A numerical "Snow Index" for reindeer (Rangifer tarandus) winter ecology (Mammalia, Cervidae)¹

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Pruitt, W. O. 1979: A numerical "Snow Index" for reindeer (Rangifer tarandus) winter ecology (Mammalia, Cervidae). — Ann. Zool. Fennici 16:271—280.

Previous work has shown that some ecological characteristics of tundra upsik that are important to small mammals can be expressed by a mathematical model or a "Snow Index". Using results of my own and other investigators' earlier work, plus results of some 460 snow profiles taken in winter 1976-77 in the vicinity of Värriö Subarctic Research Station in Northeastern Finland, in relation to the semi-domesticated reindeer of Salla North association, I have derived a mathematical model which relates reindeer activity to features of the snow cover. The Värriö Snow Index (VSI) incorporates the hardness of the hardest layer in the upper half of the snow cover, the hardness and thickness of the basal layer, the vertical hardness of the snow cover surface, the thickness of the topmost layer, the hardness and thickness of the hardest layer in the snow cover and the total thickness of the snow cover. The VSI agrees well with the winter feeding activities of reindeer near the Research Station and also correlates with the puzzling latewinter movement of the reindeer through the altitudinal tree line into the alpine zone of Värriötunturi. A field check of the VSI in the central part of northern Finland, in the northern part of Kyrö association, where herding is practiced, revealed further agreement, and indicated additional, classifiable snow-reindeer relationships.

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1. Introduction

All those who have analyzed snow cover critically have commented that it affects different species in entirely different ways. For example, an increase in thickness protects small mammals from carnivorous birds, but at the same time it hinders caribou from feeding on ground vegetation. A hard, and perhaps, dense layer in the api (for snow terminology, see p. 00.) may enable some carnivorous mammals to be supported on it (Pruitt 1957), but other mammals with greater foot-loading (e.g. Alces) may be hindered in their movements. At the same time, the hard and dense layer may aid the accumulation of carbon dioxide in the pukak (Pruitt 1957) space. This gas can accumulate in densities sufficient to cause small mammals to shift their winter range elsewhere (Bašenina 1956; Penny 1977).

Ever since the pioneering work by Formozov (1946) and Nasimovič (1955) it has been clear that snow cover is an integral factor in the environment of boreal ungulates. Edwards (1956) showed how snow cover affected altitudinal distribution of caribou in the mountains of western Canada. Pruitt (1959) showed that the distribution of barren-ground caribou on their winter range could be correlated with and predicted by certain characteristics of the snow cover. Henshaw (1968) confirmed Pruitt's thresholds of sensitivity to the thickness, hardness and density of the snow cover, even in the caribou of northwestern Alaska. Stardom (1975) showed how the winter activity of woodland caribou in southeastern Manitoba correlated closely with nival factors. He also showed that the threshold of sensitivity to thickness was greater in woodland than in barren-ground caribou. Telfer (1970), Kelsall & Prescott (1971) Skogland (1978)demonstrated that snow cover morphology could be analyzed

¹ Report no. 72 from the Värriö Subarctic Research Station of the University of Helsinki.

mathematically in time and space. Kelsall (1969) analyzed sex and age morphology in Alces alces and Odocoileus virginianus in relation to snow morphology.

Pruitt (1959) noted that the ideal nival winter range for barren-ground caribou had api that was thin, of little hardness and density, and that had not been affected by invasions of warm, moist air. In other words, their optimum winter habitat was in a cold, continental climate that enabled the heat and moisture to flow uninterruptedly from the earth through the api to the cold, dry air above. Deviations from this ideal situation result in a worsening of overwintering conditions for caribou. An extended Fall Critical Period (Pruitt 1957) may have severe effects not only on small subnivean mammals but also on caribou by aiding the formation of bodni vihki, čuok'ki or caevvi (Eriksson 1976). I also noted that an ice layer (sigulik) in the upper part of the api had a greater deterrent effect on caribou than one closer to the ground. Stardom (1975) also observed this effect in relation to woodland caribou.

One aspect of caribou winter ecology that had defied explanation is the ability of the animals to detect morphological changes in the api and to orient their movements so as to progress down a gradient to a region with api of lesser thickness, hardness or density than the one they left. I believe that the sensory mechanism lies in some part of the body in frequent contact with the api but not so frequently or violently as the hoofs or lower legs.

Caribou exhibit a body movement that seems to answer this requirement. Before digging a suov'dnji or extending a čiegar they frequently plunge the muzzle into the api to a depth of 8 to 10 cm and withdraw it quickly with a motion that has a horizontal and backward component. This movement previously has been interpreted as "smelling for lichens" (e.g. Miller 1976), but it could also provide contact between the api surface and a pressure-sensitive area in the mentum. There are physical reasons for believing that "smelling for lichens" is, at least sometimes, an incorrect interpretation.

An api-sensor in the mentum would explain some activities of Rangifer. Such a sensor would react to the hardness of the top 10 or 15 cm of the api and if this layer were soft it could initiate the cratering response (Pruitt 1960a). This could happen regardless of the hardness of the basal layers. Perhaps this is the reason that sigulik near the top of the api is more a deterrent than is sigulik at the bottom of the api. Perhaps this also is why such phenomena as bodni vihki, čuok'ki or caevvi are so detrimental to reindeer — the deer cannot detect them by their sensors, and thus are not stimulated to emigrate from the affected region but

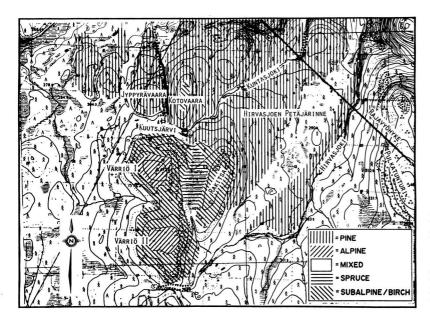


Fig. 1. General vegetationtypes of the Värriötunturi region. Adapted from Pulliainen (1976). Base map from Maanmittaushallitus Topografinen Kartta 1:50,000, no. 4714 2 + 4732 1 Värriötunturrit and 4723 1 + 2 Nuorttitunturi.

remain and continue to expend energy while getting little in return.

2. Study area and methods

The study area is situated in the vicinity of Värriö Subarctic Research Station (67°44′ N, 29°37′ E, 355 m above sea level) in Salla North reindeer association, Itäkaira, northeastern Finnish Lapland. The area is dominated by Värriötunturi. Pulliainen (1976) described the vegetation of the region. He classified the summits and slopes of Värriötunturi as typical alpine and subalpine zones. At elevations lower than the subalpine birch forests are pine forests, mixed forests and bogs (Fig. 1). For detailed descriptions of the area see Pulliainen (1971), Salo (1971) and Airola & Pulliainen (1975).

A. Snow observation procedures and methods:

Beginning 10 October I established a series of 20 standard api-profile stations (Pruitt 1959) in three irregular transects in order to encompass a variety of topographic and vegetation types (Fig. 2). Each observation profile consisted of determination of hardness, density and thickness, as well as crystal type and size of each layer of the api, vertical hardness of the api surface, temperature of ambient air and pukak and a record of any reindeer or other animal activity in the vicinity. I repeated the observations and measurements at these stations about once a week or once a fortnight, depending on change in api, weather or reindeer activity.

As the reindeer entered the region, shifted their feeding activities and finally left the region, I took, in addition, a series of api-profile stations in walls of freshlydug suov'dnji, among suov'dnji, walls of freshlydug

fies'ki, terminal walls of freshly-dug čiegar, or "systematic random" transects of stations across now-deserted feeding areas. I examined a total of 460 api-profiles in the Värriö region between 10 October 1976 and 4 March 1977. In late March and early April 1977 I examined 30 api-profiles at Kapperapalo, in the central part of northern Finland.

Pruitt (1966) derived a "Snow Index" that correlated with distribution of small mammals in a region of Low Arctic tundra in northwestern Alaska. This Snow Index employed a simple summation of the products of thickness, hardness and density of each layer of the snow cover on a number of sampling plots. In an attempt to derive a Snow Index that would model the winter activity of Rangifer I combined the previously discussed aspects of their wintering ecology and behaviour in successively different ways. I then compared the results to the actual distribution and feeding activities of the semi-domesticated reindeer in the vicinity of Värriö Subarctic Research Station. The combination that models best their winter activity I call the Värriö Snow Index:

$$VSI = (H_{1/2}H_{\rm b}T_{\rm b} + VT_{\rm s} + H_{\rm h}T_{\rm h})T_{\rm ta}/1000$$

where

 $H_{1/2}$ = hardness of hardest layer more than halfway between the substrate and the top of the snow cover.

 H_bT_b = hardness times thickness of basal layer. VT_s = vertical hardness of surface times thickness of surface layer.

 H_hT_h = hardness times thickness of hardest layer (if not H_bT_b). If basal layer is the hardest then term H_hT_h drops out.

 T_{ta} = total thickness of the api.

To test the validity of this index I derived the null hypothesis: there is no response of reindeer feeding to a low VSI.

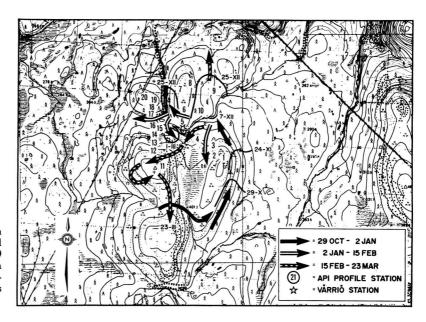


Fig. 2. Värriötunturi region showing topography and movements of reindeer 29 October 1976 to 23 March 1977, and locations of apiprofile stations. Base map as in Fig. 1.

B. Glossary of some specialized snow terminology

Although definitions of specialized snow terminology have been published by Pruitt (1957, 1960b, 1966, 1970, 1978: Figs. 1—3, 1—4, 3—1, 5—1, 5—2) and Eriksson

(1976) as well as earlier by Formozov (1946) and Nasimovič (1955), precise designation of snow phenomena continue to be misused, misspelled or ignored. For example the colour photograph on the cover of Miller (1976) is described as being of a "caribou trail" although it has the characteristics of a čiegar.

Term	Source	English Equivalent
aηmaηa	Kovakmuit (Inuit)	Space formed between drift and obstruction causing it.
api	Kovakmuit (Inuit)	Snow on the ground, forest.
bodni vihki	Lappish (Eriksson 1976)	a frozen layer of snow next to the soil; granular structure exists but crystals are intensely bonded together.
cævvi	Lappish = tsævvi (Eriksson 1976)	dense basal layer caused by the sequence of (1) unfrozen soil (2) warmer layer of snow resulting from high temperatures, followed by (3) thick snow layer which compresses the basal layer and results in a hard, dense mass with small crystals. Cævvi is severe for reindeer since it is suitable for growth of snow mould which prevents reindeer from smelling lichens; it probably also facilitates accumulation of CO ₂ under the snow cover.
čiegar	Lappish	"feeding trench" or a linear extension through undisturbed api of a sequential series of suov'dnji. Actual feeding on ground vegetation occurs only at the terminal end of a čiegar. Excavated snow is kicked back, partially filling the trench with snow that sinters and becomes very hard.
čuok'ki	Lappish	layer of solid ice next to the soil.
fies'ki	Lappish	"yard crater" or roughly circular site of thin, hard and dense snow cover caused by deer digging and extending a perimeter expanding into undisturbed api from an original suov'dnji or group of suov'dnji.
kaioglaq	Kovakmuit (Inuit)	Large hard sculpturings resulting from erosion of kalutoganiq. More precise than the loose terms "zastrugi" or "skavler".
kalutoganiq	Kovakmuit (Inuit)	Arrowhead-shaped drift on top of upsik; moves downwind
kanik	Kovakmuit (Inuit)	Ice crystals that form on cold objects when warm, moist air passes over them.
kieppi	Finnish	Hole in snow cover where an animal has plunged for shelter (pronounced "KEY-eppi").
kimoaqruk	Kovakmuit (Inuit)	"Finger drift" downwind of small obstruction.
mapsuk	Kovakmuit (Inuit)	Overhanging drift or "anvil drift".
pukak	Kovakmuit (Inuit)	Fragile, columnar basal layer of api.
qali	Kovakmuit (Inuit)	Snow on trees.
qamaniq	Kovakmuit (Inuit)	Bowl-shaped depression in api under coniferous tree.
sändjas	Lappish	Fragile, columnar basal layer of api (= pukak).
siqoq	Kovakmuit (Inuit)	Drifting or blowing snow.

Term	Source	English Equivalent
suov'dnji	Lappish	"feeding crater" or individual feeding site excavated in the api, separated from other sites by undisturbed api.
tumarinyiq	Kovakmuit (Inuit)	Small "ripple marks" which are (1) last remains of kaioglaq or (2) differential erosion of hard and soft layers.
upsik	Kovakmuit (Inuit)	Wind-hardened tundra snow.
vyduv	Russian	Spot blown bare of snow.
zaboi	Russian	Area of thick snow that persists perhaps all summer.

3. Results and discussion

A. Reindeer use of the Värriö Region

Since the advent of the snowmobile into Salla North district about 15 years ago reindeer husbandry there has degenerated into only occasional forays by the herders through the winter range. The mechanized forays climax in a violent roundup and separation in early February. The reindeer seldom see man except to be chased, and, therefore, have reverted to a feral condition.

Reindeer first moved onto the Värriö region winter range from the south on 29 October (Fig. 2). They appeared initially in the birch zone on the southern and southwestern slopes of Rakitsa and in the saddle between Värriö I and Värriö II.

Between 8 and 12 November there was a thaw with air temperatures as high as $+5^{\circ}$. By 24 November reindeer were active on the eastern side of Rakitsa and in the Hirvasjoki valley to the east. On 7 December the reindeer moved north along the eastern flank of Rakitsa, across the western end of Hirvasjoen Petäjärinne, north across the steep-walled valley of Kuntasjoki. This movement was limited to 3 well-defined trails until they crossed Kuntasjoki and reached the pine-covered "bench" along the eastern base of Kotovaara. Here they began digging suov'dnji again and feeding. They remained east of the base of Kotovaara until about mid-December, except for 10 or 20 animals that frequented the vicinity of the research station outhouse, attracted by urinesoaked snow there. The animals were more common farther east, at least as far as the border restricted zone.

On 19 December I noted that deer had

followed snowmobile trails to the eastern brow of Kotovaara and also onto Jyppyrävaara. They ventured only a few metres off the trails and climbed back onto them after a few plunging bounds in the soft api. From 22 through 24 December winds were Force 5 and 6 with sigoq and fresh snow falling, and temperatures around zero. On 25 December the deer moved onto Kotovaara, to the vicinity of snow station 6, along snowmobile trails and began feeding from these trails outwards. They dug only 5 suov'dnji but fed on tree lichens and buds. There were frequent bands of 10 to 20 animals crossing Kuntasjoki near snow stations 9 and 10, moving north, cratering and feeding as they went. On 27 December the deer began to use the grass lawn around the Station buildings. By 28 December the deer had followed the well-packed main snowmobile road west from the Station for almost one kilometre. They only ventured 3 to 4 m off the road and fed intensively in restricted areas, forming fies'ki. On 2 January the deer began to venture along snowmobile trails in the area between Värriö Station itself and the western base of Rakitsa. This movement coincided with 5 days of fresh to strong winds, siqoq and mild temperatures of 0 to -5°. The deer venturing along the western base of Rakitsa moved off the snowmobile trails to crater first the pine qamaniq (Pruitt 1957); after all the qamaniq were cratered they formed fies'ki nearby in full api. By 9 January the deer had begun to work their way up the western slope of Kotovaara, spreading out from the snowmobile trails there. On 13 January I noted that deer had worked out from the snowmobile trails on Hirvasjoen Petäjärinne, but were restricted to fies'ki. On 16 January deer moved westerly along the ravine bottom and made suov'dnji in the immediate vicinity of snow station 17.

They also cratered the steep slope between stations 17 and 19 but did not venture onto the more gentle slopes north of station 18. On 17 January the deer deserted the vicinity of stations 9 and 10, an area occupied continuously previous to this time. On this date I noted that the deer had re-excavated and fed in my old apiprofile excavations at station 6. Near station 7 they had fed in qamaniq and a η ma η a. By 20 January there was intense feeding activity along the snowmobile road leading west from the Station, on my ski trail from the road to station 17 and on the western face of Kotovaara. They fed first in the qamaniq and a η ma η a and then worked out from these sites.

In the first 10 days of February the deer underwent roundup and separation in a corral a few kilometres north of the study region. This activity was accompanied by much snowmobile use and resulted in the deer becoming exhausted and lethargic, probably from over-heating. By 12 February the deer were back in our vicinity again but now they remained in bands of 5 to 15 individuals and restricted their activity to fies'ki, from which they extended čiegar. As they extended these čiegar they tested the surface hardness of the api with their muzzles about every metre and a half. Some čiegar were as much as 10 metres long. On the "pine flats" southeast of the Station the pattern of feeding was from a snowmobile trail to a nearby gamaniq, then from one gamaniq to another. If the trees were less than 10 m apart the deer would crater the intervening api as well as the qamaniq; they avoided the gently-sloping kimoakruk (Pruitt 1960b) which reached thicknesses of over 1.3 m.

By 25 February the deer followed snowmobile trails through the birch and alpine zones of Värriö I. By 27 February they had deserted the "pine flats" southeast of the station and had moved southwesterly onto the lower slopes of Värriö I, into the birch zone. Their first feeding was on birch twigs, then they cratered around the bases of the birches. On the northern slope of Värriö I they went from one individual, scattered birch or pine to another. These animals reached their feeding site by moving along a snowmobile trail that branched from the main snowmobile road west. By this date the deer had deserted the areas where they had been common earlier - e.g. Stations 9 and 10, Kotovaara, Station pine flats — and were to be found in the immediate vicinity of snowmobile trails

on Rakitsa and on the northwestern slope of Värriö I. By 7 March they had ventured along snowmobile trails on the northern and northwestern slopes of Värriö I and were making fies'ki and čiegar there. They also were feeding in this fashion on the top of Jyppyrävaara. By 20 March deer activity was limited almost entirely to the upper birch zone and alpine zone on Värriö I. Here the api was changed into upsik (Pruitt 1960b) and the deer sank in only 8 to 10 cm. The animals moved from one birch shrub to another, stripping twigs and what lichens remained. They even scraped crustose lichens from large dead and dry pine stubs. Some birches were completely stripped and broken. Junipers and pines had buds eaten and branches broken. By 23 March there was a dramatic decrease in deer sign on Värriö I and only 3 animals were observed. The entire upper birch zone and the alpine zone had been cratered and the roughened surface filled in and smoothed by fresh upsik. Indications were that the deer moved to the south along the Värriötunturi chain.

C. Reindeer activity and Värriö Snow Index

Fig. 3 displays ranges, means, standard deviations and standard errors of the means of log VSI of both "reindeer feeding" and "no reindeer feeding" stations. Paired one-tailed "Student's t" tests for a significant difference in mean log VSI at each instance (I through X in Fig. 3) proved all the differences significant at the 95 % level, with the exception of instance "V". Therefore it is clear that api through which reindeer fed had lower VSI than did api through which they did not feed.

The situation in instance "V" accompanied a major storm, characterized by gale winds, siqoq and warm temperatures. Several large pines, up to 70 cm dbh, were felled and numerous large branches broken; qali disappeared almost entirely.

By mid-January the deer had changed their activity in relation to feeding sites. They now had utilized the ideal api in the vicinity of stations 9 and 10 so thoroughly that almost all the api had been disturbed and recrystallized. They then deserted this area and shifted their feeding activities primarily to the western slope of Kotovaara. In mid-February they moved to the pine flats between the Station and the base of Rakitsa, later moving farther southwesterly

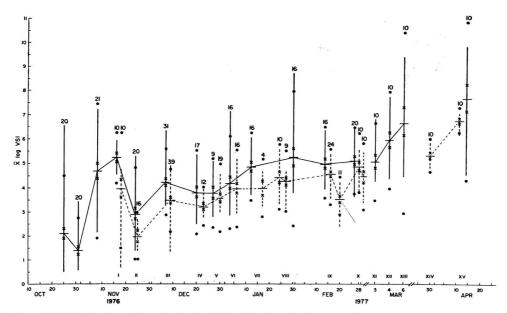


Fig. 3. Log VSI of both "reindeer feeding" (dashedlines) and "no reindeer feeding" (solid lines) stations. Vertical dashed or solid lines = ranges; horizontal bars = means; distance between black circles = \pm 2 SD; distance between x's = \pm 1 SE. Numbers above each instance signify numbers of api profiles examined.

onto the lower northeastern slopes of Värriö I and still later onto the northern slope, thence to the western slope in the upper birch zone and the alpine zone by mid-March.

In early March I set a series of profiles in a transect across the sequentially-deserted areas. Each transect consisted of 10 api-profiles taken 10 m apart, regardless of whether they fell in undisturbed spots or not.

In the area of Stations 9 and 10 the mean VSI of all 10 samples was 1.03×10^7 (instance "XI" in Fig. 3). Eight of the 10 samples fell in old craters; their mean VSI was 1.02×10^7 . The two samples that fell in undisturbed snow had an average VSI of 5.59×10^4 . Thus 80 % of the area was no longer suitable for the deer to feed.

In a similar transect taken on the western slope of Kotovaara after the deer had deserted it, all 10 samples fell in old craters and had a mean VSI of 9.124×10^6 (instance "XII" in Fig. 3).

Another transect through the now-deserted Station Pine Flats api had seven samples falling in old diggings, with a mean VSI of 1.022×10^9 . The three samples in undisturbed snow had a mean VSI of 4.59×10^4 . The mean VSI of all 10 samples was 7.16×10^8 (instance "XIII" in Fig. 3).

These data offer an explanation for this type of feeding activity that I had noted earlier (Pruitt 1959). When approximately 70 % of the api is disturbed by their own activity, the deer desert that area for another one. We should note that the area into which they now move may have api with *VSI* high enough that they previously had avoided it.

As the winter progresses the api "matures" or changes because of recrystallization from the bottom of the cover upwards. The speed and intensity of the upward expansion of the pukak layer is governed by 1) amount of heat and moisture flowing from the earth and 2) lack of heat and moisture in the supranivean air. The result is a decrease in hardness of the pukak layer. Moreover, hard layers or even sigulik in the lower half of the api are progressively eroded and softened. In the Värriö region this phenomenon had advanced sufficiently by 20 March to enable the deer to make čiegar and fies'ki in the previously-avoided api of the upper birch zone and the upsik of the alpine zone of Värriö I.

At Kapperapalo, near Nunnanen, where I made a field test of VSI, this phenomenon was strikingly evident. On 30 March the deer were using čiegar and fies'ki in the vicinity of the



Fig. 4. Fies'ki. Kapperapalo, near Nunnanen, Kyrö reindeer association. 30 March 1977.



Fig. 5. Čiegar. Kapperapalo, near Nunnanen, Kyrö reindeer district. 30 March 1977.

corral (Figs. 4 and 5). Earlier, in mid-winter, the api in this area had been subjected to severe trampling by several thousand deer undergoing roundup and separation. The api still had a hard basal layer, but the hardness varied from only 50 to a maximum of 1000 g cm⁻², with most stations in the neighbourhood of 300—500 g cm⁻². (Hardness of thoroughly trampled api is on the order of 1.0×10^9 g cm⁻²). I calculated the *VSI* of 10 sites in the walls of fies'ki to average 4.4×10^5 (instance "XIV" in Fig. 3). The maturation process clearly had been operating over the winter, eroding and softening the basal layer.

On 13 April the deer were still using this area, even though 80 % of it showed disturbance. Now, however, because of the recent, intense use the fies'ki were much harder. A 10-station transect showed a mean VSI of 7.22×10^8 (instance "XV" in Fig. 3).

The paradox was solved by closer examination of the actual feeding sites. All that I examined fit a general pattern — they were undercut beneath a hard surface trail (Fig. 6). Some were undercut a half metre from the vertical. These feeding sites had a mean VSI of 4.55×10^6 (instance "XV" in Fig. 3).

The pattern can be explained as follows. The trails, whether originally by snowmobile or rein-





Fig. 6. Modified fies'ki excavated under hard trail during Api modification Period. Kapperapalo, near Nunnanen, Kyrö reindeer association. 13 April 1977.

deer, had surface vertical hardnesses of several thousand g cm⁻². Deer did not excavate them. Thus even after prolonged use of the area there remained a series of strips of unused ground vegetation 70 to 90 cm wide and a total of many metres long, protected by the overlying very hard trails. The normal maturation of the api caused the pukak layer to expand vertically and, eventually, to soften the lower part of the hard trail sufficiently that deer could dig there. The pukak varied from 50 to a maximum of only 250 g cm⁻² hardness. Sometimes deer would excavate from both sides of the trail until the čiegar met, leaving the trail suspended unsupported in the air. Under these peculiar conditions the VSI did not model accurately the reindeer-api interactions because VSI encompasses the normal suface hardness relationships.

Table 1 presents my interpretation of the stages or "seasons" of the snowy portion of the year in relation to reindeer activity. The Värriö Snow Index (VSI) models all these relations except during the Api-maturation Period. Previous studies that have demonstrated close Rangifer-snow relationships have been on a grand geographic scale. The present study demonstrated relationships and interactions as well on a restricted geographic scale of about 15 km².

Acknowledgements. I am grateful to the universities of Oulu and Helsinki and to Professor Erkki Pulliainen for making available facilities at the University of Oulu and at Värriö Subarctic Research Station. I am grateful to Timo Helle and Dr. Erkki Lähde for making available facilities at the Rovaniemi Research Station of the Finnish Forestry Research Institute. I thank Kalevi Loisa, Martti Laitinen, Pertti Lehtinen, Pekka Ovaskainen and Jouko Iivanainen for many kindnesses and

Table 1. Stages or "seasons" of the snowy portion of the year in relation to Rangifer.

FALL CRITICAL PERIOD

- 1. Fluctuating api, possible nast' (Formozov 1946).
- 2. Intermittent use of suov'dnji.

PRE-THRESHOLD PERIOD

- Api less than threshold values for hardness, density or thickness.
- 2. Use of suov'dnji OR use of arboreal lichens.

THRESHOLD PERIOD(S)

- a) Hardness, density or thickness exceeding tolerance (not self-induced).
 - b) Searching for gradient and moving down gradient to suitable api.
- 2. Use of suov'dnji OR use of arboreal lichens.

SELF-INDUCED MOVEMENT PERIOD

- Ideal api has been hardened by suov'dnji excavation until it is beyond tolerance.
- 2. Deer leave region with previously-ideal api.

SUB-MARGINAL PERIOD

- Use of api that exceeds usual thresholds of hardness, density or thickness.
- 2. Use of čiegar and fies'ki.

API-MATURATION PERIOD

- Pukakization reduces hardness of basal layers sufficiently for deer to re-invade previously-deserted areas.
- 2. Re-use of čiegar and fies'ki; rare use of suov'dnji.

SPRING CRITICAL PERIOD

- 1. Possible nast' caused by sun and/or rain.
- 2. Use of bare south-facing slopes, bare qamaniq, bare a η ma η a.

assistance in the field. Oula Näkkäläjärvi of the Saami Institute, Kautokeino, Norway kindly provided Lappish names for certain reindeer-snow phenomena. I am indebted to Dr. N. Arnason for advice on the statistical treatment of the data. I am grateful to the University of Manitoba for a Sabbatical Leave Research Grant. Wolf Heck skilfully made the figures. I am indebted to Dr. R. E. Longton for a valuable critique of the manuscript.

References

Airola, H. & Pulliainen, E. 1975: Itäkaira — Koilliskairan kansallispuistosuunnitelman osa. (Summary: Itäkaira — part of the proposed Koilliskaira National Park). — Suomen Luonto 34: 157—162, 199.

157—162, 199.
Ваšепіпа, N. V. (Башенина, Н. В.) 1956: Влияние особенностей подснежного воздуха на расположение зимних гнезд полевок. — Zool. Žurnal 35:940—942.

Edwards, R. Y. 1956: Snow depth and ungulate abundance in the mountains of western Canada. —
J. Wildlife Managem. 20: 159—168.

Eriksson, O. 1976: Snöförhållandenas inverkan på renbetningen. — Meddel. Växtbiol. Inst. Uppsala, 1976 (2):19 pp + appendices.

1976 (2):19 pp + appendices.

Formozov, A. N. 1946: Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Moscow Soc. Naturalists, Mater. Fauna Flora USSR, N.S. (Zool.) 5:1—152. (English translation 1969: Boreal Inst., Univ. Alberta, Occas. Publ. 1:1—141).

Henshaw, J. 1968: The activities of the wintering caribou in northwestern Alaska in relation to weather

- and snow conditions. Int. J. Biometeorol. 12 (1):21—27.
- Kelsall, J. P. 1969: Structural adaptations of moose and deer for snow. J. Mammal. 50: 302—310.
- Kelsall, J. P. & Prescott, W. 1971: Moose and deer behaviour in snow in Fundy National Park, New Brunswick. — Canad. Wildl. Serv. Rep. Ser. 15:1—25.
- Miller, D. R. 1976: Biology of the Kaminuriak population of barren-ground caribou. Part 3: Taiga winter range relationships and diet. Canad. Wildl. Serv. Rep. Ser. 36:1—42.
- Nasimovič, А. А. (Насимович, А. А.) 1955: Роль режима снежного покрова в жизии копытных животных на территории СССР. Izd. Akad. Nauk USSR. Moscow. 402 pp.
- Penny, C. E. 1977: Subnivean accumulation of carbon dioxide and its effects on small mammals. Unpubl. M.Sc. thesis, University of Manitoba.
- Pruitt, W. O. 1957: Observations on the bioclimate of some taiga mammals. Arctic 10 (3):129—138.
- --> 1959: Snow as a factor in the winter ecology of the barren-ground caribou (Rangifer arcticus).
 -- Arctic 12 (3): 158-179.
- —»— 1960a: Behaviour of the barren-ground caribou.
 Biol. Papers Univ. Alaska 3:1—43.
- —»— 1960b: Animals in the snow. Scient. Amer. 202 (1):60—68.

- —»— 1966: Ecology of terrestrial mammals. In: Wilimovsky, N. J. & Wolfe, J. N. (eds.), Environment of the Cape Thompson region, Alaska: 519—564. USAEC, Div. Tech. Info. PNE—481.
- »— 1970: Some ecological aspects of snow. Proc. 1966 Helsinki Symp. "Ecology of the Subarctic regions". UNESCO series "Ecology and Conservation" 1: 83—99. Paris.
- Pulliainen, E. 1971: Helsingin yliopiston Värriön tutkimusasema. Luonnon Tutkija 5:160—164.
- —»— 1976: Birch forest damage caused by Oporinia autumnata Bkh. (Lep., Geometridae) in 1965—
 1966 in eastern Itäkaira, northeastern Lapland.
 Ann. Entomol. Fennici 42(4): 166—170.
- Salo, L. J. 1971: The last wilderness a sanctuary for wildlife research. — Look at Finland 6:46—50.
- Skogland, T. 1978: Characteristics of the snow cover and its relationship to wild mountain reindeer (Rangifer tarandus tarandus L.) feeding strategies. Arctic and Alpine Res. 10(3): 569—580.
- Stardom, R. R. P. 1975: Woodland caribou and snow conditions in southeast Manitoba. — Proc. Ist. Int. Reindeer-Caribou Symp. :324—334.
- Telfer, E. S. 1970: Winter habitat selection by moose and whitetailed deer. J. Wildl. Managem. 34:553—559.

Received 11. XI. 1979 Printed 29. I. 1980