87 ± 1.17			22.57 ± 1.32	5.55 ± 0.53
Total	16	71.11 ± 1.12			23.08 ± 1.13	5.83 ± 0.69

¹ (Y⁺): 11.5-month-old and older

² Fawns: < 11.5-month-old

APPENDIX 3. Composition and caloric content of deer collected between April 13 and April 18 on Anticosti Island

Sex and age	N	Water % ± s.d.	Fat % ± s.d.	Protein % ± s.d.	Ash % ± s.d.	Caloric value kcal/g ± s.d.
Fresh ingesta-free weight basis						
Females (Y ⁺) ¹	10	70.72 ± 2.11	1.32 ± 1.33	22.13 ± 1.23	5.84 ± 0.52	1.32 ± 0.13
Males (Y ⁺)	4	70.95 ± 1.13	0.89 ± 0.97	22.14 ± 1.12	6.03 ± 0.97	1.31 ± 0.11
Total (Y ⁺)	14	70.79 ± 1.84	1.19 ± 1.22	22.13 ± 1.15	5.89 ± 0.64	1.28 ± 0.05
Fawns ²	5	73.66 ± 1.27	0.18 ± 0.05	20.87 ± 1.08	5.35 ± 0.67	1.14 ± 0.06
Total	19	71.54 ± 2.97	0.93 ± 1.14	21.80 ± 1.24	5.35 ± 0.67	1.27 ± 0.13
Dry ingesta-free weight basis						
Females (Y ⁺)	10		4.31 ± 4.20	76.78 ± 3.62	19.92 ± 0.75	
Males (Y ⁺)	4		2.96 ± 3.19	76.32 ± 5.75	20.99 ± 2.24	
Total (Y ⁺)	14		3.93 ± 3.87	75.94 ± 4.74	20.23 ± 1.34	
Fawns	5		0.65 ± 0.17	79.21 ± 1.94	20.19 ± 2.06	
Total	19		3.06 ± 3.61	76.82 ± 4.40	20.19 ± 1.50	
Fresh ingesta-free fat-free weight basis						
Females (Y ⁺)	10	71.67 ± 1.35		22.52 ± 1.30	5.92 ± 0.59	
Males (Y ⁺)	4	71.57 ± 0.62		22.33 ± 0.96	6.18 ± 0.94	
Total (Y ⁺)	14	71.64 ± 1.35		22.47 ± 1.18	5.99 ± 0.68	
Fawns	5	73.79 ± 1.23		20.91 ± 1.08	5.30 ± 0.59	
Total	19	72.20 ± 1.60		22.06 ± 1.33	5.81 ± 0.72	

¹ 11.5-month-old and older

² Fawns: < 11.5-month-old

APPENDIX 4. Composition and caloric content of deer collected between May 15 and June 14 on Anticosti Island

Sex and age	N	Water % ± s.d.	Fat % ± s.d.	Protein % ± s.d.	Ash % ± s.d.	Caloric value kcal/g ± s.d.
Fresh ingesta-free weight basis						
Females (Y ⁺) ¹	5	71.28 ± 1.63	0.62 ± 0.63	22.99 ± 0.76	5.11 ± 0.37	1.30 ± 0.10
Males (Y ⁺)	4	70.76 ± 1.73	1.40 ± 1.55	22.97 ± 0.23	5.35 ± 0.40	1.38 ± 0.14
Total (Y ⁺)	9	70.84 ± 1.59	0.97 ± 1.13	22.98 ± 0.56	5.22 ± 0.38	1.34 ± 0.11
Fawns ²	2	72.90 ± 0.00	0.22 ± 0.03	21.62 ± 0.64	5.23 ± 0.57	1.19 ± 0.03
Total	11	71.21 ± 1.65	0.83 ± 1.05	22.73 ± 0.77	5.22 ± 0.39	1.31 ± 0.12
Dry ingesta-free weight basis						
Females (Y ⁺)	5		2.07 ± 2.00	80.10 ± 2.16	17.78 ± 0.78	
Males (Y ⁺)	4		4.53 ± 4.85	77.44 ± 4.60	18.02 ± 1.27	
Total (Y ⁺)	9		3.16 ± 3.54	78.92 ± 3.50	17.89 ± 0.96	
Fawns	2		0.82 ± 0.09	79.76 ± 2.24	19.30 ± 2.13	
Total	11		2.74 ± 3.30	79.07 ± 3.23	18.14 ± 1.23	
Fresh ingesta-free fat-free weight basis						
Females (Y ⁺)	5	71.72 ± 1.21		23.13 ± 0.89	5.14 ± 0.40	
Males (Y ⁺)	4	71.27 ± 0.50		23.30 ± 0.28	5.43 ± 0.44	
Total (Y ⁺)	9	71.57 ± 0.98		23.20 ± 0.66	5.27 ± 0.42	
Fawns	2	73.06 ± 0.06		21.60 ± 0.64	5.24 ± 0.57	
Total	11	71.84 ± 1.07		22.92 ± 0.88	5.26 ± 0.42	

¹ (Y⁺): 11.5-month-old and older

² Fawns: < 11.5-month-old

APPENDIX 5. Composition and caloric content of deer collected between June 18 and July 13 on Anticosti Island

Sex and age	N	Water % ± s.d.	Fat % ± s.d.	Protein % ± s.d.	Ash % ± s.d.	Caloric value kcal/g ± s.d.
Fresh ingesta-free weight basis						
Females (Ad) ¹	4	66.05 ± 2.09	6.00 ± 2.85	22.88 ± 1.32	5.07 ± 0.49	1.81 ± 0.21
Males (Ad)	5	65.74 ± 1.43	7.01 ± 1.83	22.11 ± 1.17	5.14 ± 0.35	1.86 ± 0.15
Total (Ad)	9	65.88 ± 1.64	6.56 ± 2.23	22.45 ± 1.23	5.11 ± 0.39	1.84 ± 0.17
Yearlings ²	7	68.83 ± 1.05	3.67 ± 1.70	22.65 ± 1.30	4.86 ± 0.62	1.57 ± 0.10
Total	16	67.17 ± 2.04	5.30 ± 2.45	22.54 ± 1.22	5.00 ± 0.50	1.72 ± 0.19
Dry ingesta-free weight basis						
Females (Ad)	4		17.36 ± 7.76	67.68 ± 7.36	14.93 ± 0.99	
Males (Ad)	5		20.38 ± 4.84	64.68 ± 4.03	15.04 ± 1.24	
Total (Ad)	9		19.04 ± 6.04	66.01 ± 5.57	14.99 ± 1.07	
Yearlings	7		11.64 ± 4.94	72.84 ± 6.15	15.56 ± 1.57	
Total	16		15.80 ± 6.62	68.95 ± 6.85	15.24 ± 1.29	
Fresh ingesta-free fat-free weight basis						
Females (Ad)	4	70.26 ± 1.18		24.33 ± 0.84	5.40 ± 0.57	
Males (Ad)	5	70.74 ± 1.13		23.78 ± 1.06	5.52 ± 0.35	
Total (Ad)	9	70.53 ± 1.11		24.02 ± 0.95	5.47 ± 0.43	
Yearlings	7	71.46 ± 0.30		23.50 ± 1.01	5.05 ± 0.74	
Total	16	70.94 ± 0.96		23.79 ± 0.98	5.29 ± 0.61	

¹ Ad: > 23.5-month-old

² Yearlings: 11.5-23.5-month-old

APPENDIX 6. Composition and caloric content of deer collected between July 14 and August 26 on Anticosti Island

Sex and age	N	Water % ± s.d.	Fat % ± s.d.	Protein % ± s.d.	Ash % ± s.d.	Caloric value kcal/g ± s.d.
Fresh ingesta-free weight basis						
Females (Ad) ¹	11	64.52 ± 4.70	8.68 ± 5.16	21.72 ± 0.69	5.08 ± 0.68	2.00 ± 0.47
Males (Ad)	3	62.57 ± 5.09	10.03 ± 5.14	22.02 ± 0.30	5.28 ± 0.35	2.14 ± 0.50
Total (Ad)	14	64.10 ± 4.65	8.97 ± 4.98	21.78 ± 0.63	5.14 ± 0.62	2.03 ± 0.46
Fawns ²	4	67.23 ± 2.86	4.38 ± 2.10	23.69 ± 1.13	4.70 ± 0.34	1.70 ± 0.23
Yearlings ³	11	65.35 ± 2.84	7.47 ± 3.10	22.39 ± 1.25	4.79 ± 0.75	1.92 ± 0.27
Total	29	65.01 ± 3.87	7.77 ± 4.22	22.31 ± 1.12	4.95 ± 0.65	1.94 ± 0.38
Dry ingesta-free weight basis						
Females (Ad)	11		23.15 ± 11.19	62.37 ± 9.02	14.58 ± 3.13	
Males (Ad)	3		25.81 ± 11.00	59.59 ± 8.01	14.64 ± 2.96	
Total (Ad)	14		23.72 ± 10.78	61.78 ± 8.60	14.59 ± 2.98	
Fawns	4		13.07 ± 5.30	72.58 ± 5.23	14.40 ± 0.87	
Yearlings	11		21.05 ± 7.01	65.07 ± 7.04	13.87 ± 2.30	
Total	29		21.24 ± 9.34	64.51 ± 8.25	14.22 ± 2.54	
Fresh ingesta-free fat-free weight basis						
Females (Ad)	11	70.60 ± 1.30		23.70 ± 1.07	5.57 ± 0.77	
Males (Ad)	3	68.61 ± 0.10		24.54 ± 1.63	5.98 ± 0.12	
Total (Ad)	14	70.36 ± 1.39		23.89 ± 1.20	5.66 ± 0.69	
Fawns	4	70.31 ± 1.63		24.79 ± 1.43	4.93 ± 0.45	
Yearlings	11	70.61 ± 0.93		24.20 ± 1.20	5.19 ± 0.87	
Total	29	70.45 ± 1.23		24.18 ± 1.22	5.38 ± 0.77	

¹ Ad: > 23.5-month-old

² Fawns: < 11.5-month-old

³ Yearlings: 11.5-23.5-month-old

APPENDIX 7. Composition and caloric content of deer collected between September 02 and November 04 on Anticosti Island

Sex and age	N	Water % ± s.d.	Fat % ± s.d.	Protein % ± s.d.	Ash % ± s.d.	Caloric value kcal/g ± s.d.
Fresh ingesta-free weight basis						
Females (Ad) ¹	4	56.63 ± 7.35	18.38 ± 8.81	20.76 ± 1.65	4.24 ± 0.35	2.87 ± 0.77
Males (Ad)	2	57.35 ± 1.91	18.17 ± 0.70	20.09 ± 0.43	4.40 ± 0.78	2.81 ± 0.08
Total (Ad)	6	56.87 ± 5.77	18.31 ± 6.83	20.54 ± 1.34	4.29 ± 0.45	2.85 ± 0.59
Fawns ²	7	61.91 ± 4.00	11.53 ± 4.63	21.89 ± 0.73	4.66 ± 0.60	2.44 ± 0.33
Yearlings ³	4	60.65 ± 3.05	13.31 ± 4.13	21.62 ± 1.19	4.42 ± 0.45	2.28 ± 0.41
Total	17	59.84 ± 4.85	14.34 ± 5.95	21.35 ± 1.19	4.47 ± 0.51	2.51 ± 0.52
Dry ingesta-free weight basis						
Females (Ad)	4		40.82 ± 12.47	49.21 ± 10.70	10.02 ± 2.11	
Males (Ad)	2		42.56 ± 0.23	47.08 ± 1.07	10.28 ± 1.36	
Total (Ad)	6		40.46 ± 9.86	48.50 ± 8.37	10.11 ± 1.75	
Fawns	7		29.47 ± 8.81	58.10 ± 7.18	12.38 ± 2.28	
Yearlings	4		33.39 ± 7.80	55.36 ± 7.09	11.26 ± 1.28	
Total	17		34.27 ± 9.77	54.06 ± 8.36	11.31 ± 2.06	
Fresh ingesta-free fat-free weight basis						
Females (Ad)	4	69.45 ± 1.97		25.53 ± 1.65	5.22 ± 0.54	
Males (Ad)	2	70.03 ± 1.71		24.55 ± 0.74	5.38 ± 0.99	
Total (Ad)	6	69.64 ± 1.73		25.20 ± 1.42	5.28 ± 0.61	
Fawns	7	69.93 ± 0.92		24.90 ± 1.04	5.27 ± 0.67	
Yearlings	4	69.97 ± 0.32		24.94 ± 0.31	5.11 ± 0.62	
Total	17	69.83 ± 1.14		24.97 ± 1.03	5.23 ± 0.60	

¹ Ad: > 23.5-month-old

² Fawns: < 11.5-month-old

³ Yearlings: 11.5-23.5-month-old

APPENDIX 8. Composition and caloric content of deer collected between November 05 and December 12 on Anticosti Island

Sex and age	N	Water % ± s.d.	Fat % ± s.d.	Protein % ± s.d.	Ash % ± s.d.	Caloric value kcal/g ± s.d.
Fresh ingesta-free weight basis						
Females (Ad) ¹	5	60.46 ± 5.33	13.03 ± 6.36	21.80 ± 1.21	4.71 ± 0.66	2.42 ± 0.56
Males (Ad)	2	60.00 ± 5.09	13.90 ± 7.69	21.54 ± 1.63	4.57 ± 0.96	2.49 ± 0.64
Total (Ad)	7	60.33 ± 4.83	13.27 ± 6.08	21.72 ± 1.20	4.67 ± 0.67	2.44 ± 0.53
Fawns ²	3	58.83 ± 3.20	15.28 ± 4.48	21.74 ± 1.03	4.45 ± 0.33	2.63 ± 0.37
Yearlings ³	0	-	-	-	-	-
Total	10	59.79 ± 4.32	13.88 ± 5.48	21.73 ± 1.09	4.60 ± 0.58	2.49 ± 0.48
Dry ingesta-free weight basis						
Females (Ad)	5		31.76 ± 11.17	56.12 ± 9.11	12.15 ± 2.82	
Males (Ad)	2		33.77 ± 14.92	54.50 ± 10.99	11.67 ± 3.88	
Total (Ad)	7		32.33 ± 11.01	55.60 ± 8.77	12.01 ± 2.80	
Fawns	3		36.43 ± 8.11	52.77 ± 6.83	10.79 ± 1.43	
Yearlings	0		-	-	-	
Total	10		33.56 ± 9.97	54.79 ± 7.94	11.64 ± 2.46	
Fresh ingesta-free fat-free weight basis						
Females (Ad)	5	69.47 ± 1.09		25.11 ± 1.21	5.43 ± 0.77	
Males (Ad)	2	69.67 ± 0.33		25.03 ± 0.33	5.28 ± 0.64	
Total (Ad)	7	69.36 ± 0.93		25.09 ± 1.00	5.39 ± 0.68	
Fawns	3	69.08 ± 0.33		25.66 ± 0.16	5.25 ± 0.31	
Yearlings	0	-		-	-	
Total	10	69.28 ± 0.79		25.26 ± 0.86	5.35 ± 0.58	

¹ Ad: > 23.5-month-old

² Fawns: < 11.5-month-old

³ Yearlings: 11.5-23.5-month-old