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Map of East Greenland between Franz Joseph Fjord and Sabine Island, Plate 1.

PREFACE

When in the summer of 1931 I went to East Greenland as a member of the Danish Three-year Expedition under the leadership of Dr. LAUGE KOCH, an investigation of the ptarmigan and its food was not included in my working programme. However, as in the autumn of 1931 I had an opportunity of ascertaining how great an insight into the food biology of the ptarmigan might be gained through a systematic investigation of the contents of its crop, I decided as far as possible not to let the crop of even a single ptarmigan pass unnoticed. This decision I adhered to, but did not for that reason kill more ptarmigans than the need for variation in food required, or the rather fortuitous luck of the hunter, never very strenuously pursued, allowed. Later on I have regretted this from a purely scientific point of view, since a statistic material can hardly be too large.

Gradually as the working up of the material advanced, it became increasingly clear to me that a systematic analysis of the contents of the bird's crop would afford great opportunities, hitherto somewhat neglected, for gaining an understanding of the conditions under which the bird lives. Even the analyses made in Greenland convinced me of this, but at the same time I realised that I would have to study the literature on the subject and various conditions of which I had not so far had any great knowledge. On drawing upon the available information of the ptarmigan supplied by zoologists, especially the East Greenland ptarmigan, I have ventured into the field of zoology, but in doing so, I have gained an insight into the occurrence and life conditions of the ptarmigan in previous years. This has increased the volume of my paper. But zoology and botany have at the same time in many respects given valuable aid to each other.

A detailed study of what access the bird has to the various food substances affords an important insight into its ecology. This is not, as many might think, an exclusively zoologic, but in part, or even to a great extent, a botanical task. The ptarmigan, to be sure, is an animal, but it is principally a plant-eating animal. Only an investigator who has studied the vegetation, its relation to the climate and the soil, the snow-cover, etc., that is to say, preferably a botanist working ecologic-

ally, will therefore be able to give a description of its facilities for obtaining food at the different seasons of the year. The literature on the ptarmigan, especially that part of it which has reference to its food, shows this very clearly, for it is almost exclusively botanists who have furnished weighty contributions to the understanding of the nature of the food on which the ptarmigan subsists.

After the first crops had been examined and the first snow-cover had formed, it was evident to the present author that the snow-cover was a factor of the greatest importance for the ptarmigan's access to food. The connection between the variation in the food at the different seasons of the year and the snow-cover was easy to establish, since an investigation of the types of vegetation and their snow-cover in winter was one of the objects of the botanical investigation during the wintering. From the first moment my attention was directed towards this object, and as the examination of the crops proceeded along with the analyses of the vegetation and the remaining botanical work, the synthesis was initiated of which the present paper is the written expression.

In Greenland no doubt thousands of ptarmigans are killed every year, and in other countries probably much greater numbers. Nevertheless only 22 systematically analysed crops of ptarmigans are available from Norway, 18 from Spitsbergen, one or three from Taimyr, and with the present work two from the Arctic-American archipelago and 78 from Greenland.

If the present paper might contribute to an understanding of the valuable material represented by the ptarmigan crops, much would be gained. But the material can best be studied by the person who has killed the ptarmigans, and has made first-hand observations on the spot if there is to be a well-founded hope of arriving at a full understanding of the great extent to which the bird is, as it were, a function of its environment. In this way it will moreover be possible to obtain so thorough a knowledge of the requirements of the bird that the question of its possible domestication, and of artificially increasing its frequency by favouring the vegetation which will supply the food most adequate for it, may be discussed. The ptarmigan, which after the introduction of the currency restrictions is not easily admitted to the Danish market, might be obtained from Greenland; and to the population there, the Danish officials included, an increase in the frequency would not be without importance. Similar investigations are desirable as regards other plant-eating land vertebrates occurring in Greenland, for instance the musk-ox, the reindeer, the Arctic hare, the lemming, the smaller birds, and the plant-eating wading and swimming birds. These are to some extent the actual bearers of that part of the Greenland trade which is associated with the catching of land vertebrates, more especially the fox, whose skin secures to the Danish State a revenue of several hundred thousand Kroner (in the year 1936

about 400,000 Kroner). For the fox lives on these animals in addition to organic materials that have been washed up into the tidal zone and on to the shore.

The acknowledgments due for assistance of various kinds during the preparation and publication of the present work are numerous. To the leader of the expedition, Dr. LAUGE KOCH, I owe special thanks for his never failing interest and encouragement. Who could better than he have planned, equipped, and conducted the multifarious work of a natural-historic geographic nature carried out during the expedition? My thanks are also due to the other members of the expedition, the ever alert GUNNAR SEIDENFADEN, responsible for the equipment, cand. mag. HELGE LARSEN, of the National Museum, the zoologists ALWIN PEDERSEN and mag. scient. HOLGER MADSEN, and Mr. ARNE SCHWARCK, all of whom have killed and handed over to me a number of the ptarmigans investigated. HELGE LARSEN likewise assisted me in sorting the contents of the crops.

Special thanks are due to the leader of the Plant-Physiological Laboratory of the University, Professor P. BOYSEN JENSEN, Ph. D., and the then assistant, the present Professor in the Agricultural College Dr. DITLEV MÜLLER; to the former, for the readiness with which he placed the facilities of the laboratory and his personal insight at my disposal during the physiological investigation of the food elements of the ptarmigan, to both of them for their never failing interest, encouragement, and advice during my work.

I further desire to tender cordial thanks to Professor KNUD JESSEN, Ph. D., and Professor AUG. KROGH, Ph. D., for the interest they have taken in my work as it progressed.

Mag. scient. FINN SALOMONSEN supplied me with valuable data concerning the systematics of the Greenland ptarmigans. Dr. KAJ L. HENRIKSEN, Dr. R. SPÄRCK, and mag. scient. S. R. TUXEN have determined the insects found in the crops. Mag. scient. R. HÖRRING, Keeper of the Zoological Museum, and Dr. O. HAGERUP, have allowed me to examine the ptarmigans from Danske Island. Mr. HELGE PETERSEN, state meteorologist, has given me certain particulars concerning the climate of East Greenland, and members of the scientific staff of the Astronomic Observatory of the University, notably Mr. A. MÖLLER, has supplied me with information concerning the illumination in the winter. To all of these gentlemen I express my cordial thanks for their help.

I am likewise indebted to Dr. K. GRAM, who kindly photographed the food elements in the ptarmigan crops brought home by me.

Copenhagen, June 1936.

INTRODUCTION

Nakatogak or Mitigak, i. e. "he at whom stones are thrown", is, according to HELMS (1926), the name by which the East Greenlanders designate the ptarmigan. On the west coast of Greenland, according to FABRICIUS (1780), the terms Akeiksek or Kauio are used, both perhaps derived from the calls of the ptarmigan. These Eskimo terms are the earliest names on record for the Greenland ptarmigan. No doubt they have been employed for centuries to denote the bird which, perhaps, was not appreciated particularly, and which could be secured merely by throwing stones, but whose intestines with their content of vegetable matter are even at the present day stated to be a delicacy much coveted by many Greenlanders. Judging from the wealth of ptarmigan images, cut in wood or tooth by the grown-up Eskimos, and excavated by archaeologists from the house ruins (cf. RICHTER, 1934, LARSEN, 1934, GLOB, 1935), it may be assumed that the ptarmigan has played a prominent part in the imagination of the East Greenland Eskimo children. Eskimo legends are associated with the ptarmigan, and skeletal fragments of the bird occur among other bones in the house ruins (DEGERBØL apud GLOB, 1935, pp. 94—96).

Wherever expeditions have pushed towards the pole, except on Novaya Zemlya, they have observed the ptarmigan, one of the birds found farthest north in the winter. The genus *Lagopus* is widely distributed along the Polar Sea, and within the genus the species *Lagopus mutus* is the one found farthest north. In more southerly regions ptarmigans related to it occur at high mountain levels. Much would seem to indicate that the area of the species has previously, probably during the Ice Age, been more continuous. Bones of ptarmigans (*L. mutus*) from the tundra age have been found in Denmark (WINGE apud LEHN SCHIÖLER, 1926). The post-glacial changes in climate split up its area as it followed the receding ice-edge towards the north, leaving enclaves in high mountain regions. Whether the species has been able to subsist in the ice-free refuges which are known to have existed at any rate during the latest

glaciation in Scandinavia, in Greenland, and in North America, is not known, but it would not, at the outset, seem to be improbable. If it survived the latest glaciation in one or several of these non-glaciated areas, its area during the Ice Age must have been more split up towards the north than it is at the present time, while its area towards the south must then have been more continuous than at the present time.



Gelting phot. April 3, 1932.

Fig. 1. Male ptarmigan in winter plumage. Granatdal, Clavering Island.

In "Vögel der paläarktischen Fauna" HARTERT (1910—23) records the following forms of ptarmigans:

Lagopus mutus mutus MONTIN, Norwegian mountain regions southward to 58° N. lat., Sweden southward to Dalarne, Russia (including Finland) from the Arctic Sea to 66° N. lat. in Lapland, and to 61° N. lat. in Ural.

Lagopus mutus helveticus THIENEM., throughout the area of the Alps down to 1700 m above sea-level in the summer and 1400 m in the winter.

Lagopus mutus cinereus MACG., mountains of Scotland, including the Inner Hebrides (Mull, Islay, Jura, and Skye).

Lagopus mutus pyrenaicus HARTERT, the Pyrenees down to 2000 m above sea-level.

Lagopus mutus hyperboreus SUND., Spitsbergen and Franz Joseph Land.

Lagopus mutus islandorum FABER, Iceland.

Lagopus mutus reinhardti BREHM, Greenland.

Lagopus mutus rupestris GMELIN, the Barren Grounds of North America from Labrador to Alaska, the Aleutian Islands and Sitka, and to the south on the mountains round the middle course of the Yukon, in the Rocky Mountains and the mountains of New Foundland.

Lagopus mutus Ridgwayii STEJNEGER, the Bering and Copper (Commander) Islands.

Lagopus mutus japonicus CLARK, the high mountains of Hondo (Japan).

Forms of *Lagopus* further occur along the Arctic coast of Siberia and on the mountains south thereof as far as Kamtschatka, on Verchokjansk, Alazeia, Altai, Baikal, Taskhajatag, and the Tarbagatai Mountains (cf. HARTERT l. c.).

Many American authors (cf. HARTERT l. c.), however, segregate several more races and forms within the North American *Lagopus mutus* group and as regards Greenland I have followed SALOMONSEN'S work from 1936 (cf. p. 48).

The total area of the *Lagopus mutus* races is of special interest; it shows that the species is arctic-circumpolar with isolated enclaves in the highlands of the temperate zones, an area which it has in common with many of the so-called arctic-alpine species.

WINGE (1898) is of opinion that the species existed as early as in Tertiary times, and presumes that it has been ousted from the high-arctic regions during the Quaternary Epoch. While no arguments have later been set forth which speak against the high age presumed by WINGE, we dare hardly at the present time give a definite opinion as to whether the species was actually in Quaternary times ousted from the non-glaciated areas which are known to have existed, for instance in the North American archipelago, during the Ice Age. Both the ptarmigan, the reindeer, the ermine, the lemming, and the musk-ox seem to have centres of distribution there, and the possibility can hardly be rejected that all or some of these animals may have survived, at any rate the latest ice age, in these regions. These animals are furthermore among those which at the present time live farthest north even in the winter. If the lemming, as assumed by EKMAN (1922), has survived the latest ice age in the non-glaciated areas of Norway, it seems very probable that the ptarmigan, too, has done so, and the possibilities of the two species having survived the Ice Age in the non-glaciated areas of North America do not seem any slighter.

BRIEF TOPOGRAPHIC-GEOLOGICAL SURVEY

The stretch of the ice-free coastal area to be discussed here is orographically a plateau, whose geological age will not be dealt with here. The plateau-like character of the country appears even from the topographical maps and has, as regards the northern parts, been described by J. P. KOCH (1916, pp. 438—39). The plateau was probably even before the Ice Age subjected to water erosion and tectonic disturbances, by which the valley systems received their first shape. This modelling of the valleys continued during the strong glacier erosion of the Ice Age, and the plateau-like character was thereby somewhat effaced, especially along the outer coast, where the valley beds are broadest and where also the late- or post-glacial transgressions caused large parts of the plateau to be worn down. The late- or post-glacial abrasion planes rose during a subsequent post-glacial regression, and at the present time accompany the eastern edge of the outer coast in the form of flat and extensive forelands (Wollaston Foreland, the foreland in the eastern part of Clavering Island, Homes Foreland, and the forelands of Hold-with-Hope and Badland Valley).

A glance at BACKLUND'S, KOCH'S, and SEIDENFADEN'S map (SEIDENFADEN, 1931) (see also pl. 1) will give a comparatively good idea of the land forms. Farthest westward, at the edge of the inland ice, the ancient plateau surface is most distinctly seen and most coherent, the valleys cut into the plateau being narrowest here. The plateau surfaces stand at an altitude of from 1300 m to 1500 m above sea-level. To the west the plateau is covered with ice, while to the east it is free from ice over wide areas. In the valleys the large glaciers issuing from the inland ice descend to the heads of the fjords (Wordie Glacier, Waltershausen Glacier). Here in the inner fjord district the average height is greatest. The edges of the plateaus are but exceptionally associated with narrow, low-lying forelands, and as a rule rise very steeply from the narrow fjords to altitudes of nearly 1300 m, where the plateau surface generally commences (Geolog Fjord, Granta Fjord, Tyroler Fjord).

Farther east, in the outer fjords, the differentiation between the high-lying plateau surface and the flat forelands is less marked. The valleys are broader and less steep, the slopes of the plateau rise gradually and are easy to climb (the west side of Clavering Island, Loch Fyne, Musk-ox Fjord). The ancient plateau surface, however, is distinctly traceable at levels of about or over 1000 m. At these levels the mountains are more or less flat-topped or have plateau-like "shoulders" (Halle Mountains and the "1000 m Plateau", the "Jernhatten", and "Pladen" on Clavering Island, Stensiö Plateau, Spath Plateau, the Giesecke Moun-



Gelting phot. Aug. 25, 1933

Fig. 2. Plateau surface (1300—1500 m above sea-level) partially covered by highland ice. Payer Land.

tains). As in the outer fjords, the plateau surfaces are less extensive and the valleys broader than in the inner fjords; the average height is correspondingly smaller.

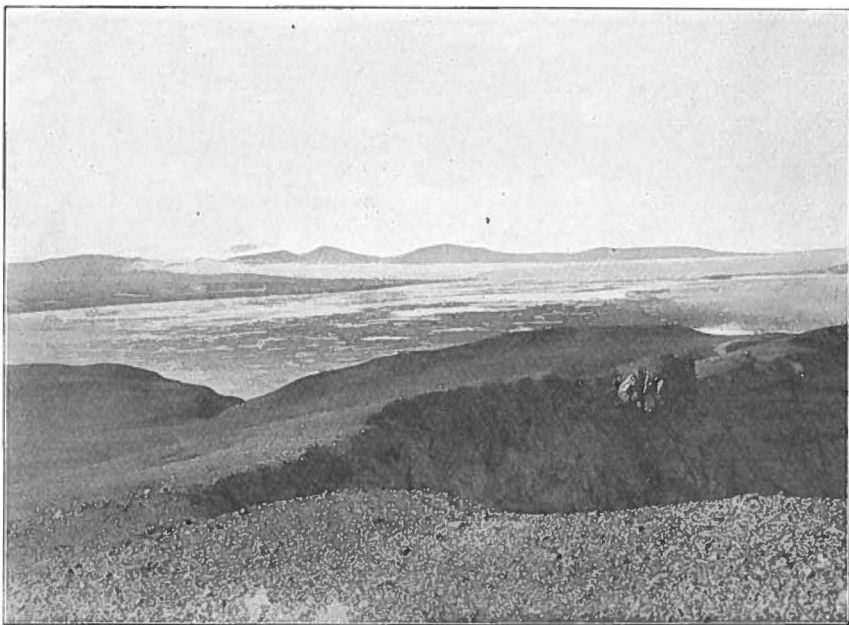
At the outer coast the ancient plateau has in most places more or less disappeared. Here extensive lowlands are found, or the coast rises very slowly to the ancient plateau heights, small remnants of which are found here and there on the flat tops of the isolated mountains (Mt. Saddle, Mt. Brinkley, Mt. Rundetaarn (800 m), the higher mountains of Hold-with-Hope).

Thus the plateau surface attains its greatest altitudes to the west, where it is most continuous, while to the east large parts of it

have entirely disappeared and have been replaced by or converted into extensive low forelands. Thus the mean altitude is slight at the outer coast and considerable near the edge of the inland ice.

The geological conditions will not be discussed in detail here, but as they are not without importance for the ptarmigan's choice of a breeding place, a brief description will be given of the geologic-topographical conditions on Clavering Island, which is the best investigated locality as regards the occurrence of ptarmigans.

The lands west of Clavering Island, viz. Payer Land, Manley Land,

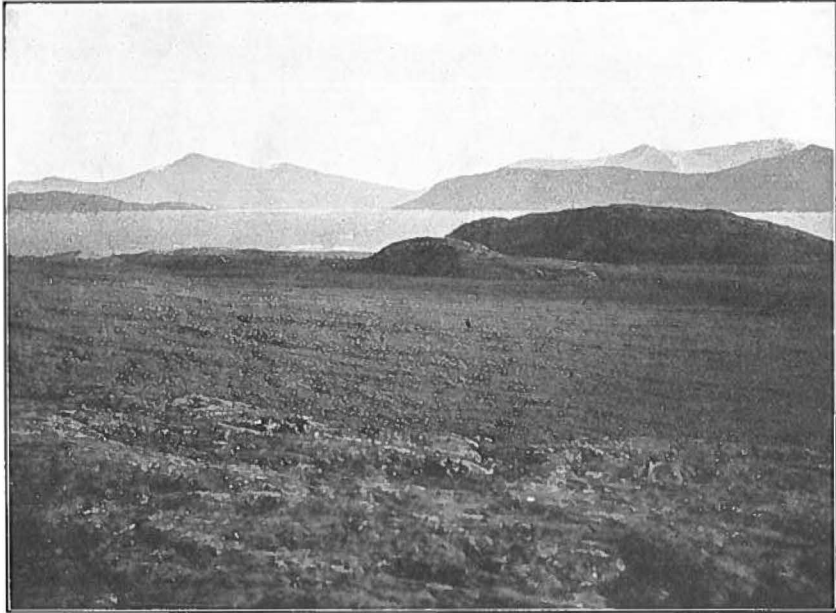


Seidenfaden phot. August 1934.

Fig. 3. Outer coast of Hold-with-Hope. Looking north from Cape Broer Ruys. To the right Holland Island. A bank of fog is approaching the coast.

and Courtauld Land, are chiefly built up of solid crystalline rocks (gneiss), which form the plateau surface. East of this area of crystalline rocks there occurs a depression in them filled up by Carboniferous sediments, sandstones and limestones with intercalated basalt intrusions and overlying basalt sheets of Tertiary age. However, the basalt is of subordinate importance. Thus Halle Mountains and Mt. Bramsen are beautifully stratified, consisting of Carboniferous limestones and sandstones with intercalated basalt intrusions. On account of the operation of the frost on the easily splitting rocks the traces of glacier erosion within this western area of Clavering Island are somewhat effaced; thrust and lee sides in the solid rocks are less conspicuous.

The central part of Clavering Island, the Central Plateau, consists of gneiss, which in the middle of the island reaches the plateau surface. From sea-level to about 1000 m above, the gneiss projects everywhere from the loose deposits. At 1000 m altitude it is overlain, locally by one or more Tertiary basalt sheets, which, however, at the present time are much worn by water and glacier erosion and often merely occur as cairn- or helmet-shaped erosion remnants. The surface of the solid rock consists mostly of a hard, highly metamorphosed,



Gelting phot. Aug. 18, 1932.

Fig. 4. Domes of crystalline rocks (raised skerries) at Eskimonæs. In the foreground an inland delta, in the background, left, a raised marine terrace.

crystalline schist, whose original stratification, however, is often distinctly traceable, particularly in the original sandstone areas now metamorphosed into coarse-grained quartzites.

The gneissic rocks are much dissected; deep ravines, crevices, and minor cracks and clefts are common phenomena. The ground is much broken, the form characteristic of crystalline rocks, and, at any rate at lower levels, scoured out by intense glacier erosion. Since the land, after being ice-covered, has been subjected to a transgression reaching some hundred metres above the present sea-level, marine deposits occur at the present day up to great altitudes, and the horizontal marine terraces set their mark on the scenery. The gently sloping mountain sides are terraced. Where the erosion terraces are interrupted for shorter or longer

stretches, they are often replaced by well preserved accumulation terraces, which are especially common in depressions in the surface of the crystalline rocks and, at lower levels, near the shore (see for instance the background in fig. 8, p. 30).

The region round Eskimonæs may justly be described as raised skerries, though they cover but a small area. The raised skerries of crystalline rocks, which are connected by raised marine plains and terraces, exhibit beautiful thrust and lee sides (cf. fig. 4); this applies to the whole gneiss surface up to a certain altitude above sea-level.

A narrow foreland extends along the coast. At Granatdal the foreland is 3—4 km broad, near Eskimonæs about 1 km, while farther eastward it is almost or entirely absent. The raised skerries of the foreland rarely attain an altitude of more than 100 m above sea-level. From the narrow foreland the surface of the crystalline rocks rises gradually to the edge of the plateau, which occurs 3—10 km inland. The latter is sculptured out into more or less isolated peaks standing at altitudes of 1100—1300 m. The Central Plateau in the middle of the island attains an altitude of about 1500 m above sea-level. The plateau surface is covered by immense fields of basalt blocks originating from the disintegrated basalt sheets. As monuments of the latter, isolated erosion remnants rise above the block fields. Otherwise block fields occur at lower levels, chiefly along the base of the ravines only, or in the inland deltas of the rivers. Thinner strewings of blocks of glacial origin occur chiefly on the polished thrust sides of the gneiss domes. The central highland ice of the island lies on the plateaus above 1000 m altitude.

The loose soils, which occur especially in the depressions between the gneiss domes, doubtless to a great extent consist of original moraine material (as indicated by the erratic boulders), but on account of the transgression they have been redeposited in marine accumulation terraces and by the rivers in fluvial deposits.

On the east the central gneiss area of Clavering Island is bounded by several fault lines, east of which the land is lower and chiefly built up of Tertiary basalt, which dominates the landscape in the form of intrusions into sediments of Mesozoic and in part also Permian age, and as sills and dykes, the basalt usually exceeding in thickness the sedimentary formations, which consist of calcareous clay and sandstones. In addition loose Tertiary sediments occur.

In the basaltic country also the glacial polish is not well preserved. Sharp-edged dykes and sills alternating with sharp-edged block fields and marine deposits form the surface of the ground.

On Wollaston Foreland and the outer coast of Hold-with-Hope, whence some of the ptarmigans are derived, extensive lowlands rest on a basaltic substratum. The region of Hold-with-Hope round Knuds-

hoved must be termed a low plateau, whose surface ranges from 70 to 300 m above sea-level.

For geological details and more exhaustive geological surveys the reader is referred to BACKLUND (1930; 1931, 1 and 2; 1932), BACKLUND and MALMQVIST (1932, 1935), LAUGE KOCH (1929, 1931), KULLING (1930), MALMQVIST (1932), EIGIL NIELSEN (1935), NOE-NYGAARD and SÄVE-SÖDERBERGH (1932), TEICHERT (1933), and WHITTARD and PARKINSON (1931). A map of the area, based on recent triangulations, is under preparation by the Geodetic Institute, Copenhagen.

BRIEF METEOROLOGICAL SURVEY

Since meteorological investigations for a series of years are not available from other stations within the area than Myggbukta, it is difficult to give a satisfactory description of the climatic conditions, which is very deplorable, since, as far as can be judged from the vegetation and what climatic phenomena have otherwise been observed by travellers in the region, we are here concerned with an area within which the climate varies considerably from place to place, and where there is a great climatic difference between the land round the heads of the fjords and the outer coast.

At Myggbukta the Geophysic Institute of Tromsø has for a series of years run a meteorologic station, and even though it has not been worked by experts, and for several periods no observations were made, the staff of the station having had to attend to the often remote fox-traps, we must be grateful for the work that has been done there.

On account of the varying meteorological conditions the observations from Myggbukta cannot be taken as a general example of the East Greenland climate in that latitude; however, as long as observations have not been made at other stations within the area, the observations from Myggbukta are most valuable as a basis for a judgment of conditions as a whole. Below I shall briefly record some main lines of the observations made at Myggbukta during a period of ten years, from 1922 to 1932, after BIRKELAND and SCHOU (1932), and point out the deviations from these which, from our present knowledge of the conditions, though it is not based on measurements, may be expected to be found inland.

The atmospheric pressure is high, the annual average being 760.7 mm. It is highest in the month of May, 766.2 mm, lowest in December, 756.3 mm.

The winds in summer are chiefly southeasterly. (This may be a local phenomenon at Myggbukta and due to the position of the station in Badland Valley. In the fjords extending east-and-west there is thus in the summer a regular change from westerly land-winds to easterly

sea-winds.) In the winter northerly and northwesterly winds prevail. Winds from the southwest are exceedingly rare. Storms are rare, most frequently they blow from the northwest and northeast. (Myggbukta is sheltered from storms from the north.) The winds from the northwest nearly always have the character of warm dry winds (foehn winds).

The temperature and precipitation will appear from table 1 and fig. 5, compiled after BIRKELAND and SCHOU (l. c.):

Table 1.

Month	1	2	3	4	5	6	7	8	9	10	11	12	Year
Mean temperature C°	-20.3	-21.4	-20.9	-16.4	-7.0	0.4	3.7	3.0	-2.5	-9.7	-15.6	-18.9	-10.5
Precipitation (mm.)	4.6	10.6	5.3	4.1	1.2	6.3	11.8	10.8	1.3	4.5	11.1	6.0	77.6

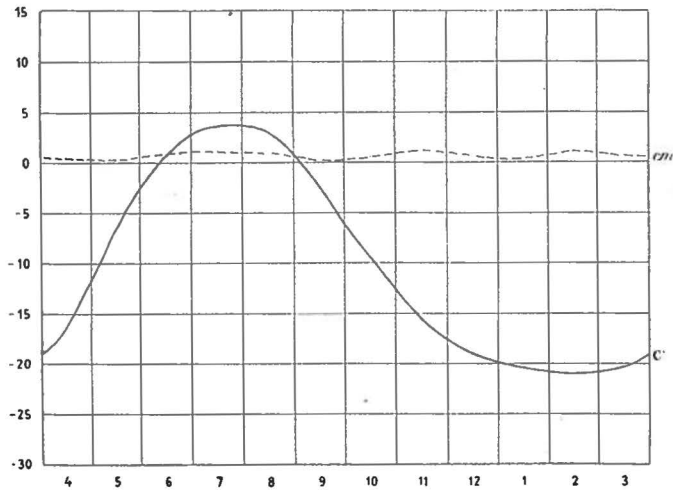


Fig. 5. Hydrotherm figure for Myggbukta. Temperature in C°, precipitation in cm.

During the first half of June the temperature curve passes zero and remains above this until the beginning of September. The warmest month is July with 3.7° C., the coldest month February with 21.4° C. below zero. The absolute summer maximum is 22.8° C. (July 25, 1929), the absolute winter minimum is 45.5° C. below zero (January 4, 1927). Northerly or northwesterly winds in the summer may cause a sudden temperature change of up to more than twenty degrees. The number of days with negative temperatures was 309. July showed seven days with negative temperatures.

The precipitation is inconsiderable, according to the incomplete measurements 77.6 mm annually. The greater part of it comes down in the form of snow, the 82 days with precipitation comprising 67 snowy days and 17 rainy days; on two days annually, on an average, it both rains and snows. During six years it snowed only once in the month of July. In 30 of the aforesaid 82 days the precipitation was less than 0.1 mm. Hail was observed once, while thunder has never been heard.

It should, however, be pointed out, as done by HELGE PETERSEN (1935), that the measurements of the precipitation at Myggbukta do not show any great agreement with the amounts of precipitation and annual course that might be expected on the basis of measurements in Scoresby Sound and at Danmarkshavn. PETERSEN (l. c.) points out that the precipitation at the Danish hunting stations Sandodden and Germaniahavn is > 199 mm. Thus the precipitation at Myggbukta is possibly affected by the local conditions.

The number of cloudless days is very considerable, viz. 93 annually. The number of days with an overcast sky is 102, that is, rather low. In the winter there hardly occurs one foggy day, whereas in the summer there are 6—7 every month. The amount of cloud is slight, only averaging 52 per cent., being highest in the summer (60 per cent.) and lowest in the winter (50 per cent.).

The relative humidity of the air is slight, the annual average about 70 per cent. In the summer it may increase to 100 per cent., but may also fall to 24 per cent. while the foehn winds prevail.

If it is borne in mind that Myggbukta is situated at the outer coast, and that WEGENER's measurements at Danmarkshavn and at Pustervig situated west thereof show with certainty, and all other observations confirm, that the climate is increasingly continental towards the interior of the fjords, the observations made at Myggbukta are of interest for an understanding of the continental character of the East Greenland fjord climate. In the fjords the precipitation must be assumed to be slighter, the summer temperature higher and the winter temperature lower, the number of foggy days lower, and the amount of cloud slighter. NORDENSKIÖLD (1916) as well as several of the botanists that have worked in Greenland (WARMING (1888), ROSENINGE (1896), HARTZ (1896), KRUSE (1912), PORSILD (1935), SEIDENFADEN (1933), LYNGE (1932), BÖCHER (1933), SØRENSEN (1933), and GELTING (1934)) have called attention to this general fact.

As to the summer temperature it is not known how much higher it is in the fjords than at the outer coast, but the measurements by TH. SØRENSEN (1933) for the summer of 1932 indicate that it may be fairly high. The vegetation and the biological conditions are indicative hereof, for instance

the degree of lignification and the thickness of the lignified parts of the woody plants (cf. KRAUS 1874).

For the surface water of the fjords, too, the higher summer temperature of the interior is of importance. According to SPÄRCK (1933, p. 19 ff.) the layer of warm surface water is thickest in the inner fjords (in Kjerulf Fjord and Musk-ox Fjord up to 25 m), and the temperature of the surface water is highest at the heads of the fjords. Plate 3 in the paper cited is exceedingly instructive. Analogous conditions were observed by THORSON and USSING (THORSON, 1934) in Scoresby Sound. The occurrence of certain boreo-arctic molluscs in the inner fjords (e. g. *Pecten islandicus*) shows unmistakably the ecological importance of the warm surface water.

Finally the rise of the snow-line towards the heads of the fjords (cf. GELTING, 1934, 1936) must be correlated with the hotter summer and slighter precipitation inland.

The wind conditions must be assumed to be of very great importance for the continentality, which increases with the distance from the outer coast. Here the measurements from a single station cannot be taken as a general example, since the wind conditions are to a great extent influenced by the trend of the fjords. Certain general features can, however, be pointed out on the basis of observations on the wind conditions in the different areas. The reader is otherwise referred to the meteorological observations made by the Danmark Expedition (ALFRED WEGENER 1912), and by HELGE PETERSEN (1934, 1935) and FRITZ LOEWE (1935).

While winds from the north, often of great violence, are common along the outer coast at any rate in the winter, winds from the north-western quarter are very frequent in the fjords at all seasons of the year. It is common to all these winds that they are dry — the north wind, however, being the least dry — but they differ greatly as regards violence and temperature, similarly as they may originate in very different ways.

The weather conditions of the Greenland coast lands are dominated by the exchanges which take place between the polar air over the inland ice and the oceanic air over the surrounding seas. The westerly winds of the east coast, which owing to the gradient system of the inland ice and the surrounding seas descend to sea-level at the heads of the fjords, must be very dry on account of the descent. If, however, Atlantic air masses make their way across the inland ice, where they give off precipitation during their ascent, their temperature will be exceedingly high in view of their immediate geographical position. If these air masses are forced back over the coast land, they will be further heated dynamically, and on reaching sea-level they will show a very high temperature and

an extremely slight relative humidity. It is these winds that are termed foehn winds. HELGE PETERSEN (1934) has shown that such air masses can descend in the form of foehn winds either on the same side of the inland ice on which they ascended, or on the opposite side, and by means of DE QUERVAIN's observations on the inland ice in 1912 he has been able (PETERSEN 1935) to trace the dynamic temperature changes of the air masses during their passage across the inland ice from Angmagssalik to Jacobshavn.

Foehn winds are of common occurrence in Northeast Greenland, but as their warm and dry condition is directly proportional to the amount of their fall, it will be understood that the mountain levels are not exposed to them to the same extent as the lowlands.

On their way from the heads of the fjords to the outer coast the direction of the foehn winds is horizontal, and their special character is therefore somewhat weakened owing to exchange with the surrounding air masses. Consequently the outer coast will not be exposed to them in their full intensity.

Of quite a different character are the fall winds blowing down from the inland ice, which in their typical form are dry and cold. They are caused by a cooling of the air masses occurring immediately above the surface of the inland ice, which consequently descend towards the edge of the inland ice. If the fall winds blow with great intensity, they may force their way towards the east and follow the fjords for a shorter or longer distance, sometimes right out to the outer coast. Fall winds also are the cause of the driving snow in the winter so frequently met with on the inland ice and described by most travellers; however, similarly as the fall winds may make their way out along the fjords, the driving snow can sometimes be traced right out to the mouths of the fjords.

In the summer dry fall winds often alternate with humid sea-winds with astounding regularity. Owing to the cold of the night the fall winds will blow in the early morning, but will in the course of the forenoon be replaced by sea-winds blowing from the east. The sea-winds often carry fog, especially in the spring, but it rarely pushes very far beyond the mouths of the fjords. BIRKELAND and SCHOU (l. c.) state that the number of foggy days at Myggbukta is but small. At Eskimonæs it is smaller still, and west of this point fog is a rare phenomenon. The great frequency of southeasterly winds at Myggbukta during the summer must be due to its position in the outer coast district where the sea-winds are of common occurrence, whereas "fjord winds" rarely reach so far. Eskimonæs is situated in the zone in which the change of the wind is particularly remarkable. Practically only winds from the

west or from the east are known in this place. Farther into the fjords westerly winds prevail.

The importance of the fall winds may be briefly stated to be that they keep the humid easterly winds away from the inland, and the effect of the foehn winds in addition that they have a heating influence. Both wind systems are dry. In a very narrow zone of the coast only the east wind sets an oceanic mark on the climate.

Another factor contributing to the continental character of the climate of the whole area is the pack-ice belt, which girdles the coast as a low "foreland of ice" (WEGMANN 1935).

Thus both the inland ice in the west and the pack-ice in the east contribute to the continental climate of the ice-free coast land.

THE VEGETATION

Introduction.

As a result of the difference in the climate of the outer coast and the inner fjord districts, the difference in the vegetation of these two areas, too, is great. This is reflected not only in the flora lists of the areas, but to an even greater extent in the vegetation. The outer fjords occupy an intermediate position, and as they form a transitional area, their number of species is the highest, representatives of both the inner fjord and the outer coast floras occurring here. The vegetation of the inner fjords is of an extremely xerically marked character, being mostly dominated by xerophilous species, whereas the vegetation of the outer coast is marked by the moisture of the ground, being mostly dominated by more or less typical hygrophytes. As a consequence of the warm summer climate of the inner fjords, their flora includes an element of southern species, to whose frequency, however, the drought often puts a limit. The more or less oceanically characterised species, in particular, show a sharp and sudden limit towards the dry inland climate, or they are here associated with damper soil than in the outer districts. On account of the usually minimal moisture of the soil and the slight humidity of the air in the inner fjords, and more especially the desiccating effects of the foehn winds on the above-ground organs of the plants, a general tendency to associate with a deeper snow-cover than at the outer coast is traceable in a very large number of hygrophytes and the communities formed by these (cf. TH. SØRENSEN, 1933, pp. 6—11, and GELTING, 1934, pp. 235—36).

In the winter, on travelling from the inner fjords towards the outer coast, one will note that the snow-free vegetation of the dry heaths of the inner fjords is gradually replaced by less xerically marked vegetation types, and at the same time there emerge from the snow-cover types of vegetation which are never seen in the inner fjords, and some of these vegetation types turn out to be entirely or partially free of snow at the outer coast during the winter. The same tendency may be observed if one climbs a mountain in the winter. Not only is the moisture of the soil

greater at the mountain levels and at the outer coast, but the vegetation period, too, is both shorter and colder than in the lowlands of the inner fjords. This factor, also, contributes to confine the plant communities to more or less snow-free soil in the mountains and at the outer coast.

On account of the snow-covering in the winter, access to the vegetation is considerably reduced during that season. As will be shown below, the food of the ptarmigan illustrates this fact; in the summer it consists mainly of snow-patch plants, in the winter mainly of species growing in soil free from snow.

In the Scandinavian plant-geographical literature snow-patch denotes the same as is expressed by "Schneethalchen" in Central Europe, especially in the Alps; and any patch which owing to its relatively deep or prolonged snow-cover becomes free of snow so late in the year that this gives the vegetation a distinctive stamp, may practically be defined as a snow-patch. As is well known, the snow-patch vegetation is often of a hygrophilous or seasonally hygrophilous character on account of the moisture due to the melting snow. Another ecologic factor is the protective effect of the snow-cover against cold as well as against desiccation. Morphologically the snow-patch plants are often distinguished by their small size, biologically by their short prefloration period, and phenologically — on account of the prolonged snow-covering — by their comparatively late development.

Plant communities constantly covered by snow during the winter are abundantly represented at Eskimonæs, thus for instance dwarf-shrub heaths such as the *Vaccinium uliginosum* heath and the *Cassiope tetragona* heath. But only in places with a deeper and more prolonged snow-cover than that of the *Cassiope* heath, will the snow-patch vegetation proper, in the sense used below, appear.

On the basis of the lignification and the systematic position of the dominating plant species it is possible to distinguish between various forms of snow-patch vegetation, viz:

- Snow-patches rich in dwarf-shrubs.
- Snow-patches rich in herbaceous plants,
- Snow-patches rich in cryptogams.

Ecologically, however, they are rather closely related. The snow-cover is thickest in the cryptogam snow-patches, thinnest in the dwarf-shrub snow-patches.

Of the dwarf-shrub snow-patches, those rich in *Salix arctica* are the commonest. The dry *Salix arctica* snow-patches constitute the ecological connecting link with the less snow-covered dry *Cassiope tetragona* and *Vaccinium* heaths; the damp *Salix arctica* snow-patches are very rich in herbs and form the ecological connecting link with the more snow-

covered herb snow-patches. Rich in herbs are also the *Salix herbacea* and *Cassiope hypnoides* snow-patches, which, as a rule, on account of their favourable exposure do not become free of snow at a later date than the *Salix arctica* snow-patches.

Various forms of typical herb snow-patches occur. They may be dominated by one or more of the following species: *Carex rigida*, *Eriogonum unalaschkensis*, *Festuca rubra*, *Luzula confusa*, *Oxyria digyna*, *Phippsia algida*, *Ranunculus pygmaeus*, *Saxifraga cernua*, and *Trisetum spicatum*. Among the dominating species there occur numerous other herbs, less conspicuous on account of the greater distance between the individuals, but still characteristic of the snow-patches, viz.: *Carex Lachenalii*, *Draba alpina*, *D. oblongata*, *Minuartia biflora*, *Ranunculus sulphureus*, *R. nivalis*, *Saxifraga nivalis* (incl. *tenuis*), *S. rivularis*, *S. stellaris* var. *comosa*, and *Taraxacum arcticum*.

Associated with certain southwardly exposed snow-patches there further frequently occurs a more or less stereotypic company of species which can hardly be designated actual snow-patch plants, inasmuch as their habitat is but sparsely covered with snow, but is irrigated by the water coming from the melting snow-patches. These species are thus distinguished from the typical snow-patch plants by being associated with a more scanty snow-covering, but are alike in that they occur on damp soil. On account of their association with the areas immediately surrounding the snow-patches, several of these species often form part of the summer food of the ptarmigan. Of these species the following may be mentioned here: *Carex capillaris*, *C. scirpoidea*, *Draba daurica* v. *rustriiformis*, *Luzula spicata*, and *Potentilla Crantzii*.

In the snow-patches rich in herbaceous plants *Polygonum viviparum* is often present in large numbers; but the species is especially numerous in the *Salix arctica* snow-patches, if their exposure is favourable and the moisture suitable. Nowhere does the species attain a greater density of individuals and a greater luxuriance than in the *Salix arctica* snow-patches, which have a favourable exposure and presumably also contain some nitrogen.

Various forms of cryptogam snow-patches occur, dominated either by mosses (especially *Polytrichum*), liverworts, or algæ. However, none of these communities seem to serve as feeding grounds for the ptarmigan.

On soil free of snow in the winter the ecology and accordingly the vegetation are quite different. The species are exposed to the winter cold in its full intensity, and to the effects of the wind. The forming of dense tufts or low espaliers is a morphologically common feature of many plants growing on such soil. The prefloration period on snow-free soil cannot be determined without detailed physiological experiments, but must be presumed to be fairly long. However, the plants will finish their

development early, which (cf. p. 154) may be due to some extent to their ability to benefit by the insolation.

It may therefore seem justifiable to assume that the physiological processes in the plants, and accordingly their content of organic substances and salts, are rather different on snow-free and on deeply snow-covered soil.

Within the areas free of snow in the winter the ecology of the plant species, however, will differ considerably on damp and on dry soil; damp soil is commonest at the outer coast, while dry soil is commonest in the fjords.

Of the plant communities free of snow in the winter it seems, in addition to the *Salix* growths of the outer coast, to be the *Saxifraga oppositifolia* communities and the different forms of *Dryas* heath which supply important contributions to the food of the ptarmigan. The chief characteristics of the areas of dominance of these two species and other species of significance to the ptarmigan will appear from the following.

Ecological conditions in the areas of dominance of the species most important to the ptarmigan.

Here we shall only deal with certain main features of the ecology of such species, as an investigation of the contents of the crops have proved to contribute considerable weights to the food of the ptarmigan at one season or another. The species in question are:

In the summer food: *Polygonum viviparum*.

In the winter food: *Salix arctica*, *Dryas octopetala*, and *Saxifraga oppositifolia*.

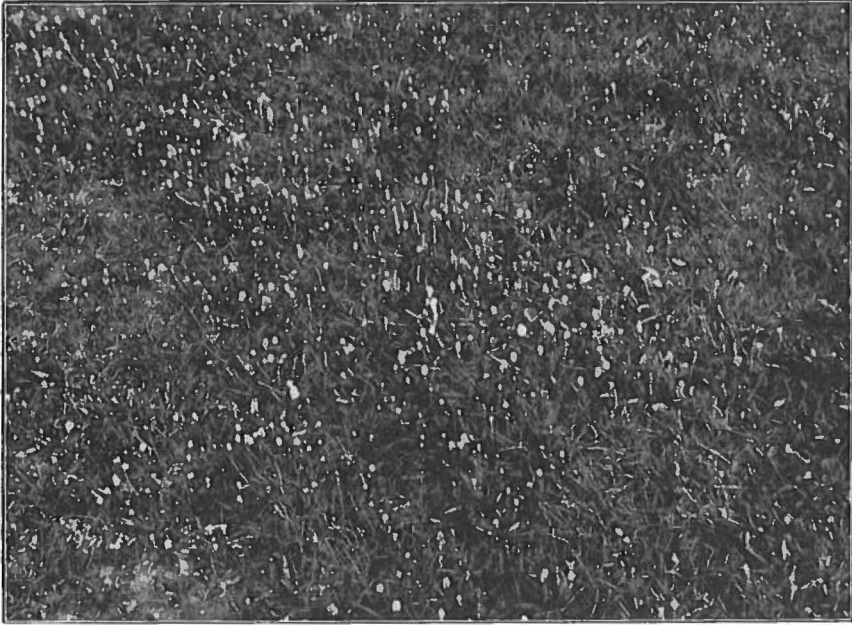
Polygonum viviparum L.

The species is a perennial herb (stem-tuber geophyte) with a subterranean storage organ in the stem-tuber rich in nutritive substances (cfr. Tab. 24, p. 153). The stem-tuber is often only 1—2 cm long and 0.5 cm thick. The above ground stem is 10—15 cm high, leafy, with a basal rosette, and a flowering spike at the top, which, however, does not produce ripe fruits, but has many bulbils in the axils of the bracts, by which the species multiplies vegetatively. It is these bulbils and the stem and bracts of the spike which constitute the most important food of the ptarmigan in the summer. In winter the ptarmigan may quite exceptionally secure the nutritious stem-tubers from the ground.

As far as I know, the species has no area of dominance, but is very frequent in numerous, mostly snow-covered, damp plant communities. The species attains its greatest frequency (co-dominance) in moderately snow-covered, favourably exposed, medium-damp *Salix arctica* snow-patches of a meadowy appearance (herb slope) due to the fresh green

luxuriance of the community and its great abundance of leaves (cf. fig. 6, below). It is these snow-patches which in summer supply to the ptarmigan its main quantity of *Polygonum* food.

In 1932 the *Salix arctica* snow-patches rich in *Polygonum viviparum* became free of snow in the lowland round Eskimonæs at the beginning of June, and on account of their favourable exposure the development of their vegetation took place rather rapidly. By the middle of June the bulbiferous *Polygonum* spikes were seen everywhere. Later in the summer



Getling phot. July 17, 1932.

Fig. 6. *Salix arctica* association rich in *Polygonum viviparum*; *Salix* is almost completely replaced by *Poa arctica*, *Festuca rubra*, and other nitrophilous grasses. The picture was taken on the manured ground near the former Eskimo habitation at Dodemandsbugten, Clavering Island.

until September *Polygonum* at the same stage may be found at higher mountain levels (800—1000 m above sea-level) near Eskimonæs. They are the *Polygonum* laggards of the unfavourably exposed snow-patches, with lower temperatures owing to their high altitude, which now develop their organs. A reflection of the abundance in summer of young *Polygonum* bulbils may therefore be found in the highlands even in the late summer, when the species has shed its bulbils in the lowland.

Thus the species shows its greatest luxuriance and density of individuals on snow-covered soil, but it also occurs, though much more sparsely, on snow-free soil if it is sufficiently damp during the summer. On slightly

snow-covered soil the spike may sometimes rise above the snow-cover, the species being a typical "winter stander" (SERANDER, 1901). The bulbils adhering longest are spread by the wind over the smooth surface of the snow. These winter standers do not contain many bulbils but to the ptarmigan they may be of importance, as they may be supposed to indicate where it is worth while to start digging for stem-tubers.

Altogether the access to *Polygonum* in the winter is immensely hampered by the snow-cover; moreover the accessible



Gelting phot. July 4, 1932.

Fig. 7. Luxuriant *Salix arctica* association rich in *Polygonum viviparum* and other herbs. Numerous spikes of *Polygonum* are seen in the background to the right. Of other herbs *Anica alpina*, *Cerastium alpinum*, and *Festuca rubra* are seen. The locality is manured by *Larus glaucus* and *Branta leucopsis*, breeding on the rocks behind. In the winter 1931—32 the locality was frequently visited by ptarmigans and Arctic hares, and in the summer by foxes looking for eggs. It is the most northerly locality known in East Greenland in which such a rich vegetation utilises manure originating exclusively from animals. If the summer temperature had been higher, a luxuriant shrub might doubtless have been found here. The picture was taken at the southern point of the cape of Eskimonæs.

fragments are either poorer in nutrient substances (poor in bulbils) or more difficult to secure (stem-tubers).

Fig. 11, 4, p. 34 may serve as a paradigm of the snow-cover in the *Salix arctica* snow-patches rich in *Polygonum*. The date of the final disappearance of the snow may, however, vary according to the climatological conditions of the year as well as to locality.

Salix arctica PALLAS (s. l.)

The species is a deciduous dwarf-shrub with creeping, espalier-forming or but slightly ascending branches, which only quite exceptionally rise more than 15—20 cm above the ground. The annual shoots are soft and light-green, but turn darker in the course of the summer. The lignification proceeds but slowly, though apparently more rapidly than in most other woody plants within the area (cf. KRAUS, 1874), probably most rapidly in the inner fjords, where the summer heat is greatest. Only exceptionally does the ptarmigan eat fragments of branches more than one year old. The bitten-off fragments of branches are, in a dry state, dark green or slightly nut-brown with a delicate smell. Leaves form but a subordinate part of the food of the ptarmigan. The catkin buds, and especially the terminal buds of the twigs, are very frequently found.

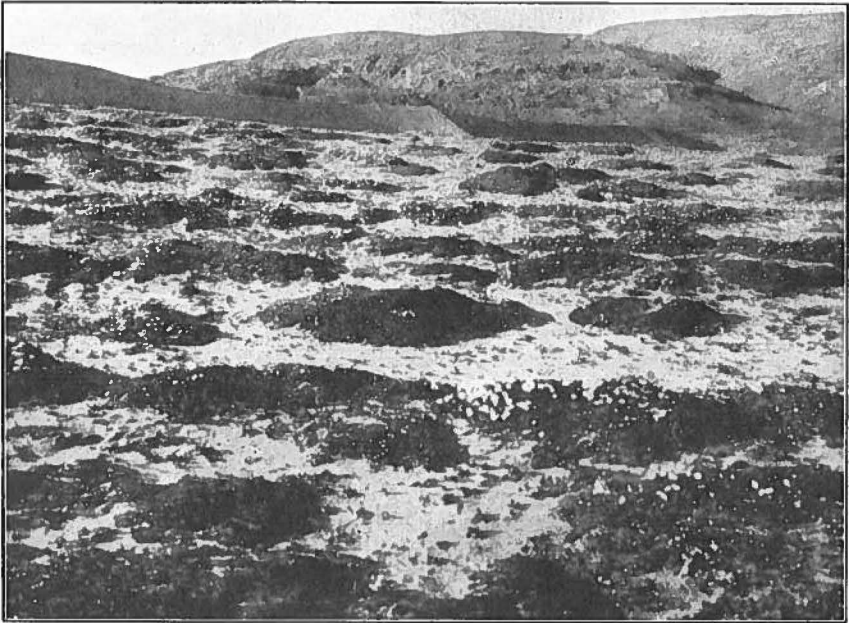
The species is one of the commonest plants within the area and perhaps the commonest dwarf-shrub. It has an exceedingly great amplitude in the various ecological scales and occurs on nearly all kinds of soil from the driest to the dampest, from the deeply snow-covered to the snow-free soil, and yet the luxuriance and density of individuals of the species within the different types of vegetation shows that it must be considered rather a hygrophyte. But if only the roots have access to the capillary water, the species can withstand very well a periodic desiccation of the upper ground in summer, as well as snowlessness in winter. The species, it is true, is somewhat resistant to the foehn winds, but it does not thrive well in localities constantly swept by these winds. In the inner fjords the species is therefore more intimately associated with deep snow-patches than in the outer districts.

On account of its hardiness the species is able to form a closed vegetation in localities of rather different ecology. We may distinguish between different types growing on superficially dry soil, which in the winter is as a rule deep and constantly snow-covered in the fjords, and various types on damp soil, which in the winter is often less snow-covered and is especially found at the outer coast, where the effect of the foehn winds is less desiccating or where the *Salix* localities are sheltered from the foehn winds, whereas in winter they are often exposed to deflation by the north winds, which are not, by far, so dry.

To understand the access to *Salix* in the winter it must be kept in mind that this access will become increasingly easy when moving from the inner fjords over the outer fjords to the outer coast.

The same tendency may be seen on going from the lowland of the fjords up into the highlands. Here, as at the outer coast, the *Salix* growths show a tendency to occur on soil that is barer of snow than in the lowlands of the fjords. However, the highlands of the fjords do not present the same favourable conditions as regards access to *Salix* as the

outer coast, since the *Salix* areas are "thinner", that is, the density of the individuals is not so great. But as high as 1000 m above sea-level *Salix* areas that are more or less free of snow in the winter may be met with locally, which may be supposed to be accessible for the ptarmigan at such times of the winter when the lowlands of the fjords are concealed below a snow-cover of a hampering thickness. The larger quite mechanical effects of the wind at the mountain levels are traceable here, and the mountain winds, like the north winds of the lowland, are not dynamic-



Gelting phot. June 28, 1932.

Fig. 8. *Dryas octopetala* association \pm bare of snow in the winter, much eroded by the wind. Each individual encloses a dune embryo, eroded on the windward side and covered by the over-ground parts of *Dryas* on the lee-side. Each of these individuals sends one thick tap-root down to the capillary water over the icy substratum, which here possibly occurs 4—5 m below the surface of the ground. The sand areas between the tufts are covered with *Chamaenerium latifolium* and *Festuca rubra*. In the background a distinctly raised accumulation terrace and several erosion terraces in the solid rock. Eskimonæs, Clavering Island.

ally heated in the same degree as the hot foehn winds of the lowland.

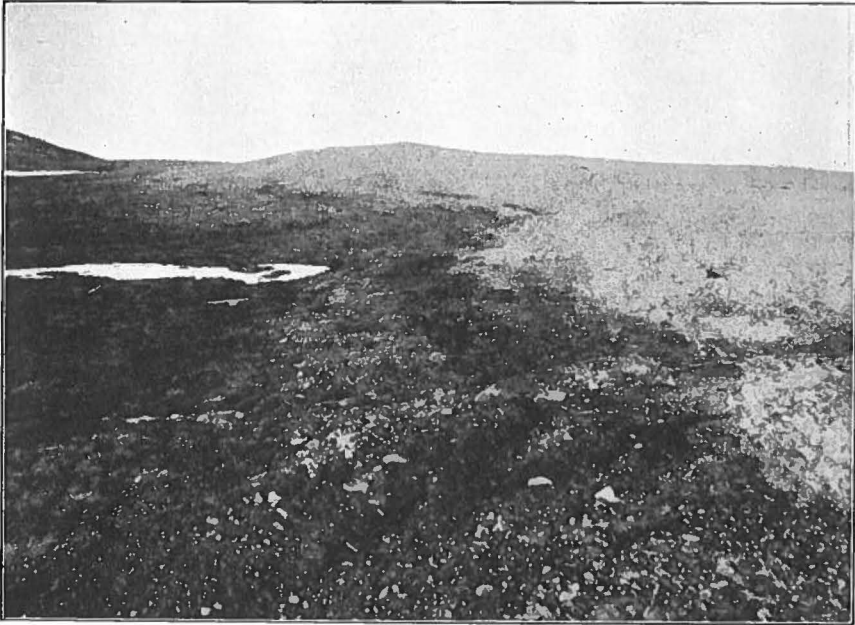
The snow-cover on a commonly occurring dominance area of *Salix arctica* at Eskimonæs is illustrated in fig. 11, 4, p. 34.

Dryas octopetala L.

The species is an evergreen dwarf-shrub, forming continuous vegetation mats, which only exceptionally rise more than 10—15 cm above

the ground. The greater number of the annual shoots are some few centimetres long at the most, crowded with leaves, that is to say, they are typical short shoots. According to JESSEN (1913), long shoots up to 10 cm long seem to be frequent in other parts of the Arctic. Long shoots have also been observed in Northeast Greenland, but seem to be rare. It is only the leaves which enter in considerable quantities into the food of the ptarmigan.

The species is one of the commonest plants of Northeast Greenland.

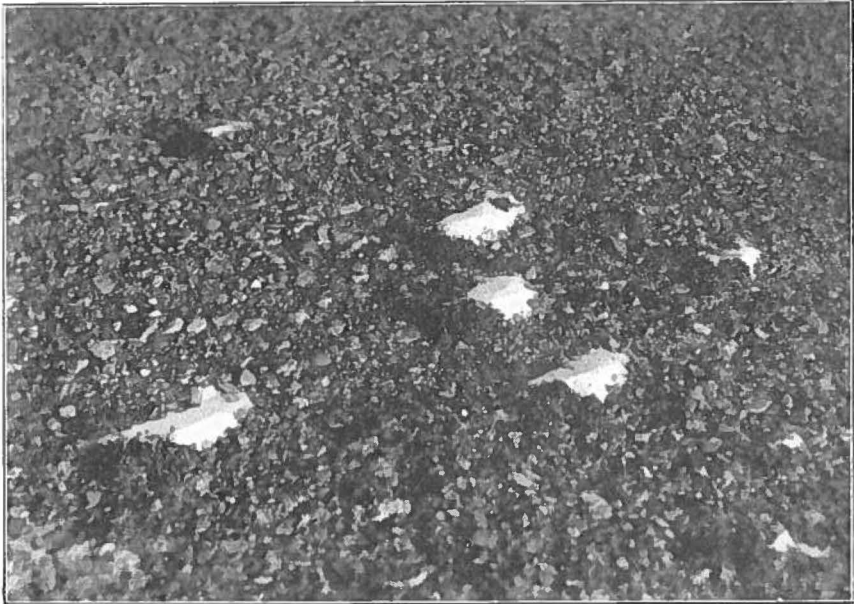


Gelting phot. May 17, 1932.

Fig. 9. Photograph showing the influence of differences in the snow-cover. To the right a really dry "Hamada" or "Fjældmark" \pm snow-free in the winter, almost bare of vegetation and subjected to deflation both summer and winter. To the left in the picture, where the snow-cover is constant during the winter, there is a fairly luxuriant *Carex* heath bordered by *Dryas octopetala*. Eskimonæs, Clavering Island.

Like *Salix arctica*, *Dryas* has a wide amplitude in nearly all the ecological scales, but while *Salix* is chiefly associated with moist soil snow-covered in winter, *Dryas* is preferably associated with dry soil snow-free in winter. The *Dryas* heaths are often very rich in grass (or more correctly rich in glumiflores, since the *Carex* species are the commonest co-dominants), and one is often in doubt whether to term an association a *Dryas* heath rich in glumiflores or a glumiflore heath rich in *Dryas* (cf. also SAMUELSON, 1916, and NORDHAGEN, 1928, 2, and 1936). *Dryas* may exceptionally form dense growths in places with a thick snow-cover, but as a rule

the communities rich in *Dryas* are scantily snow-covered or often free of snow in the winter, being often only snow-covered during a prolonged or quiet snowfall, but laid bare by the first light winds setting in. The *Dryas* tufts are extremely resistant to the desiccating effect of the wind, and the species is excellently equipped against deflation on account of its deep-striking tap-root and its cushion form. The size of the leaves varies according to the degree of moisture of the soil and the wind exposure of the locality. On soil free of snow in the winter the species



Gelting phot. October 4, 1931.

Fig. 10. Marginal part of a *Saxifraga oppositifolia* association free of snow in the winter. Eskimonæs. Clavering Island.

occurs almost exclusively with very small leaves (forma *minor* HOOKER), while on soil snow-covered in the winter it has big, well-developed leaves, whose margins are but slightly revolute.

Since *Dryas* occurs with great frequency at the outer coast as well as in the fjords, the access to it in winter, on account of the scanty snow-covering of its habitats, will not present the same differences as is the case with *Salix*. However, this species, too, will probably be most easily accessible at the outer coast.

The snow-cover on two dominance areas of *Dryas octopetala* at Eskimonæs is illustrated in fig. 11, 2 and 3, p. 34.

Saxifraga oppositifolia L.

The species is an evergreen, partially lignified herb, which on dry soil forms densely tufted blocks (*f. pulvinata*), whose stems are often so closely compressed that the surface of such a block may be formed exclusively of the terminal buds of the dense-set perennial shoots, whereas on damp, more or less snow-covered soil it forms looser tufts with longer internodes (*f. reptans*). It is almost exclusively the terminal buds of *f. pulvinata* that serve as food for the ptarmigans.

The species is exceedingly common within the area, and on account of its wide amplitude in the various ecological scales may be found everywhere and at all seasons of the year. It enters into a large number of plant communities as a subordinate species. As a pioneer of vegetation the species occurs on the horizontal planes, snow-free in the winter, of the raised marine terraces, and here withstands complete bareness of snow throughout the winter. Precisely because of their lack of snow the *Saxifraga* areas leave their impress on one's memory of the wintertime, when so many other species are burried by snow. On snow-free or slightly snow-covered soil the species forms very open growths with interstices of about 1 m or more between the individuals (root competition). On soil with a somewhat deeper snow-cover similar growths may be found, in which, however, the bottom is covered by a more or less continuous layer of lichens (*Stereocaulon*). These associations are less suitable feeding places for the plant-eating animals than the *Dryas* and *Salix* associations on account of the large spaces between the individuals. However, they may be used, though possibly not very often, if the access to other food is hampered.

The snow-free *Saxifraga oppositifolia* associations must be supposed to be almost equally frequent within all districts. However, I have but few observations of them from the inner fjords, where they frequently seem to be replaced by dry grass heaths, especially *Elyna* heaths.

The snow-cover of the *Saxifraga oppositifolia* association pictured in fig. 10 is illustrated in Fig. 11, 1, p. 34.

Measurements of the snow-cover on the types of vegetation of importance to the ptarmigan.

In order to gain an idea of the snow-cover of the different plant communities during the year I made various measurements in the outer fjords near Eskimonæs in the winter of 1931—32. These measurements, which were made for purely ecological, and not meteorological, purposes, were made in the following way: 50 bamboo sticks were placed in ten different plant communities, five in each community. This was done in September. With the exception of a single snowfall on August 23, which

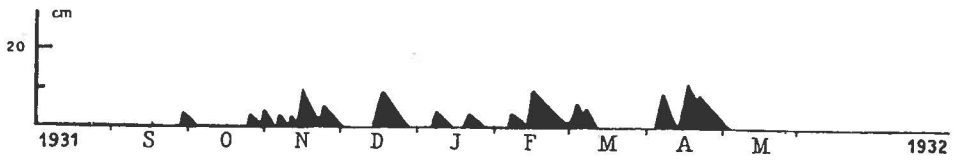
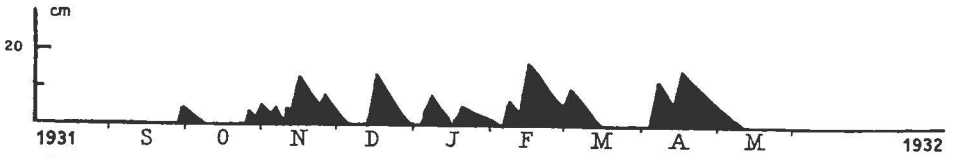
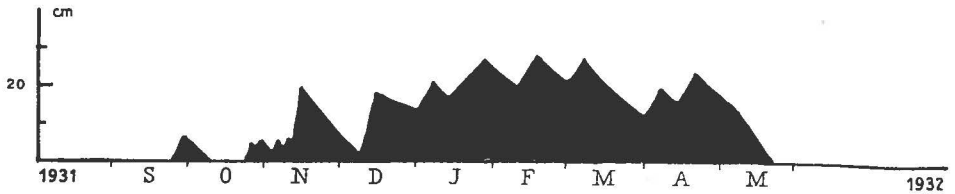
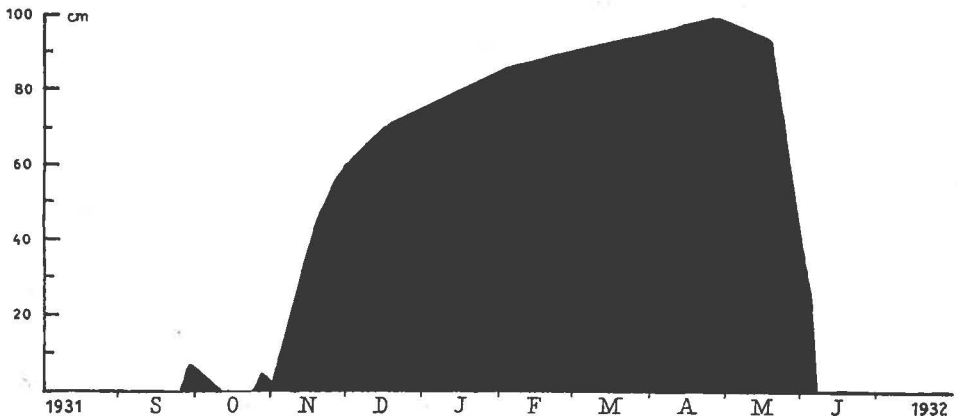
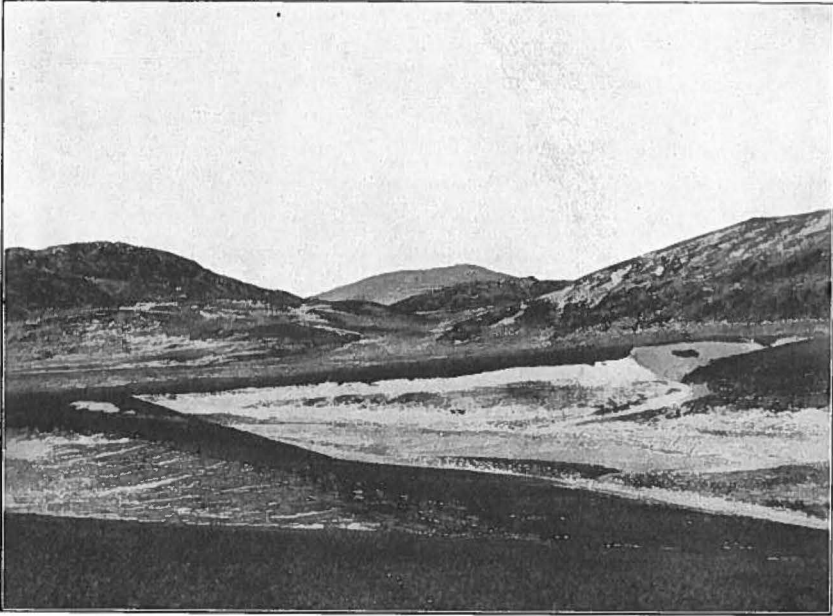
1: Open *Saxifraga oppositifolia* - ass.2: Open *Dryas* - ass3: *Dryas*-ass rich in species4: *Salix arctica* - ass rich in
Stereocaulon alpinum

Fig. 11. The snow-cover on different types of vegetation at Eskimonæs 1931—32.

immediately melted, I succeeded in registering the snowfall throughout the winter. The thickness of the snow-cover was measured on the sticks, on which notches were cut at each 50 cm. For the intermediate intervals a centimetre tape-measure was used at each observation.

Measurements on the sticks were made at the following dates in 1931: $28/9$, $29/9$, $3/10$, $12/10$, $25/10$, $26/10$, $31/10$, and $1/11$. In the Christmas week all the plant communities were found to be snow-covered though in different degree, and further the snow-cover on the *Salix arctica* heath was found to be about 70 cm thick. In 1932 the snow-cover was measured at the following dates: $2/2$, $28/4$, $17/5$, and $2/6$. At the station of Eskimonæs a register was kept of snowfall and force of the wind. By combining the



Gelting phot. October 2, 1931.

Fig. 12. When the autumnal snowfalls set in, the depressions in the ground are first covered, because they are sheltered from the wind, which carries the snow from hills and plains into the depressions, where it forms snow-patches. Snow-covered: various snow-patch communities and *Salix arctica* ass. Slightly snow-covered: *Cassiope* heaths. Snow-free: *Dryas* and *Saxifraga opp.* ass. Eskimonæs, Clavering Island.

direct measurements with the register of snowfall and wind-force it is thus possible to plot the approximate curves of the snow-cover.

Fig. 11, p. 34, gives the snow-cover for four characteristic plant communities at Eskimonæs in the winter of 1931—32. The snow-cover is given in centimetres. Further it should be premised that the precipitation that winter must presumably be considered to be slighter than normally; nothing certain is known, but it was the general opinion of the trappers. It is known, however, that in the two ensuing winters the precipitation was higher.

Apart from the snow which came down on August 23, and which immediately melted, the first persistent snow-cover was formed at the

end of September. Gradually, however, it was swept away and redeposited by the wind, and from the beginning of October all the communities investigated were again bare of snow till the 27th October, when a slight snowfall occurred. This initiated the actual snow-covering period. From that date on there was throughout the winter a characteristic difference between the snow-patch communities and the more or less snow-free communities: while the snow-cover of the *Salix arctica* association rich in *Stereocaulon alpinum* showed a constant increase, the communities more or less free of snow were only covered during quiet snowfalls, and subsequently the snow-cover was removed, entirely or partially, by the wind. The *Dryas* association rich in species occupies an intermediate position, though it approaches the more or less snow-free communities, for as late as the middle of December, 1931, openings were seen in the snow-cover, through which the vegetation was visible. Even though the average snow-cover of the *Dryas* association rich in species in January, 1932, was about 15 cm, a single patch free of snow was seen. Not till the end of January was the heath definitely covered, and bare patches were not seen till the melting of the snow in the spring.

Thus in 1931—32 the following rule could be ascertained for the slightly snow-covered communities: until midwinter there was snow-bareness alternating with a scanty snow-covering; not till after midwinter were they completely covered with snow.

Communities which, like the open *Saxifraga oppositifolia* association, throughout the winter are alternately covered and bare of snow I would designate more or less snow-free.

The following rule applied to the snow-patch communities: apart from a short period in the late autumn, the snow-cover increased until the spring, when it decreased by sublimation and melting of the snow.

The importance of the snow-cover for the zonation of the vegetation and the access to it.

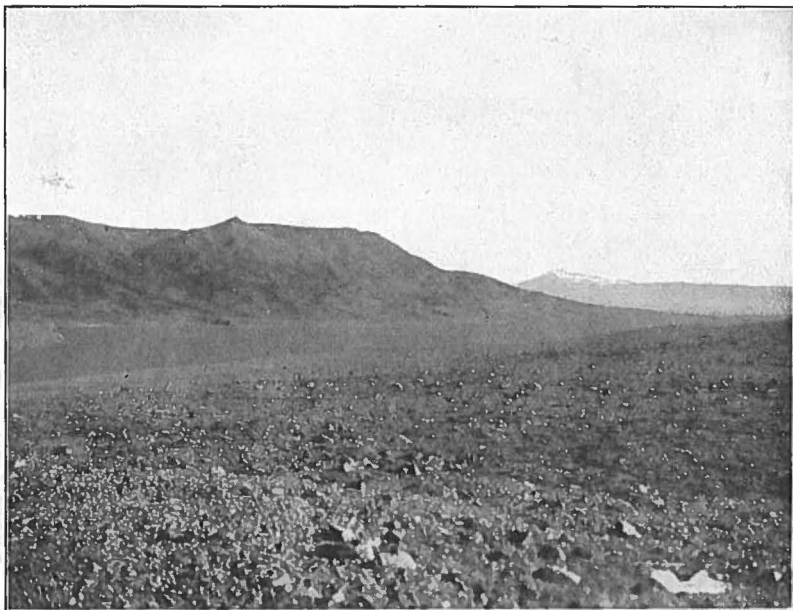
Throughout Northeast Greenland the thickness and duration of the snow-cover give rise to definite and law-regulated zonations of the vegetation. Particularly in areas with well preserved, often linear, raised marine terraces, plant belts arranged with nearly geometrical precision are conspicuous. *Cetera paribus* a certain type of vegetation corresponds to a given snow-cover.

As, however, the difference in climate between the outer coast and the fjords influences the requirements of the individual species in regard to the thickness and duration of the snow-cover, the snow-cover in the dominance areas of the species will be different in the fjords and at the outer coast. The rule is, as mentioned on p. 23, that the dominance area

of the same species is less snow-covered at the outer coast than in the fjords.

This phenomenon will be demonstrated in the following by some examples and is illustrated in figs. 15 and 16 (p. 39). A characteristic zonation at Eskimonæs in the outer fjords is diagrammatically represented in fig. 15.

In the figure the broken line indicates the thickness of the snow-cover at the beginning of October, 1931, the continuous line may be taken



Gelting phot. July 28, 1933.

Fig. 13. Coastal plain in the inner fjords free of snow in the winter. A dry "Fjældmark", almost bare of vegetation with the exception of the most xerophilous species: *Elyna Bellardii*, *Carex nardina*, *Dryas octopetala*, *Saxifraga oppositifolia*, and other species. Its importance for the ptarmigan as a winter feeding place is no doubt slight on account of the absence of *Salix arctica*. (The plateau surface (cf. p. 11) is distinctly seen). Revet, Payer Land.

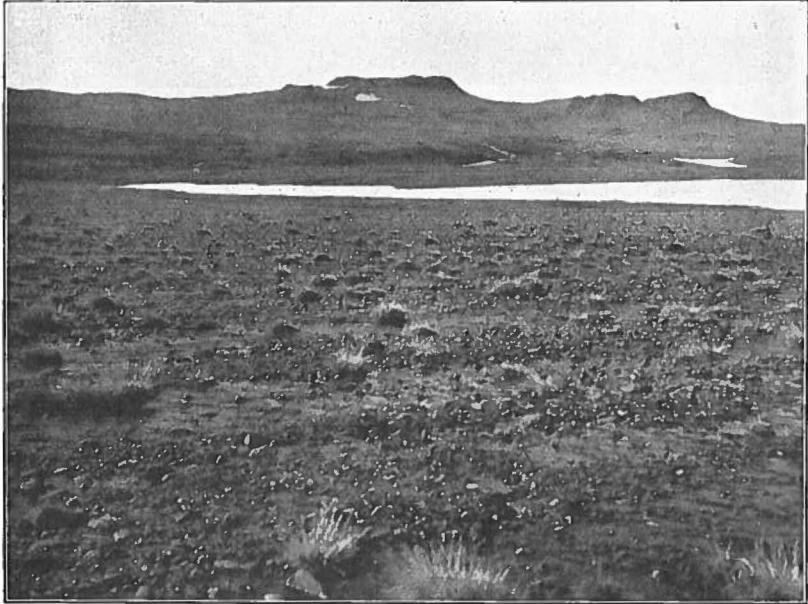
to indicate its thickness either after a quiet snowfall or later in the winter (January). Whichever alternative is chosen, the figure shows very clearly that an increasing snow-cover will impede the access to *Salix* to a much greater extent than to *Dryas*, which again is less easily accessible than *Saxifraga oppositifolia*, even though the difference between the two latter is not very great.

The situation outlined here is that of the ptarmigan in the winter at Eskimonæs or in the fjord districts in general.

In addition to the *Salix arctica* snow-patches, which are constantly

snow-covered in winter, there occur at Eskimonæs, as well as in other places in the fjords, *Salix* growths which are less snow-covered in winter than those described here; thus on moist, swampy soil (KRUUSE's tufted bogs, 1912). However, the latter decrease in frequency towards the interior of the fjords at the same time as their snow-cover increases in thickness. Even at Eskimonæs they are so deeply snow-covered that it is difficult for the ptarmigan to gain access to them in the winter.

A characteristic zonation at the outer coast is illustrated in fig. 16,



Gelting phot. August 16, 1933.

Fig. 14. Coastal plain at the outer coast more or less snow-free in the winter, irrigated in the summer by the water running off from perennating snow-drifts. Its importance for the ptarmigans as a winter feeding place is no doubt considerable on account of the abundant *Salix arctica* growths on the hills and the drier parts of the otherwise very moist soil. The grass tufts are formed of *Deschampsia arctica*. In the background Mt. Rundetaarn. Lervig, Clavering Island.

which is drawn on the basis of observations made in Grønnedal on the northeast coast of Clavering Island on May 3, 1932. As the vegetation in question is situated on a glacier of moving soil, and such are characteristic of many ptarmigan feeding grounds at the outer coast, I consider it reasonable to discuss in greater detail, when necessary, the water supply and the mechanics of the solifluction (cf. also TH. SORENSEN, 1935).

In the lee of the basalt dyke to the left an immense snow-drift has been deposited, whose nucleus, at any rate in certain years, persists during the summer. The marine terrace seen to the right in the figure,

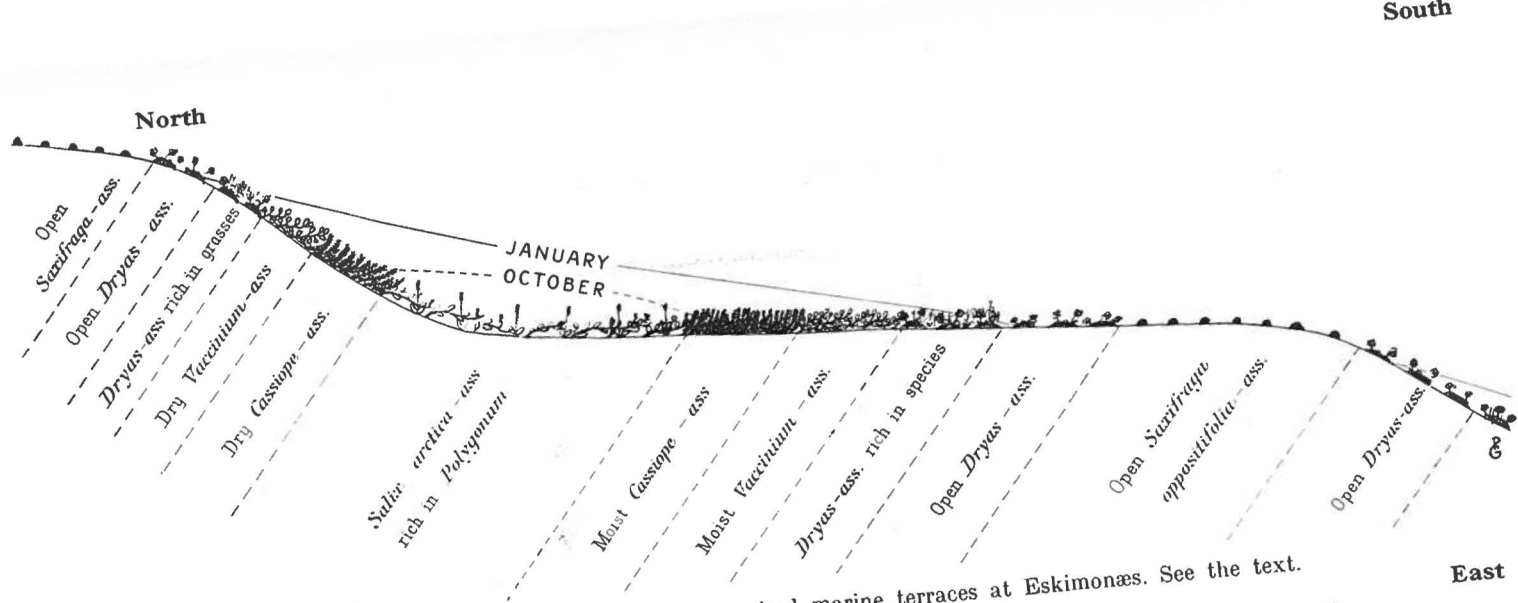


Fig. 15. Zonation of the vegetation on raised marine terraces at Eskimonæs. See the text.

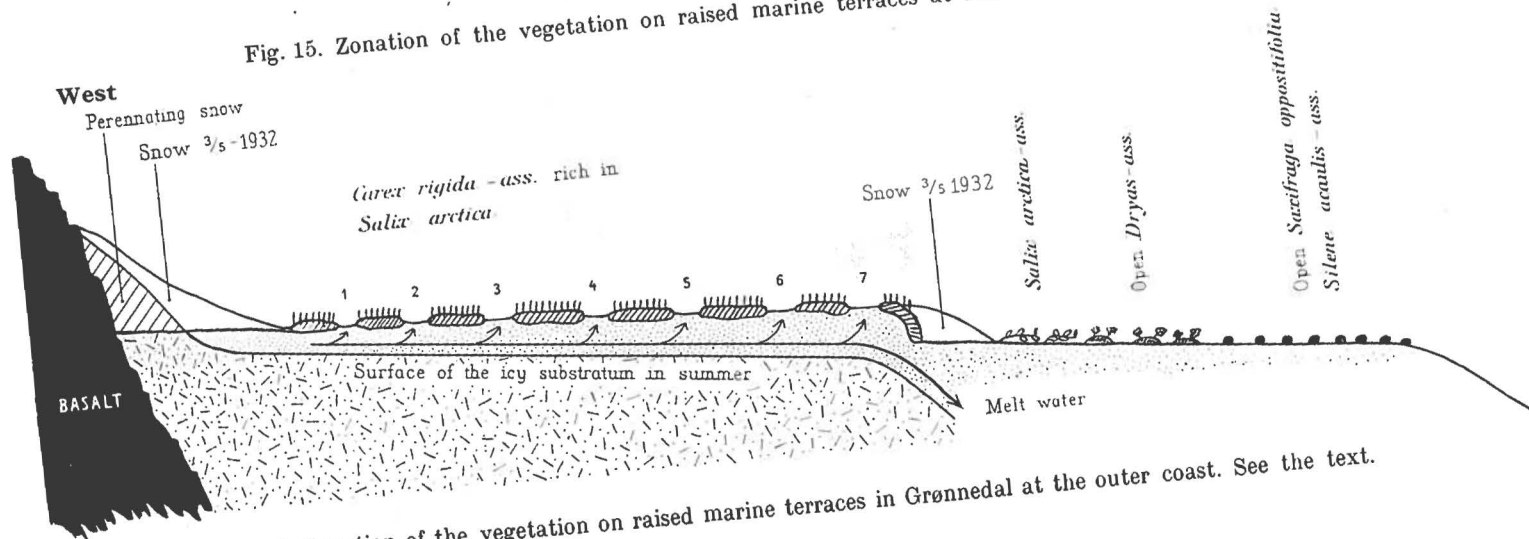


Fig. 16. Zonation of the vegetation on raised marine terraces in Grønndal at the outer coast. See the text.

formerly extended quite close to the snow-drift, but on account of the melt-water seeping out from the latter a glacier of moving soil has formed, which quite slowly, year by year, has moved over the surface of the terrace to the east. The surface of the moving soil glacier, which at first had almost the same inclination as the original terrace surface, has gradually, by deposition of moving soil at the distal end of the glacier, become almost horizontal.

The figure shows the surface of the icy substratum in the summer,



Gelting phot. May 3, 1932.

Fig. 17. Glacier of moving soil, Grønnedal, Clavering Island, seen from the north-northwest (cf. fig. 16, p. 39). *Carex rigida* association rich in *Salix arctica* and mosses. On account of sublimation due to insolation on the days before the picture was taken the snow only persists in the cup-shaped depressions.

as found by digging and measurements, in one of the characteristic moving soil glaciers at Eskimonæs.

At the eastern edge of the glacier of moving soil there are, as usual, conditions for the deposition of a minor snow-drift. East of this extends the terrace surface, sloping slightly and farther east cut through by a rivulet. In winter the whole area, with the exception of the easternmost, not damp, parts of the terrace, is frozen to the surface of the ground. In spring melting sets in, and the surface of the icy substratum gradually subsides nearly to the level indicated in the figure. The water from the

melting snow-drift seeps eastward, first superficially, subsequently underground. The water follows closely the icy substratum, which is so compact that the water cannot sink through it. At a certain time the moisture of the soil will be so much greater at a certain level below the superficial sod that the interior, water-saturated parts of the glacier of moving soil will begin to flow. The edge of the moving soil glacier moves some distance eastward. At the same time the sod on its surface will crack and old crevices will widen, and soft masses of soil saturated with water will pour forth into new and old fissures. Often the sod proves to be so resistant that it will rise in bulges (German: Brodelstellen, cf. GRIPP, 1927, 1929, 1932) before cracking.

Such "Brodelstellen" in every stage of development may be found in most large glaciers. Between the vertical movements in the "Brodelstellen" and the horizontal movements caused by deflation a certain cooperation is gradually established, which may go on for a number of years, and which results in a removal of the fine-grained material of the moving soil glacier. Wind erosion especially takes place in the winter in the "Brodelstellen", whose content of ice will rapidly sublimate, and then the mineral particles, being loosened from each other, will be carried away by the wind. Next spring the solifluction commences again. The various "Brodelstellen" receive fresh water-saturated material from the interior of the moving soil glacier. Next winter the fine-grained particles of this fresh material are removed entirely or partially by the wind, and so on.

The traces of deflation on the moving soil glacier in Grønnedal showed that here the erosion of the "Brodelstellen" was chiefly caused by winds blowing from the north-northwest, and in many places the effects of the wind had been so strong that the original convexity of the "Brodelstellen" had disappeared and been replaced by cup-shaped depressions (fig. 16, 1—7). Many of the depressions were of such early date that the vegetation was regenerating by variants of the surrounding vegetation. In fig. 17 the depressions appear as snow-patches, the weather having been calm for some length of time, for which reason the snow had disappeared by sublimation from the whole area except the depressions, in which the snow-cover had been thickest.

The vegetation on the moving soil glacier in question consists, as indicated in the figure (16), of a *Carex rigida* association rich in *Salix arctica*. The moss layer is continuous. Macroscopic vegetation is lacking in some of the cup-shaped depressions only. However, many regenerate by association fragments rich in algæ and dominated by *Alopecurus alpinus* and *Arctagrostis latifolia*. Apart from the two distinct snow-



Gelting phot. July 20, 1933.

Fig. 18. Raised foreland at the outer coast. Hird Bay, Clavering Island. To the left, raised marine terraces, which afford shelter for long-lingering and perennating snow-drifts, which supply the coastal plain with water during the summer. To the right, Gael Hamkes Bay with ice-floes.



Gelting phot. May 10, 1932.

Fig. 19. Final stage of solifluction in a plain free of snow in the winter. The finer material is carried away by the wintry north winds, leaving behind the stones and the plants, which are fastened by long tap-roots. In nearly each "Brodelstelle"-centre there is a *Salix*, much attacked by ptarmigans and hares. Germaniahavn, Sabine Island.

patches and the cup-shaped depressions the whole area was free of snow on May 3, 1932, and the frequent traces of deflation showed with all desirable distinctness that the vegetation must, as a rule, be free of snow or but very scantily snow-covered throughout the winter. For traces of deflation due to the decidedly wintry north winds were rarely observed even in fairly constantly snow-covered communities.

The stages of solifluction briefly outlined here are phenomena of extremely common occurrence at the outer coast, where they are far



Getling phot. February 16, 1932.

Fig. 20. Incipient deflation in a hill covered by a glumiflore heath (*Elyna Bellardii*, *Carex nardina*) rich in *Dryas octopetala*. In the foreground numerous traces of deflation and erosion-remnants enclosed by the roots of the densely tufted glumiflores and the cushions of *Dryas*. In the background, left, the almost undisturbed optimal phase of the *Elyna* heath. The direction of deflation and corrosion traces is north-south.

Knudshoved, at the outer coast of Hold-with-Hope.

more common than in the fjords. The intensity of the solifluction, too, is greater at the outer coast.

The final stages of the solifluction are characterised by an abundance of big boulders and coarser material in the moving soil glaciers (cf. fig. 19, p. 42). The finer particles are removed by the wind (and the thaw-water), and the vegetation consequently becomes poorer. Finally, often merely systems of circular or polygon-shaped "boulder craters" are left, and here *Salix arctica* is often one of the few plants still able to withstand the extremely violent physical conditions. Probably its long root plays an important role in this respect.

The undisputed dominance of the *Salix arctica* areas at the outer coast is closely connected with the greater moisture of the soil as well as the greater humidity of the air there. The moisture of the soil, again, gives rise to solifluction, and for this reason I have briefly described one of the most conspicuous solifluction phenomena, the glacier of moving soil.

The *Dryas* and *Saxifraga oppositifolia* associations shown in fig. 16, p. 39, differs little from those of the fjords.



Gelting phot. May 10, 1932.

Fig. 21. Final stage of wind erosion in a plain free from snow in the winter. Detail picture of the foreland at Germaniahavn, Sabine Island. *Salix arctica* individuals, which on account of the north winds lie closely pressed to the surface of the ground. Direction of individuals north-south. Each stone gives shelter to a *Salix* individual. The individual in the foreground is almost undermined by deflation. The snow-free ground allows hares and ptarmigans to seek their food unhampered in the winter.

Bearing in mind what we have learned about the snow-cover of the different plant communities in the various districts, we shall find, on glancing at fig. 15, p. 39, that by midwinter the snow-cover in the fjords have reached the *Dryas* heaths, while as early as October—November it covered the *Salix arctica* snow-patches rich in *Polygonum*, and consequently the access to food must be very considerably reduced. For the ptarmigans there seem to be three possibilities, viz.:

- 1) to dig into the snow for food,
- 2) to make a change to other, less snow-covered plants,

- 3) to move to areas where the vegetation is better able to satisfy its demands.

Let us consider more closely these possibilities.

1) The ptarmigan digs into the snow for food. The foot of the ptarmigan is excellently suited for scraping away soil and snow, and the claws of its toes are shed several times a year. The claws are broad, shovel-shaped, almost nail-like. Hence there should be nothing to prevent the ptarmigan from using its feet to secure enough of the snow-covered food it requires. However, towards midwinter, during the increasing snow-cover and the decreasing day-light, this procedure will hardly be sufficiently economical considering the time it takes. That the ptarmigan scrapes away new-fallen snow with its feet has been ascertained by observation, but in the snow-drifts hardened by the wind and often overlying the *Salix arctica* growths, this procedure will hardly be of any great importance. The Norwegian trapper FOLDVIK states in "Polar-Årboken" (1933, p. 142) that the ptarmigans gather round the holes in the snow-cover made by the musk-oxen in a further search for food.

2) The ptarmigan changes to other and less snow-covered plants. This possibility seems to be extensively resorted to by ptarmigans. As will be shown below (p. 118), the increasing snow-cover must precisely be assumed to be the cause why the food from summer to midwinter shows the characteristic change from *Polygonum* to *Salix*, *Dryas*, and *Saxifraga oppositifolia*.

3) The ptarmigan moves to areas where the vegetation will better satisfy its demands. As stated in the above (cf. fig. 16 and the text pp. 36—44), this possibility, too, is open to the ptarmigan; and, as will be shown below (pp. 63—69), it does, in fact, make use of it. And conditions seem to be such that a roaming may be assumed to be the rule in the winter.

Thus, while digging after food may be considered a subordinate exception, at any rate during the dark time, we consider that possibilities 2 and 3 will be accepted to an extent which will depend on the climatological development of the particular year.

THE PTARMIGAN, ITS OCCURRENCE AND FREQUENCY IN NORTHEAST GREENLAND

Nomenclature.

As stated above (p. 8), the Greenland ptarmigan had several Eskimo names. However, the attempts of FABRICIUS (1780) to classify the Greenland specimens as *Tetrao lagopus* L. initiated a period of many years during which the species led a rather knock-about life in the systematical works, and even at the present day it is perhaps hardly definitively placed.

As the present paper aims primarily at investigating biological conditions with regard to the food of the ptarmigan within an area in which its race seems to be elucidated, a brief treatment of the systematic-nomenclatural questions must be allowable, all the more so since the author is unable to contribute anything new to this field.

The East Greenland ptarmigan, with which we are here specially concerned, was first observed by Europeans in the summer of 1822, when the crew of WILLIAM SCORESBY jun.'s ship the "Baffin" of Liverpool encountered it on Jameson Land, Scoresby Sound, and on Traill Island, where it was so little shy that, as SCORESBY puts it (1823, p. 421), it "was knocked down with stones".

As done by FABRICIUS (1780) and GIESECKE (1816), SCORESBY, too, refers the Greenland ptarmigans to *Tetrao lagopus* L.

The ptarmigans brought home by the Second German Northpolar Expedition from Sabine Island, Clavering Island, and Wollaston Foreland are mentioned by FINSCH (1874, p. 195) as *Lagopus alpinus* NILSS.

The specimens brought home by BAY (1894, p. 25) from Scoresby Sound, also, are stated to be indistinguishable from European ones (now classified as *Lagopus mutus* MONT.). Since then the East Greenland ptarmigan has always been referred to *Lagopus mutus* MONT., though under different race- and variety-designations.

WINGE (1898) claims that many futile attempts have been made to separate the Greenland ptarmigan from the European one, and he

places all the forms occurring in Greenland under the variety name *var. rupestris* GMELIN.

MANNICHE (1910), who was the first to give detailed information about the moulting of the East Greenland ptarmigan (contributions had, however, already been given by FINSCH (1874) and DEICHMANN (1909)), omits a systematic discussion and lists the species under the name *Lagopus mutus* MONT.

A systematic treatment of the Greenland ptarmigans was made by



Gelting phot. April 3, 1932.

Fig. 22. Male ptarmigan (No. 39) on a scantily snow-covered *Dryas* heath rich in *Carex nardina*. Granatdal, Clavering Island. Note the foot-prints in the snow to the left showing the jumps in the snow, which is 3 to 5 cm deep. There is hardly any doubt about the importance of the loose snow as a factor hampering the movements of the ptarmigan; the bird always jumps in the loose snow, while it is able to run on the surface of the hard snow.

LEHN SCHIOLER (1925, p. 108). He arrived at the result that three races of *Lagopus mutus* MONT. occur in Greenland, viz. *rupestris* in the northern part of the west coast, *Reinhardtii* in the southern part of the west coast, while for the east coast he erects a new race, *groenlandicus*.

Until quite recently later authors have adopted LEHN SCHIOLER'S nomenclature, thus HELMS (1926), ALWIN PEDERSEN (1926, 1930), LÖPPENTHIN (1932), and SCHAANING (1933).

According to PETERS (1934) the Northeast Greenland ptarmigan must, on account of a prior claim to the name *groenlandicus*, be given a

new name, and he proposes the designation *captus* PETERS (= *groenlandicus* SCHIÖLER). Under that name the ptarmigan figures in the paper by DEGERBØL and MØHL-HANSEN (1935).

Having learned that the ornithologist FINN SALOMONSEN had just finished an examination of all the skins of *Lagopus mutus* from Arctic areas kept at the Zoological Museum of the University of Copenhagen, as well as of many skins kept at other museums and collections, I applied to him for the information required. With great readiness SALOMONSEN placed his knowledge at my disposal. From this it appeared that LEHN SCHIÖLER's distinction between the two races in West Greenland can hardly be maintained, and SALOMONSEN therefore regards them as one race, *rupestris* GMELIN. According to SALOMONSEN, the skins brought home from Angmagssalik and Kangerdlugssuak on the southeast coast of Greenland must also be referred to *rupestris*. The southern limit for the Northeast Greenland ptarmigan *captus* must, according to SALOMONSEN, be drawn at the Blossville Coast. I am very grateful to FINN SALOMONSEN for this detailed information. For further particulars the reader is referred to SALOMONSEN's work, which has just appeared in: Medd. om Grøn. Bd. 118, Nr. 2, 1936.

After SALOMONSEN's revision the case stands thus: In Greenland there only occurs one species of *Lagopus*, viz. *Lagopus mutus* MONT., which is represented by two races, *rupestris*, present throughout the west coast and along the east coast northward to Kangerdlugssuak, and *captus*, living in Northeast Greenland northward from Blossville Coast. The northernmost locality established with certainty for *rupestris* on the west coast is Upernivik; however, since *rupestris* is at hand from Grinnell Land (82°46' N. lat.) not far from the north coast of Greenland, it must be supposed to occur on the west coast up to a similar latitude, where ptarmigans are known to occur, for instance at Thule (cf. FREUCHEN 1921). The northernmost locality ascertained with certainty for *captus* on the east coast is Danmarkshavn; but ptarmigans have been observed farther north, too, thus at Cape Bridgman (latitude 83°13' N.). The limit between *captus* and *rupestris* must lie on the north coast of Greenland, but where is not known with certainty, no material having been brought home. Finally, it should be stated that *captus* has not been observed outside Northeast Greenland, and is accordingly endemic for that area.

According to systematists, there are rather considerable differences in the Greenland races of ptarmigans. Thus *captus* is the biggest, the size, according to SALOMONSEN, increasing with the geographical latitude. Two of the botanists who have made analyses of the contents of ptarmigan crops, and one zoologist state the weights of the ptarmigans investigated. The table below gives the weights for Northeast Greenland (73°—74° N. lat.), Spitsbergen, and Jotunheimen (Norway), after SCHAA-NING (1933), ARBO HØEG (1929), and LID (1927).

Table 2. Total weight of ptarmigans from various areas.

<i>Lagopus mutus</i> MONT.	East Greenland SCHAANING 1933	Spitsbergen ARBO HØEG 1929	Jotunheimen LID 1927
Season at which the ptarmigans were killed.....	July—August 1930--31	End of Sept. 1928	January—March and June—August
Number of killed ptarmigans (all grown-up).....	5	6	18
Mean weight in g.....	502	704	439

As will be seen, the number of ptarmigans weighed is but small, but at any rate the Spitsbergen ptarmigan seems to be distinguished by a great weight. As far as I know, no weighings of the West Greenland ptarmigan are available; however, since weight is an easily definable concept and can far more easily be uniformly determined than length of wings, total length, and other biometric concepts, I should much recommend to future investigators to undertake determinations of weight. Made at different seasons of the year and at different places, they may also furnish valuable data as to the state of nutrition of the ptarmigan.

Occurrence and frequency.

Between Cape Dalton and Danmarkshavn the ptarmigan (*Lagopus mutus captus*) has been observed in all areas ever visited and by nearly all travellers. To and including Sabine Island (74°30' N. lat.) the species has been observed at all seasons of the year, and must accordingly as far north as this place be considered a stationary bird, even though in winter it roams about a good deal in order to find snow-free stretches with sufficient food. North of Sabine Island the species has, indeed, been observed once even at midwinter, but information of larger flocks from the wintertime is, as far as I know, not available.

However, it would be too hasty a conclusion on that ground to reject the possibility that the bird may winter in greater numbers in this high geographic latitude, since ornithological investigations in these regions have only been made in altogether three winters in two different places. It must be borne in mind that the darkness essentially impedes observation, not only on account of the failing daylight in itself, but also because it hinders the undertaking of journeys. The two ornithologists who have wintered in these regions, remained, as far as can be gathered from their reports, indoors during the dark time, or at any rate within the very limited area that may be traversed on foot in the moderate light in the middle of the day lasting hardly more than

two hours. Their areas of investigation in the dark time¹), therefore, constitute only two points of this vast country. When, moreover, it is taken into consideration that the ptarmigan precisely in winter principally gathers in places where the snow-free vegetation is of such a kind that it is suitable food for it, it seems natural to assume that the negative or very sparse positive results relating to the presence of the ptarmigan obtained by the ornithologists during the dark time are due partly to the failing light, partly to the fact that their wintering places may possibly have been poor feeding grounds for the ptarmigans. As regards the northern part of the west coast of Greenland BERTELSEN (1932, p. 55) has raised similar objections against a denial of the occurrence of the ptarmigan on the basis of negative results gained during the dark time, since here, too, they may actually be due to deficient investigations. The question as to whether the ptarmigan passes the winter in large numbers north of Sabine Island must therefore for the time being be left open (cf. however p. 54). Observations from the area between Franz Joseph Fjord and Sabine Island show, however, that by midwinter the ptarmigan is often not observed for weeks, or even months, if one is staying in areas with a deep or moderate snow-cover, while in other, less snow-covered areas numerous ptarmigans, often in flocks, may be observed all through the winter even in the dark time. Since the vegetation conditions of these winter feeding grounds are but slightly affected by the deviations of a single year from the climatic norm, but should rather be regarded as to some extent conditioned by the norm, I consider it probable that the ptarmigan may here, as a rule, find the conditions it requires, and consequently that the ptarmigan in normal years will winter in the area in the same numbers in which it is present in the respective years.

Since, as far as is known, winter feeding grounds may possibly be present even north of Sabine Island, I do not consider it improbable that future investigations may establish the occurrence of the ptarmigan as a stationary bird northward to and including Germania Land.

In the following pages the earlier literature on the occurrence and frequency will first be considered, and next my own investigations on the subject will be given.

Earlier investigations.

A fairly copious literature is available on the occurrence and frequency of *Lagopus mutus captus* in Northeast Greenland, part of which has been cited above. It would take us too far to quote in detail all the

¹) By the dark time I mean the period of the year when the sun is constantly below the horizon, viz. c. November 9 to February 4 (in latitude 74° N).

available literature on the subject, all the more so since part of this literature is already known and has shown with certainty that the ptarmigan may be met with practically along the whole coast; but apart from this, it often does not supply us with certain data for an estimate as to the frequency of the ptarmigan at the different seasons of the year or of its seasonal migrations. Often the information given about the latter is very sparse, simply because there has been no opportunity of obtaining a knowledge of them in whole or in part, or, what is even worse, the information is directly misleading, since attention is not called to the deficient investigations during the dark time, which has already been mentioned in the preceding pages. So long as ring-marking has not taken place, a demonstration of the seasonal migrations will always be connected with great difficulties and remain somewhat uncertain. If, however, variations in the access to food at the different seasons and in the different areas, based on reliable investigations of the vegetation and the nature of the food, can be connected with remarkable fluctuations in the stock of ptarmigans, we shall have a clue to an understanding of the cause of the seasonal migrations, and accordingly a greater or smaller guarantee of a correct interpretation of the ptarmigan migrations, which may seem rather confusing on a superficial view. Moreover there will be a possibility of distinguishing within the literature on ptarmigans which details are essential and which are unessential in this respect.

Since, as will appear from the following, I believe that within my botanical working field I have gained an insight into the dependence of the ptarmigan migrations on the access to the vegetation at the different seasons, I take this as a guide to what to point out of the earlier literature as essential for an understanding of the seasonal migrations. I shall therefore in the following disregard travelling reports and hunting stories. On the other hand, attention has been paid to all the scientific literature which is based on personal investigations for this purpose during stays in the area, wintering, etc.

PANSCH (apud FINSCH 1874, p. 202) is the first to mention the annual variation in the food of the ptarmigan, and credit is also due to him for having given the first contribution to an understanding of the seasonal migrations of the ptarmigan. Since his precise information, on account of a deplorable misprint or error in writing, has unfortunately been ignored, I feel justified in quoting him in extenso. He writes as follows (l. c.).

“Schneehühner waren den ganzen Winter über sehr zahlreich auf der Shannon-Insel, namentlich in den Niederungen nahe dem Hafen. Sie hielten sich während dieser Periode in Ketten von 6—20 Stück und waren so wenig scheu, dass wir sie mit leichter Mühe erlegen konnten, ja sogar mit dem Ladestocke wurden einzelne erschlagen. Die Kröpfe

der erlegten fand ich meist mit jungen Weidenschösslingen vollgepfropft, aber auch mit Blättern und Sprossen von *Saxifraga*, *Cerastium* und *Ranunculus*, dagegen in denen, welche wir Anfang August erhielten, hauptsächlich Samenkapseln von Cruciferen, nebst Blättern und Sprossen verschiedener Pflanzen.

Mit dem Erscheinen der Sonne wurden die Schneehühner auffallenderweise selten und auf unsern zahlreichen Excursionen durch die Insel bemerkten wir keine. Nur am 1. Mai sah Dr. Copeland ein Paar fliegen, die noch das Winterkleid zu tragen schienen. Auch Ende Mai wurden von dem genannten Forscher hin und wieder Männchen beobachtet und eins von ihm erlegt. Dasselbe trug noch das vollkommene Winterkleid, nur auf den kleinen Flügeldecken mit einzelnen braunen Federn gemischt; der nackte Hautkamm über dem Auge war stark ausgebildet, ebenso die Testikeln. Die Stimme des Schneehuhns bekamen wir nur einmal, Ende Mai, zu hören; sie bestand in einem knarrenden Tone.

Ich vermuthe, dass die Schneehühner grösstentheils während des Sommers mehr ins Innere ziehen, wo eine reichere Vegetation herrscht, während die Niederungen der Küste ihnen im Winter insofern günstiger sind, als die heftigen Stürme die Ansammlung von Schnee mehr verhindern, sodass die Vögel leichter zu den zahlreich vorhandenen Weiden gelangen können."

This description, extraordinarily detailed for his time, gives an insight into the ecology of the ptarmigan which according to our present knowledge must be said to be brief but to the point in all essentials; in one particular only is there a demonstrable error in that the investigations are stated to have reference to Shannon Island; the expedition visited that island in the month of August, 1869, and in May—June, 1870, only. However, to anybody who studies the report of the expedition (*Die zweite deutsche Nordpolarfahrt, etc.*, bearbeitet von den Mitgliedern der Expedition, Leipzig 1874) more carefully and with a little willingness, it is immediately obvious that we are here concerned with a misprint or an error in writing, and that Shannon should be replaced by Sabine. If the description is transferred to Sabine Island, it fits on all points. Everybody who has read the report of the expedition will know that the expedition ship did not lie in any harbour at Shannon Island, but that it wintered in "Germaniahafen" at Sabine Island, and that in several places in the report "Germaniahafen" is simply termed "der Hafen" (e. g. Vol. II, pp. 208 and 218). So when PANSCH (l. c.) says "den Niederungen nahe dem Hafen", it is evident that he is referring to Sabine Island.

On looking into the report of the expedition (Zehntes Kapitel: Die ersten Monate des Jahres 1870, p. 449), we shall find that TRAMNITZ and COPELAND, in the days between January 1 and 3, went on a hunting

excursion in the vicinity of Germaniahavn and brought back four ptarmigans to the ship, which then lay in "der Hafen". The succeeding mention (p. 449) of the results of an investigation of the crops of these ptarmigans indicates that they are the very same ptarmigans which are referred to by PANSCH (op cit.). If the reader has still some doubt as to whether ptarmigans occurred in Germaniahavn during the dark time of 1869—70, he should look in FINSCH (1874, p. 196), where, in the passage mentioning the winter-dress of the ptarmigan, it is stated that four ptarmigans were killed on Sabine Island on the following dates: December 9, 1869, January 2, 1870, and February 5, 1870; furthermore FINSCH, without stating the precise dates, mentions that three ptarmigans were killed in January, 1870. Accordingly, when PANSCH states that the ptarmigan was of common occurrence on Shannon Island all winter, we may safely take it for granted that he is referring to Sabine Island.

We should be deprived of a great deal of our knowledge of the life conditions of ptarmigans in previous years in Northeast Greenland if on account of the above-mentioned obvious error we were to ignore PANSCH's brilliant observations. As a point of special importance with regard to the seasonal migrations of the ptarmigans I may point out PANSCH's assumption that the rare occurrence of ptarmigans at the outer coast in the summer is due to the fact that at that season they can find better feeding grounds in the interior of the country. His supposition that it is the snow-free *Salix* areas which attract the ptarmigans to the outer coast by midwinter, is beautifully confirmed through recent investigations of the vegetation and through analyses of the contents of ptarmigan crops (cf. pp. 23 and 145).

BAY (1894, p. 26), who wintered at Danmark Island in Scoresby Sound in 1891—92, states that in November, December, and more especially in January but few ptarmigans were shot; subsequently they increased in number, and at a certain time in the spring no small numbers were killed, and at the same time numerous tracks were observed. Thus conditions at Danmark Island in 1891—92 were highly reminiscent of conditions at Eskimonæs, Clavering Island, in the year 1931—32. And since Danmark Island, where BAY wintered, is situated at the southeast side of Milne Land in the centre of the Scoresby Sound district, similarly as Eskimonæs is situated at the southeast coast of Clavering Island in the centre of the Gael Hamkes Fjord complex, both sheltered from the prevalent winds, it seems natural to assume that the conditions of snow-cover in the two localities are much alike, and that the decrease in the number of ptarmigans by midwinter is due to the migration of the ptarmigans to more snow-free regions, and that their great frequency for some time in the spring is due to the return of the ptarmigans; subsequently there is a decrease because a number of the ptarmigans, when circum-

stances permit, travel farther into the fjords to the summer feeding grounds, in the vicinity of which their nests are built. Viewed from this angle BAY's observations agree excellently with observations from Clavering Island. BAY states that the ptarmigans usually move about singly or by two, more rarely in small flocks. This is quite correct in so far as it applies to the greater part of the year. But evidently he has not observed the ptarmigans in good winter feeding places, where they may occur even in very great flocks; and as a matter of fact he is of the opinion that the hunters of the expedition had not learned to seek the ptarmigans in the right places at midwinter. BAY further states that in the winter the ptarmigans particularly haunt places free of snow.

DEICHMANN (1909, p. 145) observed several flocks of ptarmigans on Jameson Land in Scoresby Sound, and further a female ptarmigan with a flock of newly hatched chickens on Sabine Island. This shows that the ptarmigan may also be found with young even on the outermost islands, where, by the way, it must be assumed to be considerably rarer during the summer than in many places farther towards the interior of the fjords.

MANNICHE (1910, p. 111) has given a particularly detailed account of the occurrence of the ptarmigan at Danmarkshavn and the adjacent parts of Germania Land, and further supplied the very few data at hand concerning ptarmigans north of this area. It appears from his account that the ptarmigan occurs, though sparsely, from the outermost coast right in to the nunataks lying north of Dronning Louise Land, thus on the Ymer Nunatak 60 km westward from the edge of the inland ice. Despite careful investigations in the dark time neither ptarmigans nor tracks were observed during that time. Hence there is hardly any doubt that MANNICHE is right in his conjecture that the ptarmigans left the region round Danmarkshavn during these years. In his opinion they moved towards the south, though probably not for long, since they returned immediately when the sun again appeared over the horizon. This may be possible, but it is quite possible, too, that the ptarmigans merely moved to the coast, extending in the direction north-south, east of Danmarkshavn, where the north wind has free play, while Danmarkshavn, at any rate judging from the topographical maps, has a comparatively sheltered situation. For this reason the snow-cover is fairly constant round Danmarkshavn, which was already pointed out by WEGENER (1912, p. 352) and appears also from the photographic material of the expedition. The vegetation should not present any obstacle even to a slight northward advance of the ptarmigans. Thus TH. SØRENSEN has informed me that the Skærfjord harbours an astonishingly rich vegetation, even though the area must be said to be poorer in vegetation than regions lying farther south. Great Koldewey Island and

Shannon Island must be presumed to afford good life conditions for the ptarmigans in winter. More especially on the latter, where large stocks of musk-oxen are able to find sufficient *Salix* and glumiflores all winter, there must be assumed to be snow-free *Salix* growths large enough to supply food for hundreds of the quantitatively far less exacting ptarmigans.

MANNICHE further states that in October, towards the time of their departure, the ptarmigans appeared once more on the coastal plains round Danmarkshavn, to disappear again in the dark time. Thus MANNICHE's observations show as distinctly as those of BAY that the wintering place of the ornithologist was no winter feeding ground for the ptarmigan. However, this need not mean, as BAY states for Scoresby Sound, that the winter feeding place was very distant; this is also the opinion of MANNICHE, though he assumes that it lies south of Danmarkshavn.

MANNICHE's statement that ptarmigans were observed by KOCH and BERTELSEN in 83°12' N. lat. and that they must have been of frequent occurrence on the west side of Danmark Fjord, where thirteen ptarmigans were killed, is of the greatest interest, it being thereby proved that in the period May—August the ptarmigan is able to sustain life even in the northernmost parts of Greenland. The diary of JØRGEN BRØNLUND (edited by ALF TROLLE 1934) contains some notes on ptarmigans from Danmark Fjord. In 1907 the following numbers of ptarmigans were shot on the following dates: May 8, two; June 4, two; August 6, two; August 12, one; August 26, thirteen ptarmigans.

From the fact that thirteen ptarmigans were killed on August 26, 1907, it cannot, perhaps, be definitely concluded that the ptarmigan multiplies in these latitudes, but it is very probable. Flocks of thirteen in the month of August are likely to consist in part of chickens. As moreover, judging from the vegetation, it may be considered probable that there will not be any particularly long distance to fly from localities where conditions permit the ptarmigans to sustain life during the summer to areas with snow-free *Salix* flats in the winter, the idea that it might be possible for the ptarmigan to uphold life here all the winter, cannot at the outset be rejected. However, the long duration of the dark time in these latitudes tells against this. In the northernmost parts of Greenland the dark time lasts for about five months, and it is a question whether the ptarmigan in the long period in which the lack of light probably would compel the bird to eat what first and most frequently presents itself, can actually endure the uniform winter food. For ecological reasons it would probably be better for the ptarmigan of these northern regions to migrate southward during the dark time.

ALWIN PEDERSEN (1926, p. 218) states as the cause of the sparse

occurrence of the ptarmigan in the eastern part of Jameson Land that the *Cassiope* heath is the predominant type of vegetation here. I can confirm this observation; in no place have I observed larger areas of *Cassiope*, and moreover the species forms but a small part of the food of the ptarmigan. However, no inconsiderable *Salix* areas, which may at any rate partially come into consideration as winter feeding grounds, are found on Jameson Land. But so far no information as to the frequency of the ptarmigan on Jameson Land in the winter is available. The cause of its scarcity in the summer might be, not the dominance of *Cassiope*, but rather the scarcity of *Polygonum* snow-patches and the lack of the preferred breeding biotope. Jameson Land is flat and sandy and devoid of the slightly broken rocky country preferred by ptarmigans in the summer. Personally I did not observe a single ptarmigan during a stay in Scoresby Sound, partly in Jameson Land, in the summer of 1933.

ALVIN PEDERSEN (l. c.) is possibly right in his supposition that the ptarmigans of Scoresby Sound pass the winter in the interior of the country, if by the interior of the country he refers to Jameson Land, since the *Salix* flats precisely in this flat lowland must in part be kept free of snow by the wind. PEDERSEN assumes that the reason why the ptarmigans live in the interior of the country in the winter is partly a richer vegetation, partly a less severe winter; however, this is a mixture of facts, but in part properly understood, and of partially erroneous conclusions. That the vegetation is richer in the interior of the country than at the outer coast is to some extent correct; but this is due, not to a warmer winter, but to a hotter summer; the winter must be assumed to be severest, that is, coldest, in the interior of the country, as is also indicated by WEGENER's measurements at Danmarkshavn and Pustervig situated west of it. The relatively luxuriant vegetation in the interior of the country, however, is of no benefit to the ptarmigan in the winter, when it is covered with snow, and the snow-free vegetation must be even more xerically marked in the inner parts of Scoresby Sound than in the interior of the more northerly fjords, which do not extend so far inland. This also appears from HARTZ's investigations of the vegetation (1896, 2). The winter feeding grounds within Scoresby Sound can hardly be situated farther west than Jameson Land.

Of interest are PEDERSEN's statements about the frequency of the ptarmigans round Amdrup Harbour, where he spent two winters. The land is here extraordinarily sterile. Only west of the colony situated there, is there a valley with a fairly luxuriant vegetation; however, it gives the impression of being snow-covered in the winter. Round the colony proper, which I visited in 1933, the substratum consists of crystalline rocks, which, however, where not polished by the ice, are

covered by a thick carpet of moraine blocks and marine pebbles. There is a constant risk of straining one's feet, and as a botanist I was on the verge of despair on account of the lack of vegetation. Only on some steep rock walls, where water oozes down, are there some continuous green patches of vegetation; however, they are inaccessible to human beings without the aid of ropes. It is therefore not to be wondered at that ALWIN PEDERSEN (l. c. p. 219) states that if the ptarmigan was rare in the winter, it was not observed at all during the summer. For it would be almost impossible and at any rate dangerous for the unfledged young to feed on the steep rock walls. Farther westward, in the broken ground round C. Hope, PEDERSEN found the ptarmigan to be rather frequent, but in the country round Hurry Inlet he saw only some few specimens.

During ALWIN PEDERSEN's second wintering the ptarmigans were more frequent, and in the winter haunted the vegetation of the steep rock walls, whereas they seem to have been of sparse occurrence in the summer. However, their nesting places were found. Finally PEDERSEN assumes that during the breeding period the ptarmigan is most frequent in the interior of the land.

PEDERSEN (1930) remarks in passing that by midwinter an invasion of ptarmigans from the north was traceable. However, this question must be left open, for the birds may very well have come from the interior of the land, where PEDERSEN himself believes that the ptarmigans are most frequent in the summer.

LØPPENTHIN (1932, p. 45) states that within the area of Gael Hamkes Bay and Franz Joseph Fjord the ptarmigan is presumably most frequent in the interior of the country during the summer.

SCHAANING (1933, p. 15) supplies the first figures of value for an estimate of the numbers in which the ptarmigan may occur. The figures are based on statistics of the ptarmigans killed at the Norwegian hunting stations, worked out by the leader of the Norwegian Svalbard Office, Professor A. HOEL. In the following I shall quote SCHAANING's figures; in order to facilitate a general view, I have arranged the various districts according to their distance from the outer coast. In this connection it should be mentioned that the region designated Clavering Fjord by SCHAANING is not identical with that called by this name on some of the Norwegian maps, but in the main comprises only the area round Cape Stosch and round Payer Land. The subjoined table is therefore only approximately correct as regards the placing of the localities in relation to the outer coast, but it may serve to guide future investigators so that they take this circumstance into consideration.

Considering that the figure 800 for Revet and Cape Stosch represents the number of ptarmigans secured during two winters, whereas all the

Table 3.
Number of ptarmigans killed at the hunting stations.

	Year	Inner parts of the fjords	Outer coast and outer parts of the fjords
Revet + Cape Stosch.....	1928—30	800	
Revet + Cape Stosch.....	1930—31	100	
Musk-ox Fjord.....	1930—31	30	
Dusén Fjord.....	1929—30	164	
Dusén Fjord.....	1930—31	86	
Cape Peterséns.....	1930—31	20	
Myggbukta.....	1930—31		300
Vega Sound.....	1929—30		1000
Vega Sound.....	1930—31		130
Antarctic Harbour.....	1930—31		10
Total 1929—30 (+1928 Revet and C. Stosch)		964	1000
Total 1930—31.....		236	440

other figures refer to those secured during one winter, the table must be said to show with great distinctness that in both the years in question the largest number of ptarmigans were killed in the outer districts. They were all shot during the winter. The question now suggests itself: How many of the ptarmigans were killed during the dark time proper, when the sun is below the horizon? As to this SCHAANING's figures give no information; however, I was lucky enough to meet with one of the ptarmigan hunters from Vega Sound, viz. the Norwegian archaeologist SØREN RICHTER, who informed me that in the period from December, 1929, to about the 10th January, 1930, he and his companion at Vega Sound shot about 300 ptarmigans. How large a number were killed during the rest of the dark time, he could not state with certainty, but it was no small number. Altogether, RICHTER informs me, the largest number of ptarmigans were observed in the dark time, when they were seen in great flocks in a snow-free tract of land immediately south of a pass in a mountain-chain striking west-and-east, through which the north wind had free play. On his approaching the place on skis in the grey of dawn, the ptarmigans swarmed out of the holes in the snow into which they had dug themselves for the night. RICHTER's observation clearly confirms what is otherwise known of the behaviour of the ptarmigans in the winter, viz. that they secure their food in areas swept bare of snow by the wind.

SCHAANING gives no data from the Cape Wynn station. However, the geologist R. BØGVAD, who wintered at Sandodden in 1929—30 and visited Cape Wynn in the course of the winter, informs me that ptarmi-

gans were frequent on the outer coast of Wollaston Foreland, where there was a specially favourable place at Cape Wynn haunted by numerous ptarmigans throughout the winter.

In the year 1932—33 ALWIN PEDERSEN wintered at Hochstetter Foreland. He has published the preliminary results of his investigations (1934). He observed only a single ptarmigan during the dark time proper, and makes the following comments on PANSCH's observations from Sabine Island in 1869—70 (l. c. p. 17): "Von der zweiten deutschen Nordpolarfahrt liegt eine in der späteren Litteratur oft erwähnte Beobachtung vor (FINSCH 1874 p. 202), nach welcher sich Schneehühner in Ketten von 6 bis 20 Exemplaren während des ganzen Winters auf der Shannon Insel aufgehalten haben. Es hat aber keiner von den Expeditionsteilnehmern im Winter die Shannon Insel besucht. Das Überwinterungsquartier an der Sabine Insel wurde erst am 8. März verlassen. Hiernach kann keine Zweifel darüber bestehen, dass, wenn nicht überhaupt ein Irrtum vorliegt, diese Beobachtung für die Sabine Insel gemeint ist. Hier wurden aber im Winter nur wenige Schneehühner gesehen, erst gegen Schluss der Dunkelzeit wurden sie häufiger, was genau mit den neueren Beobachtungen übereinstimmt und die Rückkehr der Schneehühner nach Norden betrifft."¹⁾

As already stated, I quite agree with PEDERSEN that PANSCH's statement must be assumed to contain an error, and that the observation should be referred to Sabine Island. However, apart from this error, PANSCH's description bears so distinctly the stamp of being based on the author's own observation that all idea of other errors may safely be rejected. (cf. p. 51 ff.) As I did not understand PEDERSEN's statement, that in 1869—70 but few ptarmigans were seen at Germaniahavn during the winter, I applied to him for an explanation. PEDERSEN referred me to the popular report on the expedition²⁾. But here it is not stated that the ptarmigans were only observed in small numbers during the winter. On the contrary, in the record of January 1—3, it is said: (l. c. Bd. 1, p. 449): "Herr Tramnitz und Dr. Copeland unternahmen einen Jagdausflug und brachten vier Schneehühner an Bord".

It is also doubtful what PEDERSEN means by his statement that in 1870 the ptarmigans increased in frequency towards the end of the dark time, for PANSCH (apud FINSCH 1874, p. 202, quoted pp. 51—52 of the present paper) states: "Mit dem Erscheinen der Sonne wurden die Schneehühner auffallenderweise selten und auf unsern zahlreichen Excursionen

¹⁾ Spaced by GELTING.

²⁾ Die zweite deutsche Nordpolarfahrt in den Jahren 1869 und 1870. Erster Band, Leipzig 1874.

durch die Insel bemerkten wir keine. Nur am 1. Mai sah Dr. Copeland ein Paar fliegen, die noch das Winterkleid zu tragen schienen”.

Since PANSCH's statement is accompanied by several specimens of ptarmigans killed at Germaniahavn in the period December—January 1869—70, we may safely let his words stand.

The author's own investigations.

My own investigations of the occurrence and frequency of the ptarmigan are chiefly limited to the south coast of Clavering Island, where I spent by far the greater part of my wintering time in 1931—32. However, on my journeys I obtained a fairly good knowledge of the vegetation and the animal life at the outer coast between Hold-with-Hope to the south, over Jackson Island, Clavering Island, and Wollaston Foreland to Sabine Island in the north. In the interior of the country, at the heads of the fjords, I stayed for some weeks in the summer, thus on Payer Land and in the inner parts of Wollaston Foreland. To Loch Fyne I paid short visits both summer and winter. I have only travelled twice through Musk-ox Fjord in the winter. At the station at Mt. Gunvor in Nordfjord I stayed for some weeks in the winter. Thus it is principally the occurrence of ptarmigans at the south coast of Clavering Island I am able to describe.

During the first half of August, 1931, ptarmigans were not common in the lowland at the south coast of Clavering Island. From about August 20 to September 11 only some few ptarmigans were seen in the lowland between Eskimonæs and Eskimobugt. On September 16, shortly after a slight snowfall, a flock of ten to twelve were seen on the slopes of the cape of Eskimonæs. They flew from one patch of vegetation to another, and often used their wings to gain a foothold, which I have never observed ptarmigans do except in this place, where narrow rock ledges alternate with steep walls. As far as I could observe, they were all in winter plumage.

On September 27 I climbed the mountains in company with the archæologist HELGE LARSEN. On the plateau behind Eskimonæs, at an altitude of 900—1100 m, we came upon several flocks of ptarmigans, all in winter plumage. The plateau was largely free of snow, the wind having swept the snow into flat, firm drifts (cf. fig. 23, p. 61). The birds were at work in the naked soil, where *Polygonum* was present, though not in very great quantities. The still bulbiferous winter standers were seen at intervals on the frozen soil. Whenever we approached a flock, the birds took wing and settled on a snow-drift nearby, over whose surface they were seen to run with great rapidity before stopping after their flight through the air. It was remarkable that it was possible to approach considerably nearer to the ptarmigans when they were sitting on the

snow-drifts than when they were on the snow-free ground. In fact, it seemed as if the birds felt safer there, and on account of their white winter plumage it was actually more difficult to distinguish them. Now and then the warning calls of the male birds were heard, which have been best rendered by HARTERT (1923) as "orrrr, orrrr" with rolled r's. On October 9 I again visited the plateau. In a valley with patches of vegetation free of snow a small flock of about ten ptarmigans was observed. On October 8 ALWIN PEDERSEN killed three ptarmigans at



Getling phot. September 27, 1931.

Fig. 23. The 1000m Plateau at Eskimonæs, where the ptarmigans were observed on September 27. In the background the plateau surface is distinctly seen, as also the basalt sill in the mountain "Pladen". The cairn-like erosion-remnant is Steinnmann Spitze.

Eskimonæs. On October 11 two were seen at the Granatdal. From this date till December 20, as far as I know, no ptarmigans have been observed by any of the members of the wintering party at Eskimonæs. It must be presumed that there have not been very many, at any rate in the lowland.

From November 2 to December 19 I undertook a journey from Eskimonæs through Loch Fyne and Musk-ox Fjord and onward to the head of Geolog Fjord. The return journey was started through Musk-ox Fjord, but since the heaviest snowfall during that winter occurred on this journey, we did not succeed in travelling through Musk-ox Fjord, but had to return to Nordfjord and go through Franz Joseph Fjord via

Myggbukta and Loch Fyne to Eskimonæs. On this journey ptarmigans were only observed twice, viz. a flock of about 20 birds at the head of Loch Fyne on November 3, and a flock of ten at the foot of Mt. Gunvor on November 16.

In the days before Christmas, 1931, the snow-cover was deep at Eskimonæs. Nevertheless SCHWARCK killed two ptarmigans here on December 20. During Christmas time we only made short strolls immediately outside the house and consequently saw no ptarmigans. However, one ptarmigan was killed on January 2, 1932.

By the middle of January I heard for the first time after a long interval the orrr-orrr of the male ptarmigan, and on the slopes of the cape of Eskimonæs observed a flock of some 5 or 6 birds. However, the few observations made from Christmas time till then were probably due to the lack of outdoor excursions. On February 1 or 2 the trapper HERDAL made an excursion on skis in the territory round Eskimonæs for the purpose of shooting ptarmigans to be used for catching foxes, but he had no success. On February 11 I left Eskimonæs, travelling with the trapper EWALD RASMUSSEN via Jackson Island to Knudshoved on Hold-with-Hope. On March 17 I returned to Eskimonæs. During this interval ptarmigans were but rarely observed at Eskimonæs, according to the reports of my comrades at the station. At Knudshoved, however, numerous ptarmigans were seen from and including February 13, moving about in flocks, sometimes numbering some 20—30 birds, on the flat land round the station, where there was nearly everywhere sufficient *Salix* food for them. I made several sledge trips across the inland of Hold-with-Hope, which was free of snow over wide stretches, whereas the low flat valley systems extended for miles into the country, forming snow-clad thoroughfares for sledging. Practically every day I saw ptarmigans. In Tobias Valley, behind Carlshavn, ptarmigans were also observed. The Gaasepas and the Slædepas in the headland of Knudshoved had been visited by ptarmigans for some time, to which the numerous large and fresh heaps of excrements in the block fields testified. Here ptarmigan No. 9 was killed just as it was leaving its shelter from the wind in the block field.

On my return to Eskimonæs on March 17 the stock of ptarmigans there had for some time been increasing. On the same day ALWIN PEDERSEN shot six ptarmigans, one of which was an old cock, the remainder being young hens. On March 19 four ptarmigans were killed, one was an old cock, the others were hens. During the subsequent time ptarmigans were rather frequently observed in the lowland, but the flocks grew smaller and smaller, and even in April rarely more than two birds at a time were seen. From April 29 to May 15 I travelled through Young Inlet and along the outer coast to Germaniahavn. On May 4, between 2 or 3 in

the morning, I observed a small flock of ptarmigans, five or six, feeding on the small morainic spit east of Zackenberg (cf. fig. 44, p. 139).

On May 19 I shot an old cock at Cape Mary. On May 27, judging from observations made at Baadsted, the copulation was in full progress; here a hen, partly in summer plumage, and a cock, apparently entirely in winter plumage, were seen. On June 1 a hen in full summer plumage was seen on Falske Næs west of Eskimonæs, which, judging from its behaviour, might be presumed to have its nest there. It continued to return to the place where I first observed it, uttering the same clucking sounds as hens do when they have chickens. I assume it had eggs.

From that date to the end of July ptarmigans were hardly seen. On July 20 I shot an old cock, and from the end of the same month hens with chickens were common in the lowland at Eskimonæs and Granatdal. Thus I shot a hen and one chicken nearly ready to fly at Eskimonæs on August 1. There was no great difference in size between the mother and the chicken. During the whole first half of August ptarmigans were numerous in the lowland, but a decrease in frequency was noticeable by the middle of the month. In August, 1933, their frequency was about the same as in 1932 on the south coast of Clavering Island, perhaps slightly higher; on August 24, 1933, the crew of the s. s. "GUSTAV HOLM" killed about a score of ptarmigans.

Seasonal migrations.

If we compare the data from Vega Sound, supplied by RICHTER, and those from Cape Wynn, supplied by BØGVAD — two areas the former of which lies nearby, the other at the outer coast proper — with my observations from the outer coast at Knudshoved, the conclusion must be drawn that by midwinter of the years in question a migration actually took place from the interior to the outer coast. PANSCH's data from Sabine Island indicate that a similar migration took place in the winter 1869—70.

PANSCH assumed even then that in the summer the stock of ptarmigans was richer in the fjords than at the outer coast — a fact about which all seem to agree at the present time. — His ground for this assumption was that the vegetation inland was richer, and this has been confirmed by recent investigations of the vegetation, at any rate as regards the species of importance to the ptarmigan in the summer.

However, since conditions in the winter are quite different on account of the snow-cover, and the relation of the vegetation to it, and the actual ptarmigan feeding grounds in the fjords are, as a rule, confined to soil covered with snow, while at the outer coast they are associated with less snow-covered, often wind-eroded, soil, it may be assumed that a migration to the outer coast of the ptarmigan stocks of the fjords is

the rule in the winter. The vegetation here supplies us with the indications necessary for supplementing the relatively sparse observations on the migration and the frequency of the ptarmigan. Of these the results for three winters agree.

Without investigations of the vegetation and without systematic analyses of the crop contents, the scarcity of ptarmigans in the fjords in midwinter might easily suggest that the ptarmigan is in part a migratory bird which goes south in the middle of the winter. However, the frequency of ptarmigans at the outer coast in the winter would seem to show that this is not so, but that it migrates eastward roughly in the same latitude. Accordingly the ptarmigan may be characterised as a stationary bird with a tendency to roam.

Further we are now able to understand the older, but no doubt erroneous, views held by HELMS (1926) and ALWIN PEDERSEN (1930), according to which the bird moves towards the south in the middle of the winter.

Both authors explain the sudden, but very varying, rise in the stocks of ptarmigans during the winter in the outer districts of Scoresby Sound and Angmagssalik as due to an immigration from the north; but for both districts the true explanation may quite well be, that here, as in the more northerly areas, a migration takes place from the interior of the country in the winter.

A migration southwards to Scoresby Sound, cannot be proved without marking with rings the ptarmigans living along the coast north of Scoresby Sound; for the ptarmigan occurring in Scoresby Sound does not differ from that occurring north of this place. They both belong to the race *captus*. As regards Angmagssalik, an immigration of ptarmigans from the north may for the time being be denied, so long as the race *captus* has not been killed at Angmagssalik. For the ptarmigan indigenous to this locality belongs to the race *rupestris*. As regards its food, there is no reason for the ptarmigan to go south, since the snow-free vegetation of the outer coast must be supposed to afford more than abundant feeding for the ptarmigan stock of Northeast Greenland. Altogether it will be difficult to point out plant species more frequent in Northeast Greenland than *Salix arctica*, *Dryas octopetala*, and *Saxifraga oppositifolia*, the three plants which form the main part of its winter food. Moreover, the snow-cover in the winter increases enormously on the east coast of Greenland with decreasing geographical latitude, at the same time as the crust-snow, so hampering to the ptarmigan, and due to alternating positive and negative temperatures, grows more common. The illumination also is not particularly good at Angmagssalik in the winter. The increasing cloud-covering and the growing number of days with precipitation make themselves felt.

The question as to whether the ptarmigans on the east coast of Greenland north of 74°30' N. lat. are stationary birds that, like their more southerly relatives, migrate largely within one latitude only, or whether, as presumed by MANNICHE, they move some distance towards the south in the winter, must for the time being remain open. If they go south, this may partly be the cause of the abundance of ptarmigans in the winter along the outer coast between 72° and 74° N. lat. According to our present knowledge, it would be of little use for them to go still farther south, since the outer coast between Traill Island and Scoresby Sound does not, like the more northerly coasts, present any fertile areas.

Between Scoresby Sound and Germaniahavn, a slight shifting towards the south of the ptarmigan stocks possibly takes place in the winter, as is the case in northern Europe with the crows (*Corvus cornix*); however, no opinion can be given on this question until a systematic ring-marking has been carried out.

In addition to the migration to the outer coast various trends in the migrations of the ptarmigan can be demonstrated at different seasons of the year. Thus a migration into the mountains analogous to that recorded in the literature from other parts of Greenland (WINGE 1898, BERTELSEN 1921), can be shown to take place.

This migration into the mountains, which on Clavering Island in 1931—33 took place in August—September, may be connected with the period when the snow-patches melt and with the degree of development of *Polygonum* in snow-patches with different periods of melting. From the analyses p. 153 it would seem that the young bulbils, and on the whole the young spikes, are richer in proteins than the older ones. It further appears from the contents of the crops that it is principally the young organs that are devoured by the ptarmigans. As long as the young spikes and bulbils are present in sufficient quantities in the lowland, where the snow-patches first become free of snow, the ptarmigan remains there. In normal years this will probably be the case until the middle of August. At that time the *Polygonum* spikes will, as a rule, be full-grown, and their food value will decrease day by day, the bulbils falling to the ground, whereas at higher levels, where the *Polygonum* snow-patches become free of snow later in the year, and the development of the vegetation is on the whole delayed, they are still found in the younger stage rich in proteins. The observations given in p. 60 ff. may therefore be explained as observed stages in a migration of the ptarmigan up the mountains in search of *Polygonum*, commencing in August and not yet completed at the top of the plateaus (900—1100 m) at the beginning of October.

It is true that examined crop contents from September are not at hand, but the direct observations showed that it was *Polygonum* which

the ptarmigan ate in the mountains. However, from Spitsbergen we know, from analyses of the contents of crops made by ARBO HØEG (1929), that in September the ptarmigan there lives chiefly on *Polygonum*. As the summer is very short, and it is almost exclusively in that period that the ptarmigan has access to food rich in proteins, the ptarmigan may be presumed to change to the winter food poor in proteins as late as possible. At any rate a food rich in proteins will be of importance for the growth of the young birds, and it is a question which should be subjected to future investigation whether the migration into the mountains cannot be considered the last stage of the maternal care of the hen. It is a fact, however, that the ptarmigans seen in the snow-patches of the lowland in the month of August are largely mother-hens with their young not yet grown up, while the birds seen in the mountains are apparently grown-ups.

Finally, the time of the disappearance of the ptarmigan from the lowland in the years 1931, 1932, and 1933 agrees remarkably well with the above-mentioned state of development of *Polygonum*. According to the testimony of the wintering parties in the different years, the summer occurred earlier in 1931 than in 1932, and in 1932 earlier than in 1933, and in all three years this was also noticeable in the vegetation. In accord herewith, on August 4, 1931, the ptarmigans had practically disappeared from the lowland, while in 1932 they lingered till about the middle of the month, and in 1933, on August 25, when I left the island, they seemed to be numerous in the lowland.

Apart from these two main trends in the annual movements of the ptarmigan, which, for the sake of brevity, I will call the outer-coast-migration and the mountain-migration — the former a winter and *Salix* migration, the latter an autumnal and *Polygonum* migration — so far only the breeding-ground-migration which takes place in the winter or early spring and broadly speaking is nothing but a return to the fjords after the stay at the outer coast, is known. Although very diffuse, it is noticeable. In 1932, on the south coast of Clavering Island it occurred in the first half of March, when the ptarmigans increased considerably in number, and it may no doubt go on till the beginning of April. While thus the trappers HERDAL and BRANDAL at Revet, Payer Land, west of Clavering Island, in January and February, 1932, observed but few or no ptarmigans, BRANDAL informed me on May 21 that now the ptarmigans had come to the inner fjords round Payer Land. MANNICHE's and BAY's data from Danmarkshavn and Scoresby Sound respectively may be interpreted in a similar way.

Even though a variation in precipitation and wind in the individual years may probably considerably change the life conditions and accordingly the course of the seasonal migrations, it may be assumed with

great certainty, partly on the basis of the observations on the frequency of the ptarmigans, partly from the clue supplied by our knowledge of the vegetation, that the main features outlined here will prove to be correct.

The main lines in the ptarmigan migrations in 1931—32 may then be expressed as follows: On August 4, 1931, ptarmigans were of rare occurrence in the lowland at the south coast of Clavering Island, and accordingly the mountain-migration may be supposed to have commenced. As late as the end of September and the beginning of October many ptarmigans were seen in the mountains (the stay in the mountains was not yet over). In November a heavy snowfall occurred, and there were very few ptarmigans in the lowlands of the fjords; they must therefore be assumed to remain in the mountains or to have commenced their migration to the outer coast. In February, 1932, ptarmigans were abundant at the outer coast near Knudshoved (they were still staying at the outer coast). In February—March the stock increased in the outer fjords on the south coast of Clavering Island (the migration to the breeding places had commenced), and by the beginning of May the inner fjords had received their summer stock (the migration to the breeding places had stopped). On June 1 the first female ptarmigan that must be presumed to have a nest and eggs was seen at Eskimonæs (the breeding time had set in).

Whether in 1931 the ptarmigans ever returned to the lowland of the fjords from their migration into the mountains, or whether they one day took wing and went to the outer coast, is not known. But it is very probable that the migration to the outer coast took place before the winter solstice, since at this time the lowlands of the fjords seemed to be almost devoid of ptarmigans. They could hardly stay in the mountains any longer, since here, too, the snow was apparently deep, and probably did not accumulate into drifts or was swept entirely away by the storms until January. Observations of this, in connection with investigations of the vegetation and soil made in the summer, can be made even at midwinter, more easily than might be expected. For even if the investigations of the vegetation and soil are made in the summer, they may be helpful if we are to form an idea of the conditions in the winter, the vegetation being largely dependent on these conditions. And the driving snow whirling off the windswept mountains is such a magnificent and conspicuous phenomenon that, on merely stepping outside the door, one cannot help observing it. Huge formations of clouds often crown the windward side of the mountain, while the leeward side gives off a cloud of snow, which descends from the mountain over a distance of several kilometres, and at the same time the snow-patches on the leeward side of the mountain and the lowland below will increase. Thus

after such a period, when the mountains are swept bare, the lowlands will receive a further contribution of snow. After their stay at the outer coast the ptarmigans may therefore very well travel to the mountain ranges of the fjords, where in the late winter the snow-cover is often less deep than in the lowland. If so, the migration to the breeding grounds may possibly take place in two stages, an ascent in the winter and a descent in the spring. Not till the spring are the snow-covering conditions such that the lowland, now largely free from snow, can compete with the mountain regions as regards snow-free stretches. Finally, in early summer, the lowland becomes almost totally free of snow, while the highland, on account of the lower summer temperatures, exhibits white spots formed of lingering or perennial snow-patches.

If thus there is a possibility that the migration to the breeding grounds may have two vertical stages, the possibility of the existence of two horizontal stages must be left open, too. For in the spring the melting of the snow will set in so much sooner in the inner fjords that they may exhibit young plants in a state of incipient development before the outer coast, where the melting of the snow in the spring is often impeded by fog. It may, therefore, be assumed that at any rate certain ptarmigans go directly to the inner fjords after their stay at the outer coast, to migrate subsequently to the outer coast and the outer fjords to build their nests. As will be seen, ring-marking is much needed, among other things to ascertain whether the birds breed in their native place.

That the outer coast of Hold-with-Hope seems to be a winter eldorado for the ptarmigans, is due to the abundance of localities with a particularly favourable vegetation along this coast, more especially as regards snow-free *Salix* areas, which form the most important feeding grounds of the ptarmigan in the winter. Floristically the *Salix* heaths are not very luxuriant; however, this is a botanical phenomenon of no concern to the ptarmigan, at any rate in the winter.

Even though examples of similar localities may be found in the fjords, too, they will probably be rare. The botanists who have been at work in the area have directed their attention to this possibility, but so far no such localities have been found. And being aware that it is not due to a mere chance that the ptarmigan localities are found at the outer coast in the winter, I have by employing the terms outer-coast-migration and outer-coast-stay pointed out the special importance of the outer coast as a winter refuge for the ptarmigan.

If now, keeping in mind the conditions in Northeast Greenland described here, we turn to the available information of the life conditions and frequency of the ptarmigan in West Greenland, we shall notice certain conspicuous features in which they agree. WINGE's statement

that in many localities the ptarmigan is more frequent in the winter than in the summer, indicates that in West Greenland, too, a migration takes place to the outer coast in the winter. For the records of the frequency of the ptarmigans here are chiefly derived from the colonies, settlements, and outlying stations, the greater number of which are situated near the outer coast, the hunting of the Greenlanders being mainly associated with the sea. AD. S. JENSEN's statement (1928, pp. 65—66) that the ptarmigan moves to the coast in the winter when the crust-snow renders access to food difficult in the interior of the country, supplies direct information about the cause of the winter migration. VANHÖFFEN's information that in the winter of 1892—93 the ptarmigan was commoner at the head of Karajak Fjord than in the preceding and the succeeding summer, is, as far as I know, the only record we have from the west coast stating that the ptarmigan may be more frequent in the fjords in the winter than in the summer.

Summer and winter habitats.

Just as important to the ptarmigans as suitable winter feeding grounds is the presence of suitable places for the building of their nests and the hatching of their young and for feeding in the summer.

As has been shown in the above, there is an essential difference between the summer and the winter habitats.

Summer habitats.

The breeding biotope no doubt always comes very close to the summer feeding biotope, and for this reason they can here be treated together. The broods are most frequently found in places with good summer feeding grounds.

However, other factors, too, may play a part, thus the presence of suitable places of refuge for the chickens not yet ready to fly when they are pursued by animals of prey.

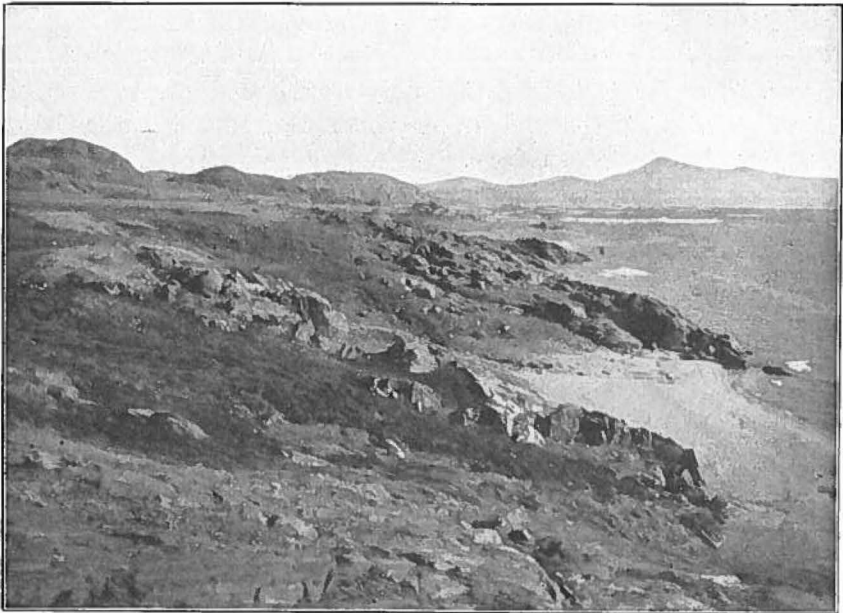
The place of the nest itself I have only observed once, viz. in Granatdal about 200 m above sea-level. The nest was situated at the base of a steep rock wall 1.5 m high, on sandy soil with a southward exposure. The place was covered by a dry heath vegetation of *Salix arctica*, among which were a number of *Carex rigida* and *Stereocaulon alpinum*. The nest consisted of a small depression in the ground. It contained two eggs not hatched.

Observations of the terrain in which the ptarmigan-broods live show that in the breeding season the ptarmigans principally stay in the slightly broken gneiss terrain, where the steep lee-sides of the rocks afford shelter for the winter snow to settle and form lingering snow-

patches, whose vegetation consists mainly of *Salix* and herbaceous plants. That is to say, precisely the types of vegetation which are rich in *Polygonum*. Such places will not be very distant either from ravines in the solid rock or block fields, where the chickens, in case of external danger, may find shelter (cf. fig. 26, and fig. 27 p. 71—72).

A proof of their persecution by birds of prey is supplied by the owl gulps, in which I have repeatedly observed the easily recognisable ptarmigan claws.

In the old Eskimo settlements one is almost always certain to meet



Gelting phot. August 8, 1932.

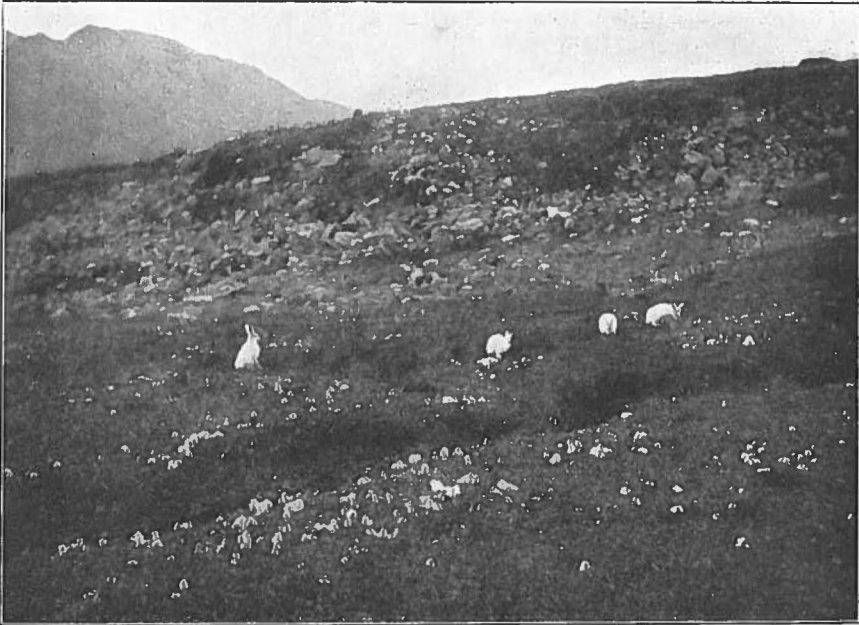
Fig. 24. Breeding biotope and summer feeding ground for the ptarmigan. In the background, left, crystalline rocks (former islands), forming domes between the raised accumulation terraces, of which the one that appears most distinctly in the figure stands at a level of about 40 m above the sea. In the lee of the rocks in the middle of the picture, numerous orographically conditioned snow-patches (now melted) with a luxuriant snow-patch vegetation are found. The darker patches indicate *Cassiope* and *Vaccinium* heaths, the light-coloured areas indicate the *Salix* heaths in the depressions. South coast of Clavering Island, looking eastward from Granatdal. In the middle of the background, Eskimonæs. To the right, Gael Hamkes Bay with Mt. Steensby in the background.

ptarmigan mothers with their broods. The archæologist HELGE LARSEN has informed me that in the summer of 1932 no ptarmigans were seen on his arrival at the Eskimo house ruins at Dødemandsbugten. On July 4 the first female ptarmigan appeared with her young. Subsequently several broods arrived, and until August 3 they were observed every day;



Gelting phot. June 24, 1932.

Fig. 25. West Harbour at Eskimonæs. The coastal plain is made up of raised sea-bottom, divided into terraces, which connect the polished moutonnée rocks. Snow-patches and breeding ptarmigans were of frequent occurrence among the rocks. In the background Norlund Alps (left) and Jordanhill (right).



H. Larsen phot. July, 1932.

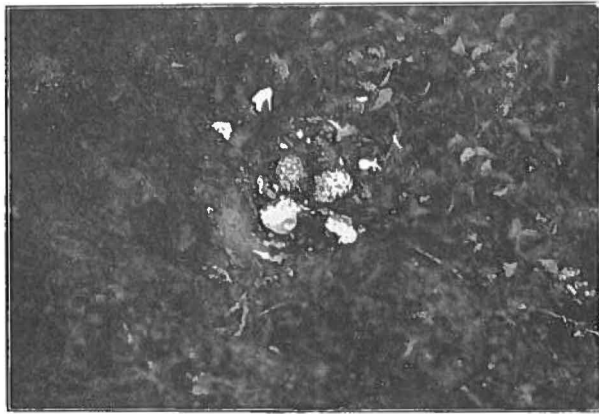
Fig. 26. Feeding biotope for the Arctic hare, here feeding on *Salix arctica*, whose catkins are seen. Among the stones in the back-ground the snow lingers long, and gives rise to the development of the snow-patch vegetation. Here is the summer feeding biotope of the female ptarmigan with its chickens. Dødemandsbugten, Clavering Island.



H. Larsen phot. July 1932.

Fig. 27. Female ptarmigan in summer plumage. Sitting quite motionless herself, she warns her chickens, which are hidden among the stones, by a persistent clucking. Dodemandsbugten, Clavering Island.

but in the evening, when the sun was low in the sky and shadows began to fall over the place, they withdrew to the ravines of the mountain sides, where they spent the night in the block fields, to appear again



Scidenfaden phot. July 30, 1932.

Fig. 28. Nest of ptarmigan in a *Salix* heath in one of the numerous terraces cut in the crystalline rocks east of Granatdal, about 200 m above sea-level. At the time the nest was found, it had been left by the hen, and the two unhatched eggs had long since rotted.

next morning among the house-ruins. On August 3 they disappeared, to return no more.

The much dissected gneiss territory between Dødemandsbugten and Granatdal presents an ideal terrain for ptarmigans, and nowhere along the whole south coast of Clavering Island was *Polygonum* more abundantly represented in the snow-patches. Thus the common occurrence of the ptarmigan here seems to be due to the possibility of securing food in the summer. Insect life, too, was more abundant here than in other



H. Larsen phot. April 27, 1932.

Fig. 29. Landscape of crystalline rocks (gneiss) at Baadsted, the south coast of Clavering Island. The photograph was taken in the winter when only the polished rock surfaces and the wind-eroded edges of a raised terrace (in the middle of the picture) were free from snow. The numerous snow-patches give rise to a luxuriant snow-patch vegetation, and the ptarmigan therefore breeds and feeds abundantly here in the summer, while in the winter it is rare or absent altogether.

places along the coast. Future investigations may possibly show that insects constitute greater quantities, at any rate in the food of the chickens, than shown by the present examination of the contents of the crops.

Winter habitats.

As already ascertained by the hunters, the winter habitats of the ptarmigan are quite different from the summer habitats.

The winter habitats are the open plains, the flat plateaus, and, to some extent, the raised marine terraces, if only sufficiently numerous

and broad. In the winter habitats the wind has free play, sweeping off the snow and thus rendering the vegetation accessible to the ptarmigans.

Since, as has been stated above, the prevalent winds of the area are of fundamentally different character as regards the humidity of the air, the westerly winds being exceedingly dry, while the northerly and north-easterly winds are generally but little dry, it will be immediately obvious that the plains which are kept free of snow in the winter by the westerly winds cannot present the same hygrophilous vegetation of *Salix arctica* as the areas which are kept free from snow by the northerly winds. It is therefore quite evident, as mentioned above, that it is the outer coast which offers the best feeding grounds for the ptarmigans in the winter (cf. figs. 17, 19, 20, 21).

In the winter of 1931—32 good feeding grounds for the ptarmigan were found along the outer coast near Knudshoved, in Grønnedal on Clavinger Island, and at Sandodden on Wollaston Foreland. Arctic hares were exceedingly frequent in the same localities. Thus in Haredal at the outer coast of Wollaston Foreland some 300 to 400 hares were observed on May 14, 1932. Similar flocks may, however, be met with in the highlands of the fjords during the winter, at times when the lowland is almost devoid of hares.

On p. 39 the importance of the snow-cover for the zonation of the vegetation is illustrated by two figures. These may also serve as illustrations in the plant-geographical characterisation of the summer and winter feeding grounds of the ptarmigan, which may be expressed as follows: In the summer the ptarmigan principally seeks its food in the types of vegetation situated inside the *Cassiope* belt, that is, in places with a deeper wintry snow-cover; in the winter it obtains its food practically exclusively from the types of vegetation situated outside the *Cassiope* belt. Since the latter (cf. GELTING, 1934) is a very prominent feature in the vegetation of Northeast Greenland, it will hardly be possible to draw a more precise limit, plant-geographically as well as with regard to the terrain.

FOOD

PREVIOUS INVESTIGATIONS

East Greenland.

Although the East Greenland ptarmigan was recorded from Jameson Lând in Scoresby Sound and from Traill Island by SCORESBY jun. as early as 1823 and from Jordanhill inside Godthaab Gulf by CLAVERING (1830), a long time passed before information was gained of its food. It was the energetic naturalist ADOLF PANSCH, a member of the Second German Northpolar Expedition, who supplied this first information (apud FINSCH, 1874, p. 202). He found that the crops of the ptarmigans killed in the winter were mainly filled with young buds of *Salix*, to a less extent with *Saxifraga* (no doubt *S. oppositifolia*), *Cerastium*, and *Ranunculus*. However, the crops of ptarmigans killed at the beginning of August chiefly contained capsules and seeds of Crucifers as also leaves and shoots of various other plants.

Probably the crops from August examined by PANSCH further contained bulbils of *Polygonum*; but he can hardly have distinguished them from the Crucifer seeds, the identification of which was no doubt made on the basis of the characteristic capsule fragments mostly accompanying them. Apart from this presumed deficiency in the investigation, PANSCH, as will be seen later, has given us an insight into the variation of the food of the ptarmigan which the recent and more comprehensive investigations have been able to add to, but not to alter materially.

EDV. BAY (1894), who wintered in Hekla Harbour at Danmark Island in Scoresby Sound on the expedition to East Greenland under the leadership of RYDER in the years 1891—92, says of the food of the ptarmigan that it consists of buds, leaves, and twigs of willow, birch (*Betula nana*), and the blue-berry plant (*Vaccinium uliginosum*), and further fruits and leaves of sorrel (*Oxyria digyna*), blue berries, and black crowberries (*Empetrum nigrum*).

From the investigations on the food of the ptarmigan made by

LINDHARD and MANNICHE on the Danmark Expedition (MANNICHE, 1910, p. 111) we know that the ptarmigans killed at Danmarkshavn in February—March had chiefly eaten *Salix arctica*, but also *Dryas octopetala* and leaf buds of *Saxifraga oppositifolia*, while the birds shot in August—September had eaten various plants and insects whose species were not determined.

According to ALWIN PEDERSEN (1926, p. 218), the ptarmigan in Scoresby Sound lives chiefly on "Kriechweiden". There can hardly be any doubt that he means *Salix arctica*, and that it is the winter food he is referring to.

In the crops of three male ptarmigans killed in the days July 30 to August 13, 1930, at Cape Stosch, Knudshoved, and in Musk-ox Fjord LOPPENTHIN (1932, p. 44) found leaves and flowers of *Dryas octopetala*, leaves of *Salix arctica*, and pebbles.

Thus it was known with certainty that the following species formed part of the food of the East Greenland ptarmigan:

<i>Salix arctica</i>	<i>Empetrum nigrum</i>
<i>Dryas octopetala</i>	<i>Vaccinium uliginosum</i>
<i>Saxifraga oppositifolia</i>	<i>Oxyria digyna</i>
<i>Cerastium alpinum</i>	<i>Ranunculus</i> sp.
<i>Betula nana</i>	Seeds of Crucifers

In the summer food were further found insects, and at all times of the year grit (quartz).

Distinct indications that there is a difference in the summer and the winter food are already to be found in PANSCH (l. c.), but it also appears from LINDHARD's and MANNICHE's investigations (l. c.). PANSCH, who presumably examined but a small number of ptarmigans, found *Salix arctica* only among the main species of the winter food. LINDHARD and MANNICHE ascertained the presence of all the three main constituents of the winter food: *Salix*, *Dryas*, and *Saxifraga oppositifolia*.

West Greenland.

On studying the ornithological literature on Greenland, which has gradually become rather copious, one will find scattered notes on the food of the ptarmigan, but it would take us too far to go through them here, all the more so since rational investigations of a large number of crops are not available. According to WINGE (1898, p. 125) the contents of crops from other parts of Greenland have contained leaves and buds of birch, willow, heather, and *Saxifraga oppositifolia*, and in the autumn and winter berries of *Empetrum* and *Vaccinium*. Of special importance is WINGE's statement that the young eat flies, beetles, and insect larvæ,

since it shows our knowledge, that the ptarmigan is not exclusively a plant-eater, to be of a much earlier date than assumed by GRIMSHAW (1925, pp. 69—70).

SALOMONSEN (1925, p. 127) states that the crop contents of male ptarmigans from the innermost part of Godthaab Fjord in the last half of June consisted mainly of leaves of *Betula nana* and *Vaccinium uliginosum*. Later in the summer he found the food of ptarmigans, whose sex, however, is not indicated, to consist mainly of fruits of *Empetrum nigrum*.

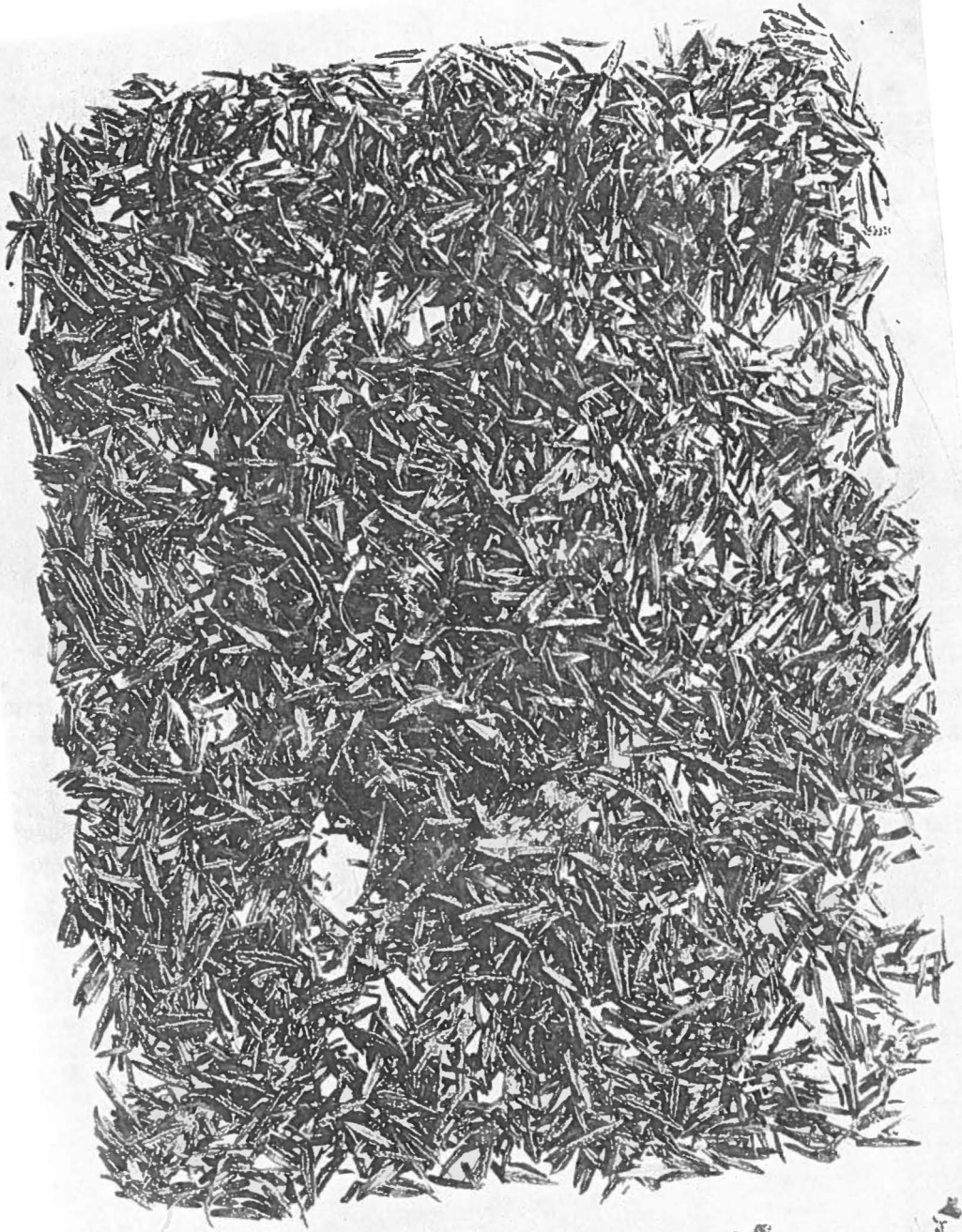
THE AUTHOR'S OWN INVESTIGATIONS

Collection and treatment of the material.

The preservation of the crops of the ptarmigans killed during the wintering was commenced in October, 1931, and continued during the subsequent months. Gradually I had collected so many that in January, 1932, I began a closer investigation of the material. This was continued all the winter whenever an opportunity offered, and it proved to be an excellent indoor work during the long winter nights. I am much indebted to my wintering companions for usually remembering to keep the crop and its contents for me when they killed a ptarmigan. Thus ptarmigans Nos. 15—17, 22—25, and 29—38 were killed by ALWIN PEDERSEN, Nos. 26—27 by SCHWARCK, Nos. 54—57 by HOLGER MADSEN, and Nos. 65—72 by the crew of the s.s. "Gustav Holm". The remainder of the ptarmigans I shot myself.

The crop of a killed ptarmigan is best taken out, and was taken out, by cutting open the breast skin by means of a sharp knife, then you grasp the crop with forefinger and thumb until you feel the narrow place where the crop passes into the gullet. The crop is then loosened by a rapid pull. In this way the crop may be taken out without breaking, and without part of the contents being lost, provided it has not been damaged by the shot which killed the ptarmigan. Subsequently the crop was put aside for some time for temporary drying.

The sorting of the material was carried out some days later in the following way. The crop was opened and the partially dried materials were emptied on to a piece of white paper for sorting and identification. The latter procedure was easy, because the material generally consisted of easily recognisable fragments of plants which are of common occurrence within the area, and the fragments could therefore mostly be identified without using a magnifying glass. By the aid of a pincet, the individual constituents were picked up and assorted, each species and its fragments being kept by itself in empty match and tobacco boxes. Finally some small fragments were left, the determination of which might sometimes cause some difficulty. Mostly, however, all the fragments could be de-



↑
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↑
3



↑
4

finitely determined, it was only in a very few cases that an unsorted remainder was left, but in no case were more than 50 mg. discarded, an amount which was quantitatively subordinate. The open boxes with the assorted material were numbered and placed in my room on a shelf to be air-dried before they were weighed.

Drying and weighing. The boxes remained on the shelf for two or three months. Then the material was weighed on a chemical balance, whose smallest unit was 50 mg. The quantities weighed, with a single exception (cf. foot-note p. 96), are therefore weighed with an accuracy of 50 mg, which with the drying method employed must be regarded as quite sufficient for our purpose. Even though, on account of the air-drying employed, there may be some difference in the water content of the material, I do not believe that air-drying of similar material can be done better by any other method. The room in which the material was kept and weighed, was always dry, and I always took care that the material should be as uniformly dried and weighed as possible.

The material from ptarmigans Nos. 43—53, which were killed in the summer of 1932, was not weighed until after my return to Denmark in October, 1932, and consequently had a drying time of three to four months. The material from Nos. 54—57, which were shot in January and March, 1933, was not weighed till September, 1933, and consequently had a drying time of seven to nine months. However, since, by the method employed, the material must be supposed to be as well air-dried as is possible in the course of two months, I do not think that this difference in the drying time is of any importance for a comparison of the weights found. If the contents of crops are to be kept for a long period, I should advise against preserving it in alcohol or other extracting liquids. For if this is done, one is deprived of the possibility of analysing the material for its content of nutritive substances. In Greenland it is possible to keep air-dried material in boxes or paper bags, but on arrival at a laboratory the material should be placed in glass vessels with tight stoppers, since otherwise it may easily be exposed to attacks by noxious animals.

The weight of the fragments. Since this weight, as will be shown below (p. 131), is of great importance for the understanding of the external

Fig. 30. Total content of the crop of ptarmigan No. 78. Young bird, sex not known. Mt. Gunvor, November 16, 1931.

- 1) About 5000 leaves of *Dryas octopetala*.
- 2) 13 fragments of branches of *Cassiope tetragona*.
- 3) 2 leaves of *Vaccinium uliginosum*.
- 4) 74 buds of *Saxifraga oppositifolia*.

No *Salix* fragments were found. The preceding night it was calm snowy weather. All nat. size. (GRAM phot.)

conditions under which the ptarmigan lives at the different seasons of the year, it will already now be discussed in greater detail. We are here concerned exclusively with the four species which constitute the main food of the ptarmigan, viz. *Salix arctica*, *Dryas octopetala*, *Saxifraga oppositifolia*, and *Polygonum viviparum*.

To determine the weight of the fragments, the number of the fragments and their total weight must be known. While the latter was determined by weighing, the number of fragments was determined by counting. This was done simultaneously with or immediately after the sorting, sometimes by counting all the fragments, sometimes by weighing and counting a sample of fragments. As the fragments of the different species are rather different, it will be best here to treat them separately.

It is comparatively easy to determine the accurate number of the *Salix* fragments, which are most numerous in the winter, when they consist almost exclusively of branches with buds, or of isolated buds. Where they occurred in large numbers, the number was determined by precise counting and weighing of a homogeneous material of one-fourth or one-third of the total quantity. Often, however, all the fragments were counted. The average weight and number of the *Salix* fragments must therefore be assumed to be so nearly accurately determined as is practicable with air-drying. This is all the more fortunate for our analyses of the life conditions of the ptarmigans, because *Salix* forms the chief food of the ptarmigan in the winter, which is the longest season of the year within the area dealt with here.

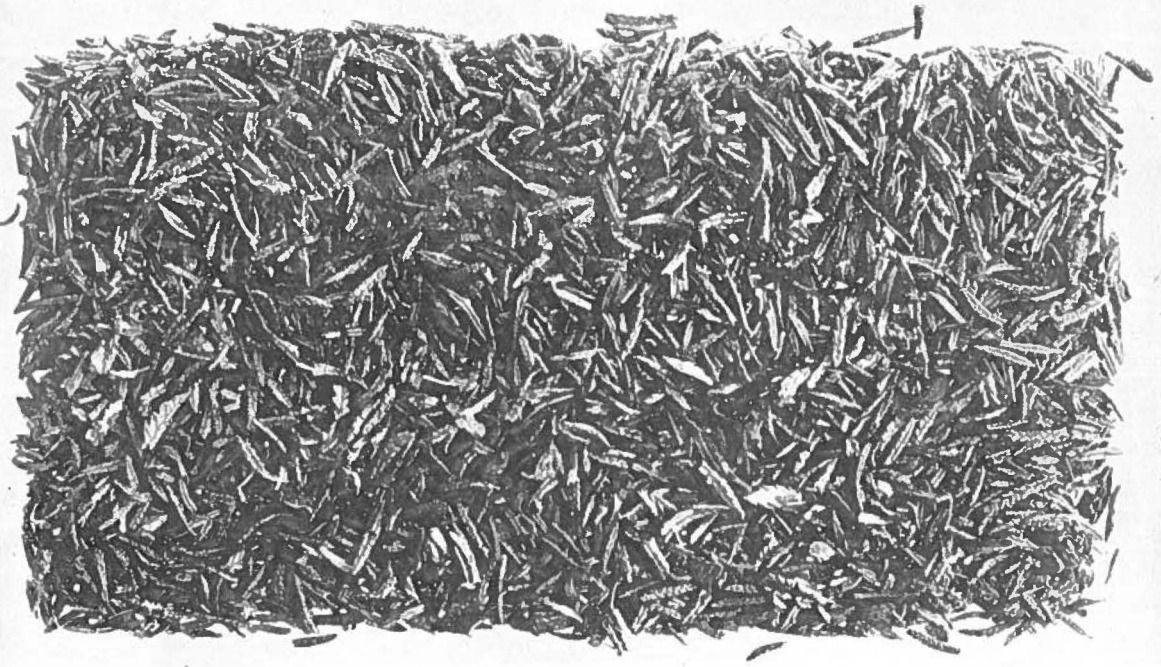
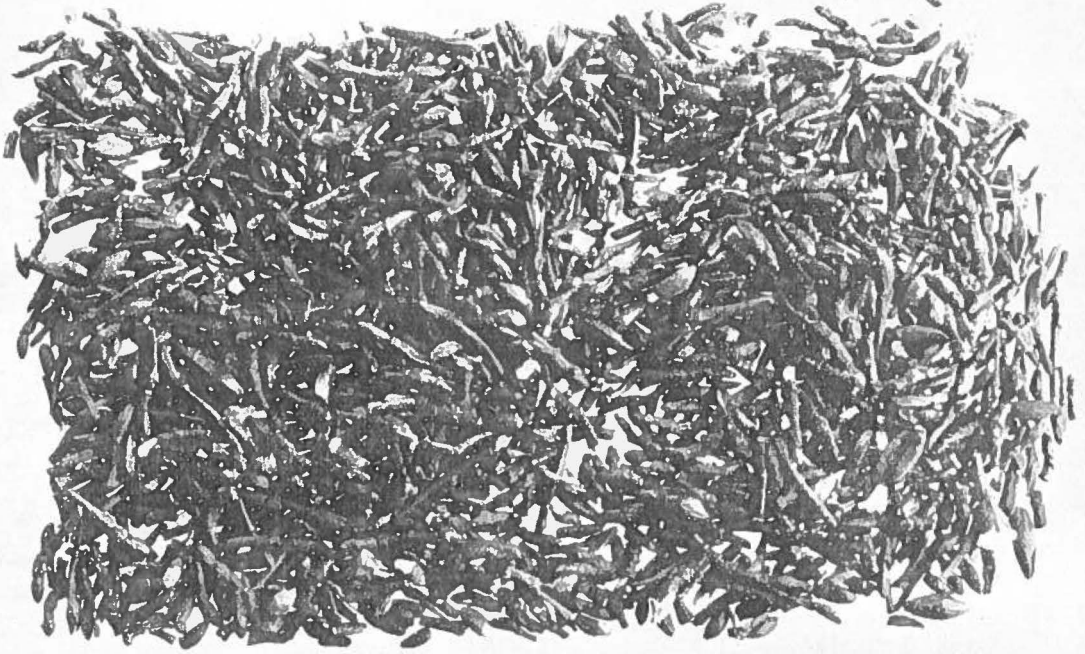
The number and average weight of the *Dryas* fragments also can be determined with fair accuracy. In the winter the material consists almost exclusively of leaves. By far the majority of these are whole and consist of the whole leaf blade, moreover often with the leaf stalk and stipules adhering. Often, however, the blade had been cut off slightly above the stalk, and sometimes it was cut off at the middle. More rarely the blade was cut off so near the apex that its size was less than half of the whole blade. In weighing the material, all *Dryas* fragments were weighed. On counting, I counted only such blades as were at least half the size of the whole blade, the smaller fragments being disregarded. The quantity of the latter was but slight, but it will be understood that the weights of fragments found by this procedure are a little too high. If when I counted the fragments I had been aware how important a factor the weight of the fragments is, I should have been able to determine it more accurately on the spot; but it was not till after my return from Greenland in 1933, when I began the final working up of the material, that I realised this; and then part of the material had been intentionally discarded because I had not a sufficient number of boxes at my disposal; this was, however, a great mistake, as I might have used paper bags.

For the time being we must be content to note that the fragment weights found for *Dryas* are somewhat, though not very much, too high. However, this is rather unimportant for their mutual comparability, the same procedure having been followed in all the *Dryas* determinations. But there is an element of uncertainty.

A similar element of uncertainty enters into my determinations of the average weight of the fragments of *Saxifraga oppositifolia*. Here the uncertainty is even greater because of the special character and fragility of the *Saxifraga* fragments, and in this case, too, it cannot be rectified.

The *Saxifraga oppositifolia* fragments consist of small parts of branches with adhering leaves. If the crop is opened immediately after the ptarmigan has been killed, the fragments will often prove to be comparatively "pure", i. e. entire. But after drying, many loose leaves are found, and it may be supposed that a large number of these leaves have fallen off during the drying. This should not influence the determination of the weight of the fragments, since we need not count the loose leaves. But the drying also makes the stems of the fragments more brittle, and accordingly they often break. I only counted the largest fragments, but weighed the total quantity of fragments, for which reason the fragment weight is only approximate. Considering the fairly large quantities of *Saxifraga* "dust" in each sample I assume that the computed weight of the *Saxifraga* fragments is somewhat too high. For the mutual comparison of these fragments at the different seasons of the year the error is of less importance than in comparisons with, for instance, the very accurately determined *Salix* fragments and with the at any rate relatively accurately determined *Dryas* fragments.

As has been shown above, the determination of the weight of fragments is difficult as regards the elements of the winter food. However, with regard to *Polygonum* a factor unknown from the winter fragments intervenes, which renders the determination of the weight of the fragments, but not of the total weight, of this species almost impossible. For *Polygonum* is mainly eaten in the summer, and the fragments which are consumed in the spring or early summer are different from those eaten in the late summer and autumn, the various organs having by then completed their summer development. It is chiefly the spike and the bulbils that are eaten; in the spring and early summer it is mainly the spike (at this time the bulbils have not yet developed), and in the autumn almost exclusively the bulbils; the time of the change from spike to more or less pure bulbils is of shorter or longer duration according to the temperature and whole climatic development of the summer, and for similar reasons the change takes place sooner or later. Thus 1932 was an early year, and the crops of the ptarmigans shot in August contained



almost exclusively bulbils; the year 1933, on the other hand, was later, and in August the ptarmigans had large fragments of spikes in their crops.

On drying the material the bulbils fall in large numbers from the spike fragments, and it is therefore no easy matter to determine the number and average weight of the latter. As regards the autumnal fragments, among which spike fragments apart from the bulbils are but sparsely represented, counting of the bulbils and subsequent weighing may give some idea of the weight of the bulbils. Unfortunately, during my stay in Greenland, I was not aware of the fact that the weight of the fragments of *Polygonum* might be of great interest, and therefore made no thorough investigation of them. However, they were not so necessary as investigations of the average weight of the winter food elements, for in the summer the ptarmigan seems to eat large quantities of this species only, while in the winter three species yield considerable contributions to the food.

It will be very difficult to ascertain how many bulbils the ptarmigan secures in one pick of its beak, but no doubt the number varies considerably. The average weight of the spike fragments (i. e. the stem of the spike plus the organs adherent to it (bulbils, bracts, floral elements)) is fairly high.

I have now mentioned the known sources of error in the determinations of the weight of the fragments, because it is such an important factor for the understanding of the life conditions of the ptarmigan at the different seasons of the year, and because this is a point that needs revision, which it will be easier to undertake when the difficulties have beforehand been pointed out to the revisor. If nevertheless in the succeeding pages I make use of the weights of fragments found, though they are encumbered with errors, it is because I have found through my analyses to which side the error tends in most cases, and accordingly in the average. In spite of the errors I have therefore a relatively good control of the results arrived at.

The weights of the *Polygonum* fragments, however, must be left entirely out of consideration.

Gram phot.

Fig. 31. The complete content of the crop of ptarmigan No. 4. Adult ♀.

Knudshoved, February 18, 1932. All nat. size.

Above, left: Buds and branches of *Saxifraga oppositifolia*.

Above, right: Various other plant fragments (cf. Table 4).

In the middle: Buds and branches of *Salix arctica*.

Below: Leaves of *Dryas octopetala*.

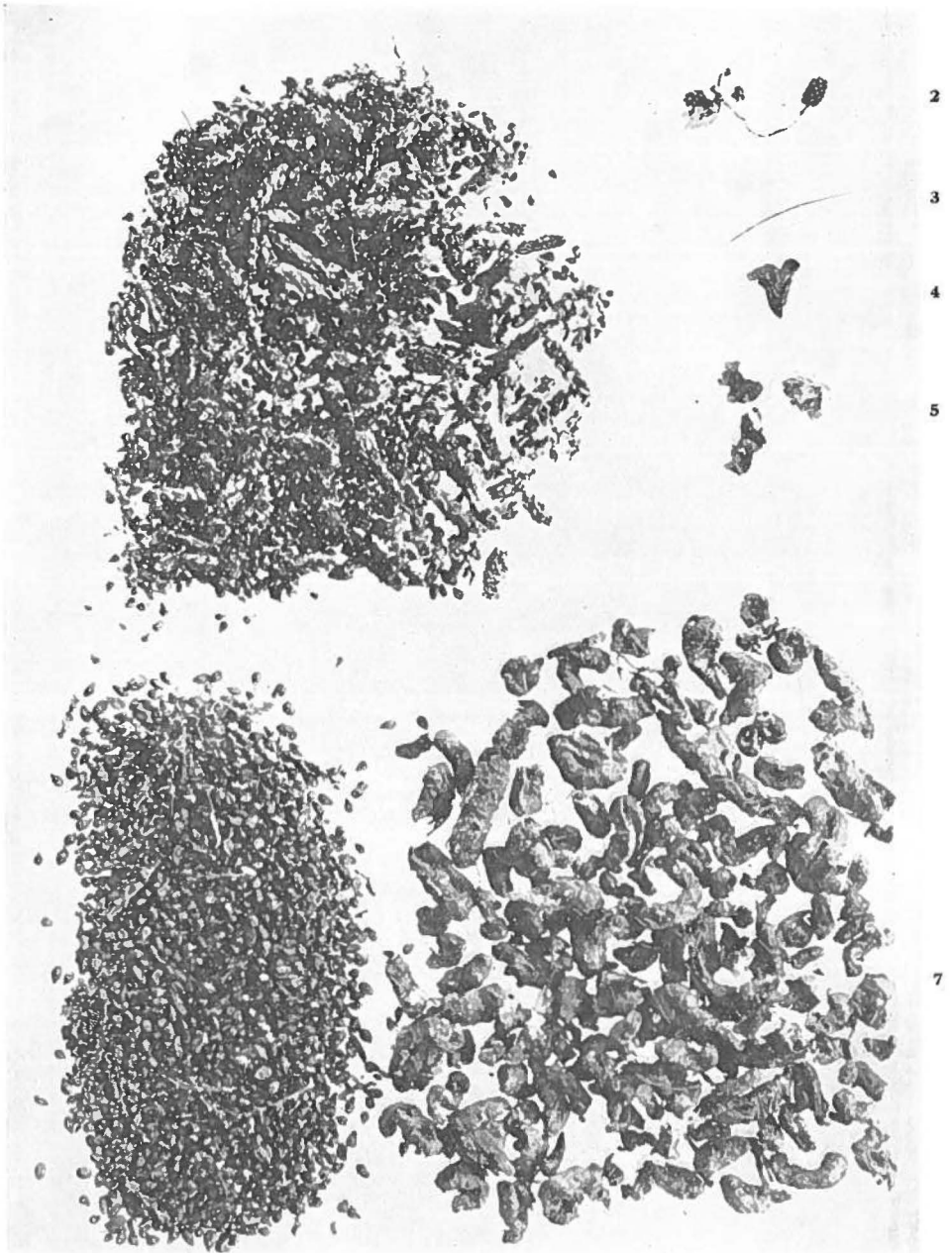


Fig. 32. 1—5, the content of the crop of ptarmigan No. 59. Young chicken. Sex unknown. Eskimonæs, August 12, 1933. — All nat. size.

- 1) Spikes of *Polygonum viviparum* with loose bulbils.
- 2) Fragment of *Ranunculus pygmaeus*.
- 3) Leaf (of *Festuca rubra*?).
- 4) Leaf of *Oxyria digyna*.
- 5) Leaves of *Saxifraga cernua*.
- 6) Unusually big bulbils of *Polygonum viviparum* from ptarmigan No. 25. Adult ♂. Head of Loch Fyne, November 3, 1931. — Nat. size.
- 7) Stem-tubers of *Polygonum* from ptarmigan No. 5. Adult ♀. Knudshoved, February 18, 1932. — Nat. size. (GRAM phot.)

Tables showing the constituents found in the crop content.

The ptarmigans killed are derived from different localities whose situation will appear from the map (fig. 33). The localities can be referred to the different districts, in accordance with GELTING (1934, p. 12), as follows:

- | | | |
|-------------------|---|------------------------|
| Sandodden | } | Outer coast localities |
| Cape Mary | | |
| Hird Bay | | |
| Knudshoved | | |
| Eskimonæs | } | Outer fjord localities |
| Granatdal | | |
| Head of Loch Fyne | | |
| Mt. Gunvor | | Inner fjord locality |

In the tables the crop material from the ptarmigans are arranged in accordance with the position of the localities, as follows

- The crop content from the outer coast in Tables 4—5
 — — — — - — fjords - — 6—10
 — — — — - inner — - — 11

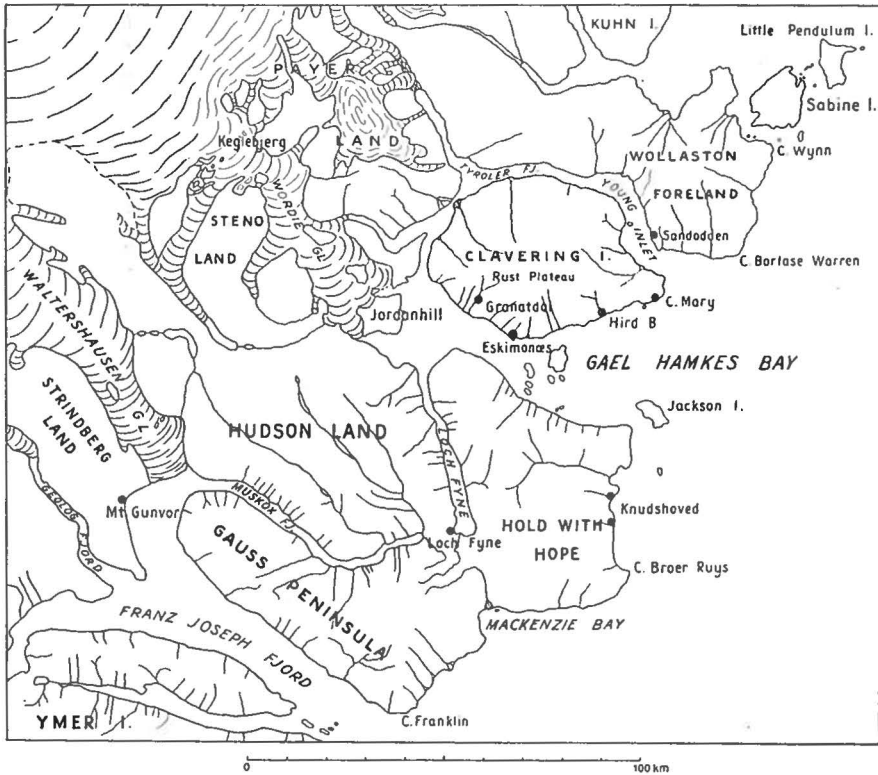


Fig. 33. Map showing the localities in which ptarmigans where shot.

The uppermost horizontal lines of the tables indicate locality, date, year, and hour, the number of the ptarmigan, sex and age, and the total weight of the plant materials found in the crop.

The vertical columns indicate the species of the plants and the nature of the fragments. The succeeding columns to the right indicate the number of the fragments (N) and their weight after air-drying (W).

The lowermost horizontal column indicates the occurrence of minerals in the crop content.

The constituents of the food are arranged in accordance with the

Table 4. Crop content from the outer coast.

Locality					
Date, year, and hour					
Ptarmigan No.		1		2	
Sex and age		♂ ad		♂ ad	
Total weight of vegetable crop content (mg).....		15350		27800	
Species	Fragments	N	W	N	W
<i>Salix arctica</i>	Buds and twigs	1000	8650	4000	20600
<i>Dryas octopetala</i>	Leaves.....	3000	5600	4000	7200
— —	Flowers.....
<i>Saxifraga oppositifolia</i>	Shoot apices	25	150	4	..
<i>Polygonum viviparum</i>	Bulbils	3	..
— —	Stem-tubers.....	22	600	2	..
<i>Cerastium alpinum</i>	Buds and leaves.....	3	..	3	..
<i>Draba subcapitata</i>	— — —	150
<i>Equisetum variegatum</i>	Sporophylls and stems	8	50	5	..
<i>Stellaria longipes</i>	Buds and leaves.....	..	150	2	..
<i>Alopecurus alpinus</i>	Leaves and stems	3	..	3	..
<i>Carex rigida</i>	Leaves.....
<i>Draba oblongata</i>	—	2
<i>Erigeron cf. uniflorus</i>	—
<i>Eriophorum polystachyum</i>	—
<i>Juncus biglumis</i>	Capsules	1	..
<i>Minuartia rubella</i>	Shoot apices	1
<i>Poa arctica</i>	Leaves.....
<i>Potentilla nivea</i>	—
— <i>pulchella</i>	Buds and leaves.....	2
<i>Sagina intermedia</i>	— — —
<i>Saxifraga flagellaris</i>	Rosettes	1	..	2	..
— <i>nivalis</i>	Leaves.....
<i>Silene acaulis</i>	Shoot apices
A fungus.....	Stalk and pileus.....
Quartz.....	Grains.....	2	..

grouping given in pp. 102—112, into main constituents, subordinate constituents, and sporadic constituents.

All weights are in mg.

All the succeeding tables, with the exception of those belonging to the physiological and eco-geographical sections, are computed on the basis of these tables.

In Tables 12 and 13 I have shown the absolute and the relative quantitative relations of the examined crop contents.

Ptarmigans Nos: 1—9.

Knudshoved 18/2 1932 3—4 p. m.										Knudshoved 19/2 1932 12 n.		20/2 1932 9 a. m.
3 ♀ ad 13800		4 ♀ ad 21600		5 ♀ ad 21150		6 ? 17700		7 ? 13650		8 ♂ ad 2500		9 ? 0
N	W	N	W	N	W	N	W	N	W	N	W	
2000	10200	1638	10250	1891	11550	2409	13550	2000	12050	300	1400	The crop was empty.
1500	2400	4500	10950	2500	5750	1800	3900	800	1500	400	1000	
..	..	1	
3	..	75	250	6	..	10	20	100	
..	..	4	7	
43	1200	165	3750	6	100	8	100	
1	..	2	..	2	..	4	2	..	
4	..	4	..	5	..	1	
3	..	3	..	1	..	2	..	1	
1	150	..	100	..	150	3	
5	..	12	..	4	
..	1	
..	
..	..	1	
..	1	
..	
1	..	2	..	3	
..	..	2	2	
..	..	8	..	1	
1	..	1	
1	..	1	..	4	
..	..	3	
..	1	
..	1	
..	..	3	2	

Table 5. Crop content from the outer coast.

Locality.....		Knudshoved				Knuds-	
Date and year.....		25/2 1932				26/2	
Hour.....		c. 12 n.				9 a. m.	
Ptarmigan No.....		10		11		12	
Sex and age.....		♀ ad		? ad		? ad	
Total weight of vegetable crop content (mg).....		28650		4000		600	
Species	Fragments	N	W	N	W	N	W
<i>Salix arctica</i>	Buds and twigs.....	3000	16550	376	1900	92	600
<i>Dryas octopetala</i>	Leaves.....	2000	4000	202	500	25	..
— —.....	Flowers.....	1
<i>Saxifraga oppositifolia</i>	Shoot apices.....	6	..	7	..	3	..
<i>Polygonum viviparum</i>	Bulbils.....	3
— —.....	Stem-tubers.....	125	2000
<i>Cerastium alpinum</i>	Buds and leaves.....
<i>Draba subcapitata</i>	— — —.....	1	..	2	..
<i>Equisetum variegatum</i>	Sporophylls and stems ..	549	5450	800	1600
<i>Eriophorum Scheuchzeri</i>	Leaves and flowers.....	..	650	5
<i>Papaver radiculatum</i>	Capsules.....	1
<i>Stellaria longipes</i>	Buds and leaves.....	10	..	1
<i>Carex rigida</i>	Leaves.....	1	..
<i>Draba nivalis</i>	Rosette leaves.....
<i>Minuartia rubella</i>	Shoot apices.....
<i>Potentilla pulchella</i>	Buds and leaves.....	1
<i>Saxifraga caespitosa</i>	Leaves.....
<i>Sedum roseum</i>	—.....
Quartz.....	Grains.....

Table 6. Crop content from the outer fjords.

Locality		Eskimonæs					
Date and year		8/10 1931					
Hour		2—3 p. m.					
Ptarmigan No.		22		23		24	
Sex and age		?		?		?	
Total weight of vegetable crop content (mg)		8700		12350		8600	
Species	Fragments	N	W	N	W	N	W
<i>Salix arctica</i>	Buds and twigs	559	6700	1905	8750	1570	7450
— —	Leaves	4	..	1	..
<i>Dryas octopetala</i>	Leaves	197	800	816	1800	204	450
— —	Flowers
<i>Saxifraga oppositifolia</i>	Shoot apices	65	700	99	400	160	600
<i>Polygonum viviparum</i>	Bulbils	27	1000	..	100
<i>Cassiope tetragona</i>	Fruits and shoots	400	..	100	3	..
<i>Cerastium alpinum</i>	Buds and leaves	2
<i>Draba cinerea</i>	Capsules, seeds	100	1	..	1	..
<i>Equisetum variegatum</i>	Stems	217	300	2	..
<i>Papaver radicum</i>	Capsules
<i>Stellaria longipes</i>	Buds and leaves	1	..	1	..
<i>Vaccinium uliginosum</i>	Fruits and leaves	7
<i>Carex nardina</i>	Spikes
— <i>cf. rigida</i>	Leaves	1	..	1	..
— <i>rupestris</i>	Spikes, leaves	3
<i>Chamaenerium latifolium</i>	Seeds
<i>Minuartia rubella</i>	Shoot apices
<i>Saxifraga nivalis</i>	Leaves	2
<i>Astrophyllum medium</i>	Shoot apices
<i>Polytrichum cf. alpinum</i>	— —
Quartz	Grains
Earth	Sand and clay

1) The crop contents of ptarmigans Nos. 30—31 were mixed before weighing.

Ptarmigans Nos. 22—32.

Head of Loch Fyne		Eskimonæs				Eskimonæs		Eskimonæs					
3/11 1931 2 p.m.		20/12 1931 3—4 p.m.				2/1 1932 2 p.m.		17/3 1932 ?					
25 ♂ ad 5300		26 ? 4300		27 ? 4100		28 ♂ ad 25000		29 ♂ ad 3500		30 + 31 ¹⁾ ♀♀ jun's 9450		32 ♀ jun 250	
N	W	N	W	N	W	N	W	N	W	N	W	N	W
113	900	70	500	25	300	1196	18100	19	150	332	3200	8	50
..
651	1400	1500	3800	1700	3800	1000	1900	1700	2850	2800	6100	108	200
..	1	..
2	..	4	..	1	..	935	5000	209	500	64	150	4	..
..	2950	25	..	5	..	3	1
..	50	1	3	..	1
..
9
..	1
1	..	1	..	4	..	1	2
..
..	12	..	1
..	1	2
..	3
..	1
..	1
..
..	3
..	3
..	1	700
..	400

Table 7. Crop content from the outer fjords.

Locality		Eskimonæs			
Date and year		17/3 1932			
Hour		?			
Ptarmigan No.		33		34	
Sex and age		♀ jun		♀ jun	
Total weight of vegetable crop content (mg)		4550		4100	
Species	Fragments	N	W	N	W
<i>Salix arctica</i>	Buds and twigs	91	850	241	1900
<i>Dryas octopetala</i>	Leaves	2000	3700	1400	2150
<i>Saxifraga oppositifolia</i>	Shoot apices	17	..	31	50
<i>Polygonum viviparum</i>	Bulbils
<i>Arctostaphylos alpina</i>	Leaves
<i>Cassiope tetragona</i>	Fruits and shoots	2
<i>Cerastium alpinum</i>	Buds and leaves
<i>Equisetum variegatum</i>	Stems
<i>Stellaria longipes</i>	Buds and leaves
<i>Vaccinium uliginosum</i>	Leaves	1
<i>Carex nardina</i>	Spikes	2
<i>Carex cf. rigida</i>	Leaves	3	..	2	..
<i>Draba lactea</i>	Rosette leaves
<i>Equisetum arvense</i>	Stems
<i>Hierochloë alpina</i>	Leaves
<i>Juncus castaneus</i>	Capsules
<i>Minuartia rubella</i>	Shoot apices	1
<i>Saxifraga nivalis</i>	Leaves
Quartz	Grains	1

Table 9. Crop content from the outer fjords

Locality		Eskimonæs		Eskimonæs	
Date and year		15/8 1932		16/1 1933	
Hour		5—6 p. m.		?	
Ptarmigan No.		53		54	
Sex and age		♀ jun		♀ jun	
Total weight of vegetable crop content (mg)		1250		25000 ¹⁾	
Species	Fragments	N	W	N	W
<i>Salix arctica</i>	Buds and twigs	8	50	800	11000
— —	Leaves
<i>Dryas octopetala</i>	Leaves	10000	10100
— —	Flowers
<i>Saxifraga oppositifolia</i>	Shoot apices	1000	3900
<i>Polygonum viviparum</i>	Bulbils	1050
— —	Stem-tubers
<i>Carex misandra</i>	Spikes	2
<i>Cerastium alpinum</i>	Leaves
<i>Oxyria digyna</i>	Fructiferous raceme
<i>Saxifraga cernua</i>	Leaves
<i>Stellaria longipes</i>	Buds and leaves
<i>Vaccinium uliginosum</i>	Fruits	17	150
<i>Carex capillaris</i>	Spikes
— <i>rupestris</i>	Spikes	2	..
<i>Draba daurica v. rupestriformis</i>	Capsules
— <i>lactea</i>	Rosette-leaves
<i>Festuca rubra?</i>	Leaves
<i>Ranunculus pygmaeus</i>	Leaves, receptaculum
<i>Saxifraga nivalis</i>	Leaves
— <i>rivularis</i>	Leaves

¹⁾ A small quantity of the crop content has been lost.

Ptarmigans Nos. 53—62.

Eskimonæs		Eskimonæs						Eskimonæs							
18/1 1933 ?		12/3 1933 ?						12/8 1933 5 p.m.							
55 ♀ jun 33600		56 ♂ ad 2400		57 ♂ ad 850		58 ♂ ad 2650		59 ? jun 1700		60 ? jun 1200		61 ? jun 450		62 ? jun 500	
N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W
1000	15250	20	200	18	50	5
..	1	100	1	100
10000	12250	1000	1800	400	600	1000	1800	1
..	50
1400	6100	75	400	40	200	200	800	1	..
..	1650	..	1100	..	300	..	400
..	1	50
..
1
..	1	100
..	50
..	..	9	3
..
..	1	..
2
..	4	..
..	..	10	..	3	..	4
..	1
..	3
..	1
..	..	2

Table 10. Crop content from the outer fjords

Locality		Eskimonæs			
Date and year		12/8 1933			
Hour		5 p.m.			
Ptarmigan No.		63		64	
Sex and age		? jun		♀ ad	
Total weight of vegetable crop content (mg)		850		1250	
Species	Fragments	N	W	N	W
<i>Salix arctica</i>	Leaves	2	100
<i>Dryas octopetala</i>	Leaves
— —	Flowers	300
<i>Polygonum viviparum</i>	Spikes and Bulbils	750	..	800
<i>Cerastium alpinum</i>	Capsules	2	..
<i>Luzula arcuata v. confusa</i>	Fruits	3	..
<i>Oxyria digyna</i>	Fructiferous raceme	100	2	..
<i>Papaver radicatum</i>	Capsules
<i>Pedicularis flammea</i>	—	4	50
<i>Salix herbacea</i>	Leaves	1
<i>Stellaria longipes</i>	Buds and leaves	4	..
<i>Ranunculus nivalis</i>	Receptaculum, nuts
<i>Rumex acetosella</i>	Fructiferous raceme	4

Table 11. Crop content from the inner fjords

Locality			
Date and year			
Hour			
Ptarmigan No.		73	
Sex and age		♂ jun	
Total weight of vegetable crop content (mg)		3950	
Species	Fragments	N	W
<i>Salix arctica</i>	Buds and twigs
<i>Dryas octopetala</i>	Leaves	2000	3900
<i>Saxifraga oppositifolia</i>	Shoot apices	16	50
<i>Cassiope tetragona</i>	Shoot apices
<i>Vaccinium uliginosum</i>	Leaves
<i>Carex nardina</i>	Spikes
— <i>rupestris</i>	Leaves	2	..
<i>Potentilla nivea</i>	Leaves
Quartz	Grains

Ptarmigans Nos. 63—72.

Eskimonæs															
24/8 1933 6—12 p.m.															
65 ♀ ad 2200		66 ? jun 2300		67 ? jun 1450		68 ? jun 1500		69 ♀ ad 4050		70 ? jun 1800		71 ? jun 3150		72 ? jun 2250	
N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W
..	..	1	1
..	1
1
..	2200	..	2300	..	1450	..	1500	..	4000	..	1800	..	3050	..	2550
1	1	100
..
..
1	50	1	..	1
..
..
2	1	..	2
..	1
..

Ptarmigans Nos. 73—78.

Mt. Gunvor, Strindberg Land									
16/11 1931 2 p.m.									
74 ♂ ad 4400		75 ♂ ad 7700		76 ♀ ad 7950		77 ♀ ad 11350		78 ? jun 10200	
N	W	N	W	N	W	N	W	N	W
28	300	18	200	6	50
2500	4100	4000	7250	4500	7600	5000	9100	5000	9850
7	..	49	250	84	300	433	1800	74	300
..	..	1	..	2	50
..	450	2	..
..	..	2	2
2	1
1
..	1

7*

Table 10. Crop content from the outer fjord

Locality		Eskimonæs			
Date and year		12/8 1933			
Hour		5 p.m.			
Ptarmigan No.		63		64	
Sex and age		? jun		♀ ad	
Total weight of vegetable crop content (mg)		850		1250	
Species	Fragments	N	W	N	W
<i>Salix arctica</i>	Leaves	2	100
<i>Dryas octopetala</i>	Leaves
—	Flowers	300
<i>Polygonum viviparum</i>	Spikes and Bulbils	750	..	800
<i>Cerastium alpinum</i>	Capsules	2	..
<i>Luzula arcuata v. confusa</i>	Fruits	3	..
<i>Oxyria digyna</i>	Fructiferous raceme	100	2	..
<i>Papaver radiculatum</i>	Capsules
<i>Pedicularis flammea</i>	—	4	50
<i>Salix herbacea</i>	Leaves	1
<i>Stellaria longipes</i>	Buds and leaves	4	..
<i>Ranunculus nivalis</i>	Receptaculum, nuts
<i>Rumex acetosella</i>	Fructiferous raceme	4

Table 11. Crop content from the inner fjords

Locality			
Date and year			
Hour			
Ptarmigan No.		73	
Sex and age		♂ jun	
Total weight of vegetable crop content (mg)		3950	
Species	Fragments	N	W
<i>Salix arctica</i>	Buds and twigs
<i>Dryas octopetala</i>	Leaves	2000	3900
<i>Saxifraga oppositifolia</i>	Shoot apices	16	50
<i>Cassiope tetragona</i>	Shoot apices
<i>Vaccinium uliginosum</i>	Leaves
<i>Carex nardina</i>	Spikes
— <i>rupestris</i>	Leaves	2	..
<i>Potentilla nivea</i>	Leaves
Quartz	Grains

Ptarmigans Nos. 63—72.

Eskimonæs

24/8 1933
6—12 p.m.

65 ♀ ad 2200		66 ? jun 2300		67 ? jun 1450		68 ? jun 1500		69 ♀ ad 4050		70 ? jun 1800		71 ? jun 3150		72 ? jun 2250	
N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W
..	..	1	1
..	1
1
..	2200	..	2300	..	1450	..	1500	..	4000	..	1800	..	3050	..	2550
1	1	100
..
..
1	50	1	..	1
..
..
2	1	..	2
..	1
..

Ptarmigans Nos. 73—78.

Mt. Gunvor, Strindberg Land

16/11 1931
2 p.m.

74 ♂ ad 4400		75 ♂ ad 7700		76 ♀ ad 7950		77 ♀ ad 11350		78 ? jun 10200	
N	W	N	W	N	W	N	W	N	W
28	300	18	200	6	50
2500	4100	4000	7250	4500	7600	5000	9100	5000	9850
7	..	49	250	84	300	433	1800	74	300
..	..	1	..	2	50
..	450	2	..
..	..	2	2
2	1
1
..	1

7*

Table 12. The total crop content in the different months (mg.).

Month.....	1	2	3	4	5	6	7	8	9	10	11	12	Total
Number of ptarmigans	3	14	13	3	5	0	1	27	0	3	7	2	78
Total weight of vegetable crop content.....	83600	173150	34200	7000	14750	0	2050	45200	0	29650	50850	8400	448850
Average weight of vegetable crop content.....	27867	12361	2631	2333	2950	—	2050	1674	—	9883	7264	4200	5754
<i>Salix arctica</i>	Buds and twigs	44350	113050	8950	50	10400	—	650	—	22900	1450	800	202600
—	Leaves.....	..	+	—	3150	—	+	3150
<i>Dryas octopetala</i>	Leaves.....	24250	43350	21850	6850	3450	—	+	—	3050	43200	7600	153600
—	Flowers.....	..	+	+	—	450	—	450
<i>Saxifraga oppositifolia</i>	Shoot apices	15000	550	3350	100	+	—	+	—	1700	2700	..	23400
<i>Polygonum viviparum</i>	Bulbils and spikes ...	+	+	+	—	650	39500	—	1100	2950	44200
—	Stem-tubers.....	..	7750	50	—	—	7800
<i>Arctostaphylos alpina</i>	Fruits and leaves....	+	..	—	100	..	—	100
<i>Cassiope tetragona</i>	Fruits, shoot apices..	+	..	+	..	+	—	..	+	—	500	100	600
<i>Carex misandra</i>	Spikes.....	—	1050	50	—	1100
<i>Cerastium alpinum</i>	Buds, leaves, capsules	+	+	+	..	850	—	..	100	—	+	..	950
<i>Draba cinerea</i>	Capsules	—	—	100	+	100
— <i>subcapitata</i>	Buds and leaves....	..	150	—	—	150
<i>Equisetum variegatum</i>	Sporophylls, stems	7100	+	—	—	300	..	7400
<i>Eriophorum Scheuchzeri</i>	Leaves, flowers.....	..	650	—	—	650
<i>Luzula arcuata v. confusa</i>	Fruits	—	..	300	—	300
<i>Oxyria digyna</i>	Fructiferous raceme..	—	..	200	—	200
<i>Papaver radicans</i>	Capsules	+	+	..	+	—	100	50	—	150
<i>Pedicularis flammaea</i>	Capsules	—	+	50	—	50
<i>Salix herbacea</i>	Leaves.....	—	..	100	—	100
<i>Saxifraga cernua</i>	Leaves.....	—	..	150	—	150
<i>Stellaria longipes</i>	Buds and leaves....	+	550	+	..	50	—	..	150	—	+	+	750
<i>Vaccinium uliginosum</i>	Fruits and leaves....	+	—	150	300	—	+	450	900

A + indicates that the species is represented by less than 50 mg.

Table 13. The percentage composition of the crop content in the different months.

Month.....	1	2	3	4	5	6	7	8	9	10	11	12	Total	
Number of ptarmigans.....	3	14	13	3	5	0	1	27	0	3	7	2	78	
Total weight of vegetable crop content (mg)....	83600	173150	34200	7000	14750	0	2050	45200	0	29650	50850	8400	448850	
<i>Salix arctica</i>	Buds and twigs.....	53.1	65.3	26.2	0.7	70.5	—	..	1.4	—	77.2	2.8	9.5	45.3
—	Leaves.....	—	..	7.0	—	0.7
<i>Dryas octopetala</i>	Leaves.....	29.0	25.0	63.9	97.9	23.4	—	—	10.3	85.0	90.5	34.2
—	Flowers.....	—	..	1.0	—	0.1
<i>Saxifraga oppositifolia</i>	Shoot apices.....	17.9	0.3	9.8	1.4	..	—	—	5.8	5.3	..	5.2
<i>Polygonum viviparum</i>	Bulbils and spikes....	—	31.7	87.4	—	3.7	5.8	..	9.9
—	Stem-tubers.....	..	4.5	0.1	—	—	1.7
<i>Arctostaphylos alpina</i>	Fruits and leaves....	—	4.9	..	—	+
<i>Cassiope tetragona</i>	Fruits, shoot apices..	—	—	1.7	0.2	..	0.1
<i>Carex misandra</i>	Spikes.....	—	51.2	0.1	—	0.2
<i>Cerastium alpinum</i>	Buds, leaves, capsules	5.8	—	..	0.2	—	0.2
<i>Draba cinerea</i>	Capsules.....	—	—	0.3	+
— <i>subcapitata</i>	Buds and leaves....	..	0.1	—	—	+
<i>Equisetum variegatum</i>	Sporophylls, stems....	..	4.1	—	—	1.0	1.7
<i>Eriophorum Scheuchzeri</i> ...	Leaves and flowers..	..	0.4	—	—	0.1
<i>Luzula arcuata</i>	Fruits.....	—	..	0.7	—	+
<i>Oxyria digyna</i>	Fructiferous raceme..	—	..	0.4	—	+
<i>Papaver radicum</i>	Capsules.....	—	4.9	0.1	—	+
<i>Pedicularis flammea</i>	Capsules.....	—	..	0.1	—	+
<i>Salix herbacea</i>	Leaves.....	—	..	0.2	—	+
<i>Saxifraga cernua</i>	Leaves.....	—	..	0.3	—	+
<i>Stellaria longipes</i>	Buds and leaves....	..	0.3	0.3	—	..	0.3	—	0.1
<i>Vaccinium uliginosum</i>	Fruits and leaves....	—	7.3	0.7	—	..	0.9	..	0.2

A + indicates that the species is represented by less than 0.1 per cent.

Constituents found in the crop content.

The crop materials examined were found to contain in all fifty-two vascular plants, two mosses, one fungus, two insects, and several small particles of quartz and earth (cf. Tables 4—13).

Paying regard to the quantities in which the individual species occur in the crops, it is possible to distinguish: main constituents, subordinate constituents, and sporadic constituents in the food. This classification will be maintained here, a distinction being further made between winter food and summer food as regards the main constituents.

In this section a brief account will be given of what parts of the respective species have been found in the food of the ptarmigan. Within the two groups richest in species but quantitatively more sparsely represented, subordinate constituents and sporadic constituents, the species are given in alphabetical order.

Main constituents.

Summer food.

Polygonum viviparum L. Of this species it is principally the various organs of the spike, above all the bulbils, that are eaten. The material varies considerably as regards size of fragments and content of bulbils according to the stage of development of the plant, which again depends on the time of melting of the snow in the habitat, its exposure, the moisture of the soil, and the climatological conditions of the year (cf. p. 81). It may serve as a clue that until the beginning of August fragments of spikes up to 1 cm long and consisting of floral elements, bracts, and bulbils will probably as a rule be found, while the percentage quantity of the bulbils will increase in the course of the month and finally they will be the sole constituents. However, since the ptarmigan moves about during the summer, fragments of young spikes may very well be found at later dates. As late as the beginning of November *Polygonum* may form a considerable part of the contents of the crops. The time when *Polygonum* will become dominant in the food will further vary according to year and place, but it will hardly be before the middle of June. In addition to the spike fragments foliage leaves occur occasionally.

Stem-tubers of *Polygonum* have only been found in the winter (crops Nos. 1—3, 5—7, 10, and 58), but for practical reasons they are mentioned here. Their size and weight vary considerably, they may measure from 3 to 18 mm in length and weigh from 10 to 80 mg. They are present in large numbers in crops Nos. 1, 3, 5, and 10 only, all of which are derived from the outer coast in February.

I happened to observe ptarmigans digging for *Polygonum* stem-tubers. They removed the soil by scraping with their feet, and then by energetic jerks of the head they pulled out the stem-tubers from the soil, which was here loose and sandy, with their beaks. The stem-tubers consumed were surprisingly clean and free from earth, almost like fresh potatoes from loose sandy soil.

Winter food.

Salix arctica PALLAS. The fragments most frequently found are unquestionably buds and tips of young branches, the much developed terminal buds being particularly numerous. The size of the branch fragments consumed increases in the course of the winter, the maximum size being reached in January, and then subsequently decreasing (cf. p. 134). In the autumn and in early winter their length hardly exceeds 1 cm. In January, crops of ptarmigans killed at Eskimonæs were found to contain branches 3—4 cm long, the maximum length being 5 cm.

As the species is deciduous, fresh leaves have, as a matter of course, only been found in the summer food, mostly in inconsiderable quantities (Nos. 44—45, 47—50, 59—64, 66, and 69). Only exceptionally did *Salix* leaves dominate in the individual crops, thus in Nos. 44 and 45. The *Salix* leaves consumed had been cut into pieces, which were often but partially separated from each other, and it is therefore impossible to ascertain the number of fragments (cf. fig. 34). Quite exceptionally withered leaves of *Salix* were found in the winter food (Nos. 23 and 24).

Even though no ptarmigans were killed during the catkin period proper, it is noteworthy that neither catkins nor capsules of *Salix* have been found in the food. However, in winter the buds contain catkin embryos, and curiously enough, in several of the crops derived from Knudshoved in February, 1932, their bud-scales had burst and the downy catkins were visible. Even though buds with bursting scales may occur on the plants at this season of the year (cf. GELTING 1934, p. 115), it is probable that the greater number of the buds have opened in the crop under the influence of the body-heat of the bird.

An examination of the branch-fragments consumed in the winter shows that they are collected one at a time, being cut off by the sharp

edges of the beak. In the thin fragments from the autumn and spring the cut surfaces are most frequently smooth and straight, which shows that the ptarmigan has snapped them off by one well-directed cut with the beak. As regards the larger and thicker fragments (maximum thickness 3—4 mm) from midwinter, the case is different, their cut surfaces being rough and frayed, which seems to show that branches of this thickness represent nearly the limit of what the ptarmigan beak is able to cut through (see fig. 41, p. 133). The cut surfaces often show that in



Gram phot.

Fig. 34. Leaves of *Salix arctica* from ptarmigan No. 45. Adult ♀. Eskimonæs, August 1, 1932. Natural size.

the thickest branches the cut goes through the cambium but only some distance into the wood, whose central part has either been detached by a second cut or by a jerk of the head. Sometimes the branches exhibit marks showing that a ptarmigan has tried in vain to cut the branch in one place but has had greater success in another place.

The *Salix* individuals so placed in the ground that they project somewhat above the snow almost every winter, sometimes show distinct signs of frequent visits from ptarmigans during the winter. Thus a small *Salix* growth at the south side of the cape of Eskimonæs showed distinct evidence of having been cut down to the surface of the snow in the winter in all three years in which I observed it. The annual shoots were particularly long in the ensuing summer, a phenomenon which is otherwise known from garden plants which are cut back.

Dryas octopetala L. The elements most frequently found in the crop are the evergreen leaves. Although the latter are so close-set on the short-noded shoots that it might probably be possible for the ptarmigan to take more than one at a time, the material at hand indicates that the ptarmigan directs its cut towards the individual leaf and but rarely secures more than that in one cut. For the greater number of the leaves found are beautifully cut off in the petiole proper or very near to it. Sometimes the leaf is cut so near its base that even the stipules adhere to the leaf-stalk. Thus the material reveals the ptarmigan as a systematic collector, at any rate of *Dryas* leaves.

While the weight of the *Salix* fragments culminates by midwinter, the *Dryas* leaves attain their smallest size during the same period (cf. p. 134).

Dryas is further represented in the crop content by its flower at all seasons of the year and in all stages of development. In the summer a fairly considerable number of flower buds may occur.

The material of *Saxifraga oppositifolia* L. consists almost exclusively of tips of stems, which contain the terminal bud for the ensuing vegetation period surrounded by 8—12 close-set leaves. This is the case at any rate during the greater part of the winter, when mostly only the short-noded form *f. pulvinata* is accessible. In the early autumn and in the spring there also occur larger fragments of *f. reptans*, consisting of several straight internodes.

Capsules occur but exceptionally, thus in a number of one or two in each of ptarmigans Nos. 24, 28, and 73.

The *Saxifraga* fragments, too, must be assumed to be collected one at a time, but as mentioned in p. 81, the determination of the number of fragments is difficult.

Subordinate constituents.

This designation refers only to the quantity of the elements, not to their quality, which may very well be of importance by a specific physiologic effect. The limit between the quantitatively subordinate elements and those of sporadic occurrence (cf. p. 109) has been drawn thus: only such species as are represented by at least 50 mg in at least one crop are regarded as subordinate, while such as are always found in quantities less than 50 mg are considered sporadic.

Some few of the subordinate constituents may at times be present in fairly considerable quantities, thus for instance *Equisetum variegatum* in ptarmigans Nos. 10 and 11, *Cerastium alpinum* in No. 17, and *Carex misandra* in No. 43. On the whole it is among the subordinate constituents that substitutes for the main constituents may be expected to be found when a still larger material is available.

Arctostaphylos alpina (L.) SPRENG. is represented by a leaf in No. 39 and by some fruits in No. 43. According to verbal information from TH. SØRENSEN, fruits of this plant were abundantly represented in a ptarmigan killed in the summer of 1932 in Carl Jacobsen Bay at Ymer Island.

Carex misandra R. BR. is present in six crops (Nos. 43, 44, 46, 48, 51, 52, and 53). The species has only been found in ptarmigans from July and August and is represented by female spikes and fragments of spikes containing more or less mature fruits. Ptarmigan No. 43 is an example showing that *Carex misandra* may at times be a main constituent of the content of the crop.

Cassiope tetragona (L.) DON. is found in the food at all seasons of the year, but only in quite small quantities. The most frequent elements are the fruits, which are especially eaten in the autumn and early winter. Thus the species was only represented by fruits in Nos. 22—26 and 28, otherwise almost exclusively by apices of branches up to 1.5 cm long.

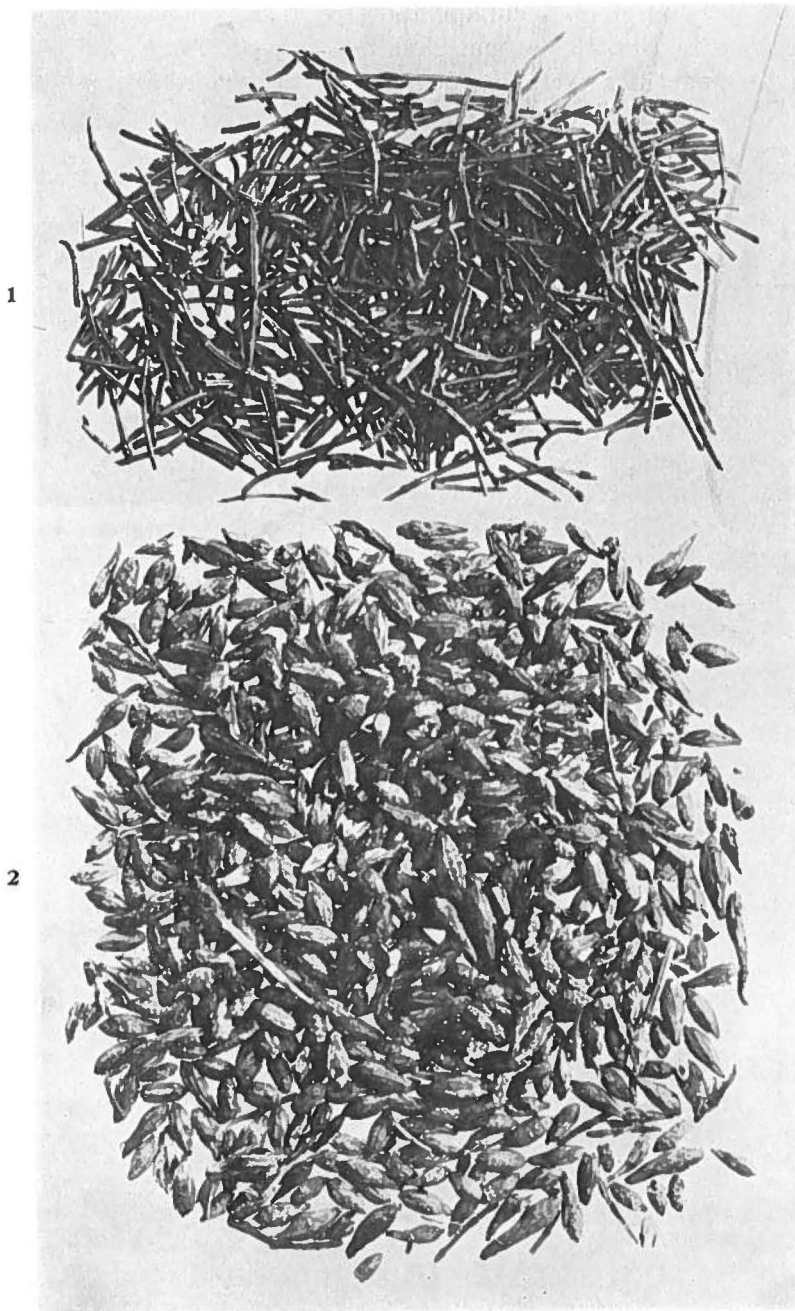
The species has never previously been found in the food of *Lagopus mutus*; ARBO HØEG (1929) assumes it is because the aromatic substances of the species repel the ptarmigan. The species having now actually been found in the food, it would perhaps seem more probable that in the summer more desirable plant organs are accessible, while in the winter the access to *Cassiope* is much impeded by the constant snow-cover which characterises its areas of dominance.

Cerastium alpinum L. is present in twenty-one crops (Nos. 1—6, 8, 13, 14, 17, 20, 21, 23, 37, 41, 51, 55, 64, 65, 70, and 71) distributed over the whole year, but in quantities above 50 mg in the months May and August only. Capsules are sparsely represented. The most frequent fragments are the buds from the axils of the leaves. These are formed at least one year before developing, and persist green all through the winter.

Draba cinerea ADAMS occurs in four crops only (Nos. 22—25 from October and November), and is merely represented by the capsule or fragments of it (valves and replum with adherent seeds). Quantity exceeding 50 mg in No. 22 only.

Draba subcapitata SIMM. Present in seven crops (Nos. 1, 3—6, 11, and 12) all from the outer coast, February. Quantity exceeding 50 mg in No. 1 only. Represented by basal leaf rosettes containing a floral primordium. These rosettes will form in great number one year, at the latest, before flowering, and persist green all the winter.

Equisetum variegatum SCHLEICH. (fig. 35, p. 107) was found in twelve crops (Nos. 1—7, 10, 11, 23, 24, and 37) distributed over the months February, March, and October. All the fragments found are derived from



Gram phot.

Fig. 35. 1) Stems of *Equisetum variegatum* from ptarmigan No. 11; sex and age unknown. Knudshoved, February 25, 1932. 2) Sporophyll heads of same from ptarmigan No. 10; adult ♀. Same locality. Nat. size.

the above-ground stem, including the often very big heads of sporophylls. Only in Nos. 10, 11, and 23 (see fig. 35, p. 107) was the species present in quantities exceeding 50 mg. In ptarmigans Nos. 10—11 the species constitutes about 25—40 per cent. of the content of the crop (cf. p. 160).

Eriophorum Scheuchzeri HOPPE. Found in two crops (Nos. 10 and 11) from Knudshoved, February. In No. 10 more than 50 mg. Represented only by fragments of stem and floral primordium, which is formed the year before it is developed, and which in February, 1932, was up to 1.5 cm long and, surrounded by the leaf sheaths of the rosette of the preceding year, rose up to 2 cm above the surface of the ground.

Luzula arcuata (WAHLBG.) SW. *var. confusa* (LINDEB.) KJELM. (fig. 38, p. 117). Found in three crops (Nos. 47, 51, and 64), all from Eskimonæs, August. The fragments found consist mostly of mature fruits. Quantity above 50 mg in Nos. 47 and 51.

Oxyria digyna (L.) HILL. Found in four crops (Nos. 59, 61, 63, and 64), all from Eskimonæs, month of August. Represented by leaves and fragments of the raceme containing mature fruits. Quantities exceeding 50 mg in Nos. 61 and 63 (fig. 32, p. 84).

Papaver radicum ROTTB. (s. l.). Present in eight crops (Nos. 10, 17, 30, 43, 65, and 69—71) from February, March, May, July, and August. In July and August only in quantities exceeding 50 mg (Nos. 43 and 69). Represented exclusively by capsules.

Pedicularis fluminea L. found in three crops (Nos. 43, 52, and 64) all from Eskimonæs, July—August. Only represented by partially mature but still unopened capsules. Quantity above 50 mg only in No. 64.

Salix herbacea L. Found in two crops (Nos. 50 and 63) both from Eskimonæs, month of August. Represented by leaves only. Quantity exceeding 50 mg in No. 50 only.

Saxifraga cernua L. Found in two crops (Nos. 51 and 59), both from Eskimonæs, month of August. Represented by the fleshy rosette leaves. Quantity in both crops more than 50 mg.

Stellaris longipes GOLDIE (fig. 38, p. 117). Found in no less than thirty-three crops (Nos. 1—7, 10, 11, 14, 17, 20, 21, 23—28, 31, 37, 41, 42, 47, 49, 51, 52, 56, 60, 64, 65, 68, and 69) distributed over all seasons of the year but with distinct maxima in midwinter and midsummer. Quantity exceeding 50 mg in Nos. 1, 4—6, 41, 47, and 51. Represented by stem fragments, buds, and leaves. In January the species is especially represented by the young buds, which hibernate in the green state before developing the next summer.

Vaccinium uliginosum L. *f. microphylla* (LGE.) NATHORST (fig. 30, p. 78). Found in nine crops (Nos. 23, 33, 43, 46, 50, 51, 53, 77, and 78),

all from the fjords, March, July, August—November. Quantity exceeding 50 mg in Nos. 43, 46, 53, and 77. Frequently represented by leaves only; but in Nos. 43, 46, 50, 51, and 53 only more or less ripe berries. Thus in the 78 ptarmigan crops examined, only 56 berries of this species have been found, although no small number of the ptarmigans were killed in the month of August when the berries are ripe and occur in such abundance that both human beings, gulls, and bears eagerly search for the *Vaccinium* heaths to eat the delicious berries.

Sporadic constituents.

Vascular plants.

While the line of distinction between the main constituents and the quantitatively subordinate ones is exceedingly distinct, the line between the latter and the sporadic elements must be rather arbitrarily drawn. As mentioned in p. 105, elements which are always present in the crop in quantities less than 50 mg are considered sporadic. Often they occur in much smaller quantities. In fact, one is compelled to believe that they have often slipped into the food quite casually, together with some other elements. But sometimes their size and number would seem to indicate the opposite, and the frequent occurrence of the sporadic constituents in the period July—August shows precisely that not all of them have been "casually" included in the food. In the February-food from the outer coast, too, they are more commonly represented than in the January-food from the fjords. I have therefore chosen the neutral term sporadic to denote these elements.

Alopecurus alpinus SMITH. Found in five crops (Nos. 1—5), all from the outer coast, February. Represented by stem and leaf fragments and fragments of the panicle.

Carex capillaris L. A single spike fragment with ripe fruits found in crop No. 62.

Carex nardina FR. Found in eight crops (Nos. 29, 30, 33, 43, 46, 49, 75, and 77), distributed over the months March, July, August, and November. Mainly represented by spikes and fruits.

Carex cf. rigida GOOD. Found in ten crops (Nos. 6, 12, 14, 23, 24, 27, 30, 31, 33, and 34), distributed over February, March, and October. Represented exclusively by leaf fragments. Some of the identifications doubtful.

Carex rupestris ALL. Found in eight crops (Nos. 23, 28, 52, 54, 55, 73, 74, and 76), distributed over January, August, October, and November. Represented by leaf and spike fragments.

Chamaenerium latifolium (L.) SWEET. Represented by one seed in crop No. 28.

found in the crops of chickens of *Lagopus lagopus* (cf. LID and MEIDELL, 1933) and of the grouse (cf. GRIMSHAW, 1911), it may be supposed that an examination of the crop content of the quite young chickens would reveal a greater number of insects in the food.

Mineral constituents.

The content of grit in the gizzard was not examined. But in the crops small pieces of quartz were frequently found. Thus in ptarmigans Nos. 2, 4, 7, 13, 17, 27, 28, 33, 51, and 77. That the ptarmigan prefers quartz as grit in the gizzard appears with all desirable distinctness from the available material, no other rocks being represented except a small lump of soil found in ptarmigan No. 30 and sand grains in varying quantities in various crops. BAY (1894), too, mentions quartz as the rock frequently found in the ptarmigan crops; the same was observed by ARBO HØEG (1929). Thus it would seem that the ptarmigan actually chooses. HAMMOND SMITH and RASTALL (1911), too, mention quartz as grit frequently found in the crop of the grouse (*Lagopus scoticus*).

The total quantitative proportion of the examined contents of crops.

The contents of the crops of in all 78 ptarmigans, killed at different seasons of the years 1931—33, have been examined. In an air-dried state the total crop content of these ptarmigans weighed 448.85 g. As the sporadic constituents were not weighed, the quantitative relations of the main constituents and the subordinate constituents only can be discussed.

These quantitative relations of the whole of the food examined will appear from Table 12 (p. 100) and fig. 36.

The figure shows that the four species, *Salix arctica*, *Dryas octopetala*, *Saxifraga oppositifolia*, and *Polygonum viviparum*, are the quantitatively most important species, while the remaining sixteen species constitute a quite subordinate part of the food.

Since insects form only sporadic constituents, which were not weighed, the term crop content in the following refers exclusively to plant food.

In the following pages the seasonal variations in the crop content will be discussed on the basis of the material examined. It may rightly be pointed out that the crop content of 78 ptarmigans is a rather small material from which to draw far-reaching conclusions; however, it should be remembered that in addition to the crop content analysed numerous direct observations in the field are at hand on the life conditions of the ptarmigan, and moreover that within the area here treated only

163 vascular plants are available as food for the ptarmigan. In the highlands of Norway, where a much greater number of species are available — much larger, because here the ptarmigan often lives far below the tree limit in the winter — as well as in Scotland, where conditions are probably very like those of Norway, a far greater number of crops will be required to constitute as valid a material as the Greenland material here submitted. From Norway so far only investigations on the food of 22 ptarmigans have been published and in the British Islands in all 399 grouse (*Lagopus scoticus*) have been closely investigated during the years in which the Grouse Committee has been at work. Thus Green-

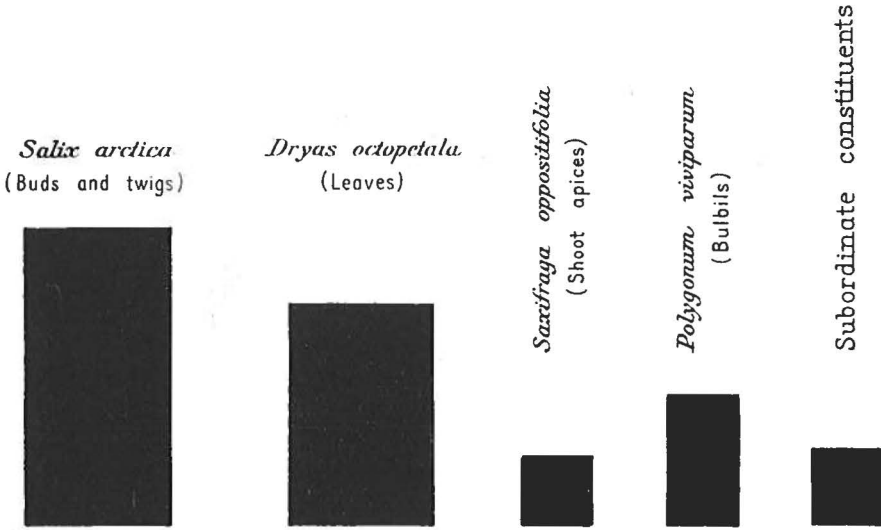


Fig. 36. Showing the relation of different constituents in the food.

land must be said to be fairly plentifully represented, even though the collecting of the material there is attended with greater difficulties, among other reasons because the shooting of ptarmigan is not a trade and only to a small extent a sport.

The annual variation of the food.

Table 13 gives the percentage representation of the different food elements in the individual months as well as in the total crop material examined. If on the basis hereof a calculation is made of the percentage representation of the main winter food elements (*Salix arctica* — *Dryas octopetala* — *Saxifraga oppositifolia*), the main summer food elements (*Polygonum viviparum*), and the subordinate elements (including stem-tubers of *Polygonum*, leaves of *Salix arctica*, and flowers of *Dryas octopetala*) for the different months, the main lines of the annual variation of the food will be arrived at. These are given in Table 14 and fig. 37.

Table 14. Annual variations in the quantitative relations of the different constituents of the food.

Month.....	1	2	3	4	5	7	8	10	11	12
Number of ptarmigans.....	3	14	13	3	5	1	27	3	7	2
<i>Salix</i> (buds and twigs) <i>Dryas</i> (leaves) + <i>Saxifraga oppositifolia</i> (shoot-apices).....	100	90.6	99.9	100	93.9	—	1.4	93.3	93.1	100
<i>Polygonum</i> (bulbils).....	—	—	—	—	—	31.7	87.4	3.7	5.8	—
Subordinate constituents.....	—	9.4	0.1	—	6.1	68.3	11.2	3.0	1.1	—

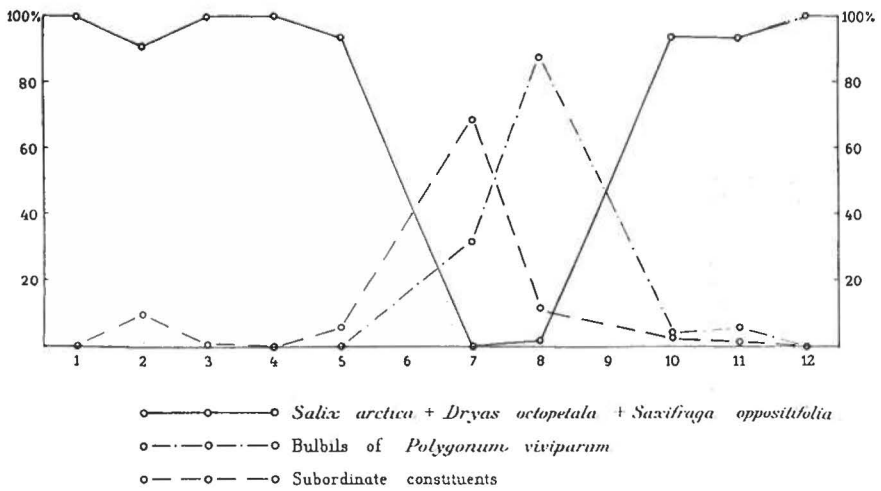


Fig. 37.

The figure and the table show that in the months October—May incl. *Salix*, *Dryas*, and *Saxifraga oppositifolia* constitute 90.6 to 100 per cent. of the total quantity of food; in August, the only summer month which is abundantly represented in respect of material, bulbils and spike fragments of *Polygonum* constitute 87.4 per cent. of the total food.

The subordinate constituents show a maximum in July. Thus they actually dominate only at the time of the year when the transition from winter food to summer food takes place.

The periods when the most important changes in the food occur.

It has been shown above that a distinction can be made between a summer and a winter food. The question then arises: when do the changes in the food take place?

Unfortunately no crop material from the months June and Septem-

ber has been examined, which is all the more deplorable since these two months, judging from our present knowledge, must be assumed to be near the times when the changes in the food occur.

We know, however, that in August *Polygonum* constitutes the main food in Northeast Greenland. From ARBO HØEG's investigations (1929) in Spitsbergen we know that in September the ptarmigan chiefly subsists on *Polygonum* bulbils, and it may be assumed that the same applies to the ptarmigan in Northeast Greenland. Conditions at Eskimonæs in September, 1931, were such that the ptarmigan might very well be assumed to live mainly on *Polygonum*, since the belated individuals of the late-melting snow-patches, at any rate at a certain height above sea-level, could be found with numerous bulbils in the spike. As late as November 3 a single ptarmigan was shot (No. 25), whose crop content showed a weight percentage of *Polygonum* of about 60. The change from *Polygonum* to winter food and the dominance of the latter will probably by future investigations be proved to take place in the course of October. It can hardly occur very much later, since the fading daylight (cf. p. 129) will render it increasingly difficult for the ptarmigan to secure a sufficient quantity of food from the winter standers, which become poorer and poorer in bulbils.

As has been shown above, the ptarmigan lives chiefly on *Salix*, *Dryas*, and *Saxifraga oppositifolia* in the winter, at any rate till May. What food the ptarmigan subsists on in June is not known. For June is the breeding time of the birds, and only a small number of them are seen, which the observer does not like to kill, knowing that they have eggs or newly hatched chickens. At Eskimonæs a voluntary protection was established, but a protection ought to be secured by law.

In May—June there can be but little access to *Polygonum*, since the above-ground organs do not develop until June, and the ptarmigan must therefore be assumed to continue to subsist on the winter food elements or to seek other kinds of food.

If it is taken into consideration that at this time of the year the winter food has lasted for six or seven months, it cannot surprise that the ptarmigan, the snow-covering having already decreased considerably, now changes to more varied food. And if so, many young buds and partly developed young plant organs may be expected to be at its disposal even at the end of May, since the plants are now beginning their spring development (cf. GELTING 1934, p. 310). Such young plant organs may be assumed to serve as resources until *Polygonum* has attained the stage of development sufficient to serve as food for the ptarmigan. However, very little is known about which plant species these may be, but they might possibly be assumed to be the same as form subordinate constituents later in the summer. This assumption seems justified by the maxi-

mum shown by the subordinate constituents in July (fig. 37), in which month, it is true, only one ptarmigan was killed.

It is interesting that precisely *Carex misandra* is so abundantly represented in the food of the single ptarmigan killed in July. Already in the autumn this plant exhibits such well developed floral primordia that they can be observed with the naked eye (GELTING 1934, p. 166). As early as May, 1932, the plant was in incipient activity at Eskimonæs, and from the end of the same month the rapidly developing spikes must as a rule be accessible to the ptarmigan in no small quantities.

Especially when we take the diversified content of nutritive substances of the winter and summer food into consideration (cf. p. 153), it seems probable that in the spring, when the snow-cover has begun to disappear and the plants have commenced the building up of substances after the hibernation, the ptarmigan will as soon as possible change from winter food to other food. Hence it may be assumed that as a rule the ptarmigan changes to a more varied food of young plant organs in May or the beginning of June, to change over in the course of June—July in the main to *Polygonum*.

Variations in the summer food.

Very little can be said about the variations in the summer food. Even though the difficulties (mentioned on p. 81) in determining the weight of the fragments of *Polygonum* with sufficient accuracy at present prevent us from forming an exact estimate of the quantities of food taken by one pick, as regards the access to *Polygonum* the summer may be characterised as comprising an early-summer period, when the access increases day by day until it attains the climax, after which it decreases again. The climax occurs at the time when most of the *Polygonum* growths are in blossom. Up to that time the ptarmigan is able to secure its *Polygonum* food by cutting off relatively large fragments of the spike containing the bulbils rich in proteins. After flowering the value of the spike as food decreases from day to day, the bulbils falling to the ground and being carried away by the wind. The ptarmigan will then have either to collect the bulbils singly from the ground, or to migrate up the mountain sides, following the flowering stage of the *Polygonum* snow-patches, to be finally faced, in the course of the autumn, at the high levels of the mountains, by ripe spikes with falling bulbils. As the weight of the individual bulbils in the available material increases from August to November on account of the growth of the bulbils, it would seem that the more difficult access to them is thereby compensated to some extent. However, this needs a closer investigation.

Even though *Polygonum* is thus in August quantitatively the most important plant for the ptarmigan, qualitatively there is a rather great

variation in the food, in that the material includes other species, too, in greater quantities than at any other period of the year, but each species in quite small quantities only. Of subordinate constituents (cf. p. 105) may be mentioned: capsules and flowers of *Cerastium alpinum*, fruits of *Luzula arcuata*, *Oxyria digyna*, capsules of *Pedicularis flammea*, *Papaver radiculatum* (alcaloids?), leaves of *Salix herbacea*, *Saxifraga cernua*, *Stellaria longipes*, and *Vaccinium uliginosum*. The sporadic constituents (cf. p. 109), also, are represented by many species, for instance *Carex capillaris*, *Draba daurica* f. *rupestriformis*, *Koenigia islandica*, *Ranunculus*

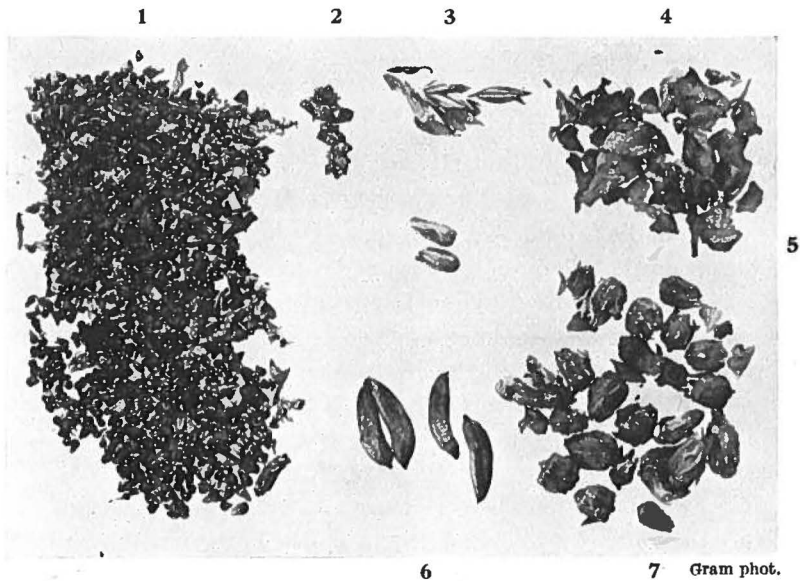


Fig. 38. Crop content of ptarmigan No. 64. Adult ♀. Eskimonæs, August 1932. 1) Bulbils of *Polygonum viviparum*, 2) clusters and capsules of *Luzula arcuata*, 3) buds and stems of *Stellaria longipes*, 4) leaves of *Salix arctica* and *Oxyria digyna*, 5) capsules of *Cerastium alpinum*, 6) capsules of *Pedicularis flammea*, 7) flower buds of *Dryas octopetala*. The *Polygonum* fragments are almost exclusively bulbils. Nat. size.

nivalis, *R. pygmaeus*, all of which are snow-patch plants or at any rate associated with the surroundings of the snow-patches, and further *Carex rupestris* and *Rumex acetosella*.

Berries are found in surprisingly small numbers, thus only some few berries of *Arctostaphylos alpina*, *Cassiope tetragona*, and *Vaccinium uliginosum*. *Empetrum* was not found at all in the available material; however, TH. SØRENSEN informs me that he has found berries of *Empetrum* in a single ptarmigan on Ymer Island.

Statements to the effect that the ptarmigan eats berries may be found in the literature, thus in SALOMONSEN (1925) and DEGERBØL and

MØHL-HANSEN (1935, p. 11). However, sometimes the ptarmigan, though seen wandering among the berries, has not actually been observed to eat them in considerable quantities. Thus it may be mentioned that ptarmigans Nos. 46—53 were killed in a *Vaccinium* heath rich in berries, but only 42 berries in all were found in their crops.

NØRDHAGEN (1928, 1) has supplied a valuable and exceedingly instructive contribution to the elucidation of the connection between years rich in berries and rich in ptarmigans and grouse. However, the accurately examined material from Scandinavia from the actual berry season is rather inconsiderable. Thus the papers of LID (1927) and LID and MEIDELL (1933) do not indicate that ptarmigans and grouse eat berries in great quantities.

Variations in the winter food.

Fig. 15 (p. 39) illustrates the access to the different food elements in the winter at Eskimonæs in the outer fjords, fig. 16 (p. 39) the access at the outer coast. Let us now examine whether the composition of the food at the different times of the winter and within the different districts really gives an expression hereof.

Since, as stated on p. 23, the vegetation differs fairly much within the different districts, I have preferred to give the statistic material for each district separately. It is true that the material for the individual districts, particularly as regards the inner fjords, is so small that it might with some right be proposed for instance to treat the material from the inner and the outer fjords as a whole, since both, though differing in natural conditions, differ distinctly from the outer coast. Admitting the justification of this objection, I shall nevertheless maintain the distinction between the two fjord districts. For if we are to compare the fjords on the one hand with the outer coast on the other, it is comparatively easy from the individual results for the two fjord districts to compute, or by interpolation arrive at, the result for both as a whole, at any rate in the present case, where the conditions of the two districts are so relatively uniform. Precisely on that account their differences, if any, will be of interest. And since future investigations, it is to be hoped, can only render the material more complete, we can hardly omit the division into the three districts outlined here. Moreover the available statistic material is distributed in such a way over the different seasons of the year that that of the outer fjords is distributed over almost the whole year, while the outer coast is only represented by the months February, April, May, and August, the inner fjords only by November. Thus, when the outer fjords cannot be compared with the outer coast, they are comparable with the inner fjords, which is of importance; for

if the variation of one external factor in one of the two districts is known, it is often possible with relative certainty to extrapolate or interpolate the conditions in the third district.

As stated above, the statistic material at hand is very incomplete. Two months (June and September) are not represented at all, others only by the crop content of one or some few ptarmigans. Thus its deficiencies are evident, and one should be extremely cautious in deducing general rules from it. If nevertheless I think it possible to deduce several such rules from it, it is because first hand observations on the day and in the place in which the material was collected, in connection with daily investigations during one winter and three summers have ensured me relative control of the material.

On the basis of Tables 4—11 (pp. 86—99) it is possible to compute the percentage representation of the main species in the crop contents in the different months and districts. This is done in Table 15.

The figures of Table 15 may also be employed for the diagrammatic representation in fig. 39, p. 121, in which the curves for *Salix arctica*, *Dryas octopetala*, *Saxifraga oppositifolia*, and *Polygonum viviparum* are given.

If we consider first the *Salix* curve (Fig. 39, p. 121) for the outer fjords (II), whence the greater number of ptarmigans are derived, it will be seen to exhibit two distinct maxima, one in October and one in May. If we compare this with the snow-cover of *Salix* at Eskimonæs (fig. 11, p. 34), which may serve as a paradigm of the snow-cover of *Salix* in the outer fjords, and whence the majority of the ptarmigans of this district are derived, we shall see that here the snow-cover exerts its controlling influence. The two maxima for *Salix* found in the food of the ptarmigan occur precisely in the months in which the snow-cover is slightest, apart from the summer months. It should further be pointed out that the curve for *Salix* is that showing the greatest fluctuations.

The *Dryas* curve (Fig. 39, p. 121) for the outer fjords (II) also shows two distinct maxima, one in December and one in April. If it is compared with the snow-covering figure, here, too, the importance of the snow-cover for the access to the plant will be seen. In accordance with the fact that the *Dryas* areas are more scantily snow-covered and become covered with snow later in the autumn and free of snow earlier in the spring, the autumn maximum for *Dryas* may occur later and the spring maximum earlier than the respective maxima of *Salix*.

The *Saxifraga* curve (Fig. 39, p. 121) shows practically only one maximum, viz. in January, but as late as March the species is comparatively abundantly represented considering the small quantities in which it usually occurs in the food. A comparison with the snow-covering figure

Table 15. Percentage quantities of the main species found in the crop contents from the different months.

Outer coast.

Month.....	1	2	3	4	5	7	8	10	11	12
Number of ptarmigans.....	..	14	..	1	3	..	3
<i>Salix arctica</i>	65.3	..	1.6	66.7	..	16.7
<i>Dryas octopetala</i>	25.0	..	98.4	27.0	..	—
<i>Saxifraga oppositifolia</i>	0.3	..	—	—	..	—
<i>Polygonum</i> bulbils.....	..	—	..	—	—	..	83.3
Subordinate constituents.....	..	9.4	..	—	6.3	..	—

Outer fjords.

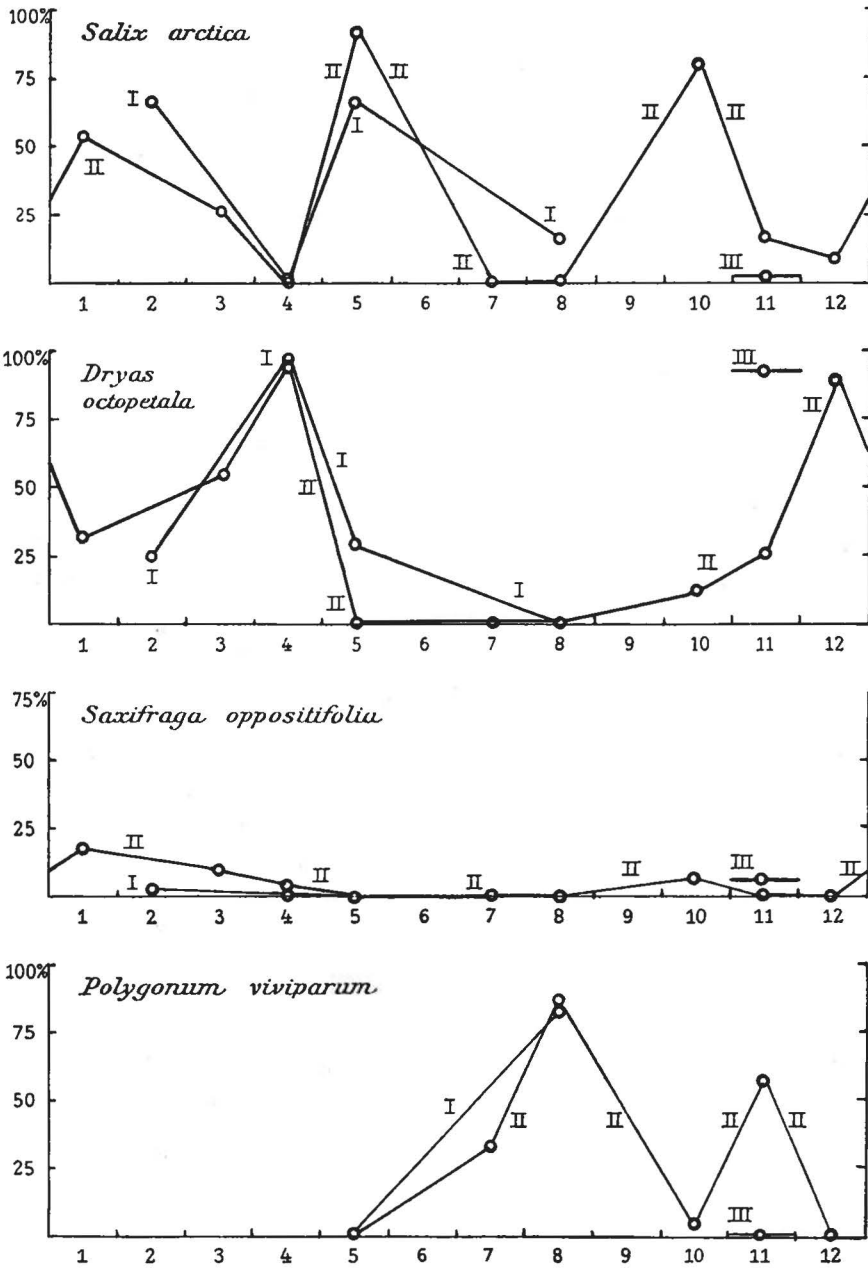
Month.....	1	2	3	4	5	7	8	10	11	12
Number of ptarmigans.....	3	..	13	2	2	1	24	3	1	2
<i>Salix arctica</i>	53.1	..	26.2	—	95.0	—	0.3	77.2	17.0	9.5
<i>Dryas octopetala</i>	29.0	..	63.9	97.4	—	—	—	10.3	26.4	90.5
<i>Saxifraga oppositifolia</i>	17.9	..	9.8	2.6	—	—	—	5.8	—	—
<i>Polygonum</i> bulbils.....	—	..	—	..	—	31.7	87.7	3.7	55.6	—
Subordinate constituents.....	—	..	0.1	..	5.0	68.3	12.0	3.0	1.0	—

Inner fjords.

Month.....	1	2	3	4	5	7	8	10	11	12
Number of ptarmigans.....	6	..
<i>Salix arctica</i>	1.2	..
<i>Dryas octopetala</i>	91.8	..
<i>Saxifraga oppositifolia</i>	5.9	..
<i>Polygonum</i> bulbils.....	—	..
Subordinate constituents.....	1.1	..

of *Saxifraga* shows that *Saxifraga* is accessible practically the whole winter; and the mostly difficult access to *Salix* and *Dryas* in January-February in the outer fjords seems to explain the *Saxifraga* maximum: the difficult access to other food elements may possibly be a concurrent cause why the ptarmigan feeds so largely on *Saxifraga*, so easily accessible, at any rate the last to be snow-covered. Finally it should be added that the curve for *Saxifraga* is that which shows the smallest fluctuations.

Thus for the outer fjords the following maxima in the winter food can be ascertained: October (*Salix*), December (*Dryas*), January (*Saxifraga*, only relative maximum), April (*Dryas*), May (*Salix*), all of which



I Outer coast. II Outer fjords. III Inner fjords.

Fig. 39. See the text.

clearly show the importance of the snow-cover, but only to a certain extent. For considering the snow-covering conditions alone, there would be nothing to prevent *Saxifraga* from exhibiting a maximum in all the winter months, nor the *Salix* maxima from being replaced by *Dryas* maxima. We are here confronted by the complicated question, what does the ptarmigan prefer? The order found must, however, to some extent be due to the fact that the ptarmigan prefers *Salix* to *Dryas* and *Dryas* to *Saxifraga*.

That the ptarmigan actually shows through its food that it has "taste", that is to say that at certain times of the year it prefers certain food elements to others, is — in that, I should think, all will agree — beyond doubt. It is proved by the material. Thus the *Dryas* leaves are accessible almost the whole year, but quantitatively are quite subordinate in the summer food. However, the different natural conditions of the different seasons of the year change the access to the different food elements as well as the food requirements of the ptarmigan. It is in the main only the former of these factors we are to deal with here; the physiological aspect will be but slightly touched in a succeeding chapter.

Inner Fjords. Turning now to the inner fjords, conditions there in November seem to be precisely as might be expected, judging from our knowledge of the vegetation. The *Dryas* maximum (fig. 39, III) seems to have shifted to the left, which agrees with the fact that in the inner fjords *Salix* is much more intimately associated with the snow-patches and deep snow-cover. The quantity of *Salix* also is at the low level that might be expected, and the quantities of *Saxifraga*, too, are somewhat larger than in the outer fjords. In view of the extremely sparse material at hand we may here with some right speak about "luck". It is satisfying to ascertain, however, that even a very small material may contain valuable matter, inciting one to establish renewed investigations for verification. But it will be obvious that to persons who have no knowledge of the vegetation and the snow-covering conditions the material would tell nothing about the phenomena discussed here.

The outer coast. In agreement with the fact that the *Salix* areas at the outer coast (cf. p. 29) compared with the fjords are always situated away from the great depths of the wintry snow-cover and tend to be more or less free from snow, or at any rate are characterised by a considerably sparser snow-cover than in the fjords, the *Salix* curve (fig. 39, I) in February is higher at the outer coast than in the outer fjords; the figure even seems to show that in 1932 this state of affairs lasted till March.

The snow-cover of the *Dryas* areas in the fjords and at the outer coast does not exhibit the same characteristic differences as that of the *Salix* areas, and accordingly the *Dryas* curves (fig. 39, I and II) are almost identical. However, here, too, there is a difference, in that the percentages

of *Dryas* must be assumed to be lower at the outer coast than in the fjords.

As not only investigations of the vegetation, but also examination of the contents of ptarmigan crops, have proved the access to *Salix* at the outer coast in February to be easier than in the fjords in the period January—March, it is not surprising that the *Saxifraga* curve (fig. 39, I) for February at the outer coast is much lower than in the outer fjords.

The attentive reader, on comparing the contents of *Salix* and *Dryas* in crops from the outer coast and the outer fjords, will no doubt note that the differences found are but small. But here a knowledge of the vegetation comes in. The ptarmigans killed in the outer fjords were killed at Eskimonæs, one of the few places in the fjords round Clavering Island in which fairly large *Salix* growths occurred, rising above the snow as late as January, and the ptarmigan killed in April at the outer coast was killed precisely on a day when the snow-cover was exceptionally coherent. A larger material would no doubt show more distinctly the difference between the life conditions in the fjords and at the outer coast.

Thus the investigations on the occurrence in the winter food of the respective main constituents show a distinct correlation to the thickness of the snow-cover, and this correlation is so evident that it is soon ascertained even in a small number of crop analyses; hence we have constantly to resort to our knowledge of the snow-cover of the vegetation if we are to read the sparse material aright.

Considering that the snow-cover in the winter does not increase gradually from day to day, but is subject to great fluctuations due to the varying climatologic conditions, it is not to be wondered at that the percentage quantities of the various constituents in the food vary considerably from day to day.

It is desirable that crop material from a larger number of consecutive days with a marked difference in precipitation and force of the wind should be available. If so, it would be possible to ascertain the daily variations in the crop content and their dependence on the weather conditions. We must here be content with the indications given by some concrete examples extracted from Tables 4—11 (pp. 86—99).

After some six or seven days' snowfall ptarmigans Nos. 73—78 were shot at the foot of Mt. Gunvor on November 16, 1931. The greater part of the lowland was covered with snow, and on account of deep, loose snow it was difficult to reach the mountain side, fairly free from snow, on which the ptarmigans moved about. An examination showed that the average content of *Dryas* in the crops of the six ptarmigans was about 90 per cent.

At the end of November and at the beginning of December the snowfall continued. After a period with no precipitation it snowed again at

Eskimonæs on December 17 and 18, and on the 20th ptarmigans Nos. 26—27 were killed here. On this day the land was covered with deep snow, the force of the wind having been inconsiderable. Again the *Dryas* percentage in the crop content was above 90.

After a long interval with no snowfalls, about 5 cm of loose snow came down in the early morning of April 3, 1932. By noon ptarmigans Nos. 39 and 40 were shot in Granatdal. In this case, too, the *Dryas* percentage was above 90.

The above examples show that after days with precipitation that has been allowed to remain where fallen (i. e. days with low forces of wind) the *Dryas* percentage may be very high, and from our knowledge of the vegetation we may assume that this is the rule. Since the snowfall occurring immediately before November 16, 1931, was one of the largest during the winter and the precipitation falling on April 3 was but small, it will be seen that the later it is in the winter, the smaller is the snowfall required to make the *Dryas* percentage in the crop content high.

At the outer coast, too, a slight snowfall late in the year may result in a high *Dryas* percentage in the crop content. Ptarmigan No. 15 (Table 5, p. 89) is an example hereof.

After a storm the *Dryas* percentage will probably fall and the *Salix* percentage rise; the same will probably take place at lower wind forces also if only they have lasted for a certain number of days. Thus ptarmigans Nos. 1—7 were killed some few days after a storm succeeded by windy days, and all the crops show a *Salix* percentage of over 50, the highest being 89 (No. 7).

A larger material may be expected to show even more distinctly that *Salix* and *Dryas* alternate in the winter food in the manner described and that *Saxifraga oppositifolia* will be present in the greatest quantities on days on which *Dryas* is abundantly represented. Thus in crops Nos. 36—38 and 73—78 *Dryas* and *Saxifraga* alternate, constituting together over 50 per cent. of the content of the individual crop.

Sometimes the weight percentage of *Saxifraga oppositifolia* in the crop content may exceed that of *Dryas*, and characteristically enough on days with so thick a snow-cover that even *Dryas* is less easily accessible (cf. ptarmigans Nos. 28 and 36). Even on such days *Salix arctica* may be present in large quantities in the crop contents, which might seem puzzling in view of the usually thick snow-cover of the *Salix* areas. It should, however, be borne in mind that firstly *Salix* has a wide amplitude in the snow-covering scale, for which reason occasional individuals may be found on soil fairly free from snow, and secondly that the branches of *Salix* are so long that in places they rise above the snow.

Apart from the main constituents only very few species were found in the winter food in such large quantities in the individual crops as to attract attention. Mention should, however, be made of stem-tubers of *Polygonum viviparum* and stems and especially sporophyll heads containing spores of *Equisetum variegatum*. Stem-tubers of *Polygonum* were only found in February—March and were particularly frequent in the ptarmigans killed on February 18, 1932, at Knudshoved at the outer coast (fig. 32, p. 84). They may constitute up to 17 per cent. of the content of the crop.

Stems and sporophylls of *Equisetum variegatum* were only found in crops of ptarmigans killed in the period October to February, and in great quantities only in ptarmigans Nos. 10 and 11 from Knudshoved, February 25, 1932, constituting 23 and 40 per cent. of their crop contents (cf. fig. 35, p. 107).

These elements must be assumed to contain something valuable for the ptarmigan, for otherwise it would hardly have overcome the extremely conspicuous difficulties in securing them. *Equisetum variegatum* rarely occurs in such large quantities that it will be worth while to spend time and energy on working at it, and the *Polygonum* has to be dug up from the soil.

In this connection it may be mentioned that I have observed Arctic hares in the winter and barnacle geese (*Branta leucopsis*) in the summer very eagerly engaged in digging out from the soil the stem-tubers of *Polygonum viviparum*, so rich in nutrient substances. The plant indeed deserves the name which was then given to it: the Arctic potatoe. The above-ground parts of the plant, too, may serve as food for the Arctic hare in the summer. The Norwegian name of *Polygonum viviparum* is "hare rye".

Summary of the annual variations in the food.

An attempt having thus been made to interpret the variations in the crop content while we have constantly had to take the snow-cover into consideration, the importance of the snow-cover for the access to food on the whole has been pointed out as one of the most important causes of the variations in the food.

The succession *Polygonum*, *Salix*, *Dryas*, *Saxifraga oppositifolia* does not only give the order of the dominance of the different main food elements in the food from midsummer to midwinter, but also gives the order of these species if grouped according to the snow-cover in their areas of dominance, *Polygonum* being covered with the thickest layer of snow, while *Saxifraga* is least snow-covered. *Polygonum* dominates in

the food during the snow-free summer time only, while *Saxifraga* is most abundantly represented at midwinter.

These results will be of importance for further investigations on the variations in the food of the ptarmigan and the access to it, and it may even now be taken for granted that even with a very small crop material at hand it will be possible to form an estimate of the access to food at the time and in the area whence the available material is derived.

A high *Salix* percentage indicates good access to food, a high *Dryas* percentage a moderately good, and a high *Saxifraga oppositifolia* percentage a poor access to food.

Similarly as a high *Saxifraga* percentage indicates the season when the access to food is most difficult, a high *Polygonum* percentage indicates the season when the access to food is easiest.

High *Salix* percentages may occur in the months October to May, high *Dryas* percentages in the period November to April.

However, the absolute quantities and dates gathered from the available material must not be regarded as general; the investigations have precisely shown that they are only general in that sense that they show an annual course of the variations, which, however, may shift to one or the other side according to the precipitation and whole climatic course of the year.

The annual variation in the food may then be summarised as follows.

The snow-cover forces the ptarmigan to leave the *Polygonum* food, and when the winter sets in, it changes to a winter food consisting of less snow-covered plants. At the beginning of the winter *Salix arctica* dominates in the food, but gradually the snow-cover renders the access to this plant so difficult that its amount in the food is reduced, while the amounts of the less snow-covered *Dryas octopetala* and *Saxifraga oppositifolia* increase. The crop content shows, however, that as soon as conditions permit, the ptarmigan principally looks for *Salix arctica*. Thus the migration to the outer coast is precisely due to the fact that the access to *Salix* is easier at the outer coast than in the fjords. After midwinter the crop content shows a gradual return to *Salix arctica* gradually as the melting of the snow proceeds, and in the course of May—June the country is so much free of snow, and the spring so advanced that the ptarmigan may change to young, growing plant parts, and in the course of June it may begin to feed on *Polygonum* again.

Thus as regards the main food constituents the variations are very great in the winter and very small in the summer. The reverse is the case with the subordinate constituents, which vary considerably in the summer food, of which they constitute about 13 per cent., while they only constitute 5 per cent. of the winter food.

The annual variation in the life-form spectrum of the plant species found in the crop of the ptarmigan.

Since in the summer, as stated above, the crop content consists chiefly of plants whose ecology deviates considerably from the plants consumed in the winter, it cannot surprise that there is a biologic and a morphologic difference, too, in the summer and the winter food elements.

An expression of this difference is gained by computing on the basis of the life-forms of the plant species (RAUNKIÆR, 1905) how large a weight percentage of the food the different life-form classes constitute at the different seasons. This is done in Table 16, below, in which the examined material from July to and including August is regarded as summer food, that from October to and including May as winter food.

The table shows that in the winter it is chiefly chamæphytes, in the summer chiefly a single geophyte which are of importance as food for the

Table 16.

Season	Winter	Summer	Life-form
Number of ptarmigans.....	50	28	
Crop content (mg)	401600	47250	
Average crop content (mg).....	8032	1688	
<i>Salix arctica</i>	50.3	8.0	Ch.
<i>Dryas octopetala</i>	38.2	1.0	-
<i>Saxifraga oppositifolia</i>	5.8	+	-
<i>Arcostaphylos alpina</i>	+	0.2	-
<i>Cassiope tetragona</i>	0.1	+	-
<i>Cerastium alpinum</i>	0.2	0.2	-
<i>Draba cinerea</i>	+	—	-
— <i>subcapitata</i>	+	—	-
<i>Salix herbacea</i>	—	0.2	-
<i>Stellaria longipes</i>	0.1	0.3	-
<i>Vaccinium uliginosum</i>	0.1	1.0	-
<i>Carex misandra</i>	—	2.3	H
<i>Equisetum variegatum</i>	1.8	—	-
<i>Luzula arcuata</i>	—	0.6	-
<i>Oxyria digyna</i>	—	0.4	-
<i>Papaver radicum</i>	+	0.3	-
<i>Pedicularis flammea</i>	—	0.1	-
<i>Saxifraga cernua</i>	—	0.3	-
<i>Eriophorum Scheuchzeri</i>	0.2	—	G
<i>Polygonum viviparum</i> , bulbils.....	1.0	85.0	-
<i>Polygonum viviparum</i> , stem-tubers	1.9	—	-

A + means quantities less than 0.1%.

ptarmigan. If it is borne in mind that the winter is more than twice as long as the summer, it will be evident that the ptarmigan chiefly takes its food from chamæphytes. This fact, which is illustrated by the even more condensed survey in Table 17, cannot surprise. As is well known, the chamæphytes occupy a greater space in the Arctic spectra (RAUNKIÆR 1911) than in the spectra from the other plant-geographical main zones, with the exception of certain desert tracts.

Table 17. Showing the percentage of the different life-form classes in the crop content of ptarmigans from the summer and the winter (extract from Table 16).

Season	Winter Oct.—May	Summer July—Aug.
Chamæphytes	95.1	10.9
Hemicryptophytes	1.8	4.1
Geophytes	3.1	85.0

To this must be added as determining for the dominance of the chamæphytes precisely in the winter food that in the Arctic regions, where the phanerophytes are absent, they are the only plants with above-ground perennating stems.

All the chamæphytes that form main constituents of the winter food will tolerate, though to a very different degree, the absence of snow in the winter, which is of importance for the access. *Salix* alone is dependent on a comparatively high degree of moisture in the soil. The reason why the heaths free of snow in the winter, and dominated by geophytes and hemicryptophytes mainly within the group of glumiflores (*Elyna*, *Carex nardina*, *C. rupestris*, *Poa glauca*, *Calamagrostis*), do not seem to contribute very much to the winter food of the ptarmigan, is no doubt that the above-ground organs of these plants die down in the winter. At any rate the ptarmigan is no feeder on glumiflores.

However, it cannot be inferred from the fact that the main food elements of the winter are lignified to a smaller or greater degree, that in the winter the ptarmigan lives chiefly on lignified plant parts. For the material shows precisely that they form but a modest part of the whole quantity, it being principally the wholly unligified or but partially ligified organs that are eaten. Of *Dryas* it is almost exclusively leaves, and the same applies practically to *Saxifraga oppositifolia*; the apices of the branches of the latter are but slightly ligified. Of *Salix* it is principally the still unligified apices of the branches that are consumed, but here the ptarmigan cannot avoid rather considerable additions of

lignified branches, at any rate in the winter. Thus the winter food can be characterised by an admixture of lignified plant organs.

If thus lignified plant organs form but a subordinate part of the winter food, they are almost entirely absent from the summer food, the main quantity of which is supplied by herbaceous plants, and of the lignified plants it is almost the herbaceous organs alone (flowers, leaves, etc.) that are eaten.

Thus in the winter the ptarmigan may be characterised as a feeder on leaves, buds, and apices of branches of lignified plants, and in the summer as a consumer of vegetative and floral organs of herbaceous plants.

The duration of the daylight and its importance for the collecting of food.

Before discussing the variation in the weight of fragments, it is necessary to point out a factor of importance for the collection of the food, viz. the duration of the daylight. At the winter solstice the daylight is astronomically reduced to nil, since at this time the sun is far below the horizon. At noon, however, a faint light can be seen to the south. Persons wintering in the area count on two hours, at the most, of fairly good light for doing outdoor work in December (cf. also SVERDRUP 1935, p. 24). In November and January conditions are more favourable.

The short duration of the light in connection with the impeded access to food must practically have the effect that not the time of the thickest snow-cover of the year, March—April, but the period of the dark time when the cover of snow is thickest (January) will be the hardest time for the ptarmigan.

The material treated in pp. 118—125 actually contributes to the elucidation of what time of the winters 1931—33 was most difficult for the ptarmigan, that is to say, the time when the possibility of securing food was most limited. The curves in fig. 39, p. 121, show that the relative percentage maximum of *Saxifraga oppositifolia* occurs in January, and since this maximum, as mentioned in p. 120, may be regarded as an indication of limited access to other food, it seems natural to assume that in the years 1931—33 the month of January was the most difficult for the ptarmigan. This was to be expected beforehand, and thus in this respect, too, the material seems to be suitable for a demonstration of the life conditions.

In describing the illumination during the dark time (see further pp. 142—147) there may be reason to examine whether the illumination by noon is more favourable in other places within the area than at sea-

level in the fjords. Some few of the latter are so narrow and surrounded by such high and steep mountains that the illumination must be assumed to be poorer than for instance at the outer coast, which consists of flat forelands, where the surface of the sea forms the horizon for about 180 degrees. But the highland, too, attracts the attention, the horizon "dipping" proportionally with the square root of the altitude above the sea. How much does this dipping of the horizon mean?

An expression of this can be found by looking in E. STRÖMGREN and B. STRÖMGREN (1933, p. 40), where the following formula is found

$$K = 1.78 \sqrt{h}$$

in which h is the height above the sea in metres, and K the dip of the horizon in arc minutes. If we insert various values for the height above the sea, we shall have the number of arc minutes which the horizon dips. An idea of what this means for the illumination at the respective levels above the sea is obtained by ascertaining by means of the "Universitetets Skriv- og Rejse-Kalender" how many days pass about winter solstice before the declination of the sun has changed a corresponding number of minutes. In this way the following table can be computed:

Darkest day at a given altitude corresponds as regards
illumination to the following dates at sea-level.

h	K	Dec.
100 m	0°18'	13
400 -	0°36'	10
500 -	0°40'	9
1000 -	0°56'	7
1500 -	1°09'	5

The table shows that at an altitude of 400 m above sea-level the illumination on the darkest day of the year (Dec. 22) corresponds to the illumination at sea-level on Dec. 10. In practice this means that by ascending to 400 m above sea-level the ptarmigan avoids the twelve darkest days preceding the winter solstice, and if it remains in the mountains, it avoids the succeeding twelve darkest days, too, in all the 24 darkest days of the year. At an altitude of 500 m above sea-level it avoids 26, at 1000 m 30, and at 1500 m 34 of the darkest days of the year. However, this does not mean that the whole dark time (i. e. the period when the sun is below the horizon) is reduced by the number of days mentioned, since the declination of the sun, when the dark time sets in about November 8, changes much more rapidly than at the winter solstice; yet it means a not quite small improvement of the illumination at midwinter. And as the improvement is directly proportional to the square root of the altitude above sea-level, a slight ascent of the mountain side will cause a comparatively greater improvement than a large ascent.

The next question must then be: Are there suitable feeding grounds in the mountains, and at what levels are the best feeding areas situated? This question can only receive a very incomplete answer.

The luxuriance and density of the vegetation decreases rapidly up the mountains, but in the fjords *Salix* areas occur occasionally up to about 1000 m altitude; these areas are but slightly covered with snow in the winter, or almost free from snow, and of such a density that they may quite well be assumed to serve as feeding grounds for the ptarmigan, at any rate for a short time. On the other hand, the areas from 300 to 800 m altitude in the fjords are as a rule less suitable feeding grounds at mid-winter, the land here being partly too steep, and hence of small areal extension, and partly covered with snow. At the outer coast, however, flat plateaus occur precisely at an altitude of some 300—400 m, which locally contain extensive feeding grounds free from snow in the winter, in places rich in *Salix*. It may therefore be assumed that in this respect, also, the outer coast offers the best life conditions to the ptarmigan, even though we cannot reject the possibility that suitable feeding places may be found locally in the mountains of the fjords in the winter.

The improvement gained in the illumination by an ascent of a certain number of metres depends on many different factors, and varies according to the duration of the faint noon-light at sea-level. When the period of light is short, a prolongation of the noon-light up to twice the normal time or more may be gained; whereas, when the light at noon lasts for more than two hours, the prolongation is less. In practice this means that the greatest improvement in the illumination will be gained if an ascent is made about the time of the winter solstice, and since at this time of the year we are probably approaching the minimum of light demanded for collection of sufficient food, I would not let these circumstances disregarded. This, however, needs a closer investigation, and measurements of the light intensity at the time of the day when the collection of food stops are desirable.

Another point is this: why does the ptarmigan not collect food during the dark night proper? It is difficult to answer, but possibly the ptarmigan, like many other birds, is night-blind.

The weight of the food fragments and its variation.

The weight of the food fragments is an aspect of the access to food which is of very great importance to the ptarmigan, irrespective of whether it secures one or more fragments by one pick of its beak. *Cetera paribus*, when the food must be secured in a short time, the plant organ of which the greatest quantity may be secured by one pick will be the most profitable. For the mutual relation of

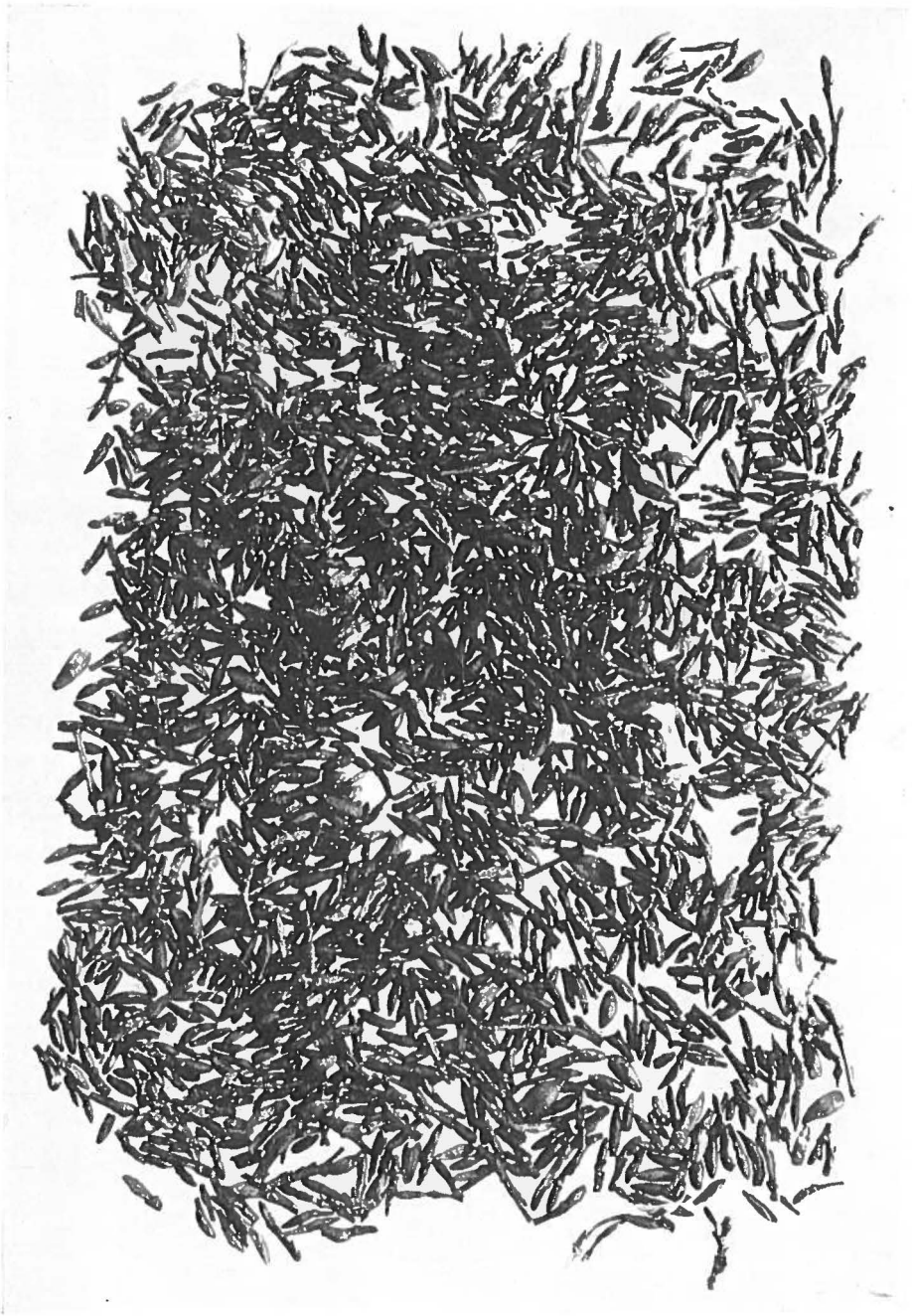


Fig. 40. The complete *Salix arctica* crop content of ptarmigan No. 23. Sex and age not known. Eskimonas, October 8, 1931. Note the small size of the fragments as compared with that represented in fig. 41. At the date in question the country round Eskimonas was almost free from snow. Nat. size. GRAM phot.

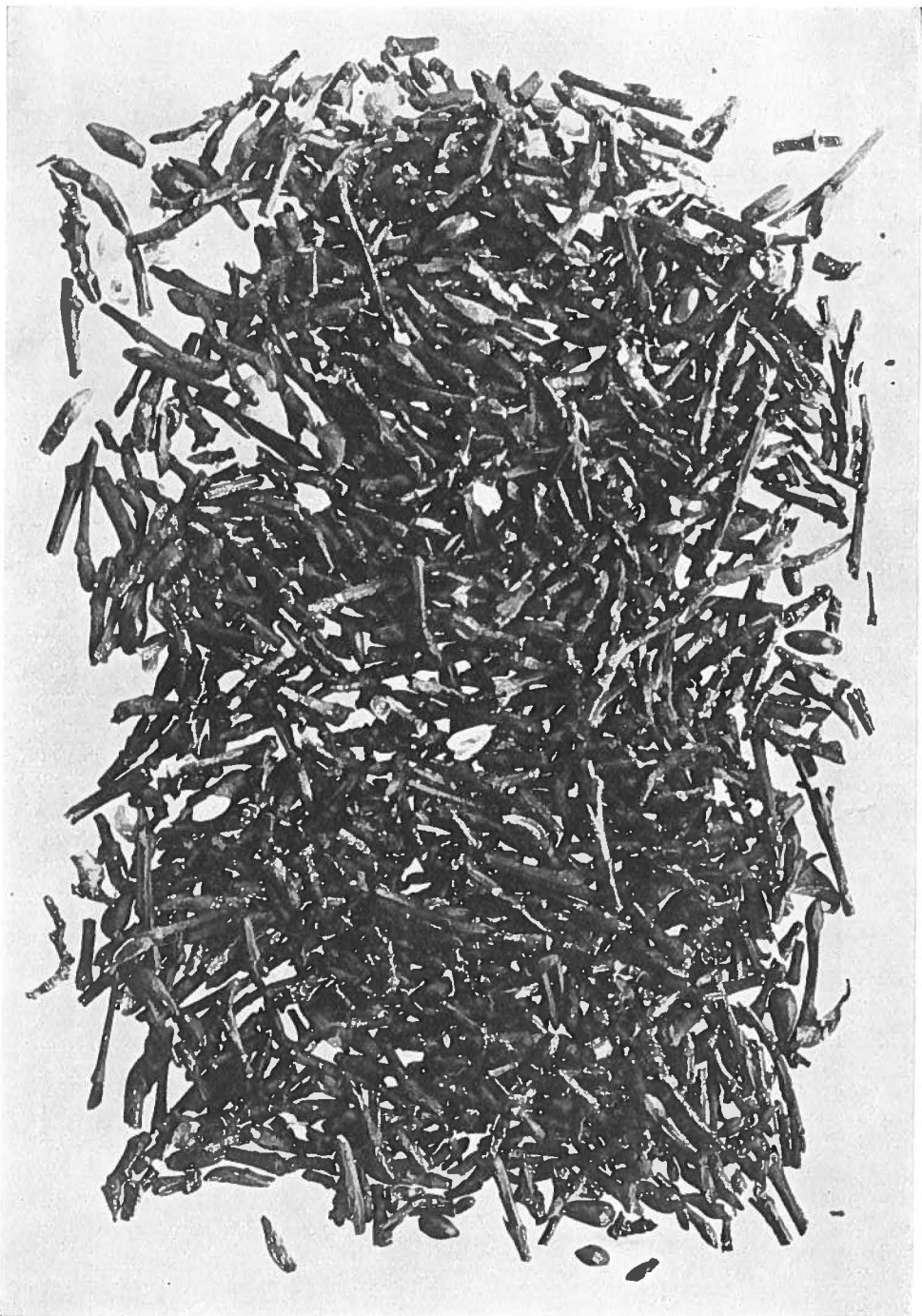


Fig. 41. The complete *Salix arctica* crop content of ptarmigan No. 28. Adult ♂. Eskimonæs, January 2, 1932. Note the big size of the fragments as compared with that shown in fig. 40. At the date in question the country round Eskimonæs was covered with snow. Nat. size. GRAM phot.

the different food fragments in this respect it is, of course, of importance to know whether the ptarmigan gets one or several fragments in one pick. As mentioned in p. 83, investigations of this are much needed. However, the investigations hitherto made seem to show that only quite exceptionally does the ptarmigan secure more or less than one fragment of the winter food elements by one pick, so in the discussion below this will be taken for granted.

Table 18 has been compiled on the basis of countings and weighings of the fragment material.

Table 18. Showing the average weight of fragments of the three main constituents of the winter food.

	Number of fragments	Weight in mg	Average weight in mg
<i>Salix arctica</i>	29679	202600	6.8
<i>Dryas octopetala</i>	85824	153600	1.8
<i>Saxifraga oppositifolia</i>	5409	23400	4.3

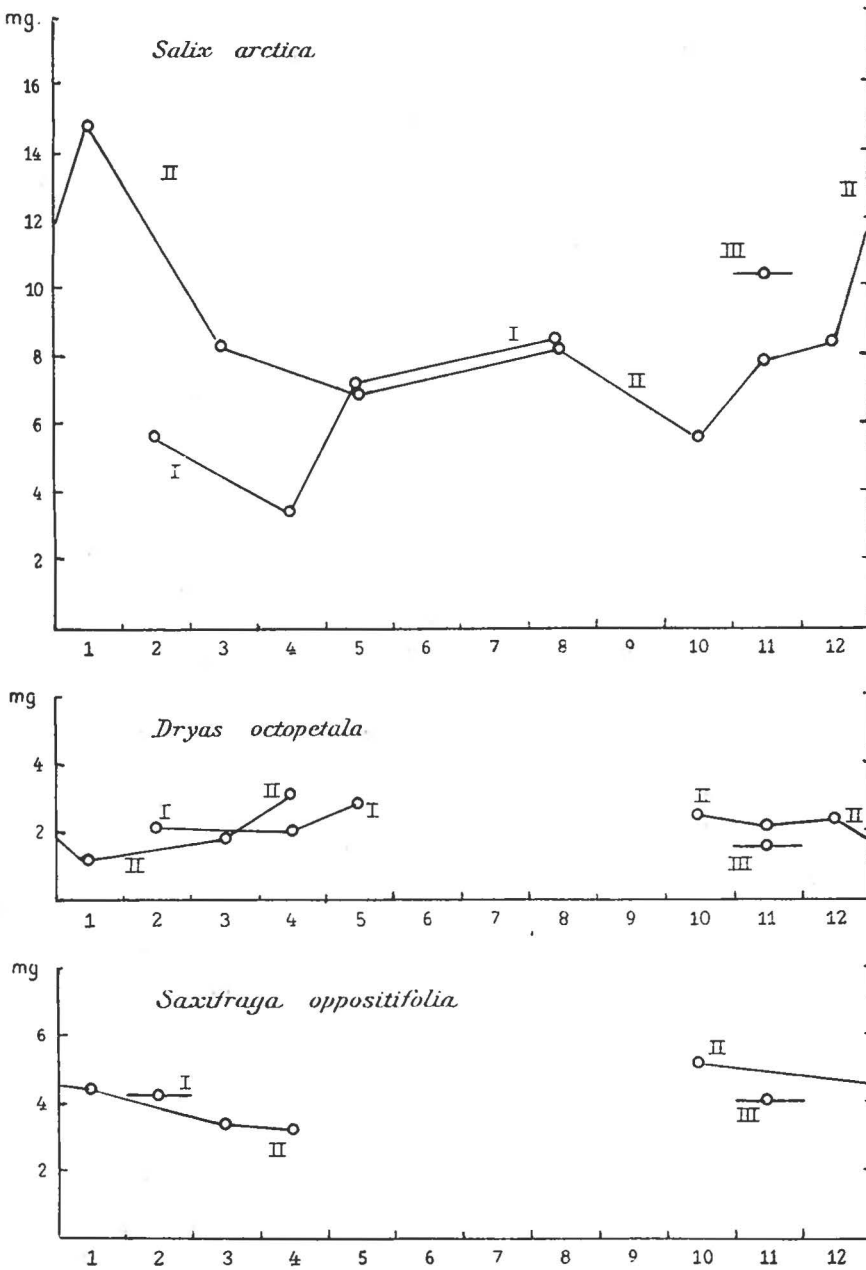
As mentioned on p. 80 ff., the value for *Salix arctica* must be assumed to be very near the true average value, while the value for *Dryas octopetala* must be considered to be a little too high, and that of *Saxifraga oppositifolia*, again, a little more too high. However, the succession of the species as regards the weights of their fragments must be assumed to be correct.

The variation of the average weights given in Table 19, and

Table 19. Average weights of fragments of various foods in different districts and different months (mg).

District	I: Outer coast				II: Outer fjords								III: Inner fjords	I+II+III
	2	4	5	8	1	3	4	5	8	10	11	12	11	Total
<i>Salix arctica</i> (buds and twigs)	5.7	(3.3)	7.1	(8.6)	14.8	8.3	..	7.0	(8.3)	5.7	8.0	(8.4)	(10.6)	6.8
<i>Dryas octopetala</i> (leaves) ..	2.1	2.0	2.9	..	1.2	1.9	3.2	2.5	2.2	2.4	1.8	1.8
<i>Saxifraga oppositifolia</i> (shoot apices)	4.1	4.5	3.6	(3.3)	5.2	4.1	4.3
<i>Polygonum viviparum</i> (stem-tubers)	21.0	21.0
<i>Equisetum variegatum</i> (sporophyll heads)	9.9	9.9
<i>Equisetum variegatum</i> (stems)	2.0	2.0

The figures in parantheses are based on weighings of a few fragments only.



I Outer coast. II Outer fjords. III Inner fjords

Fig. 42. Showing average weights of fragments of various foods in different districts and different months.

in fig. 42 is important for an understanding of the life conditions of the ptarmigan at the different seasons and within the different districts.

If the time in which the ptarmigan can secure its food is reduced, the reduction can be made up for by taking larger quantities in each pick, and thus the importance of the reduction for the total quantity consumed can be diminished.

The figures in Table 19 and the curves in fig. 42 show indeed that the weight of the *Salix* fragments culminates in January.

An examination of the *Salix* material shows that at midwinter it consists of bigger, that is to say, longer and thicker, as well as older, more lignified fragments of branches than is usual in the winter. Figs. 40 and 41 are exceedingly instructive.

Although the bigger, partially lignified *Salix* fragments might be supposed to be less tempting than the wholly or partly unligified apices of the branches, the material shows (cf. p. 104) that at midwinter the ptarmigan hardly spares itself any effort to secure them. The thickest branch fragments are often very long. The tendency is quite the same as that shown by the wood-chopper, who cuts off longer pieces of the thick branches and in this way will more rapidly have finished the wood heap. In the behaviour of the ptarmigan also, time may be considered an important factor.

Of *Saxifraga*, too, it is possible for the ptarmigan to take larger fragments by cutting at greater intervals, and the figures in Table 19 indicate that this may take place. However, this is less certain, the weights of the fragments in this case having been less accurately determined (cf. p. 81).

Quite the opposite is the case with the *Dryas* fragments, which are smallest at midwinter.

For the understanding of this fact it is of importance to recollect that, as shown by the *Dryas* material at hand, apart from some few flower-heads with adhering stem fragments occurring in the summer-food, the ptarmigan eats exclusively leaves. It seems incredible that the ptarmigan should be unable to eat stem fragments, but the material shows that it only does so to a very small extent, whatever the cause may be. But if this is the case, it will be obvious that the weight of the individual leaves will be lowest at midwinter. For investigations of the size of the *Dryas* leaves in localities with different snow-cover (cf. p. 32) have shown that in areas free from snow in the winter the *Dryas* leaves are smallest (f. *minor* HOOKER), exposed, as the localities are, to the wind and poor in nutrient substances, because the fine-grained material of the soil is removed by deflation (cf. fig. 43).

Thus the weights of the fragments and so also, to a direct observation of the crop content, the size of the fragments, supply important

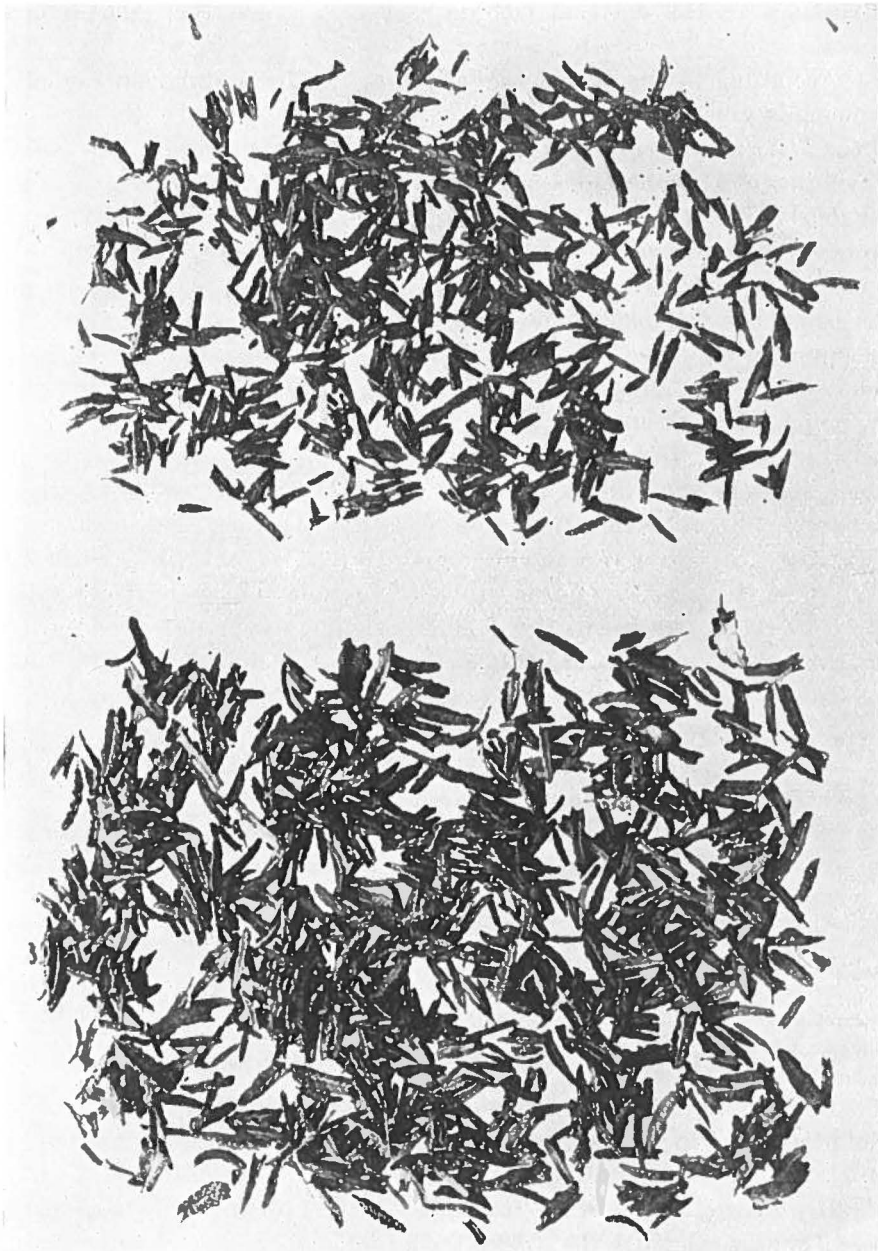


Fig. 43. Above: Leaves of *Dryas octopetala* from ptarmigan No. 36, young hen. Eskimonæs, March 19, 1932. — Below: Leaves of *Dryas octopetala* from ptarmigan No. 23, sex and age unknown. Eskimonæs, October 8, 1931. — Note the difference in the leaf sizes, due to the different exposure to the wind in the different localities. Nat. size. GRAM phot.

ON and LESLIE (1911) for *Lagopus* completely digested, or at any the night, seems to be shown by sty when at 9 in the morning of stone. An indirect proof of digestion in the resting place, is formed and at the bottom of these places. side by side, and the place of each



Gelting phot. July 17, 1932.

of course, of common occurrence in the snow-patch rich in *Phippsia algida* and have been carried into the snow-patch by covering Island. Detail of fig. 26, p. 71.

crements. An indirect proof that in food at the same time as it secures cements found in the snow-patches n that account derive some benefit or the manure must be assumed to of nitrogen, which, again, is hardly of the *Polygonum*.

verage weight of the crop content.
gated had been larger, the annual tent would, no doubt, have given us

conditions under which the food is col-

the weight of the *Dryas* fragments should he snow-covering conditions, the weights nents chiefly of the time conditions under these indications are not "true" or unmis-*lix* due to an increased snow-cover may in an increased size of the *Salix* fragments, f collecting may result in a reduction of size of the fragments consumed may also r factors, for instance the age, sex, and Thus when the access to food is limited, migans may be supposed to be greatest, "compete" about the food by cutting off es.

the weights of the fragments in d as indications of the access to from the circumstance that at mid-generally smaller at the outer coast than (fig. 42). If we follow up the thought, amples which support the supposition s may be considered as indications of the erial must be secured before the question

be stated that when the *Dryas* fragments e *Salix* fragments to increase, the hard cult access to food, commences, and this ve maximum of *Saxifraga oppositifolia* p. 129).

the food is consumed.

omplete picture of the life conditions of e must find out what information is he time of consumption of the food.

killing of the ptarmigans as appearing it of the crop content, we shall have the).

ls of this table give but few details, yet ry the crop content increases in weight een 3 and 6 p. m. Altogether it may be t in the dark time the ptarmigan only ort period every day, namely the light

Table 21. Showing the annual variation in the weight (g) of the total vegetable crop content.

Month.....	1	2	3	4	5	7	8	10	11	12
Number of ptarmigans: I.....	..	14	..	1	3	..	3
— - — : II.....	3	..	13	2	2	1	24	3	1	2
— - — : III.....	6	..
Average weight of crop content in various districts	Outer coast: I .	..	12.4 ¹⁾	..	3.1	4.3	..	1.0
	— fjords: II .	27.9	..	2.6	2.0	1.0	2.1	1.7	9.9	5.3
	Inner — : III	7.6	..
	The whole area: I + II + III	27.9	12.4 ¹⁾	2.6	2.3	3.0	2.1	1.7	9.9	7.3

¹⁾ If we disregard ptarmigan No. 9, whose crop was empty, the figure would be 13.3.

interesting details as regards the consumption of food at different times of the year and in different districts. At the present, however, we must be content with what the material at hand tells us. But it is evident that in our small material the diurnal variations in the crop content discussed on the preceding pages will greatly influence our calculation of the annual variation on the whole. But as both the diurnal and the annual variations

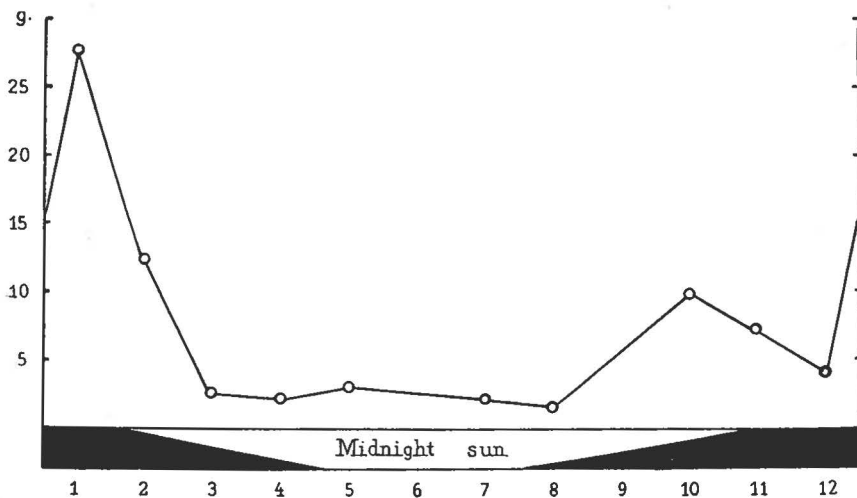


Fig. 46.

in the weight of the crop content seem to be caused by one and the same external factor, viz. the duration of the time of light for collecting food, both become expressions for the influence of this factor.

Table 21 has been compiled on the basis of Tables 4—11, and the curve given in fig. 46 was plotted on the basis of Table 21. This figure further illustrates diagrammatically the illumination, the dark time, and the time with midnight sun. Since these conditions do not differ essentially

us data of crop contents from the
r coast from January—March.

II Eskimonæs January 13		I Knudshoved February 14			II Eskimonæs March 13		
867		12361			2631		
111		3037			1061		
W	W%	N	W	W%	N	W	W%
783	53.1	1410	8075	65.3	83	688	26.2
083	29.0	1505	3097	25.0	907	1681	63.9
000	17.9	10	39	0.3	71	258	9.8
0	0.0	112	1157	9.4	1	4	0.1

W = Weight mg; W% = Weight percentage.

It does not normally live, and the hurting
on the alimentary canal show how the
under abnormal conditions, may cause
ably with our knowledge of instincts in
be interesting to study experimentally
land ptarmigan; information about the
country in the winter may be obtained
enced of the Danish partridge.

ptarmigan stock from the stormy periods of
due with unabated violence for up to
re, will therefore depend on whether or
dant that the stock in the periods left
e to gather so much food that it may
due to the storm. In view of the short
mediately obvious that the greater the
the sooner will the crop be filled. As
with regard to their content of
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e 24, p. 153), and the *Salix* frag-
h larger than the *Dryas* frag-
at an increased access to *Salix*
of the ptarmigan much more
eased access to *Dryas*.

ated. On an average the *Salix* fragments
Dryas fragments but at midwinter the
e times larger than the *Dryas* fragments.

lie nearly in the same latitude, the
le 21, is given in one curve in Fig. 46.
average weight of the crop content
uence of the duration of light sufficient
nount of the crop content is far greater
curve is encumbered with a conspicuous
December. The ptarmigans in question
rom their resting place and killed be-
bable explanation of their small crop
late in the day that the digestion of
t time had commenced and part of it

aterial tells nothing about the absolute
t seasons of the year. For obtaining
a living ptarmigans kept under obser-

the dark time proper.

he whole in the lighter periods of the
ptarmigan can collect its food quietly,
ling daylight to work intensely. This
s, indeed, the immediate impression
igan collecting its food at the different
bird possesses quite different instincts
erent habits, at the different seasons.
takes time to collect its food and has
he whole seems more easily frightened,
o move by direct shooting only, and
ly engaged in collecting food that one
idle of a flock before the individuals
sly collecting even during the flight.
; the bird fill its crop well and rapidly
her is connected with the instinct
er in flocks and roam in the winter.
the instinct of filling the crop well and
und brought into function by compe-
he flock and is thus an example of a
a this complex of reflexes might then
s devoid of suitable food. But the
solved at present, and many other
l, may play a role.

; the rapid filling of the crop during
x-storm sets in, the ptarmigan

cf. p. 134. If, therefore, we might take it for granted that *Salix* and *Dryas* were equally valuable as regards content of nutrient substances, the ptarmigan would at midwinter, by feeding on *Salix*, secure on an average twelve times as much nutrient matter in each pick as by feeding on *Dryas*. We may assume (cf. Table 24, p. 153) that *Salix* and *Dryas* are of almost the same value in this respect, but the question should be more closely investigated.

If, therefore, the ptarmigan were to increase its chances by a seasonal migration, it would have to leave the fjords at midwinter and migrate to the outer coast, which it actually does, as has been shown above (p. 63).

A closer examination of the crop content of ptarmigans killed in January, February, and March (from December only two ptarmigans are at hand, and moreover their crop content is inconsiderable) will on several points add to and throw light on the problems in these months which are so important for the ptarmigan, the access to food being impeded in different ways. The various facts relating to this material are tabulated in Table 22. While the February material is derived from the outer coast, all the January and March material is derived from Eskimonæs in the outer fjords.

If we compare, first, the conditions at Eskimonæs in January with conditions in the same locality in March, it will be known at the outset that the snow-cover has increased in thickness during this time while the illumination has improved considerably. This, indeed, appears from the material at hand, since both the average weight of the crop content and the average number of the fragments have decreased. Moreover the illumination in March should permit the ptarmigan to use the time to find *Salix*, but this species is actually much more sparsely represented in the crops in March than in January; this is due partly to the growing snow-cover, the increase of which is disproportionately large precisely in the *Salix* areas, which are here snow-patch areas, partly to the fairly long duration of the daylight, which permits the ptarmigan to feed on *Dryas*. Thus the numerical relation between the *Salix* and the *Dryas* fragments in January is 1:7, in March 1:11. The percentage representation of *Salix* and *Dryas* in the total weight of the crop content shows corresponding differences.

From February no material is at hand from Eskimonæs, when but a small number of ptarmigans were present, but it must be assumed that the month is intermediate between January and March in regard to access to food.

Considering the material from the outer coast from February, the number of fragments show that the proportion of *Salix* and *Dryas* in the

crop content is much more favourable for the ptarmigan than it may be assumed to be in the fjords in the same period. The numerical proportion of the *Salix* and *Dryas* fragments is 1:1, and the *Salix* weight percentage is 65.

Much would seem to show that conditions at the outer coast as late as March, 1932, must have been more favourable as regards the access to *Salix* than in the outer fjords at Eskimonæs 1932—33. From observations on conditions prevailing in the two districts it could not be supposed to be otherwise; for the snow-cover hardly begins to decrease on account of sublimation before April, but then always more rapidly in the fjords than at the outer coast.

The figures in Table 22 may give rise to further considerations on the conditions during these important winter months.

The three ptarmigans shot in January were killed on January 2, 1932, and January 16 and 18, 1933. These dates belong to the very dark time with only about two hours of faint light at noon. If it is taken into consideration that during the short light time of these days the ptarmigans collected on an average 9111 fragments of different kinds, the question of the time itself invites consideration. If it is assumed, for instance, that the ptarmigan is able to pick with its beak once in a second, this will give 7200 picks by continuous work during two hours. If it works at the same rate for three hours without interruption — which it may perhaps do — it will be 10,800 picks, or about the number found. This shows that there cannot be very much time to spare. There is but little time to move, and once it has arrived at the feeding place with the most important food elements, the ptarmigan must work intensely. A stay in the neighbourhood of the feeding grounds, and the presence of such snow-free areas, or areas in which *Salix* projects above the snow (*Salix* is the only species whose branches are long enough to do so), seems to be an absolute condition at this season. Personal observations, as well as the unanimous statements of the trappers, left one with the impression that in winter certain localities in the fjords are frequented by the ptarmigans. In 1932 the south point of the cape of Eskimonæs was such a locality (cf. p. 104). However, the ptarmigans had to leave the locality in the darkest time, the branches left not being suitable as food for them.

From December, an important month also, in which the faint light at noon lasts but a short time, too sparse a material is at hand to show what were the conditions prevailing, but they must be presumed to be fairly like those of January; that is, a little better as regards the snow-cover, somewhat worse as regards the duration of the faint light at noon.

As the crop material which throws light upon the life conditions of the ptarmigan during the winter months is as yet comparatively sparse, it warns us to be cautious; but the fact that the material in all essentials leads to results which agree most closely with what might be expected from investigations of the vegetation and the access to it, increases the certainty.

INVESTIGATIONS ON THE CONTENT OF ORGANIC NUTRITIVE SUBSTANCES IN THE CONSTITUENTS OF THE FOOD

In order to gain an idea of the content of nutritive substances in the different plant species a number of determinations of the content of carbohydrates, raw fats, and raw proteins in the material brought home were made at the Plant-Physiological Laboratory of the University of Copenhagen in the period January to June, 1935.

Since, as stated in p. 80, this material is incomplete, and it was moreover proved by the analyses that the quantities contained in the individual crops were often too small to allow of a thorough analysis, these investigations must be characterised as very incomplete. If from the beginning I had been working with laboratory examinations in view, the treatment of the material in Greenland could have been adapted to serve this purpose. However, despite its deficiency, the investigation supplies various data on the content of nutritive elements in the food and new clues to an understanding of the conditions under which the bird lives, and at the same time reveals problems to be solved by future investigations.

Exsiccation and equalisation.

Analyses were made of the crop content of a number of ptarmigans which had consumed such a large quantity that it might be presumed to suffice for a thorough analysis; however, this did not always prove to be the case. The numbers of the ptarmigans from which the plants and plant parts analysed were derived, will be tabulated below:

<i>Salix arctica</i>	Buds and twigs	4, 25, 28, 29—34 ¹⁾
<i>Dryas octopetala</i>	Leaves	4, 15, 25, 28, 29—34 ¹⁾
<i>Saxifraga oppositifolia</i>	Shoot-apices	28, 75—78 ¹⁾
<i>Polygonum viviparum</i>	Spikes and bulbils	25, 46 + 52, 64, 65
—	Stem-tubers	5
<i>Equisetum variegatum</i>	Sphrophylls with spores	10
—	Stems	11

¹⁾ 29—34, etc. means that the contents of these crops were analysed together.

Thus the suitable plant material from 21 ptarmigan crops was analysed.

The material was exsiccated at a temperature of 100° C. until the weight remained constant. If all the material weighed in Greenland had been brought home, this exsiccation might have supplied an expression of the effectivity of the air-drying made in Greenland. Unfortunately, however, this was not the case.

Consequently the loss in weight by complete drying can only be stated for a small part of the material investigated (see Table 23).

Tabel 23. Showing the loss in weight of the air-dried material by complete drying.

	Ptarmigan No.	Loss in weight (mg)	Loss in weight %
<i>Salix arctica</i>	} 28	2073	11.4
	} 4	1243	12.1
<i>Dryas octopetala</i>	} 28	243	12.8
	} 4	1053	9.6
<i>Polygonum</i> , bulbils	} 46	128	9.1
	} 65	233	10.6
<i>Polygonum</i> , stem-tubers.....	5	423	11.3
<i>Equisetum</i> , sporophylls.....	10	543	9.9
<i>Equisetum</i> , stems.....	11	183	11.4

As will be seen, the loss in weight ranges about 11 per cent.

As the fresh weight of the material was never measured, its absolute water content cannot be computed.

After exsiccation the material was pulverised in a quern. For *Salix* and *Dryas octopetala* the equalisation of the comminuted material presented some difficulties. While prior to the pulverisation the materials of these two species exhibit a fairly uniform appearance, a rather heterogeneous material will result from the grinding in the quern. Here the two plant species will be discussed separately.

As already stated, the *Salix arctica* material consists of fragments of branches with adherent buds. Most of the latter contain an embryonal catkin whose degree of development and whole percentage contribution to the total weight of the bud depend on the season. The later in the spring the material was collected, the larger were the embryonal catkins and the longer the hairs on the bracts. These hairs, which make the buds, when developed, appear as the well-known white silvery catkins, are filled with air and hardly particularly valuable as food. On account of the lack of protoplasm the protein content of the hairs, in particular,

must be assumed to be inconsiderable. Owing to the abundance of these hairs, which thus in regard to their content of nutrition must be assumed to differ essentially from the other *Salix* fragments, the *Salix* material after comminution appears in two widely different consistencies, viz. on the one hand the finely comminuted particles of cortex, wood, and embryonal leaf tissue and on the other hand the air-filled hairs of the bracts of the embryonal catkins. On pulverisation two groups of material are seen to leave the quern: the finely comminuted and probably highly nutritive powder below, and the silvery and presumably little nutritive felt of compressed hairs above. On cleaning the quern after separation a large quantity of the matted hair-mass is found in the quern.

It is evident that an equalisation of such a heterogeneous material is difficult, but absolutely necessary. It is of no avail to pass the material through the quern a second time; the result will be almost the same, since the hairs will pass the quern almost unchanged. Hence there was no other way out, it seemed to me, than to form an estimate of the approximate quantities of the two kinds of material found in the total mass, and subsequently by weighing the material to see that the proportions remained the same as far as possible. And the control tests showed indeed that the equalisation was successful in most cases. Ptarmigan No. 4 alone seems to form an exception (cf. footnote 3, Table 24, p. 153).

The *Dryas octopetala* material consists almost exclusively of entire leaves (blades and petioles) plus small quantities of blade fragments. Before comminution it therefore presents an extremely uniform appearance. After comminution, however, the material, like that of *Salix arctica*, exhibits two rather different masses, viz. on the one hand the finely pulverised particles of the blade tissue and petioles, and on the other hand the less finely ground, crushed, and matted parts of the strengthening tissue of the strands. The greyish-brown, matted mass, like the hairfelt of *Salix arctica*, shows a tendency to remain in the quern. In this case also, a repeated grinding in the quern is of no use, and the only way open to me was to distribute the two different masses in the analysis samples as far as possible in the same quantitative proportion as in the total mass. Here, too, the control analyses show that the equalisation must be considered to have been carried out with sufficient care.

The equalisation of the other constituents examined was not attended with the same difficulties.

Methods of investigation.

The determinations of the nitrogen content were made by the method of KJELDAHL with the modification proposed by ANDERSEN & NORMAN-JENSEN (1923), viz. to add a small quantity of graphite to the

copper salts in the destruction vessel. In most cases the macro-method was used (quantities of 500 to 1000 mg), but if it was necessary to economise with the material, the micro-method was employed (quantities 25—50 mg). The investigations showed that both methods lead to a comparable result, but if enough material is at hand, the macro-method is preferable, since by that method possible deficiencies in the equalisation will more easily be rectified.

The values of raw proteins were found by multiplying the N-values found by 6.25. The raw protein values thus arrived at are only approximate but sufficiently accurate for our purpose.

The determinations of fat were made by extraction by means of ether by SOXLETH'S method. The extraction time was in each case two hours. The amounts of substance used varied according to the abundance of the available material, the whole quantity available being as far as possible employed. The smallest quantities employed (*Polygonum* spike fragments and bulbils) were 1.3 g, the largest quantities (*Salix arctica*) 8.5 g. An important condition for the correctness of the determination is a complete exsiccation of the extracted raw fat. In the four analyses first made this was hardly complete (cf. footnote 2, Table 24, p. 153), as seems to appear from the comparatively high values of raw fat. As regards the remaining analyses a complete exsiccation was therefore made after the ether extraction and ether evaporation.

The raw fat extracted from the different plants differed in colour, the colour approaching that of the particular plant part; this was due to their content of chlorophyll and other colouring extract matter. All the raw fat values found are therefore a little too high, which, however, is of no great importance for our purpose. In practice the content of raw fat in the plant parts is, in fact, determined as the weight found by extraction with ether.

The determination of sugar was made by the method of BERTRAND. The material analysed was that from which the raw fat had been extracted by the SOXLETH method. In part of this material the determination of directly reducing sugar was made by the method of BERTRAND, while in another part the determination was made after inversion with citric acid. The difference between the first and second determination gives the amount of not directly, reducing sugar. The content of starch in the plant material from which the fat and the directly and indirectly reducing sugars had been removed, was determined by the method of REINCKE.

The content of cellulose in the plant parts was not determined. As the ruminating animals and the horse genus are probably the only groups of vertebrates in whose alimentary canal cellulose is dissolved, the cellulose cannot be taken into consideration as a food sub-

stance for the ptarmigan, but must be considered filling matter. In the succeeding pages the designation nutritive substances therefore refers only to raw proteins + raw fat + carbohydrates.

The results of the analyses are given in Table 24, p. 153. Each value is the average of two determinations.

The content of organic nutritive substances in the food of the ptarmigan.

In Table 24 the Roman figures I, II, and III indicate the outer coast, the outer fjord, and the inner fjord districts respectively. In addition, the number of the ptarmigans whence the material was derived, the dates on which the ptarmigans were killed, the mean weight of the plant fragments examined, and the percentage representation of the various substances in the food are given.

Salix arctica: It will be seen from the table that the protein content is the greater the smaller the fragments are. No exception from this rule was found in the material investigated. As the small fragments consist mainly of young buds and twigs, while the large fragments contain much lignified material, it is natural to assume that the protein content of the young fragments is larger than that of the lignified branches.

In the months January to March the quantities of raw fat seem to be fairly constant. According to the procedure adopted in the investigations the values 3.39 and 3.30 for Nos. 28 and 4 respectively must be assumed to be a little too high, and the largest and the smallest contents of raw fat known with certainty are then 3.11 and 2.90 per cent. Thus the variations in the content of raw fat are small. The content of carbohydrates in the *Salix* fragments, too, is fairly constant; however, it cannot escape notice that the small fragments are poorer in carbohydrates than the larger, more lignified fragments.

Finally it may be added that the total content of organic nutritive substances in *Salix arctica* is greatest in March (summer months not investigated), and that the addition is chiefly due to an increasing amount of disaccharides.

Dryas octopetala: The protein content in the leaves is a little higher than that of the *Salix arctica* fragments, and does not vary in a demonstrable degree with the leaf size, but shows a distinctly lower value in January than in November and February-March. This may possibly be due to differences in the soil of the habitats. Thus the soil in the snow-free January-localities must be assumed to be poorer in nutritive elements than that of the localities less exposed to the wind.

The quantity of fat in the *Dryas* leaves remains fairly constant,

Tabel 24. Showing the content of organic nutritive substances in percentages of dry matter.

	Ptarmigan No.	Date	District	Fragment weight ¹⁾ mg	Sugar		Starch ^c	Carbohydrates ^{a+b+c}	Raw fat ^d	Raw proteins ^e	Total ^{a+b+c+d+e}
					directly reducing ^a	not directly reducing ^b					
<i>Salix arctica</i>	25	3/11 31	II	7.9	—	—	—	—	—	12.00	—
Buds and twigs	28	2/1 32	II	15.1	3.39	2.27	7.28	12.94	3.39 ²⁾	9.34	25.67
	28	2/1 32	II	15.1	3.27	2.56	7.82	13.65	3.07	9.25	25.97
	4	18/2 32	I	6.2	1.76	1.55	6.71	10.02	3.30 ³⁾	13.06 ³⁾	26.38
	4	18/2 32	I	6.2	1.96	1.80	5.05	8.81	3.11	12.13 ³⁾	24.05
	29—34	17/3 32	II	8.9	3.54	4.83	6.87	15.24	2.90	10.40	28.54
<i>Dryas octopetala</i>	25	3/11 31	II	2.2	—	—	—	—	—	12.97	—
Leaves	28	2/1 32	II	1.9	—	—	—	—	4.65	8.90	—
	4	18/2 32	I	2.5	3.48	2.35	4.94	10.77	5.72	13.59	30.08
	29—34	17/3 32	II	1.9	9.40	6.22	5.18	20.80	5.34	13.06	39.20
	29—34	17/3 32	II	1.9	10.24	5.52	6.66	22.42	5.00	13.06	40.48
	15	20/4 32	I	2.0	11.55	2.33	4.50	18.38	5.34	—	—
<i>Saxifraga oppositifolia</i>	28	2/1 32	II	5.3	4.44	5.06	8.93	18.43	7.11	7.13	32.67
Shoot-apices	75—78	16/11 31	III	4.1	—	—	—	—	—	7.81	—
<i>Equisetum</i> sporophylls	10	25/2 32	I	9.9	2.18	5.71	6.61	14.50	3.62	18.62	36.74
— stems	11	25/2 32	I	2.0	—	—	—	—	4.03	11.56	—
<i>Polygonum</i> stem-tubers	5	18/2 32	I	22.7	3.45	9.20	14.08	26.73	2.21	12.93	41.87
<i>Polygonum</i> bulbils + various parts of the spike	25 ⁴⁾	3/11 31	II	—	—	—	—	—	2.48	19.75	—
	46+52 ⁴⁾	15/8 32	II	—	1.69	0.62	15.84	18.15	2.88	20.62	41.65
	64 ⁵⁾	12/8 33	II	—	—	—	—	—	—	22.09	—
	65 ⁵⁾	24/8 33	II	—	—	—	—	—	2.23	21.53	—
<i>Betula</i> twigs	— ⁶⁾	6/9 31	III	—	2.77	4.46	5.68	12.91	6.13	6.06	25.10
— leaves and catkins	— ⁶⁾	16/6 32	II	—	2.69	3.11	7.73	13.53	8.91	13.10	35.54
<i>Cassiope</i> shoot-apices	— ⁶⁾	2/7 33	II	—	2.60	3.67	3.37	9.64	10.70	6.47	26.81

1) The weight computed from air-dried material.

2) Without exsiccation after extraction with ether; the value is therefore a little too high.

3) The equalisation hardly complete.

4) The material consisted mainly of older bulbils.

5) The material consisted mainly of young bulbils + young spike fragments.

6) Herbarium material, cf. the text p. 156.

whereas the amounts of carbohydrates show a great increase from February to April. The material to illustrate this increase is but sparse, only a small amount of material having been examined; but the fact that the material examined consists of equalised samples of about 8008 *Dryas* leaves from Eskimonæs from March, about 4500 leaves from Knudshoved from February, and about 1500 leaves from the same locality from April, indicates that the increase must have taken place in a very large number of leaves of the snow-free *Dryas* individuals. Both at

Eskimonæs and at Knudshoved the increase is mainly due to the same group of carbohydrates, viz. the directly reducing monosaccharides; this, too, indicates a certain law-regulated course of the phenomenon.

The dates when the leaf material examined was collected indicate that the increase in monosaccharides had hardly begun on February 18 at the outer coast, while it was in active progress at Eskimonæs on March 17, and still going on at the outer coast on April 20, 1932.

A problem has here been revealed which cannot be definitely solved at the present time, but which on account of its great plant-physiological interest may stimulate renewed investigation. One can hardly help thinking that *Dryas*, which is evergreen, on March 17 (or even earlier) at some time or other has had an opportunity of undertaking a CO₂ assimilation by which the amount of carbohydrates has risen.

It has long been known that many arctic plants commence their vegetative activity long before the local temperature in a meteorological sense has risen above zero, but that some plants should be able to begin assimilation as early as the end of February or the beginning of March is, I suppose, a phenomenon hitherto unknown. Hence let us investigate more closely the possibility of the plant for CO₂ assimilation in the winter of 1932.

Unfortunately there was no meteorological station at Eskimonæs. Yet positive air temperatures and the consequent melting phenomena on the snow were observed on the following dates in 1932: February 12, 24, and 28. At other times, too, the air temperature was near zero, especially during the westerly foehn winds. In March positive air temperatures were, as far as I know, not registered. Since, however, it has long been ascertained by temperature measurements in the Arctic that positive temperatures may be found at the surface of the ground even when very low negative temperatures are measured in a reliable way in the higher atmospheric strata, we have thus a probability bordering on certainty that on certain days of February the evergreen plants must have been in surroundings with positive temperatures and have possibly themselves, too, been heated above the temperature threshold which the CO₂ assimilation requires in order to begin. Light was not absent in the middle of the day in February.

HARTZ's (1896) and KRUISE's (1912) measurements of the phenomena of insolation are classical. On a thermometer with a black ball suspended on a pole placed freely in the terrain, the thermometer being at a distance of 160 cm above the surface of the ground, HARTZ (l. c. p. 292) observed positive temperatures on April 9, 1892. As early as March 21 positive temperatures were registered by a thermometer suspended at a distance of 13 cm from a black wall. But earlier still positive air temperatures created by the warm foehn winds were ascertained. HARTZ made his observations on Danmark Island in Scoresby Sound, and they show that the vegetative period of the plants may begin long before the temperature in a meteorological sense rises above zero. That the plants are actually able to take advantage from these conditions is shown by examples supplied by HARTZ as well as by many others of the botanists who have wintered in Arctic regions, e. g. KRUISE (1912), WULFF (1934), GELTING (1934). KRUISE (l. c. p. 56) figures a branch of *Cerastium alpinum* which in the period March 21 to April 12, 1902, at Angmagssalik had developed six young buds. Quite similar phenomena were observed at Eskimonæs and Knudshoved in 1932, likewise in *Cerastium alpinum*. At Knudshoved the development of the *Cerastium* buds commenced at the beginning of March. These buds were often eaten by the ptarmigans.

Thus there can hardly be any doubt that in the winter of 1932 conditions in the area here treated were of such a nature that both as regards temperature and illumination *Dryas*, at certain times of the day, had a possibility of undertaking a CO₂ assimilation, which again stopped in the night and on days with persistent frost.

The increase in the carbohydrate content of the leaves may, then, presumably be viewed in relation to these facts. That the content of starch in the leaves is not higher than observed, whereas the quantity of monosaccharides has become three or four times greater in March—April than at the beginning of February, is perhaps because the root, at any rate at a certain depth, is still in frozen soil and itself, too, possibly shows negative temperatures. If so, it will be unable to receive supplies from the above-ground organs. As is well-known, the starch content of the latter is converted before transport into easily soluble sugars; but since the latter cannot be transported further, they possibly remain in the above-ground organs. This accounts for the high monosaccharide percentage in the leaves.

However, this far from solves the problem, which should be subjected to fresh investigations. Although at that time I was quite unknown with the phenomena as regards *Dryas* stated here, in view of the fact that the rosette leaves of so many arctic plants remain green and often slightly succulent throughout the winter, I set forth the supposition (GELTING 1934, p. 303) that the leaves may be assumed to serve as storage organs for nutrition which is later, at times when the frozen soil does not yet allow the intake of water, given off to the young shoots gradually as they develop. For such a transference may take place on days on which the above-ground organs of the plant are in positive air temperatures at the levels near the surface of the ground.

On the basis of this supposition, founded on observations on the development of the plants before the air temperature is climatologically above zero, the demonstration of the protein content of the plant organs investigated here obtains renewed interest. Growing organs, as is well known, require a comparatively great amount of proteins. While the plants, long before the soil has thawed, are able to increase by CO₂ assimilation their content of unnitrogenous nutritive substances, this is not the case with the nitrogenous matter, which must therefore be present even when the winter sets in. The sometimes fairly high protein content in the above-ground perennating organs is hereby probably viewed in its proper light. Very probably conditions in plants with no above-ground hibernating stems must be somewhat different. The plants dominating in the winter food of the ptarmigan, viz. *Salix*, *Dryas*, and *Saxifraga*, are all chamaephytes, and as already stated, a small increase in the disaccharide content of the *Salix* fragments can be found in March. If this increase is due to a CO₂ assimilation, this must be ascribed to the green, not yet lignified branches, the plant being deciduous; but this point, too, needs a closer investigation.

Saxifraga oppositifolia has been so little investigated that it is impossible to say anything about the variation in its content of nutritive elements. I take it as a clue, however, that the smallest fragments are richest in proteins, that is, the shoot-apices are probably richer in proteins than the older lignified parts of the stems. Moreover, the protein content in *Saxifraga* is smaller than in the *Salix* and *Dryas* fragments, whereas its content of raw fats is great.

Equisetum variegatum: The sporophyll heads and spores contain almost twice as much raw protein as the stems, and even the latter

are almost just as rich in proteins as the *Salix* and *Dryas* fragments. Thus here, too, a large protein content can be ascertained in the organs by which the species propagates during the coming vegetation period. The contents of carbohydrates and fats are intermediate between the same contents in *Salix* and *Dryas*.

Polygonum viviparum: The subterranean stem-tubers, are distinguished by being the organs richest in nutritive substances found in the food of the ptarmigan. As regards their content of proteins they are equal to the *Dryas* and *Salix* fragments; they contain but little fat, but owing to their high content of starch beat all carbohydrate records found.

The *Polygonum* spike fragments, on the other hand, beat all protein records, more especially on account of their abundance in bulbils, which, we repeat, are the organs by which the species principally multiplies. The spike fragments contain but little raw fat, but considerable quantities of carbohydrates, the amount of starch, in particular, being high.

Since after completing the analyses of the crop content I found it curious that *Cassiope tetragona* was so sparsely represented, and that *Betula nana* was not represented at all, although both plants are of common occurrence within the area, *Betula*, however, only in the fjords, I made an analysis of the organs of these plants which must be assumed to be most easily secured by the ptarmigan if it were to feed on them. I cut off with a pair of scissors the extreme tips of the branches of dried material of *Betula* collected in Granta Fjord on September 6, 1931. Furthermore I removed with my hand leaves and catkins from dried material collected at Eskimobugt, Clavering Island, on June 16, 1932. Of *Cassiope tetragona* I cut off with a pair of scissors the tips of the branches of dried material collected at Cape Hooker, Scoresby Sound, on July 2, 1933. The material of both species were dried at 100° C. and analysed like the rest of the material. The results of the analyses are given at the base of Table 24, p. 153.

Both plants show a total content of organic nutritive substances which does not deviate very much from that of the *Salix* and *Dryas* fragments, for which reason the examined fragments of *Cassiope* and *Betula* must be assumed to be able to replace them quantitatively. However, a conspicuous difference is noticeable in the protein content of the species in question. Only the catkins and leaves of *Betula* can compare with the *Salix* and *Dryas* fragments as regards protein content. In the summer, when the leaves and catkins are accessible, *Polygonum*, which is much richer in proteins, is available. In the winter *Betula* must be supposed to be able to replace *Salix* and *Dryas* in the food, but hardly outside the interior of the fjords.

Cassiope, on the other hand, has not many chances of becoming food for the ptarmigan in the winter in any great quantities, the areas of dominance of the species being then covered with a thick and lasting layer of snow. The high figure for the amount of raw fat in the analyses may be due to some extent to a high content of aromatic, non-fatty, extract substances, but whether these are actually of such a nature or taste that they are shunned by the ptarmigan, can only be decided by experiments.

Tabel 25. Showing the content of nutritive substances in certain plant parts, in percentages of dry matter, after DIETRICH & KÖNIG 1891.

Species	Notes	N-free extract matter	Raw fat	Raw protein	Total
<i>Deschampsia caespitosa</i> .	$\frac{7}{6}$; rather fertile meadow . . .	43.26	3.37	10.27	56.90
<i>Anthoxantum odoratum</i> .	$\frac{25}{5}$; in flower, clay and limy gravel	43.61	3.41	10.28	57.30
<i>Festuca rubra</i>	$\frac{6}{6}$, in flower, fairly fertile meadow	37.53	1.88	8.90	48.31
<i>Poa pratensis</i>	$\frac{11}{6}$, in flower, dry calcareous clay	43.06	2.63	10.35	56.04
<i>Carex vesicaria</i>	After flowering, swampy meadow	—	3.47	15.12	—
<i>Lotus corniculatus</i>	$\frac{10}{6}$, in flower	51.60	—	15.23	—
<i>Onobrychis sativa</i>	$\frac{8}{6}$, in flower	46.24	3.01	18.17	67.92
<i>Pisum sativum</i>	"Green peas" in flower $\frac{21}{7}$	34.59	—	24.06	58.65
<i>Trifolium pratense</i>	$\frac{19}{5}$, Young flower buds	40.16	3.75	33.04	76.95
<i>Calluna vulgaris</i>	Green stem tips	43.85	17.02	7.89	58.76
<i>Cetraria islandica</i>	From Kärnten	84.91	6.81	5.26	96.97
<i>Cladonia rangiferina</i>	$\frac{16}{6}$, Stockholm	79.68	1.55	2.87	84.10
<i>Equisetum arvense</i>	$\frac{21}{4}$, fertile stem	55.43	2.68	14.62	72.73
— —	$\frac{22}{6}$, unfertile stem	42.00	5.31	23.26	70.57
<i>Matricaria inodora</i>	In full flower	—	—	5.64	—
<i>Papaver Rhoas</i>	In incipient fructification	41.43	4.65	9.02	55.10
<i>Polygonum aviculare</i>	Partially out of flower and with seeds	—	—	17.54	—
<i>Betula alba</i>	July, leaves with soft green stems	54.47	0.33	22.87	77.67
<i>Salix alba</i>	Leaves	41.64	3.50	8.67	53.81
— <i>capraea</i>	July, leaves with soft green stems	—	—	12.34	—
<i>Pinus silvestris</i>	Young needles	36.60	9.38	10.53	56.51
<i>Solanum tuberosum</i>	Tubers, average of many samples	83.92	0.61	8.33	92.86
<i>Triticum vulgare</i>	Grains, Denmark (mean)	82.41	2.70	10.81	95.92
<i>Avena sativa</i>	— U. S. A. —	72.10	8.74	15.37	96.21

In order to form an estimate of the value of the plant species and organs which the ptarmigan eats it would be desirable to make a comparison with ptarmigan food from other regions. It is true that from the British Isles, Norway, Spitsbergen, and Northern Sibiria (Taimyr) detailed investigations are available as to which plants the ptarmigan eats; but as long as an analysis of the content of nutritive substances of these plants has not been made, a mere correlation of the plant names would be of little value. In order, however, to attempt to gain an idea of the content of nutritive substances in the Greenland plant species examined as compared with other kinds of plant food, I have correlated in Table 25, p. 157, several values after DIETRICH & KÖNIG (1891). I have chosen a number of grasses and herbs as well as woody plants, not according to their content of nutritive substances, but on a fairly casual estimate, having especially endeavoured, however, to have such species represented whose geographical distribution approaches, or extends into, the Arctic. For this reason I included for instance *Deschampsia*, *Festuca*, *Carex vesicaria*, *Calluna*, *Cetraria*, *Cladonia*, *Equisetum*, and *Matricaria*. *Betula*, *Salix*, and *Pinus* were included as woody plants; the *Papilionaceae* because they are known to be particularly rich in nitrogen owing to their bacterial root nodules. Finally some well-known agricultural plants are included. It would have been desirable to include some more actual heath plants, such being principally consumed by the ptarmigan; but very few of such plants are treated by DIETRICH & KÖNIG, and I have failed to find any information on them in other papers.

If we compare the values of carbohydrates, raw fats, and raw proteins in Tables 24 and 25, we must remember that the figures in Table 25 for N-free extract substances refer to the whole amount of carbohydrates (determination of residue), while in Table 24 the cellulose content has not been determined.

The amounts of raw fat, like the amounts of raw proteins, are quite well comparable, since they are determined in the same way in both tables; and these show that the Greenland material as regards raw fat must be said to be fairly normal, the amounts varying almost in the same way as in the plants from other regions selected for comparison. As regards the content of raw proteins conditions are somewhat different, since the *Polygonum* bulbils and stem-tubers and the sporophyll heads of *Equisetum variegatum* must be said to be very rich in proteins (their protein content is like that of the *Papilionaceae*), while the *Saxifraga oppositifolia* buds must be characterised as poor in proteins, and *Salix* and *Dryas* occupy an intermediate position.

Too great importance should not be attached to these comparisons, which still have a casual character; but as an interesting fact in this

connection we merely note that the most important food element of the ptarmigan in the summer (*Polygonum*) is rich in proteins.

When I began my investigations on the content of nutritive substances in the available crop content, I had a faint hope that it would enable me to give a reliable picture of the variations in the various elements and accordingly in the food of the ptarmigan. The material proved to be too small, and it was not from the beginning preserved with this purpose in view. Some facts which put an end to the further statistic treatment of the material will be briefly mentioned below.

It will appear from Table 24, p. 153, that the content of nutritive substances in the plant organs varies with the season. A determination carried out on the January material will not, therefore, be immediately applicable for a computation of the content of nutritive substances in the same plant part for instance in May. Since it will be of importance for a closer understanding of the conditions under which the ptarmigan lives at the different seasons to know how large a part of the supply of nutritive substances is due to the different plant parts and plant species, the access to these being highly different at the different seasons of the year, it will be of no use, if we wish to gain an idea of the life conditions of the ptarmigan, to analyse the content of nutritive substances in the individual crops as a whole; but for each crop it must be determined how large quantities of the nutritive substances are due to the different plant species and organs. If subsequently we wish to know the total amount of organic nutritive substances in the crop content, this may be determined by summing up the content of nutritive substances in the plant parts represented in the crop.

In this way we are able to keep an account of the amounts of nourishment found in the crop material. Since, however, some plant parts will always be present in the individual crops in such small quantities that they do not suffice for a thorough analysis of their content of nutritive substances, there will nearly always be a small residue in each crop whose content of nutritive substances cannot be accounted for. As this residue is, as a rule, rather inconsiderable, at any rate quantitatively, it will probably often be of little importance; but in order to avoid this source of error in the future, the following procedure might be adopted: immediately after the ptarmigan has been killed, the crop should be opened and all the species found in it noted down. Of the species and plant parts which might appear to be too sparsely represented to supply sufficient material for an analysis, about 5 g should

immediately be collected in the field, which amount will, as a rule, suffice for an analysis.

As the average weight of the fragments (cf. p. 134) was determined on the basis of the air-dried material, and the water content of the latter is known in a few cases only, the content of dry matter in the average fragments, and accordingly their content of nutritive substances, cannot be computed. An account of the amount of nutritive substances per fragment of the different plants so important for an understanding of the accessibility of the various nutritive substances, cannot, therefore, be prepared, the average content of nutrition, too, being based on too small a material.

It will be gathered from the above that the results arrived at in the analysis for nutritive substances cannot be illustrated by definite figures. At the most, certain suppositions can be set forth on the basis of scattered indications.

As has been shown above, the food of the ptarmigan in August consists mainly of *Polygonum viviparum*, which must be regarded as very rich in proteins, but very poor in fats as compared with the other main food elements. In the winter, however, the ptarmigan feeds on foods poorer in proteins, but richer in fats, viz. *Salix*, *Dryas*, and *Saxifraga oppositifolia*. Bearing in mind the great importance of the proteins for the building up of the organism, the high calorific value of the fats, and the protection against cold afforded by the deposited fats, this seems fortunate for the ptarmigan.

If it is further borne in mind what has been stated above about the access to the different food elements in the course of the year, the period midsummer to midwinter may be characterised by an increasingly difficult access, at any rate as regards the main food elements, and the period midwinter to midsummer by an increasingly easy access to proteins. To the food substances rich, or at any rate comparatively rich, in fats (*Saxifraga* and *Dryas*) there is easy access all the year round.

Since the summer, which is evidently the only time of the year at which there is easy access to proteins, is very short, it seems not improbable that the ptarmigan may need proteins in the course of the winter. A further indication of a need for proteins is the occasional occurrence in the crop content of food elements difficult of access but particularly rich in proteins, viz. stem-tubers of *Polygonum* and sporophyll heads of *Equisetum variegatum* (cf. p. 125, and ptarmigans Nos. 5 and 10).

The migration of the ptarmigan into the mountains in August—September obtains in this connection renewed interest, and may in so far be termed a protein migration as it is chiefly the access to proteins that is maintained by this migration. For the chickens which take part

in the migration the access to proteins must be of importance, as the migration coincides with the growth of the chickens.

The migration to the outer coast may be regarded as a migration for food in general, the maintenance of easy access to *Salix arctica* being a maintenance of easy access to all the groups of organic nutritive substances, though, apparently, slightest for the fats.

SOME FACTORS OF IMPORTANCE FOR THE GROWTH AND FREQUENCY OF THE PTARMIGAN

While the literature contains numerous data as to the frequency and occurrence of the ptarmigan in Greenland, very few certain clues for a comparison of its frequency in the different years are available. There can hardly be any doubt that its frequency is subject to fluctuations, but to what extent the fluctuations ascertained are merely due to the migrations of the bird or are actually an expression of a difference in the frequency of the ptarmigan in the various years, the Greenland material at hand is too insufficient to illustrate.

In countries in which shooting of ptarmigan and grouse is carried out on a large scale (for instance the British Isles and Norway), the case is different. Here we know that the stocks are subjected to particularly great fluctuations, since years exceedingly rich in ptarmigans and grouse alternate with years in which the number of the birds is shockingly low.

The cause of these fluctuations is connected, partly directly, partly indirectly, with climatic conditions (GROUSE COMMITTEE 1911, KLOSTER 1921—23, NORDHAGEN 1928, 1); but a connection of the frequency of the bird with the temperature conditions during the breeding time (FØYEN 1928) did not lead to any result.

An important element was introduced into the discussion by the ascertainment of diseases. The English grouse suffers in certain years very much from the attacks of strongylides (GROUSE COMMITTEE 1911), and the Norwegian *Lagopus lagopus* suffers much from coccidiosis (WILLUMSEN 1916, BRINKMANN 1922, 1927, 1).

The importance of birds of prey as "stock regulators" has been the subject of a vivid discussion (GROUSE COMMITTEE 1911, BRINKMANN 1927, 2, OMSTED 1927, KNUT DAHL 1927). The point of dispute is whether or not the birds of prey principally pursue the diseased birds.

NORDHAGEN (1928, 1) has supplied a perspicuous contribution to the discussion, and within the combined pathological and food-

physiological problem distinguished between the "constructive" and the "destructive" complex of factors, partly on the basis of his personal knowledge of the ecology of the feeding grounds of the bird, partly on the available literature dealing with them. By correlating the Norwegian export-curve of *Lagopus lagopus* with the berry export-curve as well as with the curve for temperature fluctuations in the Atlantic, he is able to demonstrate conspicuous agreements, and similarly he obtains agreement by connecting the golden years of the bird with years with sunspot minima.

While thus the literature on these questions is in rapid growth as regards Norway, we do not know at present the fluctuations in the frequency of the ptarmigan stock of Greenland from year to year. Even now, however, we are able, like NORDHAGEN, to point out certain variable factors in the constructive complex.

If the melting of the snow sets in later than is normal, this will cause a delay in the transition from the winter food rich in fats to the *Polygonum* food rich in proteins, which must be assumed to affect the growth of the stock, and possibly the mating and egg-laying, too, both of which require a certain addition of proteins. The temperature conditions during the months of spring as also the conditions of precipitation must here be important. If, again, the late melting of the snow causes a postponement of the egg-laying, this may affect the growth of the young chickens, whose summer of growth is shortened in this way.

However, the question is complicated, since a late melting of the snow may cause *Polygonum* to remain longer at the young stage rich in proteins, which, again, may be of advantage to the chickens. A cold summer, too, may cause *Polygonum* to remain long at the stage rich in proteins, at the same time as the insect life, which is not without importance, at any rate to the grouse (cf. LID & MEIDELL 1933), must be presumed to be poorer than in a warm summer.

A snow-cover forming early in the autumn may shorten the time in which the *Polygonum* snow-patches are accessible, and may thus be of decisive importance for the power of resistance of the stock in the ensuing winter. If some of the these factors are combined in such a way that a late summer is rapidly changed into an early autumn, this may be supposed to result in a perceptible decrease in the ptarmigan stock in the ensuing winter.

As has been shown in the above, the access to food in the winter is to a great extent controlled by the snow-cover. It would seem, however, that an actual lack of food will not often occur, since the bird by its migrations is able to escape the effects of the often merely local snowfalls. The wind conditions, too, are very variable in the winter, and along the outer coast, usually swept bare of snow by the north winds, the ptarmigan

will probably in most winters be able to find sufficient food. However, a foehn period with positive air temperatures, setting in early in the winter and after a quiet snowfall, must be assumed to be a great impediment to the access to food, since a superficial thawing of the snow with an ensuing freezing will result in the formation of crust-snow. This crust-snow can resist the erosion of the wind for a long time without being removed, and so long as this is the case, the ptarmigan will hardly be able to penetrate to the snow-covered plants. However, in Northeast Greenland crust-snow must be assumed to occur most rarely at the outer coast, where the effects of the foehn wind are smallest.

These conditions, so important for the bird, need a closer investigation. As it is not known whether the ptarmigan stock of Northeast Greenland is, or can be, infested with strongylides, coccididae or other parasites causing diseases, we must keep an open mind on this question.

As regards the state of nutrition, I had the impression that all the ptarmigans were in very good state of nutrition, they tasted fine and were fat, especially in the winter, the subcutaneous tissue being filled with fat. None of them showed any sign of disease. On May 27, 1932, I shot two ptarmigans at the Eskimo house ruins at Baadsted, Clavering Island. It was a hen in summer plumage, though still with some white feathers, and a male ptarmigan still in winter plumage. These two ptarmigans showed a remarkable difference in fatness, the female being thick and fat, the male lean. This fact is not unknown during the mating time from Scotland (cf. WILSON 1911). It is interesting in this connection to point out that of two ptarmigans wandering side by side, the crop content of the female bird consisted of sporophyll heads of *Equisetum*, which are very rich in proteins, while the other (whose sex was not determined, but possibly it was a male) had only eaten the *Equisetum* stems, less rich in proteins, which remained after the hen had secured the sporophyll heads. This shows that the hen (No. 10, p. 88) may be very eager to secure food rich in proteins.

It is not known either whether the plants on which the ptarmigan principally feeds, can be attacked by noxious animals. According to IVERSEN (1934), however, South Greenland may in certain years be largely infested by the larvæ of *Agrotis occulta*, which consume herbs and herbaceous organs of dwarf-shrubs, bushes, and lower trees. In regions where such attacks can take place, they must, of course, cause a reduced access to food for the plant-eating animals.

In Northeast Greenland the ptarmigan has several enemies, but hardly so many that their pursuits can be supposed to be of any great importance for the frequency of the bird. Of birds of prey only the falcon and the snowy owl occur (cf. p. 70). The fox as well as the ermine must

be assumed to prey on the ptarmigan, though MANNICHE (1910) observed no signs that they had succeeded in securing the bird. To the young chickens *Stercorarius longicaudus* (*Lestris longicauda*) may presumably be a danger; this bird at any rate preys on snow sparrows, as I have observed myself. The ptarmigan is hunted by the trappers and members of expeditions, but to a slight extent only. The trappers use the bird or parts of it as bait for the foxes.

THE FOOD OF THE PTARMIGAN IN OTHER COUNTRIES

Arctic American archipelago.

In December, 1935, I received for determination of their crop contents two ptarmigans from the Zoological Museum of the University of Copenhagen, killed on May 1, 1923, on the Fifth Thule Expedition on Danske Island (latitude 66° N, longitude about 83° W) by Mr. PETER FREUCHEN. The material, which since the return of the expedition had been preserved in alcohol, was derived from two ptarmigans, as already stated, both of which, according to the accompanying label, belonged to *Lagopus mutus*.

On account of the preservation in alcohol, the crop material cannot be used for a determination of the content of nutrient substances, as the alcohol extracts some of the substances contained in it. But it can quite well be employed for a determination of the quantitative proportions of the plant species represented in the food. The material was air-dried until the alcohol had evaporated, and was subsequently exsiccated until the weight remained constant.

It then became evident that when the ptarmigans were killed, their crops had been damaged, since they contained some blood, which was found to have cemented together the constituents into lumps. The cementing material had coated the majority of the fragments with a rusty-red colour. The material therefore is only suited for an approximate determination of the average weight of the fragments. As the material from both crops had been mixed together in the same glass, the crop content of the individual ptarmigan could not be determined either.

The plant species found by the analysis and their weights are given in Table 26, p. 167.

In the North American archipelago *var. integrifolia* takes the place of *Dryas octopetala s. str.* However, many naturalists regard the two species as independent and coordinate species. But for our ecological purpose it is sufficient to note that the ecology of *var. integrifolia* is very like that of the main species (WARMING, 1888, PORSILD 1920).

Table 26. Showing the crop contents of two ptarmigans from Danske Island in the Arctic-American archipelago.

Species	Fragments	Weight mg	Weight %	Number of frag- ments	Average weight of fragments mg
<i>Salix arctica</i>	Buds and twigs . .	120	1.4	33	3.6
<i>Dryas octopetala v. integrif.</i>	Leaves	7570	90.9	ca. 7000	ca. 1.0
<i>Saxifraga oppositifolia</i>	Shoot apices	600	7.2	223	2.7
<i>Equisetum variegatum</i>	Stems	20	0.2	12	1.7
<i>Polygonum viviparum</i>	Bulbils	10	0.1	20	0.5
<i>Pedicularis</i> sp.	Flowers	5	0.05	2	2.5
<i>Stellaria longipes</i>	Shoot apices	5	0.05	4	1.3
<i>Draba</i> sp.	Capsules	+	—	1	—
<i>Aphodius</i> sp.	Tibia and tarsalia .	+	—	1	—
Mussel	Shell	5	—	2	—

On the basis of the high *Dryas* and the high *Saxifraga oppositifolia* percentages we may conclude that either the ptarmigans were killed immediately after a quiet snowfall, whose precipitation had not been removed on May 1, or the winter of 1922—23 had an excessive precipitation. If that was not the case, the locality in which the ptarmigans were killed must at any rate have been exceedingly poor in accessible *Salix* areas. For in East Greenland the absolute *Dryas* maximum as also the high *Saxifraga* percentage is usually found on days after quiet snowfalls. In Table 27, p. 169, I have compared the material from Danske Island with the material from three ptarmigans killed in April in North-east Greenland. As will be seen, there is a remarkable agreement between the quantitative proportions of the species represented in the food.

Recently C. T. DALGETY (1936) has examined the crop contents of five ptarmigans (*Lagopus mutus rupestris*) from Baffin Land. The specimens were derived from the country between Eglinton Fjord and Clyde Inlet in the last half of August, 1934. According to DALGETY (l. c. p. 590), their crop contents were as follows:

“1: Entirely leaves of *Salix glauca* and *Vaccinium (uliginosum)*.

2: Approximately 40 per cent. *Vaccinium* berries, mostly ripe. Approximately 40 per cent. leaves with a few seeds of *Salix arctica*, many bulbules of *Polygonum viviparum*, heads of two species of sedge, buds of a willow, and one *Dryas* head.

3: 40 per cent. fruits of *Vaccinium*, 10 per cent. *Polygonum viviparum*, a *Ranunculus* head, *Draba* seeds, a sorrel leaf, *Salix* buds, and catkins.

4: Mostly leaves and seeds of dwarf-willow, a quantity of *Cassiope* seed and *Vaccinium* fruits, seeds, flowers, and stalks of *Polygonum viviparum*, six or more seed-heads of a large *Ranunculus*, part of a *Ranunculus* leaf, and two fragments of sorrel leaf.

5: Almost entirely buds, flowers, and leaves of *Saxifraga*, mostly *S. stellaris*, but some *S. rivularis*, also some moss-heads and one piece of branching lichen."

As will be seen, the crop contents show a composition very like that found in crops of ptarmigans from August in East Greenland. Noteworthy is the relatively great quantities of *Vaccinium* berries in Nos. 2 and 3, and the great number of bulbils and leaves of *Saxifraga stellaris* in No. 5. In crops of the Spitsbergen ptarmigan from September also (ARBO HØEG 1929) *Saxifraga stellaris* plays a role. The species is a snow-patch plant.

Taimyr.

Apart from LID's investigations (1933) of the crop contents of ptarmigans shot at "The Mortuary" (76°52' N. lat., 101°13' E. long.) on the west coast of Taimyr, no rational analyses of ptarmigan crop contents are available from northern Siberia, as far as I know. The material for comparison with the ptarmigan food in Taimyr is inconsiderable; as regards weight, it is of about the same size as the material from Danske Island.

According to LID, the crop material is derived from one or three ptarmigans, killed on April 17, 1919, in the middle of the day. The foreland, about 10 km broad, on which the ptarmigans were killed, was at that time swept partially bare by the wind, "the snow had been blown away from the highest parts of the moraines, so that they were quite free from snow" (l. c. p. 3). PAUL LØYNING, curator of the Zoological Museum of Oslo, assumes the ptarmigans to be *Lagopus mutus*¹). The crop content was taken to Oslo preserved in alcohol. The weights found by LID refer to dried (air-dried?) material. LID's figures converted into percentages of the total content are found in Table 27 (p. 169).

In the Taimyr sector of the Arctic Siberian coast, as far as can be gathered from the floristic investigations (cf. thus TOLMACHEW 1932), *Salix arctica* is wholly or partially replaced by other *Salix* species, notably *S. polaris*, *S. reptans*, and *S. rotundifolia*. In his investigations LID did not separate these species, nor is this presumably of great importance for the ecological analysis, the species being probably closely related as regards ecology. According to LID's detailed description of the *Salix* content (l. c. p. 5), however, *Salix arctica* and *S. polaris* seem to constitute the greater part of the *Salix* material, and these two species,

¹) Possibly *Lagopus mutus pleskei* SEREBR., which according to TUGARINOW and TOLMACHEW (1934, p. 19) occurs in Taimyr.

Table 27. Showing crop contents of ptarmigans from Arctic Canada, East Greenland, and Taimyr.

Snow-cover.....	?	Fairly	The hills blown free	
		continuous	from snow	
Locality.....	Danske	N.E.	N.E.	Taimyr
Year.....	Island	Greenland	Greenland	
Date.....	1923	1932	1932	1919
Number of ptarmigans.....	2	3	5	?
Total weight of crop content.....	8330	7000	14750	7101
Average weight of crop content.....	4165	2333	2950	?
	%	%	%	%
<i>Salix arctica</i>	1.4	0.7	70.5	82.0
— <i>polaris</i>				
— <i>reptans</i>				
— <i>rotundifolia</i>				
<i>Dryas octopetala</i>	97.9	23.4	11.2
— — <i>v. integrifolia</i>	90.9
<i>Saxifraga oppositifolia</i>	7.2	1.4	+	4.1
<i>Cerastium alpinum</i>	5.8	..
— <i>Bialynickii</i>	0.6
<i>Equisetum variegatum</i>	0.2
<i>Papaver radiculatum</i>	+	+
<i>Pedicularis</i> sp.....	+
<i>Polygonum viviparum</i>	0.1
<i>Saxifraga caespitosa</i>	+	1.7
— <i>navalis</i>	0.2
<i>Sieversia glacialis</i>	+
<i>Stellaria longipes</i>	+	..	0.3	0.1
<i>Arctostaphylos alpina</i>	+
<i>Cassiope tetragona</i>	+	..
<i>Draba nivalis</i>	+	..
— sp.....	+
<i>Equisetum arvense</i>	+	..
<i>Hierochloë alpina</i>	+
<i>Minuartia rubella</i>	+	..
<i>Potentilla pulchella</i>	+	..
<i>Ditrichum flexicaule</i>	+
<i>Ceratodon purpureus</i>	+
<i>Cetraria hepatizon</i>	+
Mussel shell.....	+
<i>Aphodius</i> sp.....	+
Quartz.....	+	..

at any rate, are known to be closely related ecologically. Thus in Spitsbergen *S. arctica* is entirely replaced by *S. polaris* (SUMMERHAYES and ELTON, 1923 and 1928).

Cerastium Bialynickii is closely related to *Cerastium alpinum*, and according to SCHOLANDER (1934) not specifically different from the latter. Their ecology should be roughly the same. As regards *Dryas*, LID refers the Taimyr material to *f. minor* HOOKER, which, in fact, constitutes (cf. p. 32) the main part of the *Dryas* material found in ptarmigan crops in East Greenland in the winter.

For comparison with the Taimyr material I have given in Table 27 first of all the May material from East Greenland. This, too, originates from days when large areas were bare of snow, partly due to the wind, partly to sublimation. As will be seen, here, too, the agreement between the quantitative proportions of the species constituting the food is remarkable.

Against the arrangement made in Table 27 for comparison of material from the different regions the objection may be raised that the dates do not actually agree very well, and that it ought to be the respective May materials and the respective April materials from each region which should be compared. The difference which would arise in this way, however, would only convince us that conditions vary from year to year, according to the meteorological conditions; but apart from this, there is an extraordinary agreement in the food at these fairly corresponding periods of the year and under a fairly uniform snow-cover.

Spitsbergen.

The Spitsbergen ptarmigan is at present referred by most authors to *Lagopus mutus hyperboreus* SUNDEV. Detailed investigations of its food were made in August (six ptarmigans) by O. EKSTAM (1898, p. 52) and by O. ARBO HØEG (1929), who examined the crop contents of 18 ptarmigans killed at the end of September 1928. In the August material examined by EKSTAM *Polygonum viviparum* bulbils were found to constitute the main part of the food, in which several other typical snow-patch plants, too, were represented (*Saxifraga cernua*, *S. nivalis*, *Draba alpina*, *Cardamine bellidifolia*, *Oxyria digyna*, and eight other species).

Thus a single crop was found to contain 4254 bulbils of *Polygonum*, another 3181, and a third one 2429 bulbils, but as the material was not weighed, it is impossible to form an estimate of the percentage quantitative proportions of the plant species.

O. ARBO HØEG (l. c.) gives a detailed analysis of the different plants and the quantitative relations of the different plant organs in the crops examined, and on the basis of his figures the percentage amounts of the different plant fragments in Table 28 have been computed. In order to make HØEG's figures comparable with mine from East Greenland, I have only included quantities above 50 mg in the lists, while quantities below 50 mg are indicated by a +. The August material from East Greenland is shown in the same Table.

Table 28. Crop contents from East Greenland and Spitsbergen.

Locality	East Greenland	Spitsbergen		
Year	1932—33	1928	Frequent	Typical
Month	August	September	in snow-	snow-patch
Number of ptarmigans.....	27	18	patches	plants
Total weight of crop content	45200	130108		
Average weight of crop content	1674	7228		
	%	%	%	%
<i>Salix arctica</i>	8.4	..	+	..
— <i>polaris</i>	3.3	?	..
<i>Dryas octopetala</i>	1.0	0.2
<i>Saxifraga oppositifolia</i>	+	+
<i>Polygonum viviparum</i>	87.4	83.7	+	..
<i>Carex misandra</i>	0.1
<i>Cerastium alpinum</i>	0.2	..	+	..
— sp.....	..	1.8
<i>Draba</i> sp.....	..	1.6
<i>Luzula arcuata v. confusa</i> ...	0.7	0.2 ²	+	..
<i>Oxyria digyna</i>	0.4	4.1	..	+
<i>Papaver radicum</i>	0.1	1.1
<i>Ranunculus pygmaeus</i>	+	+	..	+
— <i>sulphureus</i>	1.9	..	+
<i>Pedicularis flammea</i>	0.1
<i>Salix herbacea</i>	0.2	+
<i>Saxifraga cernua</i>	0.3	0.6	..	+
— <i>comosa</i>	0.3	..	+
— <i>caespitosa</i> var.....	..	0.2
— sp.....	..	0.4
<i>Stellaria longipes</i>	0.3	+	+	..
<i>Taraxacum arcticum</i>	+	+	..
<i>Vaccinium uliginosum</i>	0.7
<i>Carex capillaris</i>	+
— <i>rupestris</i>	+
<i>Draba daurica</i> var.....	+	..	+	..
<i>Equisetum variegatum</i>	+	+	..
<i>Festuca ovina v. brevifolia</i>	+	+	..
<i>Koenigia islandica</i>	+	..	+	..
<i>Pedicularis</i> sp.....	..	+
<i>Poa</i> sp. (<i>viviparous</i>).....	..	+	?	..
<i>Potentilla emarginata</i>	+	+	..
— <i>pulchella</i>	+
— sp.....	..	+
<i>Ranunculus nivalis</i>	+	..	+	..
<i>Rumex acetosella</i>	+
Mosses.....	..	+
Various stalks and leaves	0.5
Quartz.....	+	+
Number of species weighed ..	13	13
Total number of species.....	21	25

drawn on observations in the field in 1928, and when my personal knowledge is added to Nilsen's paper (1928, 2) as a basis.

On average quantities, it will soon be seen that the main part of the food both in winter and in summer is the same. The difference of the food at the two seasons is a small percentage in the winter and a high one in the summer.

Chamaephytes occur in the mountain regions where a tree or bush can here replace the shrub. It will be seen that in the winter trees and shrubs contribute to the food of the ptarmigan. The fact that the summer food is especially taken from the chamaephytes illustrates the importance of the perennating organs. It is immediately evident that the perennating organs will more easily rise above the snow than the above-ground organs wither and die in winter, unless the particular herbs are so low that they will soon be covered. In the chamaephytes the snow-cover in the winter food consists to a great extent of more or less snow-free soil (*Salix nana*). As regards *Empetrum* this is also the case (RDHAGEN (1928, 1). In the summer the main part of the food is largely of snow-patch plants (*Oxyria*, *Polygonum viviparum*, *Salix herbacea*,

and the access to food in the mountains, where *Salix* scrubs of the tree-limit and to the mixture of phanerophytes in the winter

(cf. pp. 2—9) will show that in Jotunheimen the lignified organs of the lignified plants (buds, buds, and tips of shoots) are to be subordinate constituents in

the food in the winter at the different seasons, and that the same is found in East Greenland.

The great difference in the winter feeding habits of the Norwegian highlands are due to the snow-covered soil, while the *Salix* scrubs of the East Greenland are associated with

the average crop content, it will be seen that the ptarmigan in September on an average had a larger crop content than the East Greenland ptarmigan in August, and that with the conditions found on p. 140 ff.

When constituting the food, we shall find a large part of it in the cases *Polygonum* bulbils constitute the main part of the crop content, and as regards the other plants the same agreement. In Spitsbergen *Salix* is the main part. In both areas *Dryas* and *Saxifraga* constitute the best place in the food at this season. The same is true to a great extent common to both areas, and is characterised by being largely snow-patch

plants. It illustrates on essential points that in the winter in which the snow-patches have melted and their fresh snow-cover, the ptarmigan receives a large amount of food, as will appear from p. 116 ff., receives an amount of food, i. e. fairly undeveloped, herbaceous plants, a gizzard and rich in proteins.

The ptarmigan in the winter must be left for future consideration. However, a priori it might be assumed, on the basis of the climate and vegetation of Spitsbergen, that the food there will be very like those found along the coast of East Greenland. But the illumination during the dark winter is much more unfavourable than in the area of the coast of East Greenland. Joseph Fjord investigated by me. The ptarmigan is a stationary bird in Spitsbergen (cf. PLESKE (1928, 1)). In support to the assumption that in East Greenland the ptarmigan is as fertile, it may be a stationary bird at the same latitude.

Iceland.

(cf. p. 50) the Icelandic ptarmigan, *Lagopus lagopus*, feeds on *Dryas octopetala*, *Empetrum nigrum*, and *Salix* (p. 191) that *Dryas octopetala* is the main part of the food in the winter.

When investigated the crop and gizzard contents of the ptarmigan near Akureyri in the days immediately after the capture of these ptarmigans in all thirteen cases where the crop was abundant were *Empetrum nigrum*, *Salix*, and *Polygonum*; and in addition the following were found: *Urtica vulgaris*, *Cerastium vulgare*, *Dryas octopetala*, *Potentilla verna*, *Salix phylicifolia*, *Salix procumbens*, and *Thymus serpyllum*.

Table 29. Showing the annual variations in the food of the ptarmigan of Jotunheimen (Norway), compiled after LID, 1927.

Season	Winter	Summer					
Number of ptarmigans.....	9	12					
Total weight of crop content (mg)	165926	37600	associated with snow-patches	associated with snow-free soil	projecting above the snow	Life-form	Weight of crop content highest in the winter
Average weight of crop content (mg).....	18436	3133					
<i>Betula odorata</i>	30.4	+	Phanerophytes	Winter food: rich in lignified plants which rise above the snow or are associated with snow free soil
<i>Salix hastata</i>	1.4	+		
— <i>glauca</i>	2.5	+		
— <i>lapponum</i>	0.2	20.2	?		
<i>Empetrum nigrum</i>	59.5	1.1	..	+	..	Ch	
<i>Loiseleuria procumbens</i>	0.7	+	..		
<i>Arctostaphylos uva ursi</i>	1.0	?	..	Chamaephytes	Summer food: rich in herbaceous plants preferably associated with snow-patches
<i>Vaccinium vitis idaea</i>	3.1	?	..		
<i>Betula nana</i>	1.3	8.5	..	+	..		
<i>Arctostaphylos alpina</i>	0.9	..	+	..		
<i>Salix herbacea</i>	44.6	+		
<i>Saxifraga oppositifolia</i>	4.4		
<i>Dryas octopetala</i>	+		
<i>Linnæa borealis</i>	+		
<i>Antennaria alpina</i>	0.5	+		
<i>Cerastium alpinum</i>	2.0	?		
<i>Sibbaldia procumbens</i>	+	+		
<i>Silene acaulis</i>	0.2		
<i>Anemone vernalis</i>	3.8	Hemicryptophytes	
<i>Astragalus alpinus</i>	0.2		
<i>Deschampsia flexuosa</i>	+		
<i>Festuca ovina</i>	+	+		
<i>Luzula confusa</i>	+	?		
<i>Oxyria digyna</i>	5.7	+		
<i>Pedicularis Oederi</i>	+		
<i>Ranunculus glacialis</i>	5.0	+		
<i>Taraxacum croceum</i>	1.6	+		
<i>Thalictrum alpinum</i>	+	+		
<i>Carex rigida</i>	+	?	Geophytes	
<i>Polygonum viviparum</i>	0.6	+		
Algae	0.2	↓ plus a diminutive addition of insects	
Lichens	+	+		
Mosses	+		
Insects	+	0.5		
Total number of higher plants	12	22		Number of plant species in the food greatest in the summer

slightly snow-covered soil or soil free from snow, and the *Dryas* and *Saxifraga* areas generally with soil even more sparsely covered with snow. We here touch upon climatic-ecological phenomena, one of which will be more closely discussed.

In the fjords of Northeast Greenland the *Salix* growths occur especially in the snow-patches, and in Scoresby Sound these growths contain the most northerly scrub found in East Greenland (HARTZ, 1896). The ecology of the Norwegian tree-limit scrubs is probably very like that of the East Greenland *Salix* growths, which are found in the interior of the fjords. An amelioration of the East Greenland climate would produce scrub in these places. The present *Salix* growths in the snow-covered lowlands of the fjords are too low to rise above the snow; the ptarmigan must therefore migrate to the outer coast to gain easy access to *Salix* in the winter, for here the low summer temperature does not allow *Salix* to become too closely associated with the deep snow-cover. This migration corresponds as regards access to food to the migration of the Norwegian ptarmigan to the tree-limit.

Below the *Parmelia olivacea*-limit of the Norwegian shrubs, which according to NORDHAGEN (1928, 2, p. 98 ff.) indicates the normal snow-cover, the shrubs, as cannot escape attention in the summer, are poor in unglorified organs, while the main part of their foliage is above this limit. Consequently the leaf and catkin buds must rise above the snow in the winter. Hence the ptarmigan, whose feet, well suited for scraping, hardly allow the bird to move on the branches of the trees, has but a small chance of feeding in the scrubs before the latter have received their normal snow-cover, that is, before the snow-cover has reached the *Parmelia olivacea*-limit and accordingly the lower limit of the occurrence of the buds. In this case the snowfall is of direct benefit to the ptarmigan.

NORDHAGEN (1928, 1, p. 11) states that the ptarmigan and the grouse (*Lagopus lagopus*) behave quite differently towards *Empetrum nigrum*, this plant not having been found in the food of the grouse (*Lagopus lagopus*). Thus the ptarmigan seems to be a specialist in this respect, which is indicative of a high degree of adaptability and possibly a prolonged adaptation to the life conditions in the mountains. Probably the ptarmigan stays in the mountains above the tree-limit as long as the *Empetrum* heaths here afford sufficient access to food, and not till these fail, does it descend to the willow and birch belts, where the snow-cover at this time has probably reached the *Parmelia olivacea*-limit.

LID's (l. c.) indications of the weights of food found in the crop at the different seasons of the year are of great interest. They are tabulated in Table 30.

The material is in itself too small to allow of a definite decision as to the actual conditions; but if we compare it with those found for East

Table 30. Showing the average weight of the crop content of the ptarmigan in Jotunheimen, compiled after LID, 1927.

Month.....	1	2	3	6	7	8
Number of ptarmigans.....	1	1	7	6	5	1
Average weight of crop content in g.	5.69	6.09	22.03	3.13	3.50	1.80

Greenland (cf. Table 21, p. 141), we shall note a conspicuous agreement and a characteristic difference. On the whole the curve shows that the quantities found in the crop in the winter are larger than those found in the summer. The maximum of the curve, however, as compared with that found for the East Greenland material, has shifted to the right, with a maximum of 22 g in March. Bearing in mind that the wintry snow-cover in Jotunheimen as a rule attains its maximum thickness about March, and that no actual dark time when the sun is below the horizon all day and night, occurs here, the conditions found for Jotunheimen, too, seem to show that when the access to food is most difficult, the instinct of filling the crop will begin to function.

Here we have exclusively dealt with the food of the ptarmigan; it should, however, be mentioned that excellent investigations and discussions on the food and biology of the Norwegian *Lagopus lagopus* are found in the papers of HOLMBOE (1924), OLSTAD & LID (1923), LID and MEIDELL (1933), and NORDHAGEN (1928, 1).

Scotland.

The food of the ptarmigan (*Lagopus mutus cinereus*) indigenous to the highlands of Scotland including the Inner Hebrides (Mull, Islay, Jura, and Skye) has so far never been closely investigated. According to W. MACGILLIVRAY (1837, p. 205) the crop content of ptarmigans shot in September, 1820, consisted of: "fresh green twigs of *Calluna vulgaris*, *Vaccinium Myrtillus*, and *Empetrum nigrum* . . . Leaves and twigs of *Vaccinium Vitis idaea*, *Salix herbacea*, seeds of various *Junceae* and *Cyperaceae*, and other plants, with berries in autumn, also form part of their food."

MACGILLIVRAY further points out — perhaps as the first — that quartz is found in the gizzard.

SEEBOHM (1884, p. 427) states that tender shoots of mountain plants, especially heather and ling, compose the food, which in the autumn is varied with berries and ground-fruit.

SELBY (1833, quoted after GRIMSHAW (1925)) gives the food as: Alpine berries, such as those of the crawcrook, cranberry and cloud-berry or knoop (*Rubus chamaemorus*), with seeds and tender shoots of alpine plants.

WITHERBY (1920—24, quoted after GRIMSHAW (1925)) adds to this list the shoots and leaves of *Salix*, and the berries of *Empetrum nigrum*.

GRIMSHAW (1925) ascertained insects in the food, viz: *Tipula* (*marmorata*?) in great quantities as well as an indeterminable Saw-fly, and in addition shoot tips of *Gallium saxatile*.

The food of the grouse (*Lagopus scoticus*) has been thoroughly investigated by WILSON and LESLIE (1911), members of the Grouse Committee (1911).

The Alps.

According to NAUMANN (Naturgesch. d. Vögel Mitteleuropas, edited by C. R. HENNICKE. Band VI, p. 63) the ptarmigan of the Alps (*Lagopus mutus helveticus*) feeds upon: buds, leaves, flowers and berries of: *Vaccinium oxycoccos*, *Empetrum nigrum*, *Calluna vulgaris*, dwarf-willow and dwarf-birch. Flowers and buds of *Rhododendron ferrugineum* and *R. hirsutum*, flowers of different species of *Ranunculus*, *Saxifraga* and *Hieracium* and many other plants.

F. VON TSCHUDI (1875) further enumerates the following species: *Salix retusa*, *Dryas octopetala*, *Azalea procumbens*, and *Saxifraga androsacea*, and mentions moreover that the chickens are fed with insects by the adults. In the winter needles of *Picea excelsa* and *Abies alba* are eaten.

CONCLUDING REMARKS

The local abundance of game in the high-arctic regions has often astounded those who have had an opportunity of experiencing it. An attempt to explain it has been made by the late Swedish botanist THORILD WULFF. During his stay in Gunnar Andersson Valley (termed also MacMillan Valley) in Wulff Land, WULFF wrote in his diary on May 18, 1917 (cf. AXEL ELVIN, 1934, p. 206) (translated from the Swedish): "A good idea. It is astonishing that the short vegetation period is able to produce sufficient substance to support the fauna of musk-ox, hare, reindeer, lemming, and ptarmigan, which is very rich in view of the scanty vegetation. Among other things the fact is no doubt of importance that the winter sets in with frost suddenly so that all salts and organic elements are preserved both in the green plant and that which has already ceased to function. No long period of rainy weather occurs in the autumn during which the organic stores are reduced through washing and fermentation."

WULFF described the fauna as "very rich" in relation to the scarcity of the vegetation. I believe that this is incorrect; I would rather express the conditions thus: the fauna is locally very rich as compared with the vegetation found in these localities; but in between these areas rich in game there are vast stretches in which no game is found, although the vegetation is just as rich as in the places where game is abundant. That this applies also to regions I have not visited personally, appears from the various expedition reports. Time after time the expeditions have sought in vain for game in places where earlier expeditions secured game. This proves, what, by the way, is well known, that the arctic plant-eaters with which we are here concerned roam far and wide, and migrations seem to them absolutely necessary to sustain life.

The animals generally move in flocks, which, when one is confronted with them, may often seem very impressive, but if distributed evenly over the area which they graze off in the course of the year, they would show a very low density of individuals.

Actually the fauna must be said to be poor in relation to the vegetation. One is convinced of the correctness of this point of view on considering that the greater part of the vegetation of the country throughout the winter is covered by a layer of snow of an impeding thickness, and the animals therefore assemble on the plains and plateaus which are swept bare of snow by the wind. A large capital of plants is present, but it is, as it were, "tied up". It is the winter conditions which provide the minimum for existence, and which are accordingly determining for the frequency of the animal species that spend the winter in the particular place. If we add to this causes of death, such as diseases, mishaps or smaller or greater catastrophes that may befall the animals, it is natural to suppose that the wintering animal stock of an arctic area is always somewhat below what the food conditions in the winter might otherwise allow.

Thus I cannot agree with WULFF in his estimate of the animal stock in relation to the vegetation. But do the other suppositions set forth by WULFF hold good? It should be said here that WULFF has in some few lines touched upon a number of problems which cannot be discussed even fairly thoroughly before physiological investigations at the most diverse points have been made, and before it is known on what plant foods the different animal species principally live.

Here it may be stated at once that the preservation supposed to take place at the setting in of the frost is of no importance for the main quantity of the food of the ptarmigan, since its food consists mostly of tips of branches and leaves of perennial plants whose organs do not normally perish in the course of the winter. The musk-ox, however, in the winter lives largely on grasses which to a great extent have turned into hay before the setting in of the frost, but which in the continental climate presumably keep a high food value throughout the winter. However, the main constituent of the food of the musk-ox is probably willow, a plant whose branches persist through the winter.

If thus WULFF's idea can only be accepted with very large modifications, the greater part of the food of the plant-eaters consists of perennating plant organs; it is, however, possible that the conservation by the frost may be of importance, viz. by preserving plants which quantitatively, it is true, are of no great importance for the plant-eaters, but may be supposed to be so qualitatively. I am here thinking of the plants of the snow-patches, more especially those of the late-melting snow-patches. Precisely their vegetation is stopped by the frost at an early stage of development. However, their growth is not stopped suddenly, since many of the plants are able to utilise the frost-free noon hours, in which the plants grow and sometimes even set flowers (cf. GELTING 1934, p. 304). Not till some time after the permanent day frost has set in, must the activity of these

cold-resisting plants be assumed to stop, since the dissolved matter in the saps causes a depression of their freezing point. To this may be added in the calm days of the autumn the possibility of sub-cooling before the sap congeals. Probably the physiological processes in the plants take place very slowly at the low temperatures in question, but precisely this fact contains a central problem. On account of their slow growth the plants remain for a long time at a young stage, and are finally preserved by the frost at such a stage; and since the investigations recorded in p. 153 seem to demonstrate that young plant parts are richer in proteins than older plant parts, it will be understood that if this is a general rule, or but partly so, the vegetation of the late-melting snow-patches may serve as a source of proteins for the plant-eaters.

In p. 160 we thought it possible to discern symptoms of a protein requirement, and throughout the summer till some time into the autumn a preference of foods rich in proteins to foods poor in proteins. In good agreement with the assumption as to the protein content of the snow-patch vegetation, the plant-eaters (the ptarmigan, the hare, and the musk-ox) are actually found to feed in the snow-patches both in the summer and the autumn.

Although the vegetation of the snow-patches is the first to be covered with snow in the autumn, it may with its frost-preserved plants serve for a fairly long period as a valuable food resource, for the snowfall may occur rather late (cf. LUNDAGER 1912, p. 383, GELTING 1934, p. 237).

The demonstration of the frequent occurrence of the snow-patch plants in the food not only of the East Greenland ptarmigan, but also in that of Spitsbergen and Jotunheimen (Norway), renders it probable that the summer and autumnal feeding of the ptarmigan in the snow-patches is a general arctic-alpine phenomenon.

The study of the ecology of the snow-patches and of the physiology of the snow-patch plants and their content of organic nutritive substances and salts may therefore be of exceedingly great interest for the understanding of the life conditions of the plant-eaters, all the more so because here the source of nutrition is represented which at any rate in the arctic regions seems to flow most sparsely, viz. the source of protein. If the plants of the late-melting snow-patches are in addition rich in vitamins, what young plants often are, it will be understood that the snow-patches, also as regards the adventive substances, may be of exceedingly great importance for the plant-eaters.

On the increase of the snow-cover, the access to the snow-patch vegetation is gradually definitely barred to the plant-eaters mentioned here. The lemming, however, has its passages below the snow during the winter, and by preference makes its nest in the snow-patches, which can hardly escape observation in the spring when the snow melts away.

The non-burrowing, or generally non-burrowing, plant-eaters, the ptarmigan and the musk-ox, however, must resort to other feeding grounds at midwinter.

The Arctic hare continues fairly long to dig down to the snow-patch vegetation, even after the snow-cover has become rather firm. Observations of this are available from the early winter of 1931—32. Finally, however, the hare, too, seeks the snow-free places.

WULFF's idea — which may almost be expressed as follows: Within certain arctic regions of a continental character the plant capital is principally consumed by vertebrates and only to a slight extent converted by micro-organisms — cannot, therefore, be contested, but it may be assumed that it is by preserving plants of a certain quality and not only a certain quantity of plants that the "frost preservation" is of the greatest importance to the plant-eaters.

The constellation of external conditions in these arctic regions consists of a number of elements, part of which are usually designated as very unfavourable; and yet nothing in the biology of the ptarmigan indicates that it does not thrive well. At many points the bird shows properties which indicate even an exceedingly great "adaptation", i. e. suitability to the arctic conditions. This might show that the bird has for a very long time been associated with the Arctic, possibly even during periods when the climate was more unfavourable and the access to food more difficult than at the present day.

WINGE (1898) assumes that the ptarmigan existed as far back as in Tertiary times, and he points out characters which show that the bird must be regarded as a highly developed gallinaceous bird; and he couples the development of these characters with an "adaptation" to the conditions during the Ice Age (l. c. p. 67). However, the reason why WINGE dared not assume that the ptarmigan had entirely or partially survived the Ice Age in Greenland, is (l. c. p. 65) that at his time it was generally supposed, owing to the traces of the Ice Age present on the outermost islands along the west coast of Greenland, that the whole country had been covered with ice.

According to our present knowledge of the extent of the glaciated areas both in the Arctic American archipelago and in the northwestern parts of the continent of America (ANTEWS 1929), the ptarmigan might quite well have survived at any rate the latest ice age there, whence it may later have immigrated into Greenland; but even the possibility that the ptarmigan has survived the latest ice age in Greenland, cannot at the outset be rejected. At the present time the bird lives in the northernmost part of Greenland, at any rate in the summer, and all the year in Spitsbergen, some of the northernmost regions of the world. Possibly

the different ptarmigan races have different climatic requirements. The bird in question, *Lagopus mutus captus*, is associated with a highly continental climate. Its area is closed to the south, since it is not known from the regions south of Blosseville Coast, which is the most important climatic boundary of the east coast (cf. BÖCHER 1933). To the north the area is not closed, since it is not known how far to the northwest the bird lives. The area opens towards the continentally marked area of Arctic America.

SUMMARY

The area between Franz Joseph Fjord and Sabine Island (Northeast Greenland), like the coast areas north and south of it, is mainly built up of a plateau dissected by broad fjords and narrow valleys. From an altitude of approximately 1300—1500 m above sea-level at the edge of the inland ice it descends to an altitude of some 800—900 m at the outer coast. To the east the plateau is bordered by low, flat or slightly broken forelands, largely consisting of the abrasion planes formed during a postglacial transgression.

The climate is continental. The hydrotherm figure shows a considerable difference in the temperatures of the summer and the winter. The precipitation is low at all seasons of the year. The greater part of it comes down in the form of snow, which to a great extent is swept out on to the sea-ice or sublimates on the numerous sunny days in the spring. Fog, which in Northeast Greenland is a rarer phenomenon than in many other arctic regions, is most frequent at the outer coast and contributes to making the summer colder there than farther in towards the interior of the fjords. Winds blowing from the northwestern quarter prevail at most seasons. The westerly winds frequently have the character of warm, dry foehn winds, but also colder fall winds occur. The foehn winds blow both summer and winter, and make themselves felt especially in the fjords. During their passage through the latter they lose part of their character by exchange with the air masses of the fjords, and their effect at the outer coast is therefore reduced. In the winter the foehn winds often cause the formation of crust-snow, a phenomenon which must be assumed to be most frequent in the inner fjords. In the summer there is often a remarkably regular daily change from westerly land winds to easterly sea winds. However, the sea winds rarely drive the fog to the heads of the fjords. In the winter northerly winds of great violence frequently prevail at the outer coast. They are generally colder and more humid than the westerly winds blowing at the same season.

Although regular observations of meteorological elements are not

available from other stations than Myggbukta at the outer coast, it may be assumed with great certainty that the continental character increases with increasing distance from the outer coast. The latter has not only a colder summer but also a milder winter than the country round the heads of the fjords.

As a consequence of the considerable climatic differences, there is a great difference, too, between the flora and vegetation of the outer coast and those of the inner fjords. The flora of the outer coast is characterised by a special outer coast element, associated with even very damp soil and forming a vegetation which ecologically as well as floristically shows resemblance to special Icelandic as well as certain Asiatic "tundra" types. The flora of the inner fjords is characterised by a special fjord element, chiefly associated with very dry soil and forming a xerophytic vegetation which notably bears an ecological, but also a floristic resemblance to the steppe and desert tracts of both the old and the new world. The species which are distributed throughout the whole area, from the outer coast to the heads of the fjords, often exhibit exceedingly characteristic differences in habitat in the various districts, more especially with regard to the moisture of the soil and the wintry snow-cover. The rule is that with increasing distance from the outer coast the area of dominance of the individual species is always associated with an increase of the wintry snow-cover or of the moisture of the soil. As a consequence the vegetation free from snow in the winter is of quite a different character within the different districts. In the winter the snow-free dry grass and dwarf-shrub heaths of the inner fjords contrast strongly with the snow-free hygrophytic meadowy or boggy plant communities of the outer coast.

The arctic willow (*Salix arctica*) belongs to the plant group whose area of dominance at the outer coast is slightly snow-covered, while in the fjords its snow-cover increases very considerably with the increasing distance from the outer coast. *Dryas octopetala* and *Saxifraga oppositifolia* seem to be less dependent on a wintry snow-cover and occur throughout the area on soil which is snow-free or but slightly covered with snow in the winter. The relation of *Polygonum viviparum* to the snow-cover agrees in all essentials with that of *Salix arctica*. The snow-cover in some characteristic areas of dominance of these species at Eskimonæs was measured in the winter of 1931—32. These measurements (diagrammatically represented in fig. 11, p. 34) may be taken as a paradigm of the snow-cover in the areas of dominance of these species in the outer fjords. It will be seen that the *Salix arctica* heath at Eskimonæs was covered with deep snow, although the snowfall that winter may be assumed to have been somewhat lower than is normal.

The wintry snow-cover gives rise to a certain law-regulated

zonation of the plant communities. As the reaction of the species to snow-cover and protection against desiccation, etc., is rather dissimilar within the different districts, not only the floristic composition of the vegetation types varies with the different distances from the outer coast, but this is also the case with their place in the snow-covering scale and accordingly with their place in the terrain. This is illustrated in fig. 15 and fig. 16, p. 39. The vegetation on the mountain plateaus in the interior of the fjords very much resembles the snow-free vegetation of the outer coast.

The East Greenland ptarmigan, *Lagopus mutus captus*, is a race endemic to Greenland and occurs from Cape Dalton in the south to Germanialand in the north. Probably the area of distribution of the race extends right to the northernmost point of Greenland, where ptarmigans have been observed, but whence no material was brought home. Between Cape Dalton and Germanialand the bird occurs from the extreme outer coast to the heads of the fjords, and even on the nunataks in the inland ice. In the breeding time the ptarmigan is mostly encountered in the fjords, where it is more numerous than at the outer coast all the summer.

In the winter the ptarmigan migrates to the outer coast, whence it returns to the fjords with the returning daylight. Here the mating takes place, and the nests are built. In May the eggs are laid, and in the course of June the young appear. In the course of the summer the ptarmigan migrates into the mountains, reaching the plateaus in September—October, when the young chickens are full-grown. These migrations may be correlated with the nature of and access to the food, since the migration to the outer coast favours the access to the *Salix* areas, which are free from snow in the winter, and on its migration into the mountains the bird follows the flowering of the *Polygonum* communities, which takes place first in the lowland and subsequently on the mountains. These migrations are also traceable in the records of the occurrence and frequency of the ptarmigan in other parts of Greenland. Further details concerning the migration can hardly be ascertained with certainty without ring-marking.

The summer habitat preferred by the ptarmigan (summer biotope) is slightly broken territory in which sudden changes in level cause the presence of numerous small snow-patches, which melt so early that *Polygonum* may occur with great frequency and vitality. On the more arid slopes of this terrain the ptarmigan may have its nest.

The winter habitats, however, are the open plains and the flat plateaus where the wind keeps the vegetation free from snow, and where the latter is of such a nature that the ptarmigan is able to sustain life on it. It is shown that the snow-free *Salix* areas of the outer coast will

principally come into question. However, the winter feeding grounds include the open snow-free *Dryas* and *Saxifraga oppositifolia* areas also. The summer feeding places, on the other hand, can be distinctly characterised, viz. as the snow-patches, or the areas round the snow-patches, which are situated within the boundary of the *Cassiope tetragona* heath (cf. fig. 15, p. 39).

The earlier literature contains several data on the food of the East Greenland ptarmigan. However, the quantities of the individual food elements have, as a rule, been left unnoticed.

The methods applied in the investigations of the crop content here discussed are described on p. 77 ff. A survey of the constituents found in the food is given on p. 85 ff. Altogether 78 crops were examined, in which the following plants were found to be represented: 52 vascular plants, two mosses, one fungus. Furthermore two insects and small quantities of quartz and earth were found.

Among the plants constituting the food of the ptarmigan four main species can easily be demonstrated, viz. *Salix arctica*, *Dryas octopetala*, *Saxifraga oppositifolia*, and *Polygonum viviparum*, compared with which all the other plant species must be regarded as subordinate or sporadic as regards quantity. In drawing the line of demarcation between the subordinate and the sporadic plant species, the term sporadic has been assigned to such as have never been found in the individual crop in quantities above 50 mg. However, the subordinate as well as the sporadic constituents may very well be supposed to be of importance by a special physiological effect.

Different plant species dominate in the food at the different seasons. The summer food consists chiefly of *Polygonum viviparum*, the winter food chiefly of *Salix arctica* with *Dryas octopetala* and *Saxifraga oppositifolia* as particularly important co-constituents. It is not known when the transition from summer to winter diet and the reverse takes place, but it must be assumed to occur in October—November and May—June respectively. However, the transition, at any rate in the spring, may quite well be supposed to take place via other species than those which have so far been found in fairly great quantities in the crop content.

Important for an understanding of the ecology of the bird is a knowledge of the variations in the food. As regards the main constituents they are small in the summer and great in the winter. This indicates that one or several factors which are of no avail in the summer exert their influence in the winter. In this connection attention may be called to the greatly varying snow-cover of the winter and the illumination decreasing steadily towards midwinter.

Table 15, p. 120, and fig. 39, p. 121, give the percentage representation

of the main food elements in the crop content in the individual months. If we compare fig. 39 and fig. 11, p. 34, in which the snow-cover of the main plant species is shown, it will be seen that it exerts a controlling influence. In the period from October to midwinter the crop content shows a change from a dominance of *Salix arctica* in October to a *Dryas* maximum in November—December. It seems natural to consider the increasing snow-cover of the *Salix* areas as the cause of this change. In the period after midwinter the opposite tendency prevails, as now the crop content shows a transition from a *Dryas* maximum in March—April to a *Salix* maximum in May. Precisely at this season the snow-cover has decreased so much that *Salix* is largely accessible again.

In midwinter and the immediately succeeding months *Saxifraga oppositifolia* is present in the crop content in small quantities, though they are larger than at any other time of the year. The scanty access to other food may here be supposed to be the cause why the species at this season is present in the food in a fairly large quantity. The great fluctuations in the *Dryas* and the *Salix* contents at this season must in some degree be due to the great variations of the snow-cover.

Some examples of the composition of the crop content on days with differing thickness of snow-cover further demonstrate the importance of the latter for the access to the different plant species. On days following upon a snowfall which on account of calm weather has remained in its original place, the *Dryas* percentage in the crop content is very high, while the *Salix* percentage is high on days after a period without snowfall or with storm. The law-regulated position of the dominance areas of the two species in relation to the snow-cover is here an important factor.

The other limiting factor in the winter is the decreasing duration of the daylight. At the beginning of November the sun disappears below the horizon, not to rise above it again till the beginning of February. From an astronomical point of view the daylight during this period is nil. Yet by noon the sun approaches so near to the horizon that the noon time is characterised by a faint light to the south. The duration of this noon light likewise decreases towards the winter solstice, but may at that season last up to two hours. In the narrowest fjords or on days when the sky is overcast it may entirely or almost fail. Owing to this total failing of the daylight and the short duration of the noon light it is not precisely the time of the thickest snow-cover (March—April) that is the critical period for the ptarmigan as regards food; the critical point must occur within that period of the dark time when the quantity of snow is largest. In 1932 this occurred in January, which must be assumed to be normal.

When in this way the lack of light reduces the time for collecting

food, the food element of which the largest weight can be secured by one pick with the beak will, *cetera paribus*, be the most advantageous. In this respect there is a considerable difference in the fragments of *Salix* and *Dryas*, the former being represented in the crop content by branches varying in size according to requirement, while *Dryas* is practically exclusively represented by leaves the size of which the ptarmigan cannot influence. Hence it is evident that in the winter *Salix* must be a more coveted food than *Dryas*. The fact that at midwinter the ptarmigan cuts off larger fragments of *Salix* than at other times of the winter, indicates precisely that time comes in as a limiting factor as regards the access to food.

Three ptarmigans killed at Eskimonæs in January had on an average consumed 9111 fragments each, and bearing in mind that these were collected during hardly two hours of faint light at noon, we receive an impression of the necessity for the ptarmigan to work rapidly and accurately as well as to find food which can supply a certain quantity in each pick. While on the long summer days the collection is done with ease and the crop has never been found full, the digestion evidently keeping pace with the collection of food, in the dark time the ptarmigan has but a short period at noon in which to collect food for all the twenty-four hours of the day. In accordance with this the average weight of the crop content is highest in January (Table 21 and fig. 46, p. 141).

Although the conditions for securing food would seem on several points to approach the minimum requirements, the ptarmigan is able to keep itself in a good state of nutrition all the winter. At midwinter the ptarmigans are fat, the subcutaneous tissue, in particular, containing a large amount of fat.

The investigations of the content of organic nutritive substances in the foods (Table 24, p. 153) demonstrate that the winter food is rich in fats, while the summer food is rich in proteins. Fat winter food is possibly a common phenomenon among plant-eaters, and seems at any rate to be useful in arctic regions, partly on account of the high calorific value of the fats, partly because of the protection against cold afforded by the deposited fats. However, since the winter in the area in question is more than twice as long as the summer, which is evidently the only season of the year when there is easy access to food rich in proteins, it is quite conceivable that the ptarmigan may in the course of the winter, especially in the late winter, be in need of proteins. This is indicated by the occasional occurrence in the winter food of elements which are particularly rich in proteins but at the same time especially difficult of access (tubers of *Polygonum* and sporophyll heads of *Equisetum variegatum*).

The investigations of the content of nutritive substances in the food

elements, however, are very incomplete, and more detailed researches should be made. These investigations have further disclosed that in 1932 *Dryas octopetala* possibly commenced the CO_2 assimilation in March.

On the basis of the investigations made into the nature of the food, the access to it, and its content of nutritive substances it is possible to point out and define more precisely some of the variable factors which must be assumed to be of importance for the thriving and frequency of the ptarmigan. However, as long as more detailed investigations on the fluctuations in the ptarmigan stock are not available, we cannot arrive at a final opinion as to the dependence of the fluctuations on the external factors.

The available literature dealing with the ptarmigan in other arctic regions and an investigation of two ptarmigan crops from Danske Island in the Arctic-American archipelago, which were handed over to me, proves that the food of the ptarmigan in the Arctic regions which it has been possible to compare, is distinguished by a relatively great uniformity at the corresponding times of the year whence material is at hand. In the Norwegian highlands, too, the conditions under which the ptarmigan lives resemble the conditions of the Arctic to such a great extent that a comparison of the food reveals certain common features in it. Interesting deviations from the food of the Northeast Greenland ptarmigan, can, however, be demonstrated and explained.

Finally, attention is called to the importance of the snow-patch vegetation as a source of protein for the arctic plant-eaters.

LITERATURE

Abbreviations: M.o.G. = Meddelelser om Grønland. København.
N.J.F. = Norsk Jæger- og Fiskeri-Forenings Tidsskrift. Oslo.

- ANDERSEN, A. C. & NORMAN-JENSEN, B. 1923: Om Kvalstofbestemmelser. — 133. Beretn. fra Forsøgslaboratoriet. København.
- ANTEWS, ERNST. 1929: Maps of the Pleistocene Glaciations. — Bull. of the Geol. Soc. of America. Vol. 40. New York.
- BACKLUND, H. G. 1930: Contributions to the Geology of Northeast-Greenland. — M. o. G. Vol. 74.
- 1931, 1: Über die Lagerungsbedingungen eines Torffundes in NO-Grønland. — M. o. G. Vol. 87.
- 1931, 2: Fjordbildningsproblemet i NO-Grønland. — Geol. Foren. Förhandl. Vol. 53. Stockholm.
- 1932: Das Alter des "Metamorphen Komplexes" von Franz Joseph Fjord in Ost-Grønland. — M. o. G. Vol. 84.
- BACKLUND, H. G. und MALMQVIST, D. 1932—35: Zur Geologie und Petrographie der Nordostgrønländischen Basaltformation Teil I—II. — M. o. G. Vol. 87. 1932 & Vol. 95, 1936.
- BARTH, J. B. 1891: Erfaringer fra Jagten paa det mindre Vildt i Norge. Kristiania.
- BAY, E. 1894: Pattedyr og Fugle. Den Ostgrønlandske Expedition udført i Aarene 1891—92 under Ledelse af C. RYDER. Tredie Del. — M. o. G. Vol. 19. 1896.
- BERTELSEN, A. 1921: Fuglene i Umanaq Distrikt. — M. o. G. Vol. 62.
- 1932: Meddelelser om nogle af de i Vestgrønlands Distrikter mellem 60° og 77° n. Br. almindeligere forekommende Fugle, særlig om deres Udbredelsesomraade, deres Yngleomraade og deres Træk. — M. o. G. Vol. 91.
- BIRKELAND, B. J., et SCHOU, G. 1932: Le Climat de l'Eirik Raudes-Land. — Skr. om Svalbard og Ishavet, Nr. 51. Oslo.
- BRAND, W. & WEGENER, A. 1912: Meteorologische Beobachtungen der Station Pustervig. — M. o. G. Vol. 42.
- BRINKMANN, A. 1922: Lirypens entoparasiter. — Bergens Mus. Årb. 1921—22. Naturv. rekke nr. 3. Bergen 1922.
- 1927, 1: Coccidiosen hos lirypen. Ibidem.
- 1927, 2: Jagtlovgivning og fredning. Naturen. Bergen.
- BRONLUND, J.: see TROLLE, ALF.
- BOCHER, T. 1933: Phytogeographical Studies of the Greenland Flora. — M. o. G. Vol. 104.
- CLAVERING, D. C. 1830: Journal of a Voyage to Spitsbergen and the East-Coast of Greenland in H.M. Ship "Griper". — The Edinburgh New Philosophical Journal, April—July 1830 (quoted after Petermann Mitt. Vol. 16, 1870).

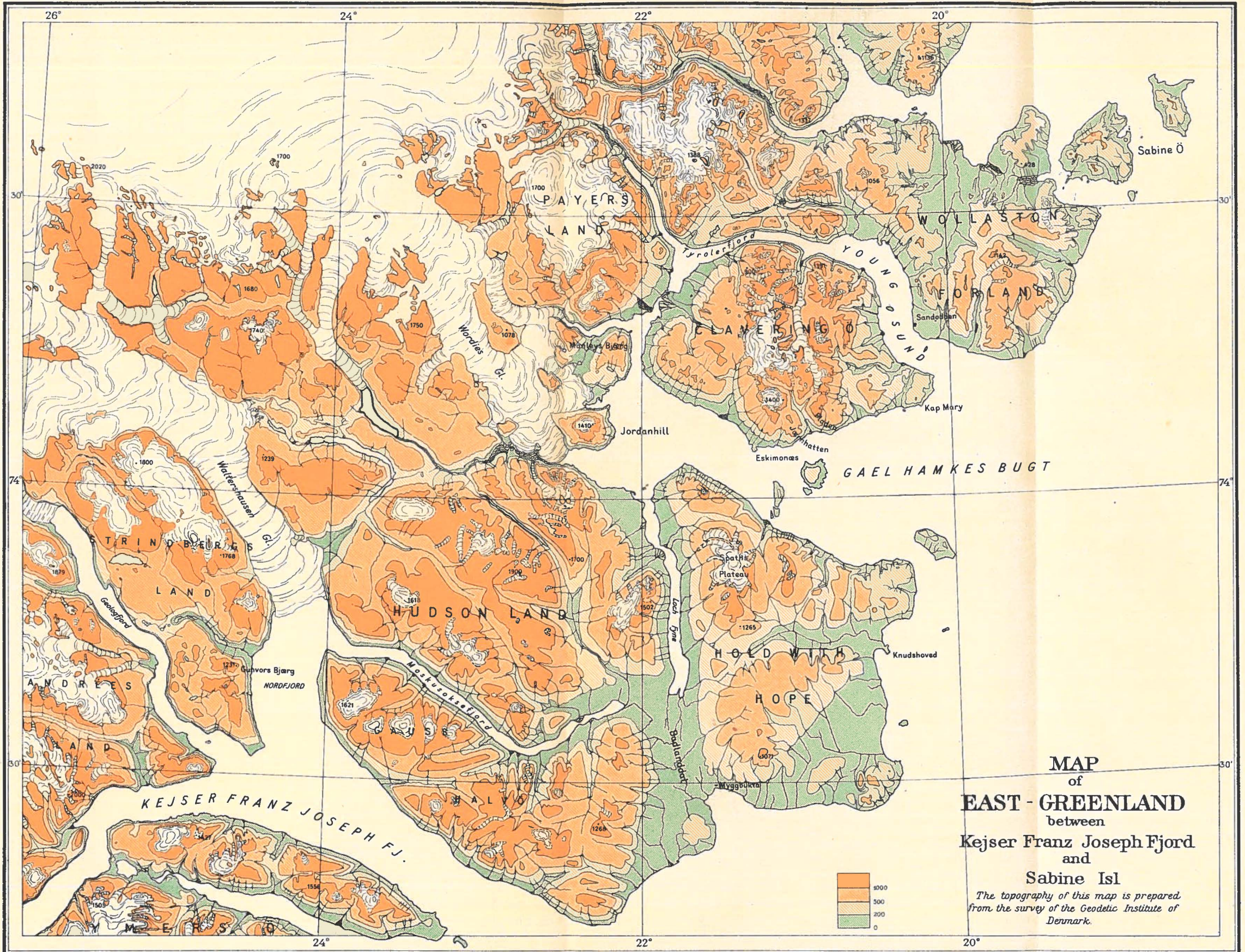
- DAHL, KNUT, 1922: Ti aars jagttagelser over skogsfugl og ryper. — N. J. F.
 — 1924: Variationer i mængden af Norges smaavildt. — N. J. F.
 — 1927: Rovvildtet i vor jagthusholdning. N. J. F.
- DALGETY, C. T. 1936: Notes on Birds observed in Greenland and Baffin Land, June—September 1934. — *The Ibis*, July 1936, p. 580—591. London.
- DEGERBOL, M. 1935: Animal Bones from King Oscar Fjord Region in East Greenland. — *Zool. Appendix apud GLOB* 1935. (M. o. G. Vol. 102.)
- DEGERBOL, M. and MOHL-HANSEN, U. 1935: Birds (Aves). The Scoresby Sound Committee's 2nd East Greenland Expedition in 1932 to King Christian IX Land. — M. o. G. Vol. 104.
- DEICHMANN, H. 1909: Birds of East Greenland. — M. o. G. Vol. 29.
- DIETRICH, TH. & KÖNIG, J. 1891: Zusammensetzung und Verdaulichkeit der Futtermittel. 2. Aufl. Berlin.
- EKMANN, S. 1922: Djurvärldens utbredningshistoria på den skandinaviska halvön. — Stockholm.
- EKSTAM, O. 1898: Einige blütenbiologische Beobachtungen auf Spitzbergen. — Tromsø Museums Aarshefter, Nr. 20.
- ELVIN, A. 1934: Thorild Wulffs grönländska dagböcker. Stockholm.
- FABRICIUS, O. 1780: Fauna Groenlandica. København.
- FANTHAM, H. B. 1911: Coccidiosis; Chapter XI; in: *The Grouse in Health and in Disease*. — Grouse Committee. London 1911.
- FINSCH, O. 1874: Vögel. Mit Noten von Adolf Pansch. — *Die zweite Deutsche Nordpolarfahrt*. Zweiter Band. Leipzig.
- FOLDVIK, NILS. 1933: Av norske fangstmenns nybyggerhistorie på Ost-Grønland. — *Polar-Årboken* 1933, utgitt av Norsk Polarklubb. Oslo.
- FREUCHEN, P. 1921: Fuglelivet i Nordvestgrønland. (Jagttagelser fra mit Vindue.) — *Dansk Ornitholog. Foren. Tidsskr.* XV. København.
- FØYNS, N. J. 1922—28: Vejret i rypedistriktene. — N. J. F.
- GELTING, PAUL. 1934: Studies on the Vascular Plants of East Greenland between Franz Joseph Fjord and Dove Bay. — M. o. G. Vol. 101.
 — 1936: Karplanternes vertikale Udbredelse i Nordøstgrønland set i Forhold til Isfremstød og Epirogenese. — *Nordiska* (19. skandinaviska) naturforskerskarmötet i Helsingfors 1936.
- GIESECKE, C. L. 1816: "Greenland" in Brewster: *Encyclopædia*. Vol. X, part. II. Edinburgh.
- GLOB, P. V. 1935: Eskimo Settlements in Kempe Fjord and King Oscar Fjord. — M. o. G. Vol. 102.
- GRIPP, K. 1927: Beiträge zur Geologie von Spitzbergen. — *Abhandl. aus dem Geb. d. Naturw.*, herausg. v. Naturw. Verein in Hamburg. Vol. 21, Heft 2—4, Abh. 1. Hamburg.
 — 1929: Glaciologische und geologische Ergebnisse der Hamburgischen Spitzbergen Exp. 1927. — *Ibidem* Vol. 22, Heft 2—4. Hamburg.
 — 1932: Diluvialmorphologische Probleme? — *Zeitschr. d. Deutsche Geol. Ges.* Vol. 84. Berlin.
- GRIMSHAW, P. H. 1911: The Insect Food of Grouse Chicks, based on an examination of crops and gizzards, Chapt. IV, Part II, in: *The Grouse in Health and in Disease*. — Grouse Committee, London 1911.
 — 1925: The Food of the Ptarmigan. — *The Scottish Naturalist* 1925.
- Grouse Committee. 1911: *The Grouse in Health and in Disease*. Being the final Report of the Committee of Inquiry on Grouse Disease. Vol. I—II. London. (As to its popular Edition see: LESLIE, A. S.)

- HAMMOND SMITH, H. and RASTALL, R. H. 1911: Grit, Chapter IV, Part IV, in: The Grouse in Health and in Disease. — Grouse Committee. London 1911.
- HARTERT, E. 1910—1923: Die Vögel der paläarktischen Fauna. — Berlin.
- HARTZ, N. 1896, 1: Fanerogamer og Karkryptogamer fra Nordøst-Grønland og Angmagsalik. — M. o. G. Vol. 18.
- 1896, 2: Ostgrønlands Vegetationsforhold. — M. o. G. Vol. 18.
- HARTZ, N. and KRUISE, CHR. 1911: The Vegetation of Northeast-Greenland. — M. o. G. Vol. 30.
- HELMS, O. 1926: The Birds of Angmagsalik. — M. o. G. Vol. 58.
- HOLBOLL, C. 1840: Ornithologiske Bidrag til den grønlandske Fauna. — Naturh. Tidsskr. IV, 1842—43. København.
- HOLMBOE, J. 1924: Hvad liryphen lever av i Norge. — Berg. Mus. Årb. 1922—23, Naturv. rekke Nr. 5. Bergen 1924.
- HOEG, O. ARBO. 1929: Food of the Spitsbergen Ptarmigan in September. — Kgl. Norsk Vid. Selsk. Forh. Vol. 1, Nr. 56. Trondhjem.
- IVERSEN, J. 1934: Moorgeologische Untersuchungen auf Grönland. — Medd. Dansk Geol. Foren. Vol. 8. — København.
- JENSEN, AD. S. 1928: Grønlands Fauna, et Forsøg paa en Oversigt. — Festskr. udg. af Københavns Universitet i Anledning af H.M. Kongens Fødselsdag 26. September 1928. København.
- JESSEN, KNUD, 1913: Rosaceae, in: The Structure and Biology of Arctic Flowering Plants II. — M. o. G. Vol. 37. København 1921.
- KLOSTER, R. 1921: Veksling i rypebestanden. Norsk opfatning. — N. J. F.
- 1922: Veksling i rypebestanden. Historie og statistik. — N. J. F.
- 1923: Vekslinger i rypebestanden paa Island. — N. J. F.
- KOCH, J. P. 1916: Survey of Northeast Greenland. — M. o. G. Vol. 46.
- KOCH, LAUGE, 1929: The Geology of East Greenland. — M. o. G. Vol. 73.
- 1931: Carboniferous and Triassic Stratigraphy of East Greenland. — M. o. G. Vol. 83.
- KRAUS, G. 1874: Einige Bemerkungen über Alter und Wachstumsverhältnisse ostgrönländische Holzgewächse. — Zweite Deutsche Nordpolarfahrt. Vol. II. Leipzig.
- KRUISE, CHR. 1912: Rejser og botaniske Undersøgelser i Øst-Grønland mellem 65°30' og 67°20' n. Br. — M. o. G. Vol. 49.
- KULLING, O. 1930: Stratigraphic Studies of the Geology of Northeast Greenland. — M. o. G. Vol. 74.
- LARSEN, H. 1934: Dødemandsbugten, an Eskimo Settlement on Clavering Island. — M. o. G. Vol. 102.
- LESLIE, A. S., assisted by A. E. SHIPLEY, 1912: The Grouse in Health and in Disease. Popular Edition of the final Report of the Grouse Committee. — London.
- LID, J. 1927: Om Fjeldrypens Næring. — N. J. F.
- 1933: Crop Contents of Ptarmigans from Taimyr. — Norw. North Polar Exp. with the "Maud" 1918—25. Scient. results. Vol. V, Nr. 2. Bergen.
- LID, J. & MEIDELL, OVE. 1933: The Food of Norwegian Grouse Chicks. — Nyt Magaz. f. Naturv. Vol. 73. Oslo.
- LOEWE, FRITZ. 1935: Klima des grönländischen Inlandeises. — Handb. d. Klimatologie, herausgg. von W. Köppen und R. Geiger, Vol. II, Teil K. Berlin.
- LUNDAGER, A. 1912: Some Notes concerning the Vegetation of Germania Land, North-East Greenland. — M. o. G. Vol. 43.
- LYNGE, B. 1932: Om udbredelsen af en del arktiske laver. — Svensk Bot. Tidsskr. Vol. 26, H. 3—4. Uppsala.

- LÖPPENTHIN, BERNT, 1932: Die Vögel Nordostgrönlands zwischen 73°00' und 75°30' n. Br. — M. o. G. Vol. 91.
- MACGILLIVRAY, W. 1837: A History of British Birds etc. Vol. I. — London.
- MALMQVIST, D. 1932: Zur Kenntnis der oberkarbonischen Sedimente der westlichen Clavering Insel, Ostgrönland. — M. o. G. Vol. 94.
- MANNICHE, A. L. V. 1910: The Terrestrial Mammals and Birds of North-East-Greenland. — M. o. G. Vol. 45.
- MOHR, N. 1786: Forsøg til en Islandsk Naturhistorie etc. — København.
- NATVIG, LEIF R. 1930: Insektlarver i rype-ekskremitter. — N. J. F.
- NAUMANN: Naturgeschichte der Vögel Mitteleuropas. herausgg. von C. R. Hennicke. Vol. VI. — Gera-Untermhaus.
- NIELSEN, E. 1935: The Permian and Eotriassic Vertebrate-bearing Beds of Godthaab Gulf, East Greenland. — M. o. G. Vol. 98.
- NOE-NYGAARD, A. & SÄVE-SÖDERBERGH, G. 1932: Zur Stratigraphie der Nordost-ecke der Clavering Insel. — M. o. G. Vol. 94.
- NOE-NYGAARD, A. 1933: Remarks on *Mytilus edulis* L. in raised beaches in East-Greenland. — M. o. G. Vol. 95.
- NORDENSKJÖLD, O., 1916: Studien über das Klima am Rande jetziger und ehemaliger Inlandeisgebiete. — Bull. of the Geol. Instit. of Upsala. Vol. 15. Uppsala.
- NORDHAGEN, ROLF, 1928, 1: Rypeår og Bærår. — Berg. Mus. Årb. Naturv. rekke, nr. 2. Bergen.
- 1928, 2: Die Vegetation und Flora des Sylenegebietes. I: Die Vegetation. — Skr. utgitt av Norsk Vid. Akad. i Oslo 1927. Matem.-naturv. Klasse. Vol. I. Oslo.
- 1936: Versuch einer neuen Einteilung der subalpinen-alpinen Vegetation Norwegens. — Bergens Mus. Årb. 1936, Naturv. rekke, nr. 7. Bergen.
- OLSTAD, O. 1922: Jagttagelser over lirypen. — N. J. F.
- 1926: Ringmærkning av lirype. — N. J. F.
- 1926: Træk af lirypens biologi. — N. J. F.
- 1927: Undersøkelser over lirypens eggægning, rugning og klækning. — N. J. F.
- 1932: Undersøkelser over lirypens forplantningsforhold. — Nyt Magaz. f. Naturv. Vol. 71. Oslo.
- OLSTAD, O. & LID, J. 1923: Undersøkelser over lirypens næring. — N. J. F.
- OMSTED, A. 1927: Aarsakerne til vekslingerne i bestanden af smaavildt. — N. J. F.
- PANSCH, A.: see FINSCH.
- PEDERSEN, ALWIN. 1926: Beiträge zur Kenntnis der Säugetier- und Vogelfauna der Ostküste Grönlands. — M. o. G. Vol. 68.
- 1930: Fortgesetzte Beiträge zur Kenntnis der Säugetier- und Vogelfauna der Ostküste Grönlands. — M. o. G. Vol. 77.
- 1934: Die Ornis des mittleren Teiles der Nordostküste Grönlands. — M. o. G. Vol. 100.
- PETERS, I. P. 1934: Birds of the World. Vol. II.
- PETERSEN, HELGE. 1934: Extrem hohe Temperaturen und Föhn in Grönland. — Metr. Zeitschr. 1934.
- 1935: Klima der Küsten von Grönland. — Handb. d. Klimatologie, herausgg. von W. Köppen und R. Geiger. Vol. II, Teil K. Berlin.
- PLESKE, TH. 1928: Birds of the Eurasian Tundra. — Mem. Boston Soc. Nat. Hist. Vol. 6, Nr. 3. Boston.
- PORSILD, M. P., assisted by A. E. PORSILD, 1920: The Flora of Disko Island and the Adjacent Coast of West Greenland. — M. o. G. Vol. 58.

- PORSILD, M. P. 1935: Stray Contributions to the Flora of Greenland. X: A Botanical Excursion to the Fiords of Godthaab District, and XI: A Botanical Excursion to the Southeastern Parts of Disko Bay. — M. o. G. Vol. 93.
- RAUNKJÆR, C. 1905: Types biologiques pour la géographie botanique. — Acad. Royale des Sc. et des Lettres de Danemark. Bull. de l'année 1905, Nr. 5. Copenhague.
- 1911: Det arktiske og det antarktiske Chamæfytklima. — Biol. Arb. tilegnet Eug. Warming. København.
- RICHTER, S. 1934: A Contribution to the Archaeology of North-East Greenland. — Skr. om Svalbard og Ishavet, Nr. 63. Oslo.
- ROSENVINGE, L. KOLDERUP. 1896: Det sydligste Grønlands Vegetation. — M. o. G. Vol. 15.
- ROSS, JOHN. 1819: A Voyage of Discovery in H.M. Ship "Isabella" and "Alexander" for the Purpose of Exploring Baffins Bay. 1819.
- SALOMONSEN, FINN, 1925: Paa Ornithologisk Undersøgelserrejse i Grønland. — Dansk Ornitholog. Foren. Tidsskr. Vol. 19, IV. København.
- 1936: Revision of the Greenland Rock Ptarmigans (Miscellaneous Notes on Greenland Ornithology III). — M. o. G. Vol. 118.
- SAMUELSSON, G. 1916: Studien über die Vegetation bei Finse in inneren Hardanger. — Nyt. Magaz. f. Naturv. Vol. 55. Kristiania 1917.
- SCHAANING, H. TH. L. 1933: A Contribution to the Bird Fauna of East-Greenland. — Skr. om Svalbard og Ishavet, Nr. 49. Oslo.
- SCHJØLER, E. LEHN, 1925: Om de i Grønland forekommende Racer af Fjeldrypen. — Dansk Ornitholog. Foren. Tidsskr. Vol. 19. København.
- 1926: Oversigt over Grønlands Fugle. — Danmarks Fugle II. København.
- SCHOLANDER, P. F. 1934: Vascular Plants from Northern Svalbard. — Skr. om Svalbard og Ishavet, Nr. 62. Oslo.
- SCORESBY, W. (jun.), 1823: Journal of a Voyage to the Northern Whale Fishery etc. Edinburgh 1823.
- SEEBOHM, H. 1884: A History of British Birds. Vol. 2. — London.
- SEIDENFADEN, G. 1931: Notes on a Map of East Greenland. — M. o. G. Vol. 87.
- 1933: The Vascular Plants of South-East Greenland 60°04' to 64°30' N. Lat. — M. o. G. Vol. 106.
- SELBY, P. J. 1833: Illustration of British Ornithology. Vol. I. London.
- SERNANDER, R. 1901: Den skandinaviska vegetationens spridningsbiologi. — Uppsala.
- SPÄRCK, R. 1933: Contributions to the Animal Ecology of the Franz Joseph Fjord and adjacent East Greenland Waters I—II. — M. o. G. Vol. 100.
- STRÖMGREN, E. und STRÖMGREN, B. 1933: Lehrbuch der Astronomie. — Berlin.
- SUMMERHAYES, V. S. and ELTON, C. S. 1923: Contributions to the Ecology of Spitsbergen and Bear Island. — Journ. of Ecology. Vol. XI, Nr. 2. Cambridge.
- — 1928: Further Contributions to the Ecology of Spitsbergen. — Journ. of Ecology. Vol. XVI, Nr. 2. Cambridge.
- SVERDRUP, H. U. 1935: Übersicht über das Klima des Polarmeeres und des Kanadischen Archipels. — Handb. d. Klimatologie, herausgg. von W. Köppen und R. Geiger, Vol. II, Teil K. Berlin.
- SORENSEN, TH. 1933: The Vascular Plants of East-Greenland. — M. o. G. Vol. 101.
- 1935: Bodenformen und Pflanzendecke in Nordostgrønland. — M. o. G. Vol. 93.
- TEICHERT, C. 1933: Untersuchungen zum Bau des Kaledonischen Gebirges im Ostgrønland. — M. o. G. Vol. 95.
- THORSON, G. 1934: Contributions to the Animal Ecology of the Scoresby Sound

- Fjord Complex (East Greenland). Hydrography by H. Ussing. — M. o. G. Vol. 100.
- TOLMATSCHEW, A. 1932: Флора центральной части восточного таймыра. ч. I. (Flora of the Central Parts of Eastern Taimyr). — Труды полярной комиссии выпуск 8, издательство академии наук сср. — ленинград. 1932. Works from the Polar Committee, Vol. 8, edited by the Scient. Acad. of U. S. S. R. — Leningrad, 1932).
- TROLLE, ALF. 1934: Jørgen Bronlunds Dagbog i Tidsrummet fra 1. Maj—19. Oktober 1907. Den i Danmarkshavn i Foraaret 1908 foreløbigt udarbejdede Oversættelse. — Publikationer om Østgrønland udgivet af Kaptajn Alf Trolle og Hustrus Legat til Minde om Danmark-Ekspeditionen 1906—1908. Nr. 1. København.
- TSCHUDI, F. VON. 1875: Dyrelivet i Alperne. Efter Originalens niende Oplag af C. Fogh. — København.
- TUGARINOW, A. J. & TOLMATSCHEW, A. J.: Материалы для авифауны восточного таймыра. (Contributions to the Bird Fauna of Eastern Taimyr). — Труды полярной комиссии выпуск 16, издательство академии наук сср. — Ленинград. 1934. (Work from the Polar Committee, Vol. 16, edited by the Scient. Acad. of U. S. S. R. — Leningrad, 1934).
- Universitetets Skriv- og Rejse-Kalender 1937. København.
- VANHÖFFEN, E. 1893: Bericht über botanische und zoologische Beobachtungen im Gebiet des Umanak-Fjords. — Verhandl. d. Ges. f. Erdkunde zu Berlin. Vol. XX, 1893. Berlin.
- WARMING, EUG. 1888: Om Grønlands Vegetation. — M. o. G. Vol. 12.
- WEGENER, A. 1912: Meteorologische Terminbeobachtungen am Danmarkshavn. — M. o. G. Vol. 42.
- WEGMANN, C. E. 1935: Eis- und Schneeformen in Nordostgrønland. — Der Naturforscher, 11. Jahrgang, März 1935. Berlin.
- WHITTARD, W. F. & PARKINSON, M. M. L. 1931: The Geological Work of the Cambridge Expedition to East-Greenland in 1929. — Quart. Journ. Geol. Soc. Vol. 87. London.
- WILLUMSEN, 1916: Coccidiose i den norske rypebestand. — N. J. F.
- WILSON, E. A. 1911: The Weight of Grouse. — Chapter VI, in: The Grouse in Health and in Disease. — Grouse Committee, London 1911.
- WILSON, E. A. & LESLIE, A. S. 1911: Food of the Red Grouse. Chapter IV in: The Grouse in Health and in Disease. — Grouse Committee, London 1911.
- WINGE, H. 1898: Grønlands Fugle. — M. o. G. Vol. 21.
- WITHERBY, H. F. 1920—24: A practical Handbook of British Birds. — London.
- WULFF, TH., cf. ELVIN, A.



MAP
of
EAST - GREENLAND
between
Keiser Franz Joseph Fjord
and
Sabine Isl

*The topography of this map is prepared
from the survey of the Geodetic Institute of
Denmark.*