by John P. Kelsa
and William Pre

Moose and deer behaviour in snow

Canadian Wildlife Service Report Series Number 15

Moose and deer behaviour in snow in Fundy National Park, New Brunswick

by John P. Kelsall and William Prescott

Canadian Wildlife Service
Report Series–Number 15

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Biographies

John P. Kelsall is a research scientist for the Canadian Wildlife Service in Edmonton, Alberta, a fellow of the Arctic Institute of North America, a regional chairman of the Canadian Society of Wildlife and Fishery Biologists, and a member of several additional scientific and professional societies. He has been a CWS researcher for over 20 years of which 12 years were spent in the Canadian Arctic and sub-Arctic. Dr. Kelsall is a graduate of Acadia University (B.A.), the University of Toronto (M.A.) and the University of Western Australia (Ph.D.), and has done post-graduate work at the University of British Columbia. Best known for his work on barren-ground caribou, and an award winning monograph on that species, he has written several dozen scientific articles on diverse subjects.

William H. Prescott is a big-game biologist with the New Brunswick Department of Natural Resources, Fish and Wildlife Branch. He received a B.Sc. (biology) from Mount Allison University, Sackville, N.B. in 1966 and an M.Sc. (wildlife management) from Acadia University, Wolfville, N.S., in 1968. His master's thesis was entitled "Winter Ecology and Food Habits of Moose in Nova Scotia." He is now in charge of white-tailed deer research and management in New Brunswick.

Acknowledgements

We are grateful to the staff of Fundy National Park, particularly Superintendent Harry Cooper, for help and encouragement during our study. Allan Smith and Peter McLaren, then of Mt. Allison University, assisted in the field in 1964–65 and 1965–66 respectively. Edmund Telfer of the Canadian Wildlife Service provided major editorial comment and suggestions on our manuscript, but he is in no way responsible for remaining errors.

The work was undertaken as an official CWS project.

Perspective

The recent history of moose and white-tailed deer in the Maritime Provinces, including Fundy National Park, has been one of great population changes. Deer were scarce or absent during the late 19th century and moose were abundant. Deer increased explosively to remarkably high populations by the 1940's. Concurrently moose populations dimished remarkably to the point where moose hunting was no longer permitted. By the 1950's deer were universally abundant throughout Nova Scotia and New Brunswick and moose were reduced to a few viable populations, mostly in local areas of high elevation, including the high country in Fundy National Park.

The high country where moose survived was characterized by, among other things, a nearly complete absence of deer in winter and a scarcity in summer. Because deer are chronic carriers of a parasitic nematode worm which is lethal in moose, and which has been one of the chief decimators of Maritime moose, any separation of the range of the two species takes on great importance.

It seemed basic to an understanding of why moose persisted in high numbers, on high ground, to examine the factors governing their presence there, and the factors which exclude deer. Snow condition, particularly depth, was superficially known to be different at the start of the study, and it was believed that occasionally extreme snow conditions sometimes controlled the populations of both moose and deer. An examination of snow morphology, in conjunction with behavioural observations of the animals, therefore seemed a logical point of attack.

Абстракт

Изучением морфологии снега и влияния последнего на поведение американского лося и оленя в Национальном парке Фанди занимались в течение трех зим, с 1963 по 1966 гг. Изучение было сосредоточено на 10 зимних станциях, находящихся на разных возвышенностях — от высоты на уровне моря до свыше 350 м. Глубина снега на каждой станции измерялась в течение всей зимы, два раза в месяц, как в местах под лесным покровом, так и в примыкающих открытых районах. Количественное описание профилей снега включало глубину, плотность, твердость, температуру, а также форму и размер кристаллов снега. На каждой станции велись записи поведения американского лося и оленя как во время непосредственного наблюдения, так и после тщательного изучения следов и измерения последних.

Глубина снега увеличивалась с повышением подъема; на каждой станции глубина снега была самой незначительной в местах, защищенных лесным покровом. Было установлено, что при глубине снега гораздо больше 20 см. олени передвигаются вниз, к незначительным возвышенностям обширных зимних пастбищ. Олени были строго ограничены в их передвижении при глубине снега свыше 40 см.; передвижение американских лосей резко замедлялось при глубине снега свыше 70 см. Плотность снега не была значительной на пастбищах американских лосей и оленей. Однако, статистически важные соотношения были обнаружены между более плотным снегом и увеличивающейся способностью выдерживать на себе передвигающихся оленей и американских лосей. Таким образом, если млекопитающие погружаются на 88% в снег глубиной 40 см. при плотности снега от 0,1 до 0,19, они погружаются только на 47% при глубине снега в 44 см. с плотностью свыше 0,49. Твердость снега представлялет довольно сложную картину в Национальном парке Фанди из-за частоты образования горизонта с последующими снегопадами. Слоев, покрытых коркой, было больше на пастбище оленей, причем больше на открытой местности, чем на местности с лесным покровом. Многие корки были достаточно твердыми, чтобы, теоретически, по ним могли передвигаться американские лоси и олени; однако, не все животные использовали эту возможность. Хотя корки иногда выдерживают передвигающихся млекопитающих, многие из них не выдерживают веса американского лося и оленя — животные проваливаются; возникает постоянная опасность ранения их ног острыми краями корки. Описываются также иные морфологические параметры снега, а также приводятся детальные результаты наблюдений глубины следов млекопитающих.

Abstract

Studies of snow morphology in relation to the behaviour of moose and deer in Fundy National Park were carried out during three winters, 1963 to 1966. Studies were centered around 10 snow stations, at varied elevations from sea level to over 350 meters. At each, snow measurements were taken twice monthly during winter, both under forest canopies and in adjacent open areas. Quantative description of snow profiles included depth, densities, hardnesses, temperatures, and description of snow crystal form and size. At each station, records were kept of the behaviour of moose and deer, both through direct observation and through scrutiny of tracks and measurement of track depths.

Snow depths increased with elevation and, at each station, were least under forest canopies. When snow depths much exceed 20 cm, deer were found to move downhill to low elevation winter ranges. Deer were restricted severely in their movement when snow depths exceeded 40 cm, as were moose when snow depths exceeded 70 cm. Snow densities did not vary significantly between deer and moose ranges but statistically significant correlations were found between increasingly dense snow and an increasing measure of support which it provided to walking deer and moose. Thus where the mammals will sink to 88 per cent of a 40 cm depth of snow at densities of 0.10 to 0.19, they sink only 47 per cent of the way into 44 cm deep snow with densities above 0.49. Snow hardnesses present a complex picture in Fundy National Park due to the frequency of horizon formation with successive snowfalls. There were more crusted layers on moose range than deer range and in the open than under canopies.

Many crusts were hard enough to theoretically support walking moose and deer and some, but not all, did so. Moose and deer broke through the rest with constant danger of lacerating their feet and legs on sharp edges. Other morphological parameters of snow are described as are the detailed results of observations of the depths of mammal tracks.

Résumé

Au cours des trois hivers de 1963 à 1966, nous avons étudié la morphologie de la neige dans le parc national de Fundy, en relation avec le comportement des orignaux et des cerfs. Nous avons choisi dix stations à des élévations diverses, du niveau de la mer jusqu'à plus de 350 mètres. A chaque endroit, nous avons mesuré la neige deux fois par mois chaque hiver, tant dans la partie boisée que dans les espaces découverts du voisinage. La description quantitative des profils de neige comportait la profondeur, la densité, la résistance, la température et la description des cristaux quant à leur forme et à leurs dimensions. Nous avons aussi consigné à chaque station nos observations visuelles sur le comportement des orignaux et des cerfs, ainsi que les résultats obtenus à la suite d'une étude sur la nature et les dimensions des traces.

L'épaisseur de la neige augmentait avec l'élévation, mais dans chacune des stations, elle était la plus faible sous les arbres. Aux endroits où l'épaisseur dépassait sensiblement 20 cm, les cerfs descendaient les collines pour se trouver un habitat hivernal à moindre altitude. Les déplacements des cerfs étaient sérieusement entravés quand la neige avait plus de 40 cm d'épaisseur, de même pour les orignaux quand l'épaisseur de la neige dépassait 70 cm. On ne remarque pas de différence significative dans la densité de la neige entre l'habitat de l'orignal et celui du cerf, mais on trouve une corrélation statistique significative entre l'accroissement de densité et celui de la capacité à supporter le cerf ou l'orignal qui s'y aventure. Ainsi, un mammifère enfonce jusqu'à une profondeur de 88 p. 100 dans une couche de neige de 40 cm d'épaisseur et ayant une densité de 0.10 à 0.19, mais il n'enfonce que jusqu'à 47 p. 100 dans une couche de neige de 44 cm ayant une densité supérieure à 0.49. La neige durcit d'une manière complexe dans le parc national de Fundy. Les croûtes superposées sont plus nombreuses dans l'habitat des orignaux que dans celui des cerfs et plus nombreuses aussi dans les espaces dégagés que dans les sous-bois.

Plusieurs surfaces croûtées étaient assez fermes pour porter, en théorie, un orignal ou un cerf, mais pas toutes. Par ailleurs, la croûte glacée de certaines surfaces se brise sous le poids des orignaux et des cerfs et les arêtes vives lacèrent fréquemment les pieds ou les pattes de ces animaux. Nous décrivons d'autres paramètres morphologiques de la neige et nous terminons par certaines conclusions fondées sur nos observations de la profondeur des pistes des mammifères.

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Fundy National Park—1963–64. Smith recording data, Prescott measuring horizontal snow hardnesses between horizons. N.R.C. snow study kit.

Introduction

In 1963 a study was designed to examine the morphology of snow in Fundy National Park, New Brunswick, to learn if altitudinal differences in depth and structure might account for an observed separation of the winter ranges of moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*). We also wished to observe moose and deer winter behaviour and, where possible, correlate it with variations in snow morphology.

Fundy National Park is heavily forested. Loucks (1962) classifies its forests largely in the Fundy Bay Ecoregion of the Maritime Spruce-Fir Coastal Forest, and partly (high and inland) in the Maritime Uplands Ecoregion. Rowe (1959) classifies them in the Fundy Coast Section of the Acadian Forest Region. Telfer (1967a and 1967b) has described comparable and nearby forests in Nova Scotia in some detail. They tend to be dense, with closed or nearly closed canopies. Spruce and fir are the dominant trees, yellow birch and sugar maple are locally dominant on high ground, and pine, cedar and hemlock are absent.

The major open areas in the park are mostly old farms, campsites, highway clearances and the like, and most of those are below 130 m elevation. The east boundary of the park is the Bay of Fundy shoreline (see Fig. 1) and inland altitudes quickly climb upward of 335 m.

The recent history of moose and deer in Fundy National Park (Kelsall, 1963) parallels their history elsewhere in the Maritime Provinces (Wright, 1956; Benson, 1957; Dodds, 1963; and Telfer, 1967b). Deer were probably scarce or absent during the late nineteenth century, and moose were abundant. Deer increased in numbers to remarkably high populations by the 1940's, but at the same time moose were dying in large numbers from *moose sickness*. By the 1950's deer were abundant throughout Nova Scotia and New Brunswick, and moose were so reduced that only a few areas of high country, including that in Fundy park, held viable populations.

In light of studies by Anderson (1963, 1965), Smith, Archibald and Corner (1964), Karns (1967) and our own observations, it appears almost certain that most of the moose sickness in Fundy park and elsewhere was caused by the nematode *Pneumostrongylus tenuis*. That parasite, chronic and apparently harmless in deer in eastern Canada, is lethal in moose when it attacks the cerebrospinal area. In Fundy park among moose which are forced by overpopulations to invade the low altitude deer ranges, as occurred in 1959–60 and 1960–61, mortality is near 100 per cent even when food is abundant.

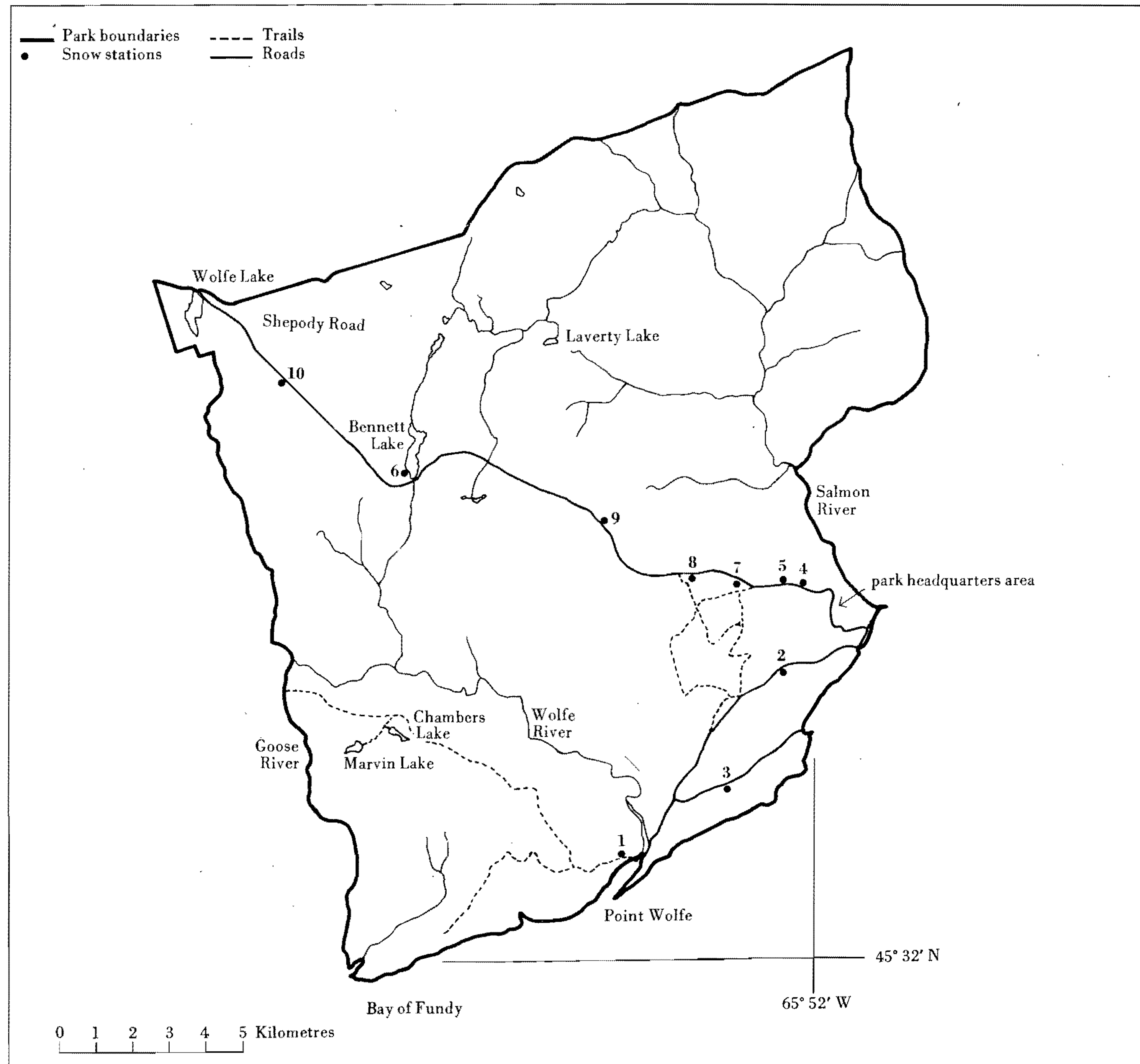
It seemed basic to an understanding of why moose were in such reduced numbers in the Maritime Provinces, and why they persisted in high numbers locally, to examine the factors which caused winter range separation. Such an understanding would be important to game management in national parks and elsewhere.

An examination of snow morphology, in conjunction with behavioural observations of the animals, seemed a logical point of attack. At the start differences in depths, densities and hardnesses at different elevations were apparent and seemed to prevent deer from invading moose range and competing there in winter. We also believed that occasionally extreme snow conditions were an important factor limiting moose and deer numbers in the park (Kelsall, 1963).

The work was designed to encompass the successive winters 1963–64, 1964–65 and 1965–66. Judging by snow depths and air temperatures, 1963–64 was moderately severe, and the other two winters were progressively milder with conditions favourable for game animals.

Figure 1. Fundy National Park, New Brunswick, showing the position of snow stations as described in the text.

Figure 1



Materials and methods

Snow study methods followed those set forth by Klein, Pearce and Gold (1950). Measurements, including those shown on the sample data sheet (Fig. 2), were taken with standard National Research Council of Canada instruments. For convenience in measuring snow depths the handle of the snow shovel was calibrated in centimeters.

Vertical as well as horizontal hardnesses were measured since the former provides a measure of the support that animals receive when in snow. Thus a standing moose having a weight loading of 700 gm/cm² would theoretically be supported by snow having an equal or greater vertical hardness.

The hardnesses we recorded tend to be maximum, because they were generally taken at the most discernable and homogeneous points in the profile pits (and thus at the thickest and strongest points). The instrument we used for measuring hardness has a bearing surface of only a few square millimeters for extreme hardnesses. Thus it will not reflect inconsistencies in variable crusts unless average hardnesses are taken over wide areas for each of many horizons. This would be too time consuming to be practical. R. Hepburn (pers. comm.) in Ontario, W. O. Pruitt, Jr. (pers. comm.) in the Northwest Territories and Verme (1968) have experimented with measuring apparatus that simulate the pressure of the hooves of deer, moose or caribou. Readings with such instruments would be a more accurate measure of animal support than the complex profile readings obtained during this study.

Ten snow measurement stations were chosen for continued study (Fig. 1 and 3). Each station included an open, treeless area (simply the wide, cleared highway right-of-way in some cases) adjacent to a forested area having a closed or nearly closed canopy. A *reading* for a station consisted of the completion of data sheets (Fig. 2) for a single profile from each of the open and closed areas, cut where snow was level and of average depth. Observations were generally made at two week intervals starting shortly after the first snowfall of each winter and going on until snow had largely disappeared from the sites the following spring. The stations were deliberately established near major park highways for speed and convenience. With deep and complex snow structures in late winter, examining 20 profile pits at 10 stations and concurrent observations of game took two full days.

To determine quantitatively whether a station was on deer or moose range we searched in a 160 m radius for animals, or tracks made since the last visit. The observations also showed, through frequency of tracks, the varying extent of ungulate movement in different snow conditions. We measured the depth of tracks in the snow to gain some indication of the support offered by varied snow conditions to walking animals. These observations were reinforced by general observations of animal activity, as opportunity permitted, in other areas of the park.

Figure 2. Record sheets were completed for each snow profile *reading* in Fundy National Park, 1963–65. Vertical hardnesses are given opposite horizon depths; intermediate hardnesses are taken horizontally between horizon boundaries.

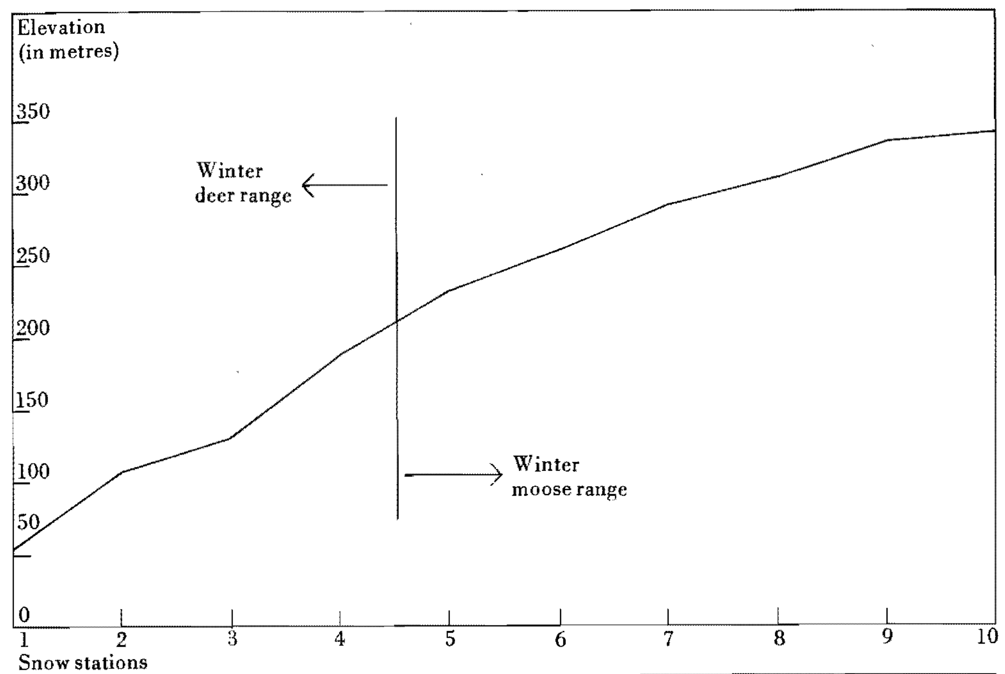
Canadian Wildlife Service Snow Survey

Station No.	9
Altitude	1100'
Exposure	Open
Observer	W.P.
Date	February 22nd, 1964
Hour	1:30 p.m.
Air Temperature	-3°C
Deer Present	No
Moose Present	Yes
Deer Track Depths	
Moose Track Depths	40 - 70 cm
Average	52 cm

Hardness	Depth	Temps.	Density	Grain Size
8 x 1 gm/cm²	84 cm			
5 x 10 gm/cm²		-2°C	60/250 .24	H & J 1-4 mm
25 x 1000 gm/cm²	47 cm			
7 x 10 gm/cm²		-2.5°C	60/250 .24	H 1-2 mm
40 x 100 gm/cm²	30 cm			
4 x 10 gm/cm²		-2°C	70/250 .28	H 1-2 mm
100 x 1000 + gm/cm²	25 cm			
3 x 10 gm/cm²		-1°C	80/250 .32	H & J 1-3 mm
3 x 1000 gm/cm²	14 cm			
3 x 10 gm/cm²		-1°C	79/250 .32	J 1-3 mm

Figure 3. The elevation above sea level of the snow measurement stations in Fundy National Park.

Figure 3



Results

Mammal distribution

Figure 4 shows the total number of observations of moose and deer, or their tracks, at the snow stations and suggests that moose are of regular occurrence in winter at elevations upward from 190 m. Deer are scarcely seen at all above 259 m. Deer dominate from 190 m downward, and moose are virtually absent below 130 m.

Snow stations 1 to 4 at elevations upwards to 190 m we considered as within winter deer range, and the higher within winter moose range. Observations elsewhere within the park suggested that such a division was sound. Working in comparable terrain and vegetation in nearby Nova Scotia, Telfer (1967b) found that in winter moose dominate above 183 m.

In each winter deer were, or recently had been, present at stations 1 to 3 at the time of nearly every snow reading. Moose were most commonly observed at station 6 in 1963–64 and 1964–65 and station 5 in 1965–66, but were observed on half or more of the visits to stations 7 to 10 in at least one of the three winters. Probably only one moose was involved in the occasional observations of that species at station 3 in each winter.

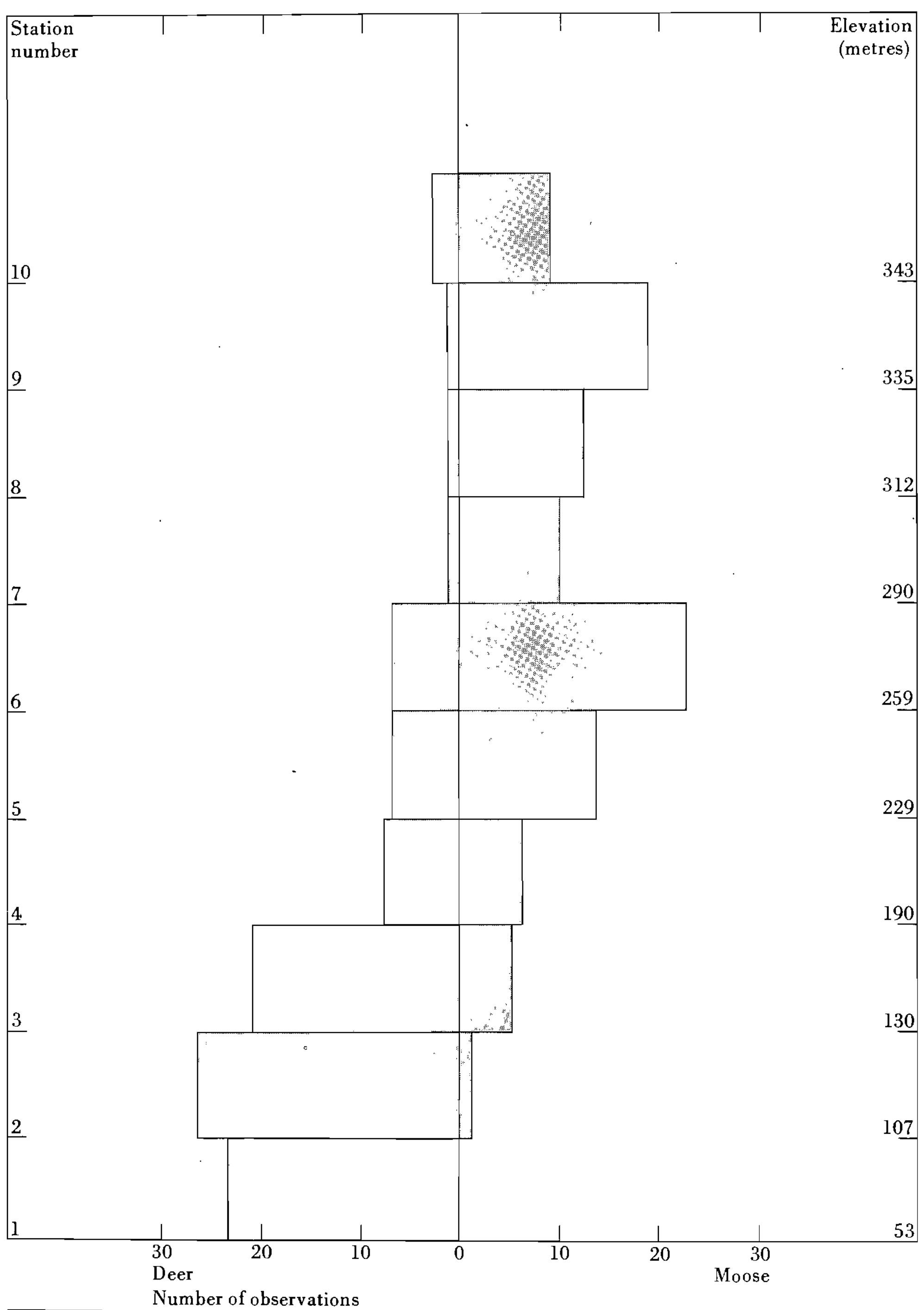
Six observations in 1963–64 of a single sick moose at stations 4 and 5 were discarded in constructing Figure 4, and for most other considerations in this paper. When first observed the animal was exhibiting typical symptoms of moose sickness, and being unable to feed it was destroyed on January 19. It proved to have *Pneumostrongylus tenuis* in the meninges of its brain.

In 1965–66 moose and deer populations at station 5, and perhaps at station 4, were artificially swollen due to extensive cutting nearby for the establishment of a new campground. The cutting operations provided packed trails for easy travel and food from fresh cut trees all winter.

Many of our observations (Fig. 2) are little used in this presentation (i.e. snow temperature, grain size and form, horizontal and many vertical hardnesses). The original data record sheets (approximately

Figure 4. Moose and deer, or their fresh trails, observed at snow stations in Fundy National Park during the three winters 1963–66.

Figure 4



600) and one typed copy of each are on file in the CWS eastern and western regional libraries respectively.

Snow depths

Mean depths of snow for open and subcanopy exposures are shown on Figures 5 and 6, and the station maximum depths are shown on Figure 7. All maximum depths in 1966 were recorded on February 27, all in 1964 on February 8 or April 5 and all in 1965 on February 6 or April 3.

The graphs comparing mean snow depths at stations considered primarily deer range and those considered moose range (Fig. 8, 9 and 10) are not quite complete for any of the winters. In 1963–64 (Fig. 8), the first snow fell in early December, but the build-up was slight until just before the first measurements on December 30. In 1964–65 (Fig. 9), there were heavy snowfalls in late November and early December. Measurements were attempted on December 6, when snow was 58 cm deep at some stations on moose range, but park highways were blocked and complete measurements were impossible until December 13. Then came record rainfalls and by the end of the month only two stations, both on moose range, had snow remaining. In 1965–66 (Fig. 10), measurements were first taken on December 5, but even then on the high moose range up to 28 cm of snow had fallen. Snow depths at the beginning of that winter increased only gradually compared to the previous two. In all three years, snow melted so rapidly after the last measurements shown on the graphs that further visits were cancelled.

It is apparent that snow is nearly always deeper in the open (Fig. 5 and 6). Twigs and branches retain snow whereas exposed areas accumulate all the snow that falls as well as that blown from surrounding trees. When thawing is advanced in late winter and spring, subcanopy areas may briefly have greater depths, since snow melts faster in the open under direct sunshine.

During the three winters, there was 45 per cent average deeper snow in the open

Figure 5. Comparison of mean snow depths in open areas at snow stations in Fundy National Park in each of three successive winters.

Figure 6. Comparison of mean snow depths in the subcanopy exposures at snow stations in Fundy National Park in each of three successive winters.

Figure 5

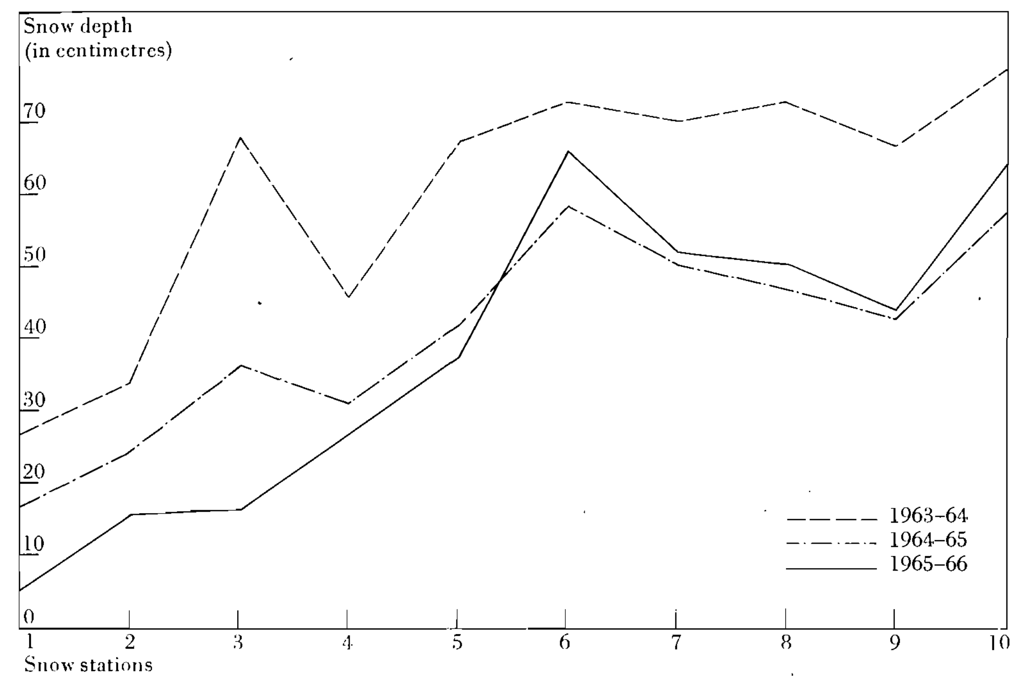
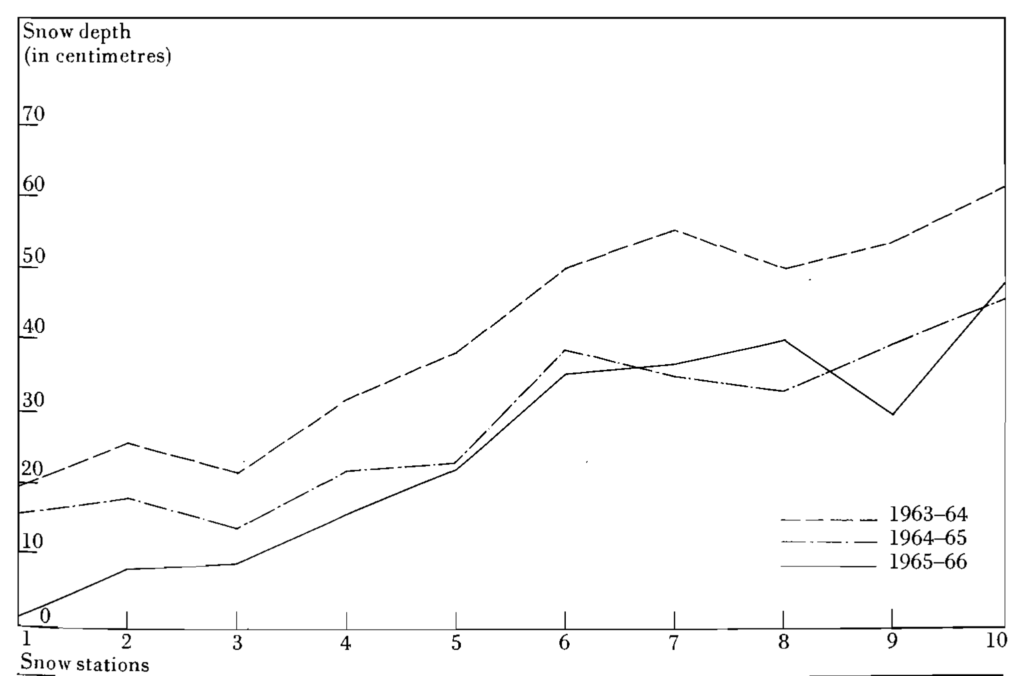


Figure 6



areas. In Quebec, Des Meules (1964) provided a similar demonstration for moose wintering areas: in general the more open the forest the deeper the snow on the ground, except in dense balsam fir sapling stands "where the snow level is boosted by the dense mat of intermingling low-lying branches." This condition was repeatedly observed but not measured in Fundy park, where the depth of snow in young spruce or fir thickets around field margins was often greater than elsewhere.

Station 3 provides results which diverge considerably from the relatively parallel results at other stations (Fig. 5 and 6). Due to the general location and topography of the site the snow depths in the open were about three times those under adjacent canopies, and the subcanopy depths were less than would be expected. We had chosen a powerline clearing paralleling a highway as an open area and thick forest between the two for subcanopy measurements. The site was near a hilltop and prevailing winds blew snow from both highway and forest into the power-line clearing. The site choice was unfortunate but comparable sites at varied elevations were not easy to choose and the problem was not foreseen.

Snow depths tended to increase (not quite directly) with altitude up to station 6 at an elevation of 260 m (Fig. 5 and 6). Beyond that the variations shown are probably caused more by site characteristics than by elevation.

Except at station 10 in 1963–64 maximum depths were recorded on the open sites (Fig. 7) and were approximately double the mean snow depths in each winter. Station mean snow depths are not shown graphically. In 1963–64 they averaged 45 per cent greater than in 1964–65 and 1965–66.

Maximum snow depths of the sort shown can be deceptive if presented without qualification. While some of the greatest snow depths during the study were recorded on moose range during 1965–66, they were of short duration and their impact on large mammals was negligible. The great depths of 1963–64, on the other hand, lasted long enough to cause physical and physiological hardship to large mammals.

Figures 8, 9 and 10 compare mean snow depths for each winter at deer and moose range stations. The figures show that there was always deeper snow on the moose range (60 to 80 per cent more on the average). The differences tended to increase as the winters advanced, especially during periods (i.e. February and March, Fig. 10) without fresh snow. The processes of maturation, tending to lessen snow depths, were more pronounced at the lower elevations.

There were some noteworthy correlations between ungulate behaviour and snow depths in the three winters. Deer remained continuously mobile in the vicinity of stations 1, 2 and 3, although they favoured established paths and beaten trails under canopies when snow depths exceeded 40 cm. This occurred in 1963–64 in February and between March 7 and mid-April (Fig. 8), in 1964–65 only briefly in February (Fig. 9) and in 1965–66 not at all (Fig. 10). In all winters deer avoided open areas, except those that were windswept and nearly free of snow (i.e. a seed potato plantation on a hilltop near station 3), whenever snow depths began to exceed 20 cm.

In early winter 1963–64 deer were active at elevations up to station 6 (260 m) until snowfalls following January 11 and 24 increased mean snow depths above 21 to 22 cm. They then withdrew to the lower elevations and were not seen again at snow stations above 190 m for the entire winter. A few individual deer, mostly large males, remained on the high country, but their movements were restricted and tracks or animals were rarely seen or reported. In 1964–65 most deer were already at stations 1, 2 and 3 when the first complete snow measurements were taken December 13, probably driven from the slopes by the deep, temporary snow that fell in late November and early December. However, we observed a total of five deer or their tracks at stations 6, 8, 9 and 10 through the winter. By contrast the average number of ob-

Figure 7. Comparison of maximum recorded snow depths at snow stations in Fundy National Park in three successive winters.

Figure 7

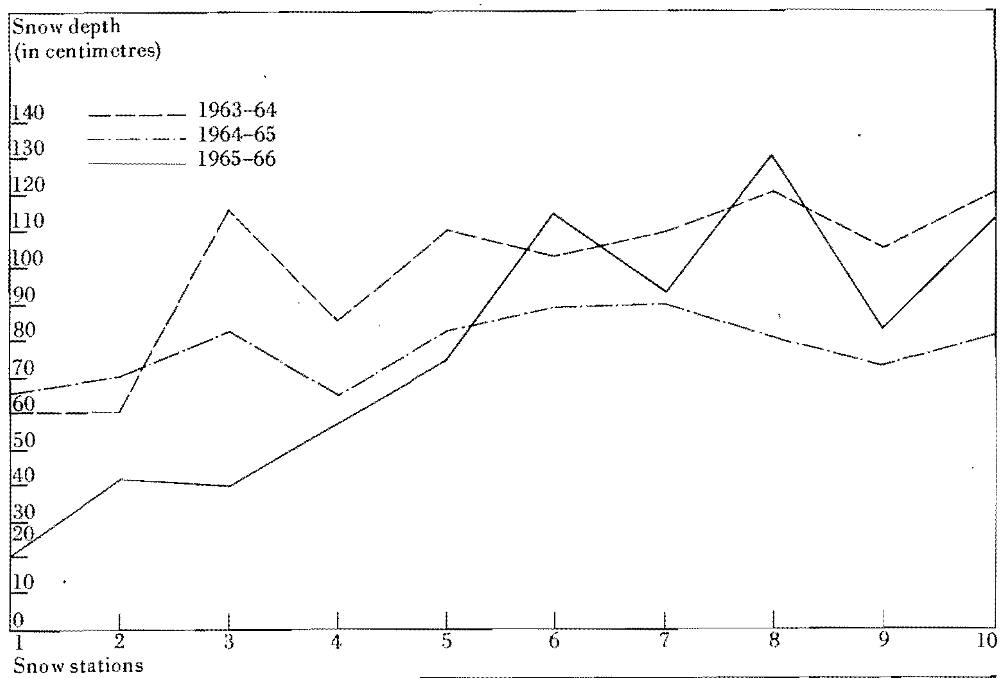


Figure 8. Comparison of mean depths of snow on deer range and moose range in Fundy National Park, 1963–64.

Figure 8

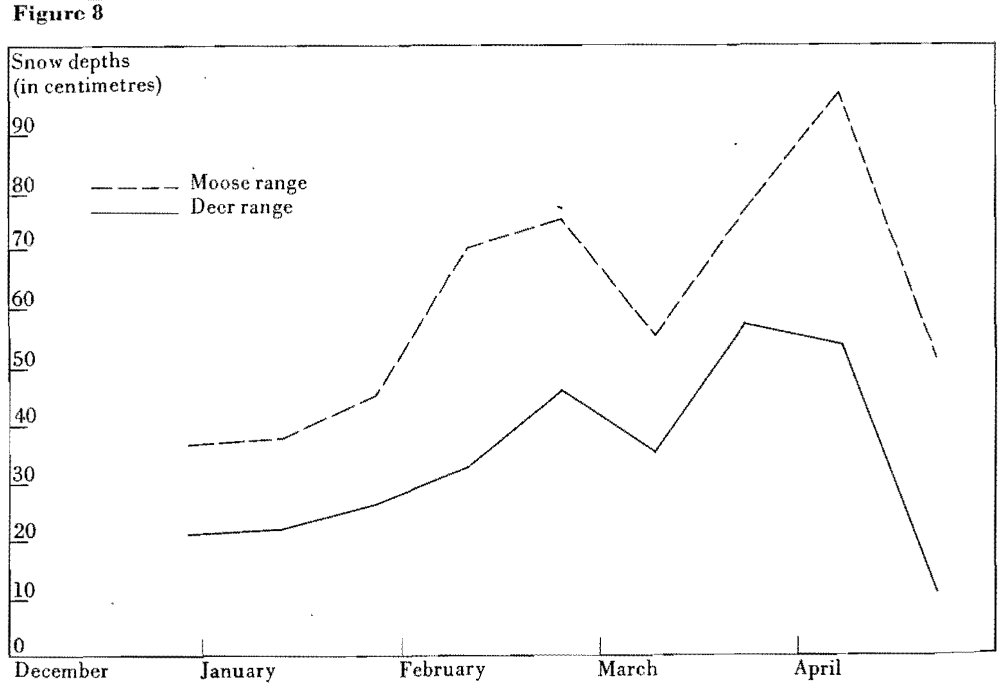


Figure 9. Comparison of mean depths of snow on deer range and moose range in Fundy National Park, 1964–65.

Figure 9

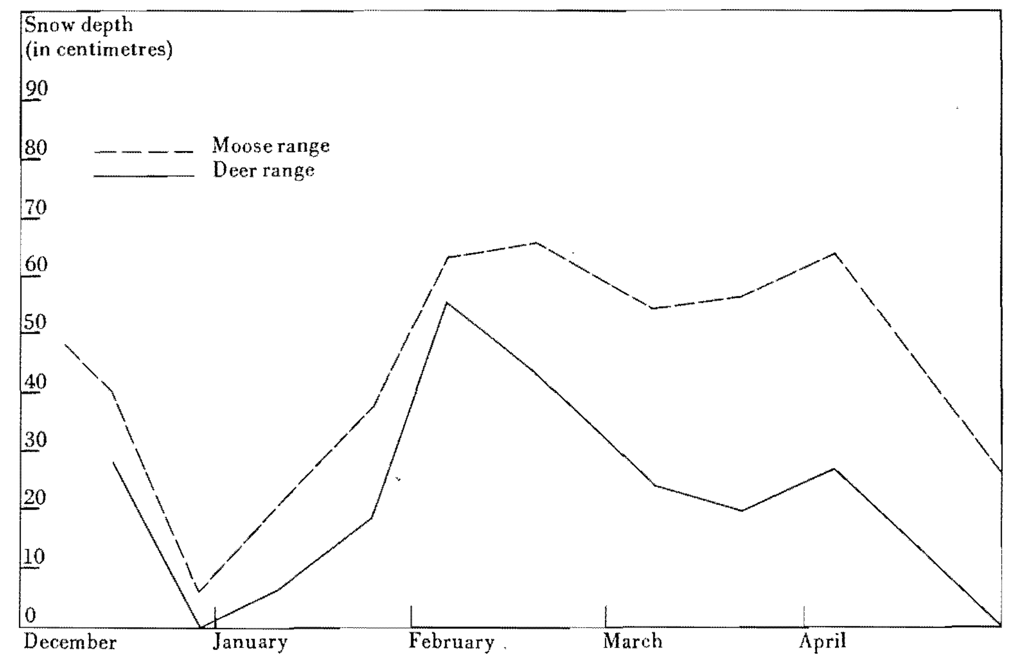
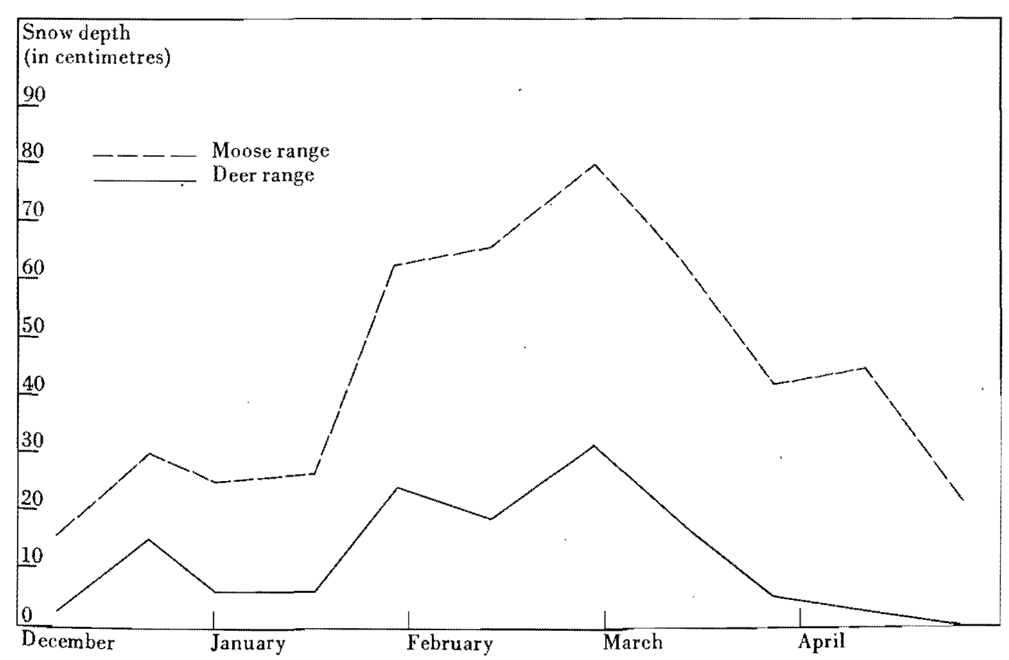


Figure 10. Comparison of mean depths of snow on deer range and moose range in Fundy National Park, 1965–66.

Figure 10



servations was eight per winter at each of stations 1, 2 and 3. We visited all stations eight to ten times each winter. Probably there were no more deer on the high country in 1964–65 than previously, but the generally lesser snow depths permitted them greater freedom to move about and be recorded. In 1965–66, due to lesser snow depths at low altitudes and the campground cutting at station 5 deer could range to higher elevations than in the previous two winters. Conditions and deer activities above station 5 were quite similar to those in 1964–65.

In 1963–64 moose were ranging downward with some regularity to station 5 and occasionally lower. They withdrew to high elevations after January 25, when snow depths began consistently to exceed 25 cm on deer range and 45 cm on moose range. Throughout the following winters, a few individual moose remained as low as 130 m elevation until late March or April.

Moose mobility was severely restricted during two periods in 1963–64, but it was only briefly restricted by the conditions encountered in 1964–65 and 1965–66. On January 25, 1964 mean snow depth on the moose range was 45 cm (Fig. 8) and moose were travelling through it freely. By February 8 mean snow depth had increased to 70 cm, and two weeks later it was 76 cm. By March 7 snow depth had dropped off somewhat, to a mean of 56 cm. From then until April 4 mean snow depth again increased sharply to 97 cm and then fell off abruptly with the onset of the spring thaws. During this period depths at individual stations frequently exceeded 110 cm. The deep snow in February restricted moose in their movements, and they were apparently confined to small local areas by the greater depths of late March and early April.

Travelling moose stayed in the shallower snow of the forest canopies in the manner described by Nasimovich (1955) and Des Meules (1964); moreover this tendency increased with snow depth until, with the mean depth at 97 cm, moose and their tracks were scarcely seen anywhere else.

Figure 11. Comparison of mean densities of snow on deer range and moose range in Fundy National Park, 1963–64.

Figure 12. Comparison of mean densities of snow on deer range and moose range in Fundy National Park, 1964–65.

Figure 11

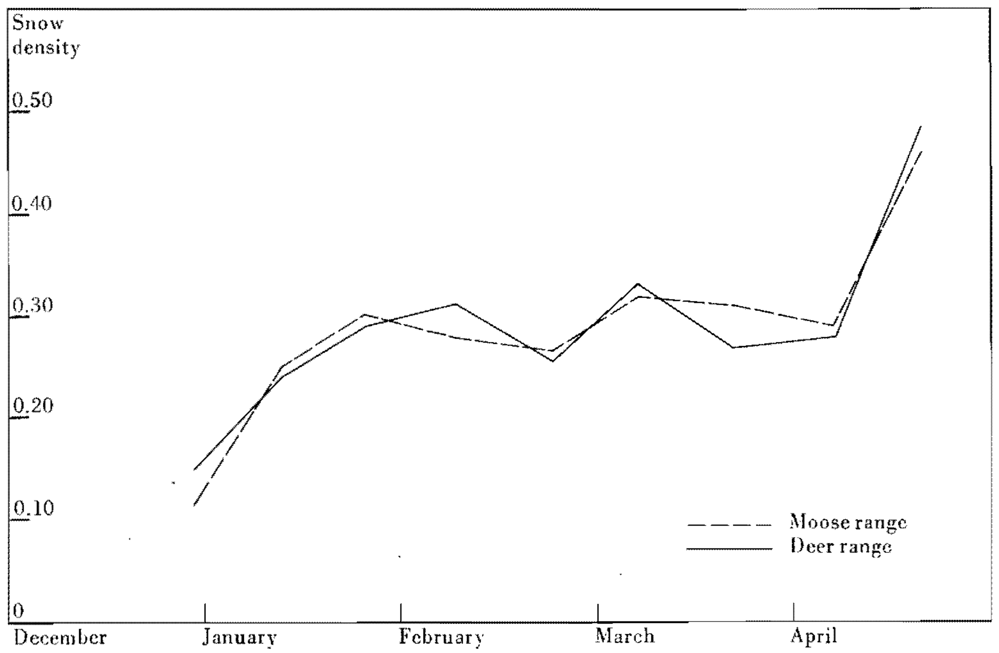
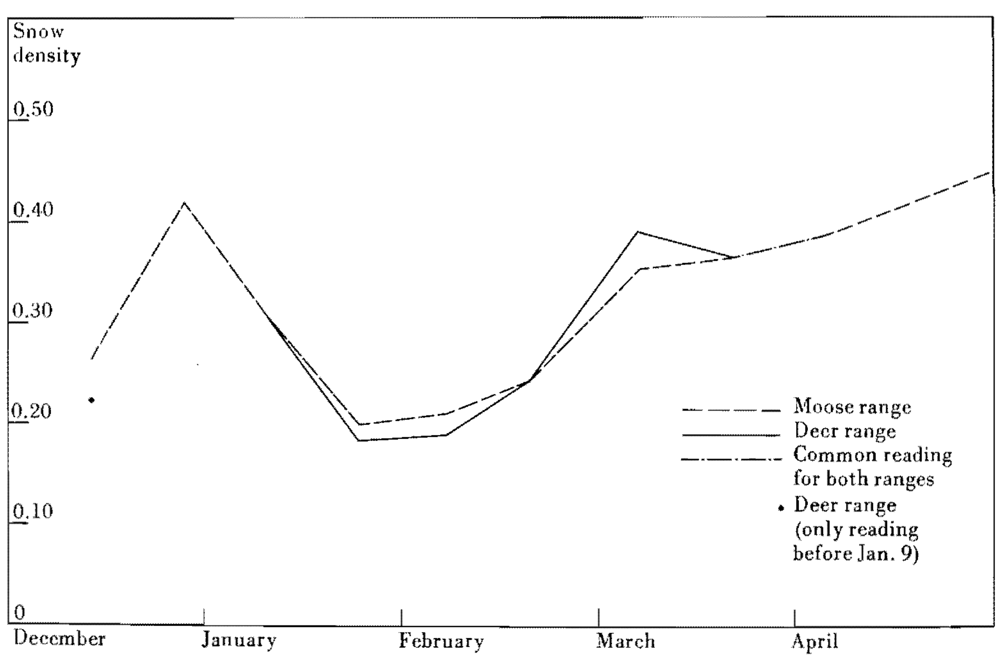


Figure 12



Nasimovich considered that Eurasian moose were greatly impeded by snow 60 to 70 cm deep unless it was light and fluffy, a condition not common in Fundy park. According to Nasimovich, in snow depths of 85 to 90 cm (and snow densities in the 0.20's) "adult moose touch the snow with the belly while running. The animals move with great difficulty." Under these conditions between March 22 and April 18, 1964 the animals in the park engaged in no movement beyond that necessary to gathering food. It is under such conditions that moose normally *yard*, and Telfer (1967a) has described typical yards for moose and deer in country comparable to that considered here. Prescott (1968) noted that moose in Nova Scotia "tended to concentrate in preferred areas" when snow depths approached 76 cm. In the park, however, high altitude ranges are overused and areas where browse is dense enough to permit moose to survive in proper yards with hard packed trails are scarce. Nasimovich considered snow depths beyond 90 to 100 cm critical for moose. In Fundy park, with browse conditions uniformly poor at high altitudes, lesser depths (probably anything above 70 cm) may well be critical, especially if long lasting. As Edwards (1956) has also noted the effect of similar snow conditions can vary between ranges with differing amounts of food and cover.

Snow densities

Figures 11 and 12 present snow densities in Fundy National Park in 1963–64 and 1964–65. Data for 1965–66 are not shown because several times during that winter the density of snow on the deer ranges could not be measured: either there was little or no snow or snow was slushy or the layers were compacted so that none could be measured individually. Such results as could be shown simply parallel those of preceding winters.

Snow densities, on the average, were slightly greater in the open than under canopies; however, the differences were not consistent and would have virtually no effect on support offered travelling animals. For these reasons subcanopy and open exposure densities are not discussed separately. When greater densities were found in the open they were due to compaction through wind action and direct sunshine.

The densities shown at each station on each date are mostly average figures derived, in late winter, from as many as 10 or more determinations made in successive snow horizons from ground level to surface (see Fig. 2). Densities were sometimes difficult or impossible to determine.

In general, densities were found to vary only slightly among the various horizons except under two conditions. As winter progressed densities in the horizons nearest ground level tended to become slightly greater than those higher up, as in Figure 2. Also, fresh snow is always less dense than snow which has been on the ground for some time. Thus just after a mid-winter snowfall the surface layer usually has densities in the 0.10 to 0.14 range while lower horizons often have densities ranging from 0.23 to 0.26. Large snowfalls are therefore reflected on Figures 11 and 12 by temporary declines in density.

Figure 11 shows nearly identical densities on both ranges throughout the winter of 1963–64. When measurements were commenced in late December the recent snow had mean densities of 0.12 to 0.15. Those values increased until on January 25 they were in the 0.29 to 0.30 range. They remained within that general range until shortly after April 5 when the spring thaws resulted in temporarily great increases.

The mean snow density pattern for 1964–65 (Fig. 12) is more variable, but it also shows similarity between moose and deer range with several common values. Following heavy rains, we could not measure the density of the snow on deer ranges on December 27 and the residual snow on the moose ranges was slushy and dense (0.40 to 0.43). When fresh snow once more started to accumulate, temperatures near and above freezing and probably high humidities as well resulted in remarkably high mean densities, to 0.31, on both ranges on January 9. They then receded to between 0.19 and 0.21 on January 23 and February 6 as fresh snow continued to amass under cooler conditions. Thereafter densities increased throughout the winter. In 1964–65 the deer ranges lost all snow following April 3, whereas five of the six stations on the moose ranges retained snow under the forest canopies until April 30.

In 1965–66 there were initially high densities under thawing conditions on both ranges (to 0.36 on December 5, 1965) declining in December (to 0.20 on December 31, 1965), then a sudden rise following a thaw in mid-January (to 0.40 on January 15, 1966). This was followed by snow accumulation and mean densities decreased to lows of 0.12 to 0.16 at some stations on January 29, 1966. There was then a gradual increase until the snow melted in April. Snow density on moose ranges could be measured at several times during the winter when that on the deer ranges could not.

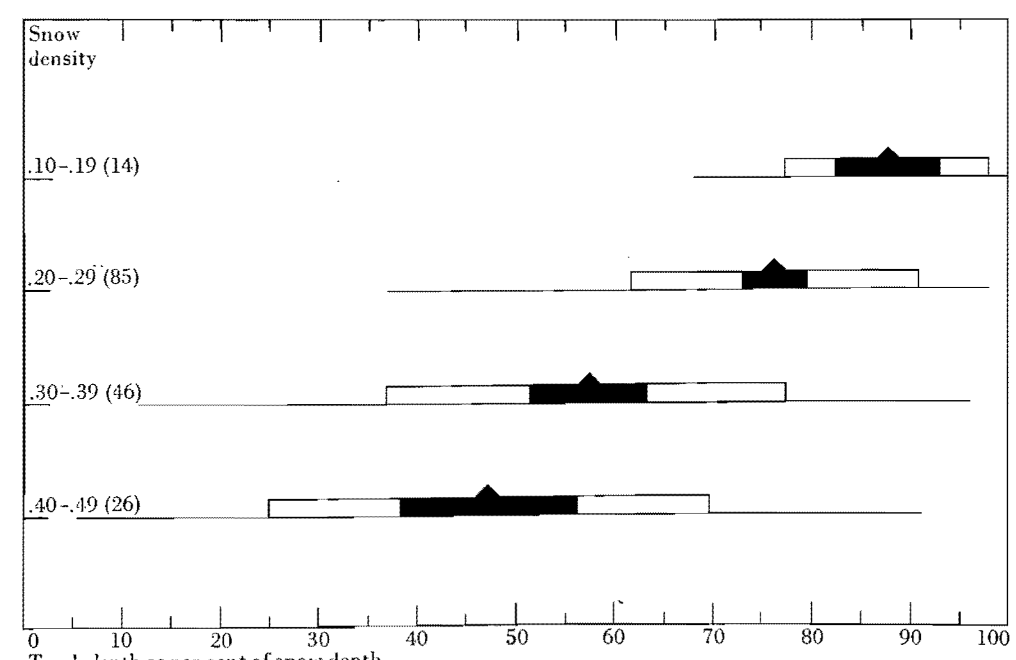
From the three winters' observations, it appears that at times when snow depth in Fundy park is important to moose and deer, there are no significant differences between snow densities on the two ranges.

Nasimovich (1955) described the effect of various snow densities on Eurasian moose in considerable detail. For instance, if snow is loose and yielding with little or no density, moose can run without difficulty in depths of 60 to 70 cm. With equal or greater depths and densities in the 0.21 to 0.22 range, the snow impedes the animals' movements. When densities reach 0.24 to 0.26 moose sink into snow "not more than two-thirds of (the) depth, and sometimes considerably less, but in that case it becomes very difficult to lift the feet from the hole in the snow and to carry them forward."

Our observations on snow density in relation to ungulate track depths, summarized on Figure 13, do not exactly parallel those of Nasimovich. Because weight-

Figure 13. Moose and deer track depths as a per cent of snow depth against four categories of snow density. Included are all observations during the study where snow depth exceeded 24 cm. In the figure the base lines represent ranges, the distance from the means (black triangles) to the outer edge of the white rectangles is one standard deviation, and the distance from the means to the outer edge of the black rectangles is two standard errors of the mean. Numbers of observations in parentheses.

Figure 13



loads-on-track for moose and deer are more variable within than between species (Kelsall 1969), both have been included together here. The figure includes only those observations of tracks where snow depth exceeded 24 cm and does not show the complicating factor of many crusted horizons of varied hardness in the snow. To some extent the different hardnesses of the crusts are mutually compensatory.

The figure shows that new snow of low density (0.10 to 0.19) will not support ungulates: mean track depth was 88 per cent (35 cm) of the mean snow depth of 40 cm. Snow density in the range 0.20 to 0.29 seems to provide some support; mean track depth here was 76 per cent (again 35 cm) of the mean snow depth of 46 cm. The difference between these two means is highly significant.

There is great difference between the first two density categories and the next—densities of 0.30 to 0.39. Here the mean track depth was only 57 per cent (28 cm) of a mean snow depth of 48 cm. Obviously real support was being provided to the ungulates. Higher densities, to 0.49, provide still greater support although the differences (see Fig. 13) are not statistically significant. The mean track depth was 47 per cent (20 cm) of a mean snow depth of 44 cm.

Moose and deer sink about equally into snow of equal densities, but equal depths affect the two species very differently. Moose walk quite easily when they are sinking only 20 to 35 cm into snow, as those depths are well below one-third of their chest height. Deer, on the other hand, are decidedly impeded by such depths which are between 56 and 70 per cent of their chest height.

There is great range to the observations in all but the lowest density categories and the standard deviations shown are great for that reason. Moose and deer will occasionally strike an air pocket or small point of soft snow, as around a buried shrub or bunch of grass, and sink deeply; on the other hand extremely local areas of good support (high density or great hardness or both) may be found in even quite soft snow—although generally not when densities are below about 0.20. Some, perhaps even most, of our extreme observations are biased in these ways.

Table 1
Snow conditions at Station 9, Fundy National Park, April 4, 1964.

	Open exposure	Subcanopy exposure
Number of distinct horizons	10	6
Range in vertical hardnesses (gm/cm²)	1 to 90,000	1 to 6,000
Mean hardness (gm/cm²)	11,105	2,600
Snow depths (cm)	105	82
Range in snow density	0.18–0.38	0.18–0.38
Mean snow density	0.28	0.27

Table 2
Maximum hardnesses (summarized) from each profile read during extreme snow conditions in Fundy National Park, March 8 to April 5, 1964.

		Deer range	Moose range
Open exposures–	Mean hardness (gm/cm)²	29,500	83,400
	Range (gm/cm²)	500–100,000	1000–100,000
Subcanopy–	Mean hardness (gm/cm²)	10,700	18,200
	Range (gm/cm²)	200–70,000	700–70,000

Snow hardness

Snow hardness is in some ways the most difficult factor to assess. As winter progresses new horizons are added to the snow profile, and most are topped by a more or less well developed crust. Our data provide extremes in variability and complexity. They will not be presented here in detail, but there are some interesting points.

Vertical hardnesses are almost invariably lower, and the crusts often less well formed, under canopies than in the open. For example, data from station 9, April 4, 1964 shows late-winter contrasts, following some fresh snow, between open and subcanopy areas (Table 1). The period March and April, 1964 when mean snow depths were the greatest observed during the study, provides additional contrasts in vertical hardnesses (Table 2). On Table 2 the hardnesses used to provide the ranges and means are the maximum recorded in each profile examination during station readings of March 8 to April 5, 1964 inclusive.

The range of hardnesses in the tabular examples are typical of late-winter conditions in Fundy park, when many successive snowfalls have complicated the snow structure. Table 1 shows again that snow depths are considerably greater in the open (by 28 per cent) and that densities are slightly greater (by less than 4 per cent). Horizons are more distinct in open areas than under canopies. Table 1 and 2 show that mean hardnesses are much greater in open areas (from 70 to 327 per cent in the examples used). During the period covered by Table 2 moose and deer were severely restricted in their movements, but the basic contrasts shown could be replicated using virtually any of the hundreds of station readings made.

The depth to which an animal sinks is not entirely dependent on the hardness of a supporting crust unless the crust is on the surface. Snow density, already discussed, is a factor. Also, when an animal steps on the snow, a pyramid-like column of compacted snow forms under its hoof. The shape of this column depends on the density and temperature of the snow, the form and size of the snow crystals, and the depth and hardness of sub-surface crusts. Apparently other factors enter in also, since attempts to correlate measurements of snow temperature, form and size of the snow crystals, and hardnesses of sub-surface crusts with track depths revealed no pattern. This is certainly an area for further investigation.

Figure 14. The mean number of crusted horizons by exposure on moose range and deer range during the three winters.

Figure 15. Mean number of crusts with a vertical hardness of 1,400 gm/cm², or more, on deer range and moose range throughout the three year study, and during the severe winter of 1963–64.

The greatest hardnesses are often found in a horizon toward the bottom of any given snow profile where the processes of maturation have been progressing the longest. The horizon is often so deep that an ungulate might not sink to it anyway. Further, while mean and maximum hardnesses were large in the samples in Tables 1 and 2, the minimum hardnesses encountered were relatively small and deer and moose would sink through most.

Expressions of hardness more relevant to ungulates are found in the number of crusts, and the number of crusts that are sufficiently hard to support (rather than impede or endanger) ungulates. Relevant data are presented graphically on Figures 14 and 15.

Figure 14 shows the mean number of discernable crusts per station by exposure on deer and moose ranges. If we ignore for the moment the hardnesses of individual crusts, a number of points are evident. The shape of the graph tends to follow that for snow depth, the greatest number of crusts being found in the deep snows of late winter. To mid-January, while there are still only one to two crusts per station the differences between stations and exposures are not as great as they are later on. Quickly, however, both mean values on moose ranges climb above those for deer ranges until, by late April, snow has disappeared on low elevations and is fast melting on the high country.

On both ranges there are more crusts per station in the open than under forest canopies, except in late April when rapid melting under direct sunlight may briefly reverse the situation. However, where there is only about one more crust per station in open areas on deer range (mean difference is 0.89 crusts), there are up to three crusts per station difference on moose range (mean

Figure 14

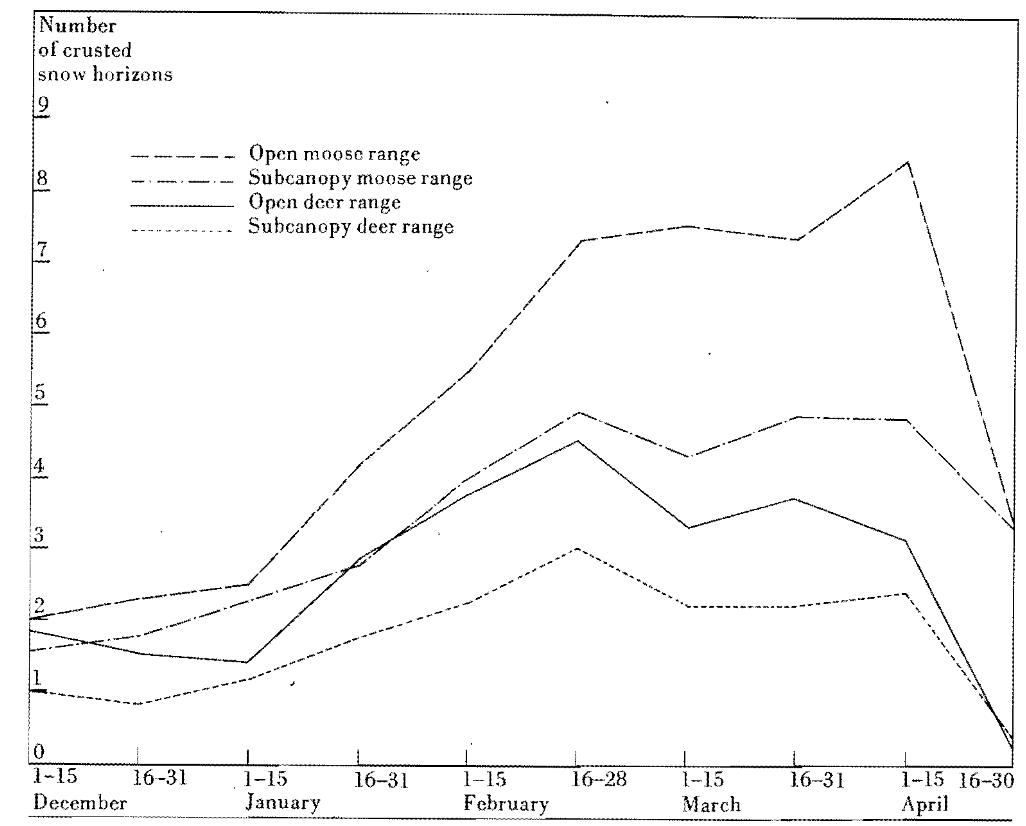
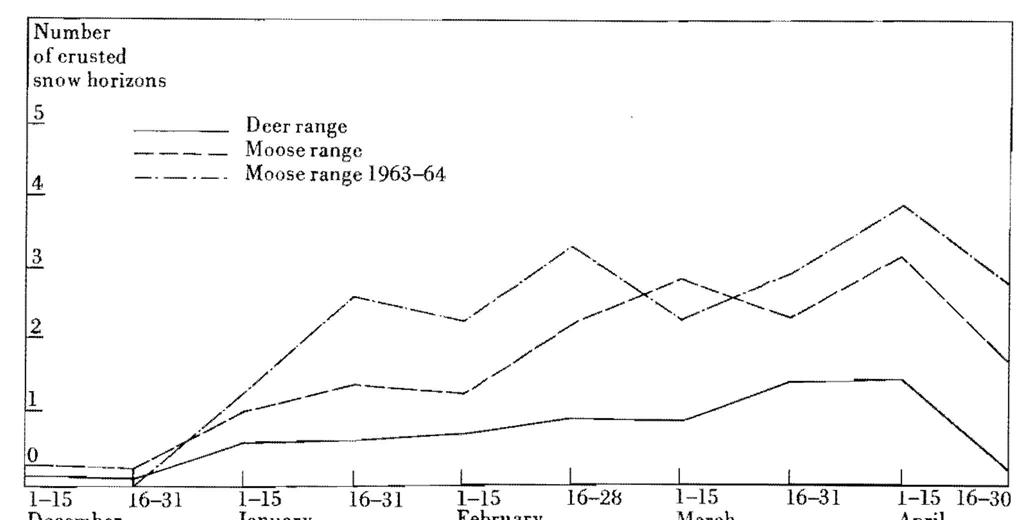


Figure 15



difference is 1.60 crusts). The few crusts on deer range result from the more rapid maturation and melting of snow at lower elevations, which tend to obscure and break up distinct crusted horizons. Also, when temperatures are near freezing, a few crusts are formed in open areas under direct sunlight.

Whatever the causes, on deer range there are only about half the crusts to impede and endanger the lower limbs of ungulates that are found on moose range. Only on moose range did we find evidence of damage to ungulates in the form of bloody hoofprints, and these were common in 1963–64. Furthermore the larger number of crusts to endanger and impede ungulates per station in the open provides a strong incentive, in addition to simple snow depth, to keep animals under forest canopies through rigorous winter weather.

Theoretically, some crusts are sufficiently strong to support ungulates. Some relevant data are given on Figure 15. The figure arbitrarily shows crusts with a vertical hardness of 1,400 gm/cm² or more, since maximum weight-load-on-track for both deer and moose is a little over 1,000 gm/cm² (Kelsall, 1969).

At any given time the number of strong crusts per station approximated one-third of total crusts. On deer range it was only in late winter that there was consistently more than one strong crust per station. On moose ranges there were two or more such crusts per station from late February to early April inclusive. However, on both ranges, from midwinter onward, at least one strong crust is found per station within a few centimeters of ground level—sufficiently deep in the snow so that it is of little or no assistance to walking mammals. Also plotted on Figure 15 is the mean number of strong crusts per station on moose range in the severe winter of 1963–64. While snow depths in that winter were about 28 per cent greater than the three year mean, they may have been partially compensated for (from the point of view of a walking moose) by the greater number of strong crusts present.

Unfortunately, it is difficult, if not impossible, to reconcile the theory of ungulate support by snow crusts with our observations. We frequently observed moose and deer penetrating crusts that should have provided support. In some cases the tracks may have been those of trotting or running animals that were imposing many times their static weight load on the snow; in most cases it seemed more likely that the snow simply was not homogeneously hard over even quite small areas. How else can one explain observations such as the following examples from the winter of 1963–64: a moose penetrated crusts of 8,000 gm/cm² at snow surface, 10,000 gm/cm² at 15 cm, 90,000 gm/cm² at 34 cm before a crust of 7,500 gm/cm² at 40 cm below snow surface supported him; another moose successively penetrated crusts of 20,000, 10,000, 30,000, 40,000 and 25,000 gm/cm² only finding support on the ground at a depth of 73 cm; and a deer penetrated crusts of 5,000 and 70,000 before finding support by a crust of 10,000 gm/cm² at 20 cm below snow surface.

In our observations cases where single hard crusts supported travelling ungulates satisfactorily are the exception. For example, on March 12, 1966 surface hardnesses of 2,000 to 30,000 gm/cm² were found at several of the stations. With temperatures of a few degrees below freezing moose, deer, and the observers found consistently good support over wide areas and the condition was considered unusual.

We concluded that while crusting and strong vertical snow hardnesses are frequent in Fundy park, they are rarely consistent enough to permit unhindered travel by walking animals. Even when one or more crusts do provide support, they are frequently buried under other crusts that make travel laborious and hazardous. This is true even when depths are not limiting. In Fundy park the hazard provided by crusts that will not consistently support ungulates is probably a more important environmental factor than the occasional crust that does consistently support them.

Air and snow temperature and snow grain size

Air temperatures were taken at snow stations most often between 9:00 AM and 5:30 PM so the temperatures tend toward the maxima. It would have been better to establish a maximum-minimum recording thermometer at each station and to systematically record daily, or weekly highs and lows. However, because the temperatures were read during visits to stations 1 to 10 which alternated with visits which began at station 10, it is felt that differences due to time of day are cancelled out and that mean temperatures are comparable between moose and deer ranges.

In 1963–64 the deer range stations (1 to 4) had a mean temperature (January 11 to April 18) of −1.1°C. The moose range stations (5 to 10) had a mean temperature of −3.2°C. In 1964–65 the mean deer range temperature (December 13 to April 3) was 0.4°C and the mean moose range temperature was −1.0°C. In 1965–66 the mean deer range temperature (December 5 to April 24) was 2.7°C and the mean moose range temperature was 2.0°C. These differences are slight, ranging from 2.1° in 1963–64 to only 0.7° in 1965–66. However, even such slight differences may be important since even a slightly more favourable metabolic rate over a long period in winter could provide an advantage to deer. Certainly observations over many years have shown that Fundy park deer on low altitude ranges are consistently in good condition and suffer little mortality in comparison with moose on the high altitude ranges (Kelsall, 1963). Telfer (1967b) found slight temperature differences between moose and deer ranges on a comparable study area in Nova Scotia, on the basis of periodically taken maximum and minimum recordings, but did not consider the differences great enough to cause ungulate movements.

Higher temperatures on deer ranges are probably critical in speeding up the processes of maturation—settling, crusting, and consolidation of the snow. In this respect deer do have an advantage. It seems

probable that a comparison of minimum temperatures would show wider differences between moose and deer range: the adjacent Bay of Fundy would tend to ameliorate low temperatures at low altitudes.

Gold (1958) and others have shown that snow matures more rapidly in above freezing temperatures and it is perhaps significant that mean deer range temperatures in 1963–64 and 1965–66 were slightly above freezing. We have seen that the deer ranges were snow free for a longer period in each of those years than were moose ranges, and that densities climbed more rapidly on the deer ranges toward the end of the snow season.

Temperatures of the snow within each horizon in each snow profile examined (see Fig. 2) were as would be expected. Temperatures in surface layers varied with the ambient air temperature although they seldom dropped below −7°C. Minimum snow temperatures were generally found in either the surface layer of snow or in the first one or two layers immediately below it, depending on the immediate past history of the air temperature. Bottom layers had the highest temperatures, and they were seldom much below freezing. In the lowest horizons, temperatures between 0° and −1°C were usual.

In general, snow grain size tended to increase from the surface to the lower horizons and the delicate configuration of freshly fallen snow changed, with increasing depth, to amorphous and icy lumps. Not infrequently the lowest layers had firn snow (loose granular snow which will flow from a shovel like sand), or heterogeneous layers incorporating everything from small grains to icy consolidations as large as a fist. These differences reflect the maturation processes that are more or less common to all snow (Gold, 1958). With the National Research Council instruments it was often difficult to secure representative 250 cc density samples of firn or heterogeneously consolidated snow.

Track measurements

Wherever they were encountered in level snow within 160 m of any snow station, we measured the average depth of moose and deer tracks. Some of these data have been given in the discussion of snow density. Table 3 presents a summary of data derived from those observations, for each winter. The data are classified by open and subcanopy areas. Only paired observations were used in the table: that is, cases where tracks of one or both species were found in both open and subcanopy areas at a station during one visit.

The data show that the advantage received by both moose and deer through confining their activities largely to subcanopy areas when deep snow is on the ground. The mean depth of deer tracks ranged from 61 to 71 per cent greater in areas of open exposure during the three winters. The mean depth of moose tracks was 76 per cent greater in areas of open exposure in 1965–66 and 52 per cent greater in 1964–65, but only 25 per cent greater in 1963–64. In the last case there was obvious bias involved. In 1963–64 moose were greatly restricted in their movements during late winter, when contrasts between snow depths were greatest, and their tracks were simply not present for measurement at the stations. Track depths taken in early winter from open and subcanopy areas were necessarily less divergent because snow depths were less divergent then.

Other biases in the data may be compensatory to some extent and no allowance is made for them. Thus during periods of great snow depth it was difficult to secure paired observations because the animals avoided walking in the open. Late in winter, when thawing was well advanced the reverse was the case. Then snow depths were briefly greater under the canopies, and animals deliberately travelled mostly in the open, meandering to avoid deep residual drifts.

Moose track depths are consistently greater than those of deer (Table 3) and this simply reflects the fact that the deer are usually found in those areas having the least snow. Deer have shorter legs than moose and would frequently have to resort to the physically wasteful process of bounding to progress in snow of the depths commonly found on moose range. Measurement studies of moose and deer in New Brunswick and Nova Scotia (Kelsall, 1969) show that the chest height of moose is nearly twice that of deer (i.e. the average chest height of 1½ year old male deer and moose are 58.9 and 98.9 cm respectively).

It is noteworthy that the track measurements take no account of snow drifts found in most open areas. At station 9, on April 18, 1964 moose tracks were 5 cm deep on the average in an open area of level snow, but they were 40 to 68 cm deep across a nearby snow drift.

Table 3
The ranges and means in track depths of walking moose and deer, under canopies and in open areas, as observed at snow stations in Fundy National Park during the winters of 1963–64 and 1964–65. Number of observations in brackets; depths in centimeters.

		Moose track depth		Deer track depth	
	Year	Open exposure	Subcanopy exposure	Open exposure	Subcanopy exposure
Range	1963–64	4–74	10–70	6–45	2–33
	1964–65	8–75	8–50	3–50	1–35
	1965–66	12–60	3–35	2–42	0–20
Mean	1963–64	40.1(22)	32.0(22)	24.3(25)	15.1(25)
	1964–65	34.9(21)	22.9(21)	22.1(14)	13.6(14)
	1965–66	29.7(19)	16.9(19)	15.4(27)	9.0(27)

Discussion

Snow studies of the sort described here have been done in Russia by Formozov (1946) and Nasimovich (1955). Severinghaus (1947) found that deep snow, particularly when it is of long duration, is the principal factor limiting North American white-tailed deer in the Adirondack region of the United States. Pruitt (1959) described snow tolerances of barren-ground caribou in detail, and Des Meules (1964) pioneered in such work with moose in North America. The present studies show that snow depths on the high altitudes frequented by wintering moose in Fundy National Park are consistently greater than on the low altitude deer ranges. They commonly exceed the depth (about 59 cm) at which most walking deer would be expected to drag their bellies. This would account for the almost complete withdrawal of deer to low elevations with the onset of winter.

The only exceptions to the use of low altitude winter ranges are those few deer that remain in high local areas with good habitat. They are never numerous. Generally large strong males best equipped to cope with difficult snow, they are often emaciated and weak in spring. Such deer probably die in particularly severe winters and, on rare occasions, their carcasses have been found. Laramie and White (1967) have described an analogous situation in New Hampshire. Other exceptions are deer which feed at quite high altitudes on steep park slopes. Snow depths are apparently much less there than on gently sloping or level areas. Such slopes commonly extend upward to 230 m, although none are represented at the snow stations.

While snow conditions prevent most deer from penetrating far into moose range in winter, and probably account for the fact that they are not numerous there at any season, moose would not be similarly restricted. In fact moose wintering at low elevations in the park should find food more abundant than at the higher levels, and snow conditions there would seldom seriously restrict their free movement. Telfer (1967b) speculated that food competition with deer and moose sickness induced by *Pneumostrongylus tenuis* might account for the absence of moose at the low elevations. Observations in Fundy park tend to confirm the latter suggestion. Moose have periodically descended to the low country and wintered there. When they do so they seem almost invariably to die before winter's end. In the spring of 1960 and 1961 approximately two dozen moose carcasses were found on deer range, many of them in areas of abundant browse where deer had wintered successfully.

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