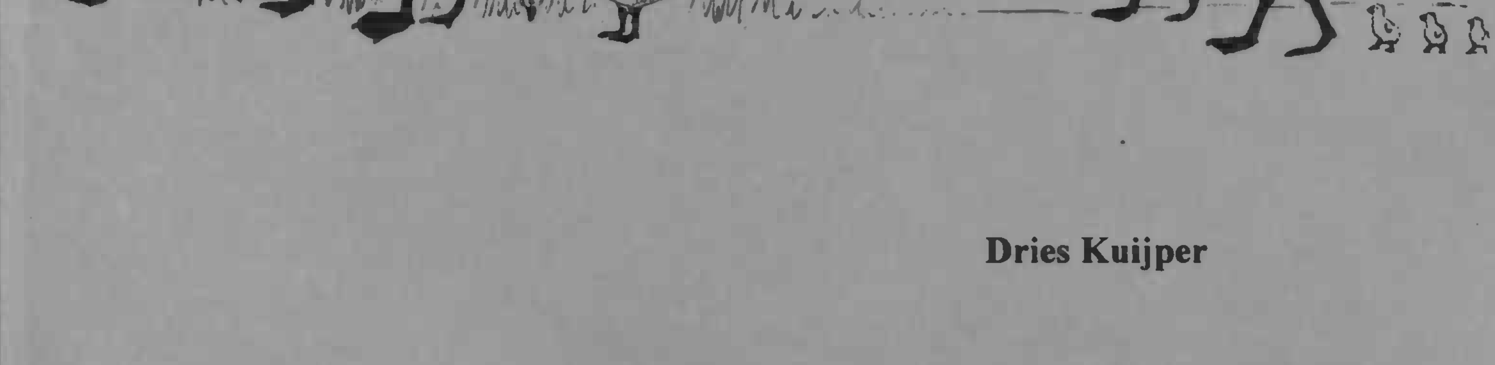
Diet and dispersal of Barnacle geese on Spitsbergen: the advantage of being first



Dries Kuijper

Diet and dispersal of Barnacle geese on Spitsbergen: the advantage of being first

M. Sc. study by Dries kuijper
Zoological la boratory,
University of Groningen

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Supervisor:
Dr. Maarten J. J. E. Loonen
Zoological Laboratory,
University of Groningen
P.O. 14, 9750 AA Haren
The Netherlands

Preface

I have been one of the lucky persons who was given the oppurtunity to do a research on Spitsbergen. This research was carried out in the summer (July-August) in 1997. It was a fantastic experience to live and work in such a high arctic environment. Walking for hours in the field without seeing a human being is something we are not used to in the crowded Netherlands.

Whithout the good company of Eric Munneke the whole stay wouldn't have been so pleasant. I learnt a lot about research in the arctic and to cooperate with other researchers from different countries.

Unfortunately our supervisor, Maarten Loonen, was not able to come to Spitsbergen himself (for the first time during this research), but we had good contact via e-mail and fax. Although sometimes technology left us. He was very busy to write his thesis at the same period, but was always there when we needed him.

The Sysselmannen på Svalbard kindly gave permission to work in the bird reserves and to ring geese. The Kingsbay Kull Compani A/S made accomodation in Ny Ålesund possible.

I like to thank Ingunn Tombre and Vergard Bunes for their help with our work, providing data lists about all the breeding pairs and for our introduction in the Ny Ålesund community. We are very grateful that we could use the computers and fax of the Norsk Polar Institutt. Nick Cox of the English station (Harland Husset) was a great help with catching geese and all kinds of practical things, during our stay. During the goose catches we had a good cooperation with Pat Butler and Tony Wokes from the University of Birmingham.

Abstract

Geese fly from their wintering grounds in the temperate climate zone to the arctic to breed. They are faced with a decrease in the quality of their food plants. Directly after snowmelt the protein content is highest and shows a sharp decline afterwards. The quantity of foodplants also shows a sharp decline during the short summer, due to grazing by geese and due to natural leaf death. In this research is illustrated that there are big changes in the diet of geese during the season, and there are big differences in the diet (and diet changes) between different areas. Geese show shifts in their habitat use during the season. There are marked changes between the dispersal of non breeders and families. Family birds disperse much more than non breeders. The family birds leave the heavily grazed areas and go to feed on areas with a higher biomass of graminoids. In this way their diet can contain more of the preferred graminoids. They first start to feed on save places close to water near the village and later move towards the fast tundra area. Early and late hatched families show the same distribution pattern during the season. The difference is that the early families are always the first ones to arrive in a certain area. So the early families have an advantage in the availability of food they encounter, and are able to have a higher proportion of preferred food plants in their diet.

Contents

1 Introduction

1.1 Objectives

Barnacle geese have to cope with several hardships during their annual cycle.
From their wintering grounds in the temperate climate zone they migrate for thousands of kilometers to their breeding places in the high arctic. At their arrival, the landscape is still covered by snow and ice and there is hardly any food. The birds have to rely on their protein and lipid reserves which they stored on their wintering grounds (Raveling 1979). Whenever spring thaw is late, much energy is lost for maintenance and not much is left for laying eggs. There is a negative relation between the start of spring thaw and the number of eggs produced (Davies & Cook 1983, Ely & Raveling 1984). When a goose arrives too early on the breeding grounds, it wasts too much energy and its breeding success will decline. Why do geese arrive so early? Their must be a strong selection pressure on early arrival, that counterbalances a selection on arriving later in the season (Sedinger & Flint 1991).

There is an effect of hatch date on the growth of goslings. Goslings that hatch early in the season grow faster. This has been illustrated in the Black Brant (Sedinger & Flint 1991), Lesser Snow goose (Cooch et al. 1991) and Barnacle goose (Loonen & van Duijn 1997). Individuals that grow slowly do not fully compensate later, and thus become smaller adults (Cooch et al.1991, Larson & Forslund 1991, Sedinger et al. 1995, Loonen et al 1997b) . The decline in growth during the season has been attributed to a seasonal decline in quality (Sedinger & Raveling 1986, Manseau & Gauthier 1993) and a decline in the quantity (Sedinger & Raveling 1986, Cooch et al. 1991) of the preferred food plants.There is a peak in the nitrogen content of the grass after snowmelt (Sedinger & Flint 1991, Lindholm et al. 1994). After this peak the N-content declines very rapidly. The level of nitrogen is strongly correlated with the protein level in plants. Protein is a very important part of the diet, especially in growing animals. Geese are very inefficient digesters and digest only approximately 40% of their food. Goslings wich have a shorter digestive tract are even less efficient in the digestion of their food (Sedinger & Flint 1991, Gadallah & Jefferies 1995). High quality food, especially in the first period of their lives is very important (Lindholm et al. 1994).

However next to this decline in the quality of foodplants there is a decline in the biomass of the preferred foodplants due to the effects of overgrazing by geese as is illustrated in Sedinger & Raveling (1986) in Canada goose and Sedinger & Flint (1991) in Black brant. This leads to changes in the habitat in the course of the season, and must result in changes in the diet.

In this study the decline in plant production and food availability due to grazing and natural mortality of plants is studied (Eric Munneke 1998) in relation to dispersion of geese and the consequences this has for their diet (this report). It is illustrated that the best growing conditions are early in the season. The food availability declines during the season due to grazing by geese and due to natural leafdeath of grasses (Eric Munneke 1998). In this report is illustrated that the Barnacle geese show a shift in the use of different habitats during the season. The diet shows considerable differences between places and changes during the season from high quality towards lower quality food plants .

1.2 Population

The Kongsfjord Barnacle goose population has only recently been established. The first record of a breeding Barnacle goose is from 1980 (Loonen et al.1997b). Since this first breeding pair the population has increased rapidly, to 326 nests in 1997 (I. Tombre pers. comm.). The Kongsfjorden goose population comprised 196 adults in 1990. From 1991 to 1992 the population almost doubled in size, but in the period 1993-1995 the population hardly grew anymore. After these years the population increased slowly (Loonen et al.1997b). The present population size is estimated at 600-700 adult individuals. During a census of the total fjord in 1997 in the last week of June we counted 682 adults.

1.3 General biology of Spitsbergen Barnacle geese

The Barnacle geese arrive the end of May, early June on the breeding grounds, at that time the tundra and thus their food is covered with snow usually until June (Tombre et al. 1996). The geese rely heavily on their body reserves. A good condition at the beginning of the breeding season is thus very important. The geese breed on small islands a few kilometers from shore. They start incubating around the beginning of June. The clutch usually consists of 3-5 eggs. Only the female incubates the eggs, the male guards her. Goslings hatch after 25 days of incubation usually in the first half of July. After hatching the parents take their offspring to the mainland to feed. Families, especially with young goslings, stay in close proximity of lakes which they use as a save place to prevent fox predation (Prop et al. 1984). In this period the gosling and the adults are unable to fly. The adults moult all their wingfeathers at this time of year. So both juveniles and adults are being restricted in their ability to disperse over the area. At the end of the very short arctic season, in September, the Barnacles migrate to their wintering quarters on the Solway Firth (Carlaeverock, in the south west of Scotland) where they arrive in the middle of October. At the end of april they start migrating north again, to the spring staging area at the Helgeland Islands. Here they gain weight for their 1500km flight to Spitsbergen (Black et al.1989), and make reserves for another breeding season.

1.4 Study site

This study was conducted on the Barnacle goose population of the Kongsfjord, a bay on the westcoast of Spitsbergen (78˚55'N 11˚ 56'E), see plate 1.
In the Kongsfjord there is a number of small islands, the main breeding sites of the geese. The most important breeding islands are Storholmen with 278 nests and Prins Heinrichøya with 78 nests (I. Tombre 1997, pers. comm.). Because in some years there are Artic foxes (*Alopex lagopus*) present hardly any geese breed on the mainland. In 1997, a year without foxes, there where 5 nests in and near the village (pers. obs.). When the eggs hatch the families swim towards the mainland, and start feeding in the "save" village, Ny Ålesund. The village is a very important feeding place. Here the presence of possible predators is the lowest. Especially the goslings are predated by the Artic fox (*Alopex lagopus*), Glacous gull (*Larus hyperboreus*), Great Skua (*Stercorarius skua*) and the Arctic Skua (*Stercorarius parasiticus*). The Arctic fox is the only predator which is able to catch an adult goose in our study area (the Snowy Owl is also a predator on the breeding grounds in Taymir of the Siberian Barnacle goos population).

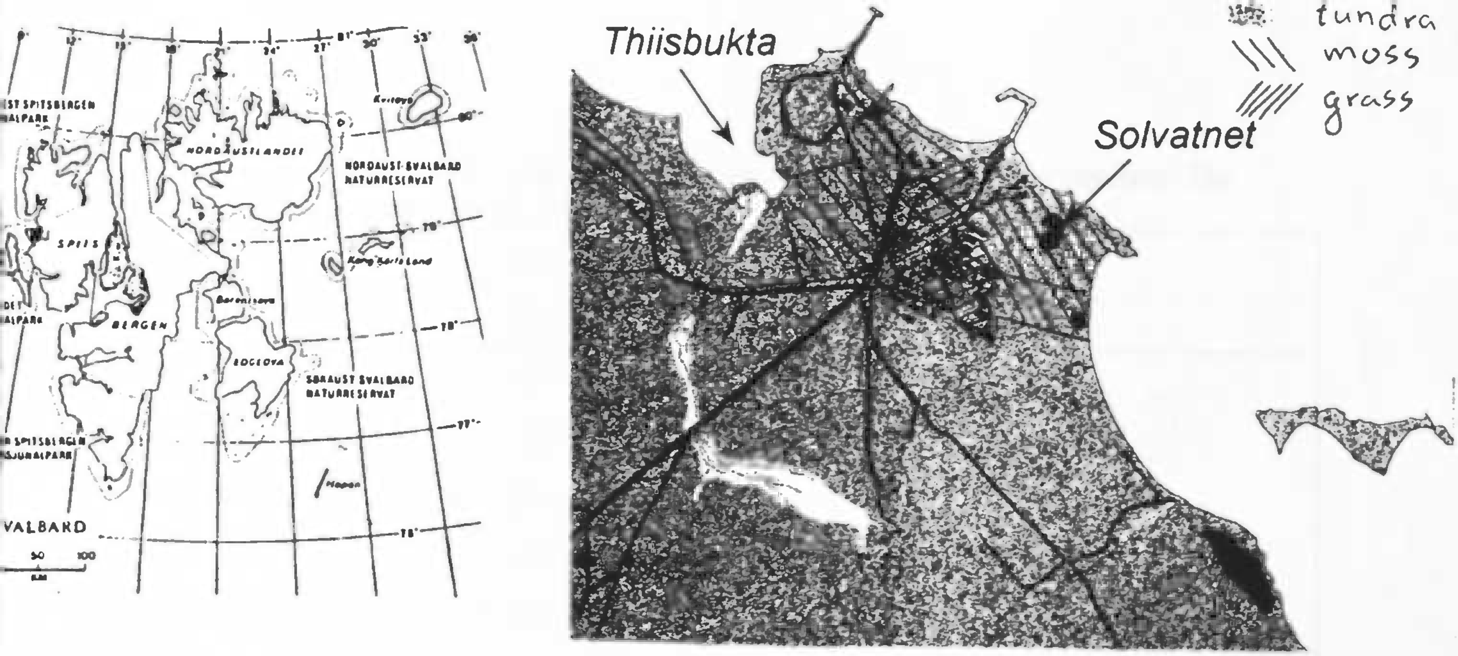

Plate 1: research area around the village Ny Ålesund. The moss, grass and tundra areas are indicated

The total research area is very divers and we distinguish three types ofhabitats that the geese use for feeding:

1) **The moss areas**. This type consists of very wet and swampy areas. Because of the permafrost the water can't percolate in the soil. The vegetation consists of a thick moss layer of more than 10 centimeter with usually a dead moss peat in the lower waterlogged part of the layer. Shoots of gras protrude through the moss layer. *Poa artctica* is the dominant grass species here. There are very little other species, some *Saxifraga oppositifolia* and *Salix polaris.* These moss areas are situated around lakes and in bays close to the shore (Solvatnet and Thiisbukta, see map). The moss areas have been the major areas for brood rearing and wing moult.

table 1a: synoptic table of the vegetation in two ***moss areas*** *(Solvatnet Bar and Thiisbukta midoost). DOM is dead organic matter. The vegetation relevees were done on 20/8/97. The mean coverage is the mean of five relevees, the frequency of occurrance is the percentage of the relevees in which the plant species occurred.*

species	**mean coverage ± S.E. (frequency of occurrance)**	
moss spec.	81.5 ± 6.5 (100)	**bare soil**
Poa arctica	0.6 ± 0.2 (60)	0 (100)
Saxifraga cespitosa	0.2 ± 0.1 (20)	**DOM**
Salix polaris	0.2 ± 0.1 (20)	18.4 ± 6.5 (90)
Saxifraga oppositifolia	0.1 ± 0.1 (10)	
Oxyria digyna	0.1 ± 0.1 (10)	

table 1b: synoptic table of the vegetation in two ***grass areas*** *(Olie and Dorpsplein). The vegetation relevees were done on 20/8 and 24/8/97.*

species	meancoverage ± S.E. (frequency)	
moss spec.	85 ± 7.7 (100)	**bare soil**
Deschampsia alpina	2.8 ± 0.9 (80)	7.2 ± 5.6 (40)
Poa arctica	0.4 ± 0.2 (40)	**DOM**
Salix polaris	0.3 ± 0.2 (30)	4.1 ± 1.4 (100)
Polygenum viviparum	0.1 ± 0.1 (10)	
Saxifraga oppositifolia	0.1 ± 0.1 (10)	

3) **The tundra areas.** The rest of the research area is called tundra area. Here, there is much a much more varied vegetation. Big parts of the tundra are very rocky places with a sparse vegetation with a lot of bare soil. The vegetated areas are again dominated by mosses. The most common monocotyledons are *Carex sp.* and *Deschampsia alpina* on the highest and driest sites and also *Poa arctica* on small wet places.

table 1c: synoptic table of the vegetation in one ***tundra area*** *(Voshoek). The vegetation relevees were done on 20/8/97.*

species	mean coverage (frequency)	
moss spec.	58 ± 11.4 (100)	**bare soil**
Salix polaris	4 ± 1.4 (100)	27 ± 11.4 (100)
Saxifraga oppositifolia	1 (100)	**DOM**
Carex spec.	1 ± 0.3 (80)	5 ± 1.2 (100)
Saxifraga cespitosa	0.6 ± 0.2 (60)	
Saxifraga hieracifolia	0.1 ± 0.1 (20)	

The geese feed in the village between the houses. Due to a long history of low disturbance the geese are somewhat used to the presence of humans. Especially at night when most people are sleeping the geese visit the village in the mid summer sun.

2 Method

2.1 Goose counts

Every day all the geese in and round the village where counted. The village was divided in different counting areas. The number of adults and the number of families were noted in all areas. Colour rings of the adults were read if possible. The number of geese near Solvatnet (an important feeding area) was counted twice a day. Every third day adults and families were counted in the total research area (from the village 4 kilometers to the east and to the west). Again as many as possible colourrings were read.
Ingunn Tombre provided data on all breeding pairs on the islands Storholmen and Prins Heinrichsøya with their clutchsize and hatchdate. This list has been used to look at the habitat selection of families with different hatch dates.

2.2 Grazing pressure

Five areas near the village were selected to study the grazing of geese in more detail. These areas consisted of two moss areas (Solvatnet west and Thiisbukta midoost see map of counting areas in Appendix), two grass areas (Olie and Dorpsplein) and one tundra area (Voshoek). On these areas biomassa samples were collected throughout the season and on Olie, Solvatnet and Dorpsplein the leaf-elongation of grasses were measured and the effects of grazing on shootgrowth were studied (Eric Munneke 1998).
To get an impression when these areas were visited by geese and how intensively they were grazed, the percentage of grazed grass shoots has been determined. A pane (20x20cm) was thrown out at random and of 50 grass leaves within this pane was counted how many had been grazed. Per area the pane was thrown out 6 times. This was done with a 2 week interval during the research period.

2.3 Diet analysis

On the 5 areas mentioned above, droppings have been collected. This was done with a 2 week interval. Per area 5 droppings on 5 different sites were collected. Only fresh droppings have been selected. Fresh droppings have a darker colour with a white part and are softer. Old droppings become much more pale and dry. These droppings have been oven-dried, 2 days at 60 °C. In the lab these droppings have been used for a diet analysis. Geese have very inefficient digestion. Approximately 40% of the food they eat is being digested. For this reason recognizable plantfragments can be found in the goose droppings. By looking at the shape of the cells, the stomata (if they are present), the cellwall structure and the way cells are arranged, plantfragments can be determined (see Appendix). There is looked at cuticula cells wich can not be digested by a herbivore (Wesselo 1984). Plant parts consisting of one or two cells cannot be determined and were not used in the analysis. The specific features of the plant species had to be learned from a microscopial reference collection. In one oculair of a stereo-microscope a grid was fitted to determine the area of the plant fragments. A method of analysing has been used as described in de Jong et al. (1995) and de Jong (1997).
In short the method is as follows:

1) Water was added to the dried dropping samples and they were grinded and mixed in a kitchen blender. In this way you get a more honogenous mixture with fine particles.

2) The mixture was washed and sieved over a 0.1 micro sieve. The dirt and very fine particles (one and two cell fragments wich are not indentifiable) will then be washed away.

3) The droppings were then mixed in water.

4) Out of this mixture 10 subsamples were taken for microscopial analysis. Per sample was looked at 10 plantfragments. The species and the area of each fragment was determined. The area was expressed as a relative area, it was not the real area. Per sample 10x10 plant fragments were determined. The proportion of the total area between the different plantspecies is the proportion in which they occur in the diet. By looking at the area of each plant species, the different fragmentation size of species is taken into account. By simply counting fragments of different species an overestimation of species wich are very fragmentated could occur (Wesselo 1984).

2.4 Goose catches

At the end of July and the beginning of August several catches have been carried out. All the unringed individuals were ringed with a colourring and metal ring. The tarsus, ulna, head and the length of the ninth primary were measured. Each bird was sexed and weighted. These data are not presented in this report.

2.5 Hatch date manipulations

Twenty four breeding pairs of the total counted 182 nest were manipulated. Their eggs were taken away and given back 5 days later. Meanwhile the geese were breeding on wooden eggs. Among the non-manipulated geese the best quality geese are probably those who lay early. Comparing early and late hatching geese is tricky in this way, because they differ in more than just hatch date. Better quality geese are expected to be dominant over lower quality geese and have better access to the best feeding places. This is the reason why manipulations are necessarry.

3 Results

3.1 Habitat choice and dispersal

3.1.1 Goose densities in village

The number of non breeding adult geese and the number of families were counted in the village every day. In figure (1) this is illustrated for five areas in different habitats.

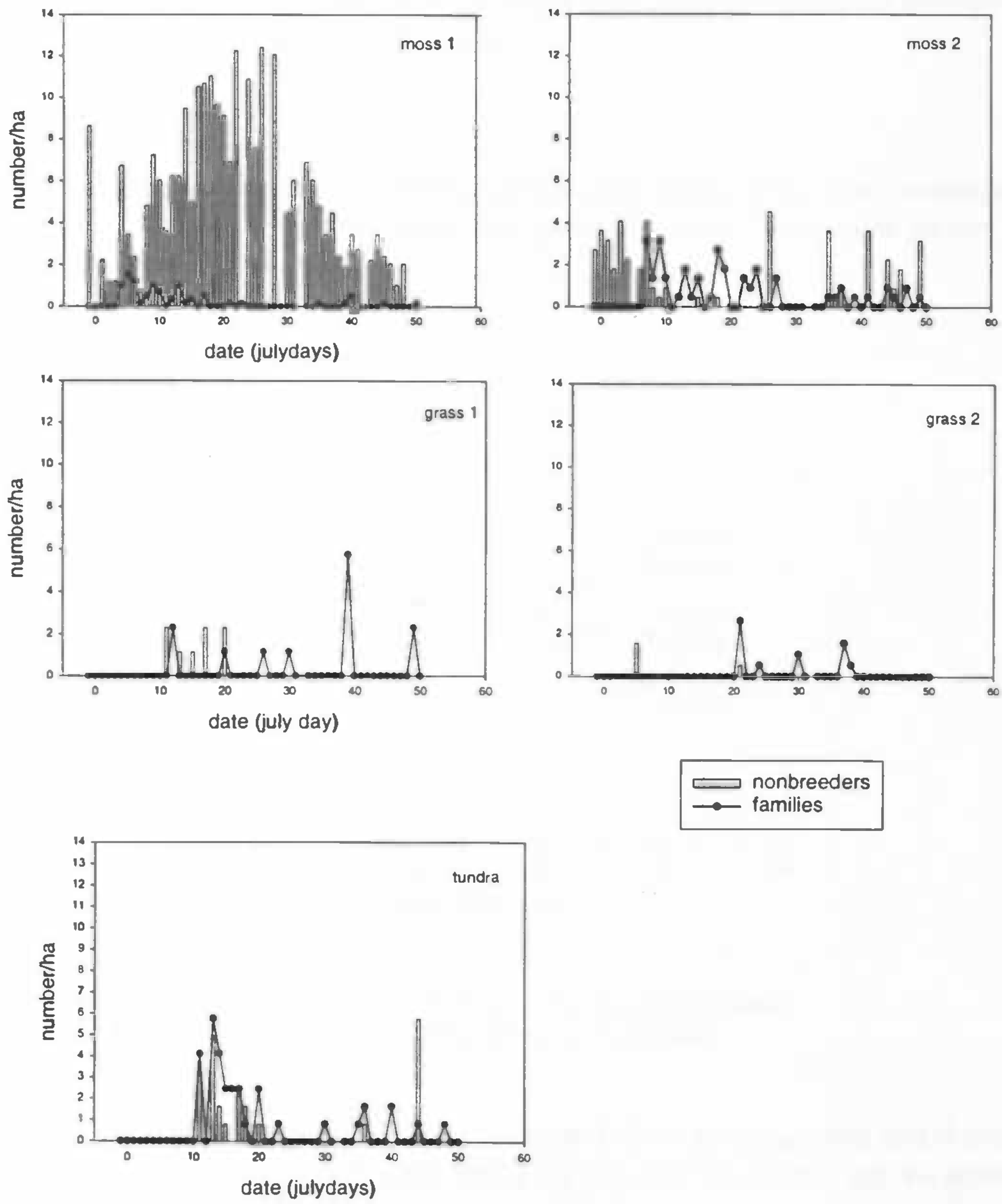

Figure (1): number of geese (families and non breeders seperately) per hectare counted on the daily census of five different areas in the village Ny Ålesund. The areas are named according to the habitat they occur in. Moss 1 is Solvanet, moss 2 thiisbukta midoost, grass1 olie, grass 2 dorp and tundra is voshoek.

In the same areas droppings for diet analysis were collected. Both the non breeders and families started feeding on the moss areas 1 and 2. On the moss area 1 the highest density of non breeders was observed during the season, they only visited the grass and tundra areas during a short period of the season. Later (between 11-7 and 12-7) the first families were seen on the grass area 1 and the tundra area. The families are much more dispersed over the areas than the non breeders. The grass area 2 is visited latest in the season. In this last area disturbance could have played an important role, because this area is situated between a lot of houses and if only one person would walk past, the geese already ran away. The goose catchings we carried out did not have a long lasting impact on the distribution of the geese. We did a catch on 26-7-97 on moss area 1. The next day no geese were counted in this area, but the second day the geese were back. On moss area 2 (the catch was on 29-7-97) it took five days for the geese to return to this area.

3.1.2 Grazed shoots

In the 5 areas the percentage of grazed shoots was determined. This is an alternative way to look when different areas are being visited by geese. In figure (2) the same pattern of grazing can be seen.

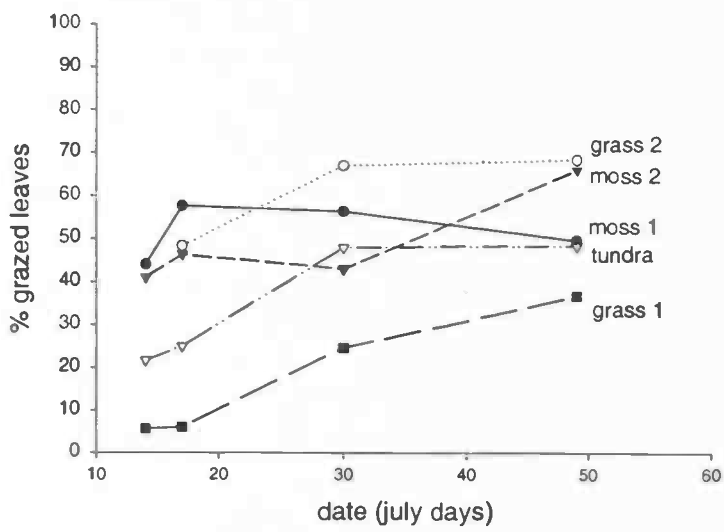

Figure (2): The percentage of grazed leaves of 50 grass leaves plotted against the date, for five different areas in the village of Ny Ålesund.

Moss area1 and 2 are the first areas that were grazed. Later the gras areas and the tundra area are grazed. The moss areas and the gras area 2 are the most intensively grazed areas over the season. Between 40 and 70% of the leaves are grazed.

3.1.3 Distribution on a larger scale

In figure (3) the distribution of non breeders and families over different habitats is illustrated. All the counting areas have been divided in three different groups according to their habitat. Because there is much fluctuation between days, the average counted numbers per three days is calculated.

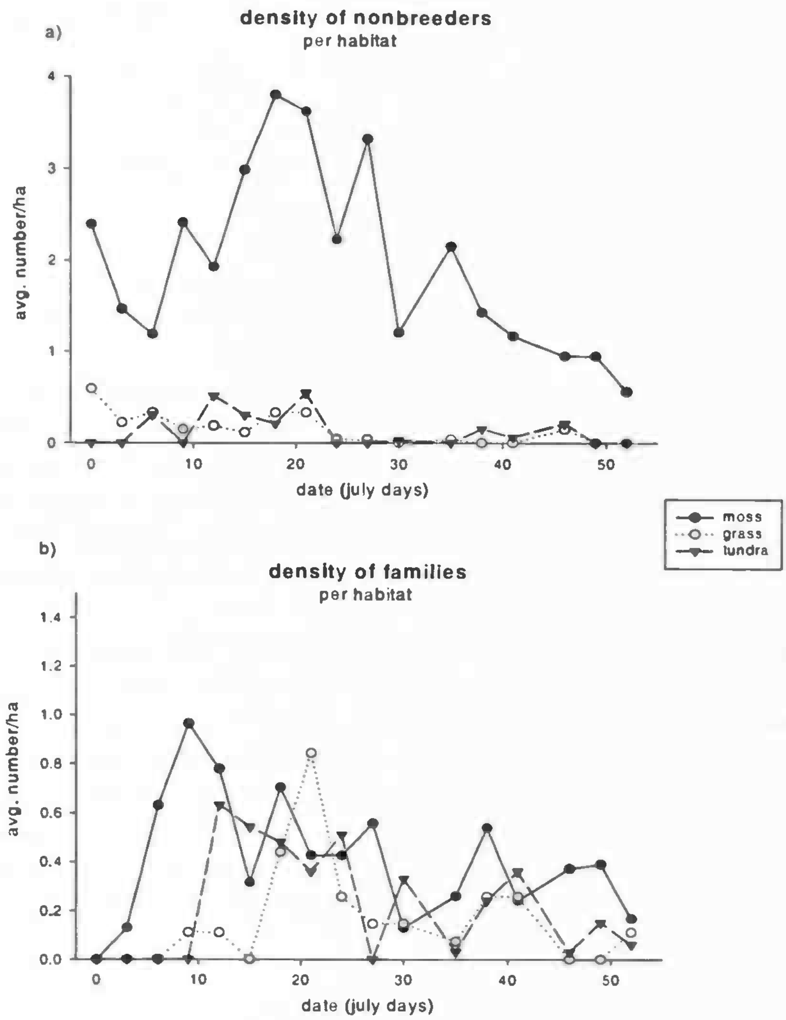

Figure (3): the average number of a) non breeders and b) families, per three day interval, per hectare on moss grass and tundra areas.

The *non breeders* are found with the highest density on the moss habitat, and there they occur in the highest density during the season. The grass and moss areas are less important.

The *families* show a different pattern. They first graze on the moss areas and then shift to the tundra and later to the grass areas. The moss area is again the most intensively used habitat during the season but the tundra and grass areas are used relativly much more by families than non breeders.

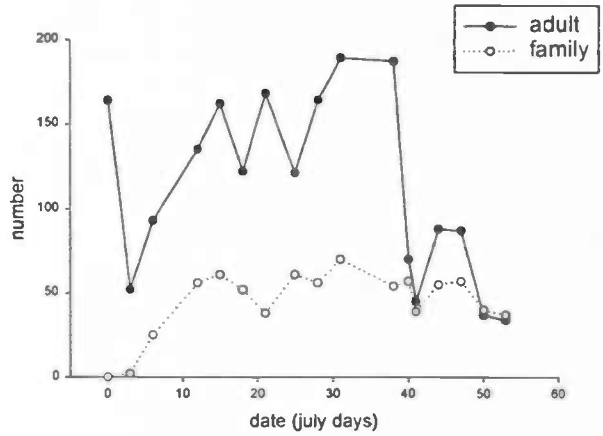

Figure (4): the number of adults and families counted during census of the total research area.

The total number of counted adults in the research area reaches a peak in the middle of the season and declines towards the end. The total number of counted families stays approximately the same during the season. As predation of adults hardly occurs and mortality predominantly occurs in goslings, this means that the nonbreeding adults are leaving the research area. The families are not leaving. Because nonbreeders can fly much earlier (their moult is completed earlier) they can disperse earlier in the season.

In figure (5) is illustrated that the percentage of families outside the village on the tundra increases during the season. They leave the village and move more and more to the far tundra to feed. The non breeders don't show a shift towards the tundra outside the village the percentages stay rather constant during the season. Because percentages deviate from a normal distribution the data were first arcsinus transformed. Then a lineair regression was performed on these transformed data. There was no significant increase in the percentage of adults counted far (R^2=0.00089, p=0.9096), but a significant increase in the percentage of families outside the village (R^2=0.44, p=0.005).

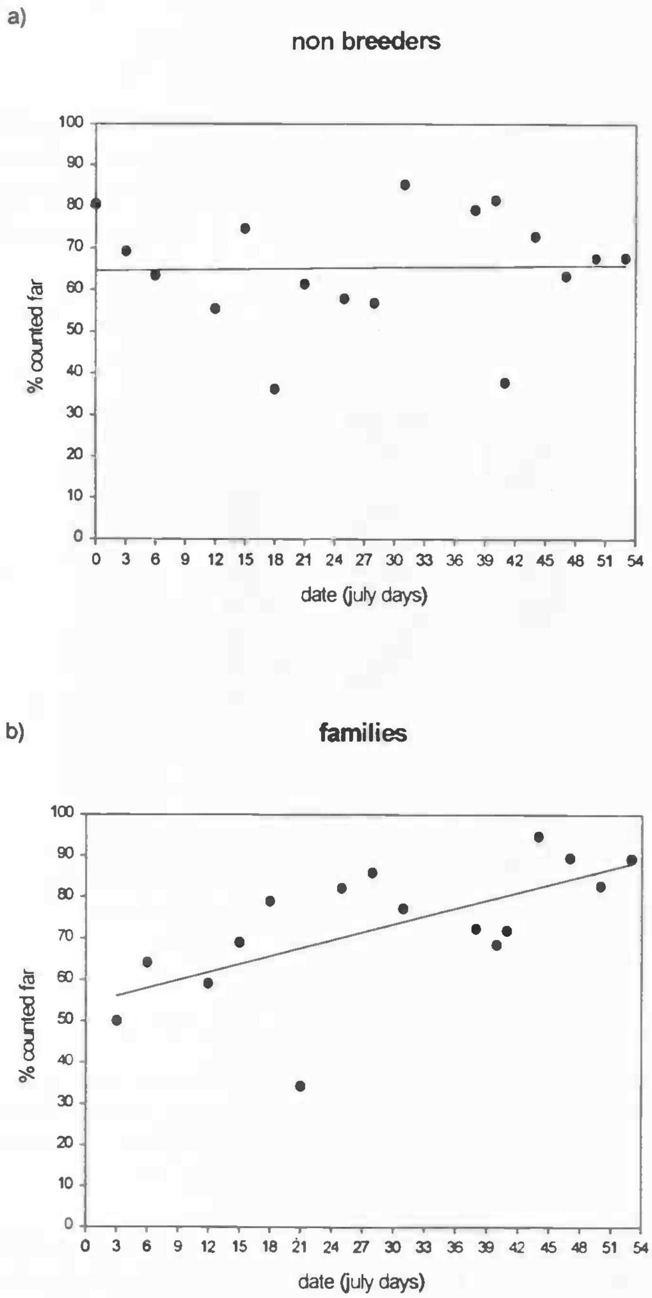

Figure (5): the number of nonbreeders (a) and families (b) counted on the tundra (outside the village) expressed as a percentage of the numbers counted in the village Ny Ålesund. The lines represent the regression of the untransformed data. The linear regression was performed on the arcsinus transformed data. For the non breeders(a): $R^2=0.00089$, $y=0.015x^2+53.82$, $p=0.910$, for the families (b): $R^2=0.44$, $y=0.43x^2+46.78$, $p=0.005$.

3.2 Diet analysis

3.2.1 Overall diet

In figure (6) the average diet over the research period is shown for four different areas. The plant species wich were found in the faeces have been grouped into four different categories. There are big differences in the proportion of monocotyls and moss species in the diet between the different areas.

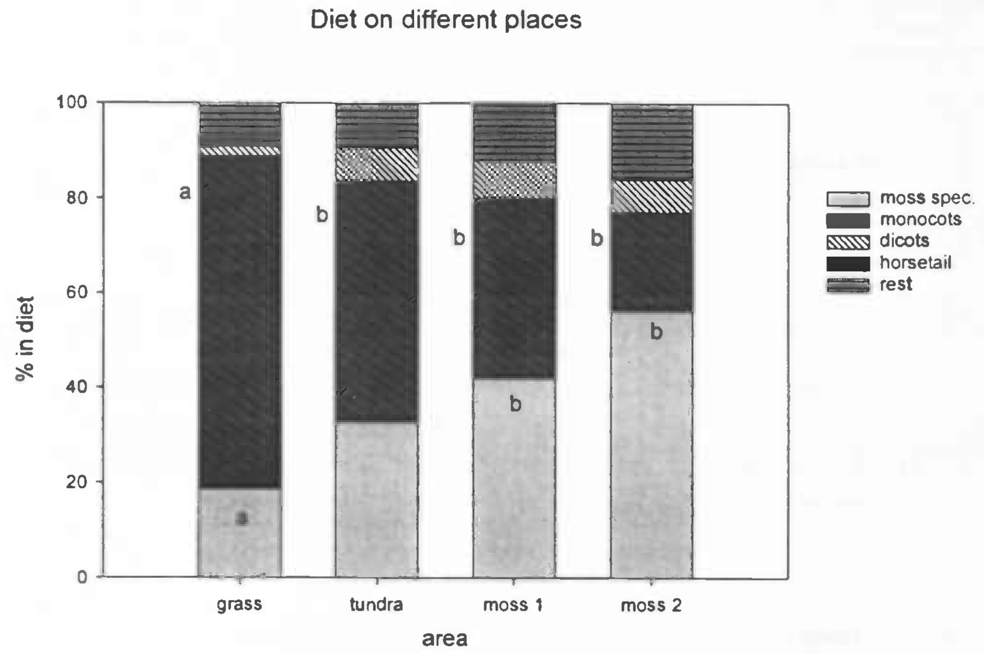

Figure (6): the overal diet in the research period in four different areas. The plant species are grouped in five categories (moss species, monocots, dicots, horsetail and a rest group of undetermined plant species). The arcsinus transformed data were tested with a Tukey test, significant differences are indicated with a 'a' and 'b' ($p<0.05$).

The data were arcsinus transformed and then tested with a multiple comparison (Tukey test). All groups (except horsetail in areas grass, tundra and moss1) were normally distributed tested with the Kolmogorov-Smirnov.

In the two moss areas the main part of the diet consists of moss species (42-56%) and monocotyls (37.9 and 20.8%). On the grass area a significant higher proportion of the diet consists of monocotyls (70.1%) and a significant lower proportion consists of moss species (18.9%). The tundra area is intermediate in its values for the two diet items. There are no significant differences in the percentage horsetail, rest or dicots eaten.

3.2.2 Changes in diet over the season

Figure (7) shows the diet in the course of the season. On the two moss areas major changes are taking place. The proportion of monocotyls in the diet declines and the proportion of moss species increases tremendously. At the end of the season the diet consists predominantly of moss species (65-86% of the diet), grass species are hardly found in the diet at the end of the season (3-14%).

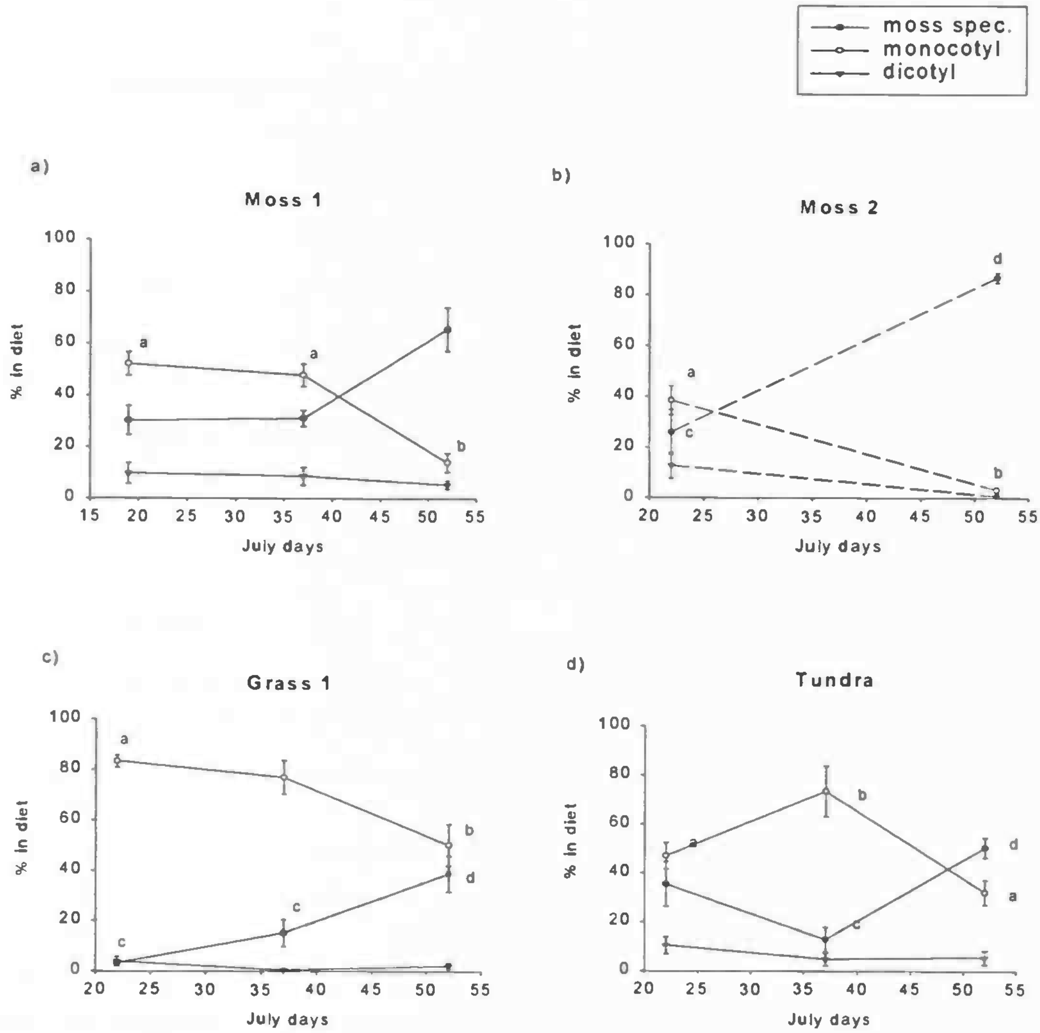

Figure (7): the proportion of three different plant categories (moss species, monocots and dicots) during the season. The figures a), b), c) en d) represent differnt areas in and round the village were droppings were collected. The small a, b, c and d's in the figures indicate significant differences, tested with Tukey multiple comparison (p<0.05).

On the grass area there is also a decrease in the proportion of monocotyls and an increase in the proportion of moss species in the diet. However these changes are not as drastic as on the moss areas. In the beginning and in the end of the season the main part of the diet consists of monocotyls (83% in the beginning and 50% at the end). In the beginning hardly any mosses are being eaten (3%, versus more than 25% on moss areas).

The tundra doesn't show such a clear picture. The percentage of monocotyls in the diet in the beginning is lower than expected (47%). However towards the end of the season the proportion of dicotyls in the diet decreases sharply (to 32%) and the proportion of moss species increases (to 50%). The first droppings were collected here on 22 July. This was just after a period that this area was visited by a high number of adult geese and families. This could be the reason of the low proportion of monocotyls in the beginning of the season, the biomass of monocotyls could thus be low after this peak in goose visits.

3.2.3 Species composition in the diet

In total 18 different plant species were found in the faeces. The most important grass species are in table (2)

table (2)a: the most important grass species with the range in which they occur in the diet.

species	proportion in diet (range)
Poa arctica	0-42%
Deschampsia alpina	0-31%
Dupontia fisherii	0-9%

table (2)b: the most important moss species with the range in which they occur in the diet

species	proportion in diet (range)
Caliergon sp.	2-73%
Oncophorus wahlenbergii	0-5%
Aulacomnium turgidum	0-2.5%

table (2)c: *most important dicotyls with the range in which they occur in the diet*

species	proportion in diet (range)
Salix polaris	0-5%
Saxifraga cespitosa	0-6%
Saxifraga oppositifolia	0-3%
Ranunculus pygmaeus	0-2.5%
Silene uralensis	0-4%

Only species that can occur with a percentage of more than 2% are mentioned in the tabels 2 a-c.
If we compare the composition of species in the diet between the different areas over the total research period, we find that there are hardly any differences in the proportion in which they occur in the diet. The geese select for the same species.
In the beginning of the season the most important food plant is *Poa arctica* except in the tundra where it is *Carex sp.* and in grass area 1 where it is *Deschampsia alpina. Carex* is found in considerable amount in the diet only on one day and on one place (13% of the diet).

On all the other days it hardly occurs in the diet. It looks like the grass species *Deschampsia alpina* and especially *Poa arctica* are the most favourite food plants. The geese start feeding on it and when the biomass of grass is high enough they remain feeding on it during the season. On all four areas, except for grass area 2, there is a sharp decline in the living biomass of grass during the season (see report of Eric Munneke). In all areas (except grass area 2) there is a change from a diet dominated by grass species towards a diet dominated by moss species. In grass area 2 the diet remains dominated by *Poa* and *Deschampsia* during the season.

3.3 Hatch date effects

3.3.1 Dispersion of families with different hatchdate

Figure (8) shows the frequency distribution of the hatchdates of all the recorded breeding pairs (data collected by Ingunn Tombre).

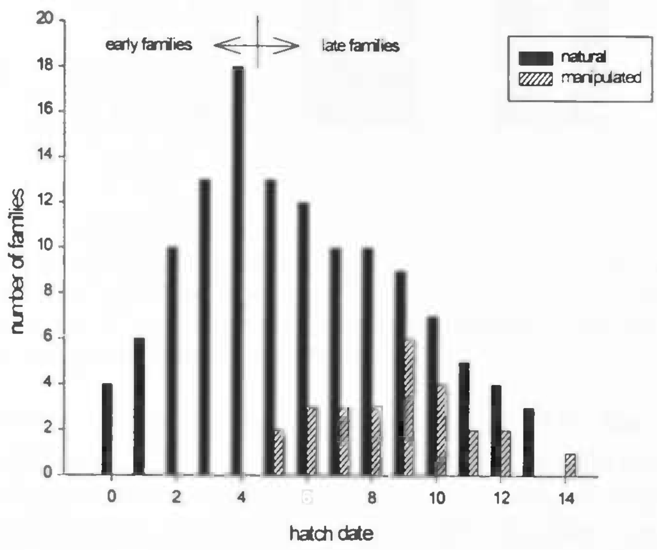

Figure (8): frequency distribution of hatch dates of families.

The pairs are divided in natural (not manipulated) and manipulated pairs. The manipulated pairs had a prolonged hatchdate of 5 days, by taking their eggs away and giving them back after 5 days (meanwhile breeding on artificial eggs). The peak of hatch date is at 4-7-97. For further analysis the pairs were divided in three groups

1) **early families**: with a hatch date on or before 4-7-97
2) **natural late families**: the not manipulated pairs with a hatch date on or later than 5-7-97
3) **manipulated families**: with a prolonged hatch date

First is looked at the distribution of these different groups over the three habitats (moss, grass, tundra) in the period 15-7 to 10-8 (figure 9). In this period all the eggs have hatched (the last at 14-7) and thus all the families of the three groups can be present. Before 10-8 no family with goslings has completed the moult yet so they are not able to fly. They are restricted in there dispersal in this way, especially in areas close to the village. When families are able to fly they can disperse much further. The average number of observationdays per family are compared. Sightings of ringed families with known hatchdates are used. Observations are grouped according to the habitat. Only one sighting per family per day is used. When there were multiple sightings on one day, the sighting of the most distant place is used, because it is likely that a lot of families return to the village regularily to drink or to sleep. The village is a relatively save place. Families that are far from the village have chosen to feed there.

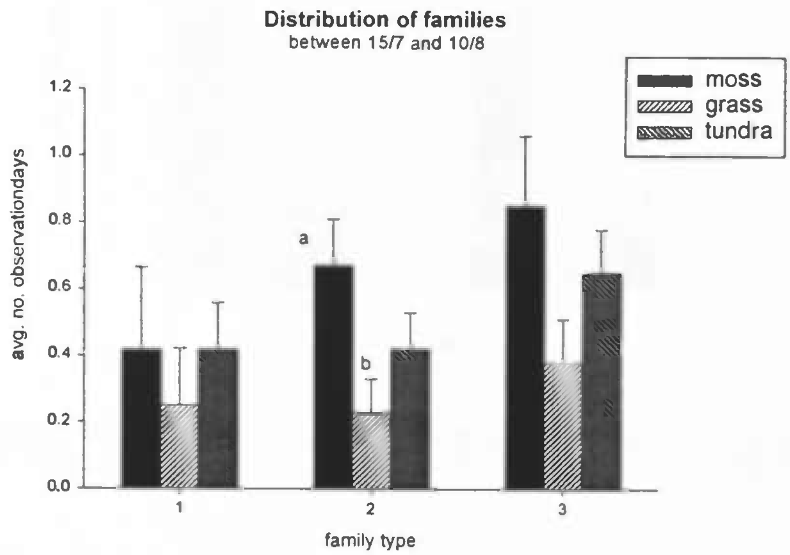

Figure (9): distribution of family types over the three habitats (moss, grass, tundra areas) in the period 1-7/14-7. In this period all the goslings have hatched and all parents are flightless. Family types are: 1) manipulated, 2) natural early, 3) natural late families. Significant differences are indicated with a and b, tested with Tukey (p<0.05)

Most families were seen on the moss areas and followed by the tundra. First a two-factor ANOVA was performed. No significant effect of family type (p=0.17) or habitat (p=0.076) was found, and no interaction (0.961). After this a multiple comparison within each family type between the habitats was conducted. The early families were seen significantly more on moss areas then on gras areas. Futher there are no consistent differences between the three types of families.

When you split this period up in two parts; 15/7-28/7 and 29/7-10/8 there are still hardly any differences between the family types. The picture looks almost the same as figure (10). Except that in the second period the tundra areas are used more, but no significant differences were found.
When you look at the distribution early in the season (figure (10)), before 14-7, the early and late families have the same pattern. There was a significant effect of habitat (p<0.00) and no effect of family type (p=0.746) and no interaction (p=0.872), tested with a two-factor ANOVA. The early and the late families are both significantly more observed on moss areas than on grass and tundra areas (Tukey multiple comparison, p<0.05). The manipulated families were not seen in this period. Not all the late families are present during this period. The last one has a hatch date on 14-7. However this doesn't influence much the total number of observationdays of families (early with 41 and late with 32 observationdays).

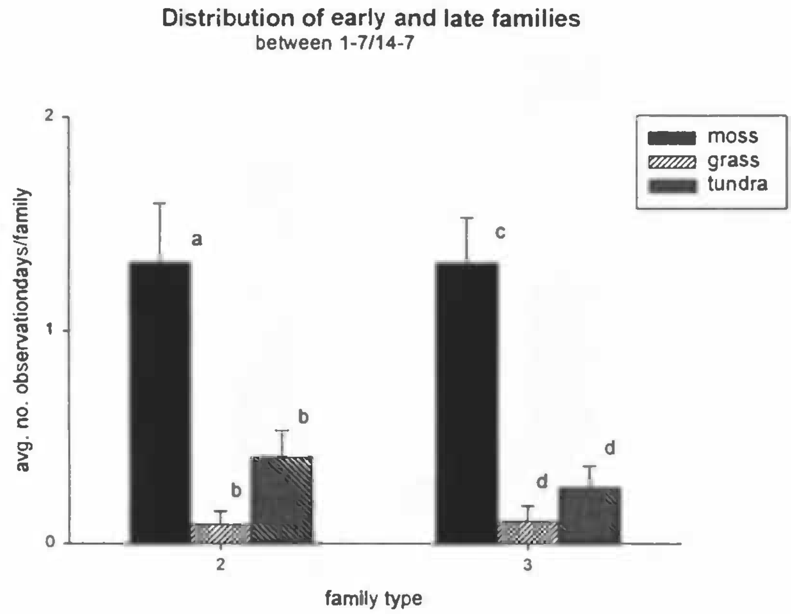

Figure (10): distribution of 2) natural early and 3) natural late families over moss, grass and tundra areas in he period 1-7/14-7. Significant differences are indicated with the small letters tested with Tukey multiple comparison.

In the end of the season, after 11-8, the distribution is totally different (figure 11). Again there was a significant effect of habitat ($p<0.00$) no effect of family type ($p=0.749$) and no interaction ($p=0.093$), tested with a two-factor ANOVA.The early and late families are found significantly more on the tundra areas (family type 3 only sign. between moss and tundra), tested with Tukey multiple comparison. The early families are almost totally on the tundra, however most of the goslings of the early families are able to fly in this period, most late families are still moulting. The late families however are more observed on the grass and moss areas.

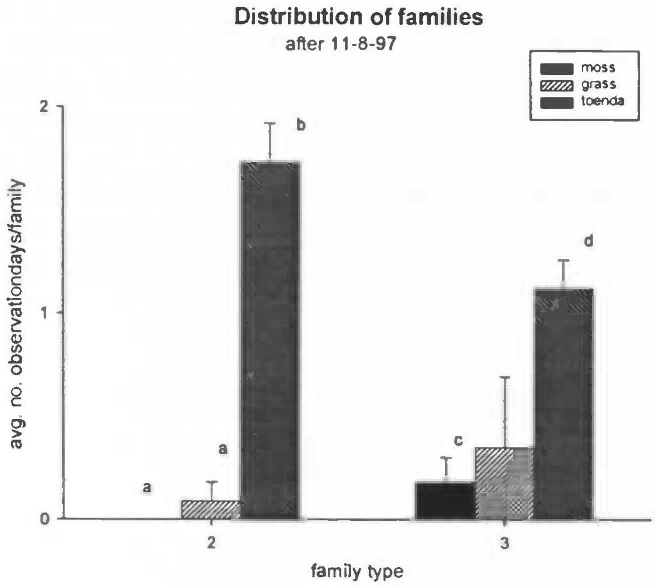

Figure (11): distribution of 2) natural early and 3) natural late families over moss, grass and tundra areas in the period 11-8 to 22-8. Significant differences are indicated with the small letters tested with Tukey multiple comparison.

So there is a temporal pattern of grazing. The families start on the moss areas and move to the tundra. It looks like there are no differences between the early and late hatched families. However the early families start to feed on the different habitats always as the first ones. The late families are delayed in their shift from one habitat to the other. The manipulated families most of the time arrive even later. So there is not an effect of parental quality on this distribution pattern.
This is illustrated in figure (12).

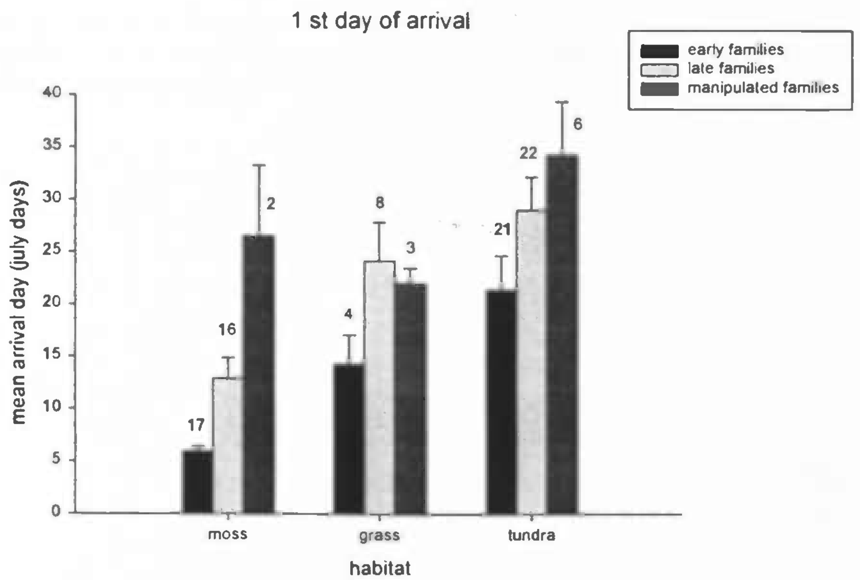

Figure (12): the mean date (±SE) of first arrival on each habitat, for the early, late and manipulated families. the numbers above the bars indicate the number of observations the average is based on.

In this way the youngest goslings are found on the moss areas and the older goslings on the tundra. In figure (13) this is illustrated.
The age of the goslings that visit a certain area is plotted for the three different habitats. The youngest goslings are indeed found on the moss and the goslings on grass and tundra areas are significantly older (Tukey multiple comparison, $p<0.05$) The goslings on the grass areas have an intermediate age.
The ages of goslings on the different habitats, splitted up for early and late families, show the same pattern. The youngest goslings are found on the moss areas and the oldest on the tundra for both the late hatched and the early hatched goslings.

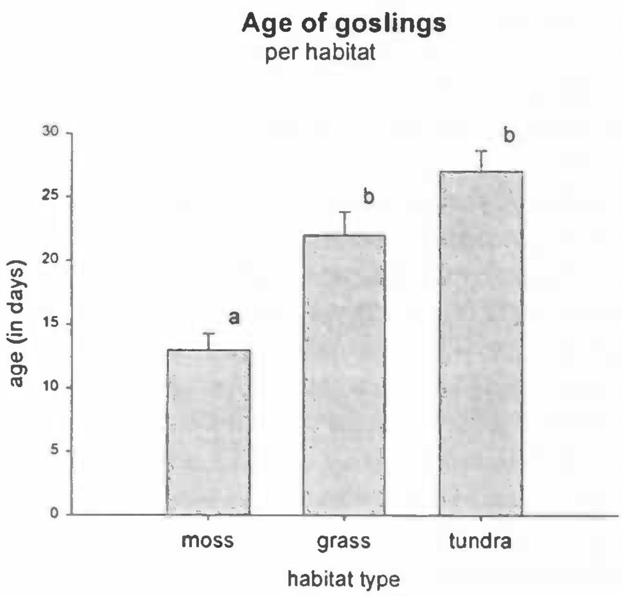

Figure (13): the average age of goslings on the three different habitats (moss, grass and tundra areas) Significant differences are indicated with a and b tested with Tukey multiple comparison (p<0.05).

4 Discussion

4.1 Habitat shift

The non breeders and the families show a different use of the defined habitats in the research area. The **adult non breeding** geese in our research area are found in the highest densities on the moss areas throughout the season. Early in the season the non breeders graze on the tundra and grass areas in the village. But at every time the density on the moss areas is much higher. The total number of counted non breeders declines during the season. Because the predation of adult geese is low in our study area (the arctic fox is the only predator that can take an adult goose, and they were not present in our study year), this means that they leave the study area. The non breeders and paired birds that nested but lost all their eggs in an early incubation phase, moult earlier than the breeders. The peaks of moult of the two categories of birds being separated by about 16 days (Loonen et al. 1997a). The non breeders start to moult in the beginning of July. Usually the birds leave the brood rearing areas after moult and go to areas with more food or with higher quality food, for example under seabirdcliffs (Loonen et al. 1997a). There they can acquire more easily reserves for their journey to the wintering grounds. So when the non breeders are in the research area they don't disperse much and stay on the moss habitat, and when they have finished their moult they leave the area.

The **families** are much more dispersed over the different habitats. The densities are approximately equal in moss, grass and tundra areas. They start feeding on moss and later visit the grass and tundra areas around the village. When you look on a larger scale, the families leave the areas around the village and go feeding more and more on the tundra far away from the village. The non breeding adults don't show this picture and don't leave the village to shift to the far tundra. There is a big impact of the polar fox (*Lagopus lagopus*) on this dispersal pattern. In our year of research (1997) there were no foxes in the area. The families were able to scattter over a much larger area than in years with foxes. In years with foxes in the area ('92-'95) the feeding area of the geese is much more restricted to save places in the proximity of water. In those years the majority of the families remain on the moss areas too. The food is much more restricted and less goslings are produced. The mean gosling weight in fox-years is 245 lighter than in years with no foxes present (Loonen et al. 1997b) The number of counted families remains roughly constant during the research period, so they remain in the area. Probably because the breeding geese moult later than the non breeders. They start to moult mid July and at the end of August most geese are able to fly (also the goslings), so they have not been able to leave the research area.

Graminoids are very attractive food plants, see later. Geese are very inefficient digesters and are known to select on high quality food (Owen, 1980).

Adult geese have a longer digestive tract than juveniles. A longer digestive tract results in a longer retention time of food and in this way in a more efficient digestion (Prop & Vulink, 1992). In Prop & Vulink (1992) is illustrated that adult geese increase the retention time two- to four-fold in the summer on the arctic breeding grounds with 24-hours of day light. In this way adult geese are able to feed on much lower quality food and they can stay on the moss habitat. Mosses are an important part of their diet. Unlike graminoids, mosses are available throughout the year and they are among the most common and widespread plants in the arctic (Rønning, 1996).

Goslings are in special need of high quality food . For their growth they need a diet with a high amount of proteins (Manseau & Gauthier 1993, Gadallah & Jefferies 1995a). Because they have a short digestive tract they are not able to digest their food very efficiently (Gadallah & Jefferies 1995a, Sedinger & Flint 1991). Graminoids are the most important foodplants for goslings (Gadallah & Jefferies 1995a, Laing & Ravelling 1993), so a high selection for these food items should be expected. This is the reason why the families are much more dispersed over the different habitats than the non breeders. In this way their diet can contain much more graminoids.

4.2 Diet

Graminoids are very attractive, high quality, food plants. They are characterized by high protein levels (20%), intermediate levels of cell content (50%) and are low in lignin (2-3%). Another group of important food plants are moss species. Mosses are generally low in protein (6%). The proportion of cell wall in mosses is high, partly due to a high lignine content (12%) very low in protein content and have a low digestibility (Prop & Vulink, 1992).
Grasses are the preferred food plants in our research area. In all the areas geese start to feed on graminoids, especially *Poa arctica* and *Deschampsia alpina* and early in the season also *Carex sp.* (on the tundra area) . And when the biomass of grass is high enough during the season they remain feeding on it. Although the cover of grasses in the vegetation relevees was very low (less than 3%), the proportion of grasses in the diet was relatively high. That means a strong selection of these food plants by the geese.
On the grass and tundra areas the biomass of grass is the highest. In the beginning of the season the biomass on the grass areas ranged between 1 and 10 g of grass per m^2, and on the tundra area the biomass was 0.3 g/m^2. The diet of the geese on these two areas also contained the highest proportion of graminoids (resp. 50 and 70%) and the lowest proportion of mosses (resp.18 and 33%). The biomass of grasses on the moss areas is much lower; in the beginning of the season it is only 0.15-0.25 g/m^2 . Due to the high grazing pressure of geese on the moss areas the grass biomass declines very rapidly during the season (Eric Munneke 1998). The average diet contains much more mosses (42-57%) and much less graminoids (21-37%). In all the areas where droppings were collected, the proportion of graminoids in the diet declines and the proportion of mosses increases during the season. However this change in diet is the most pronounced in the moss areas. At the end of the season more than 70% of the diet is composed of mosses and less than 10% of graminoids. Compared with the grass and tundra areas were the diet is composed of resp. 50% and 30% of gramonoids and resp. 30% and 50% of moss species.
Families with growing goslings (with a need of high quality food), should visit especially the areas where the biomass of graminoids is highest. However families start feeding on the moss areas
Why do all the families start on the moss areas which have the lowest biomass, where the grazing intensity is the highest and which are depleted the most? There can be two reasons for that:
a) Due to the high grazing intensity of non breeders and families there is very little grass but this is kept in the growing fase (Laing & Ravelling 1993, Gadallah & Jefferies 1995a). Young grass is known to be rich in protein and low in fiber content. So there is verry little food but of good quality, and maybe enough for growing goslings. Quality measurements were not made in our research area. In future research, special attention should be paid to quality differences of the same food plants in different habitats.
b) Especially young goslings are vulnerable to predation. In Bruinzeel (1994) is shown that there is a selection of predators on the youngest goslings. The moss areas are the safest places, they are close to the water where the families run to when there is a possible threat (for example human beings). In Stahl & Loonen 1997 is illustrated that in years with foxes present

in the area, the families stay more in the village close to open water. In this way their feeding range is restricted to a small area near the village. Hardly any geese forage on the "unsave" tundra in those fox-year. In our research year there were no foxes present. Artic Skuas and Glaucous gulls, also two important predators of goslings, are always present. They hardly occur in the village, and in this respect the village is still the savest place. It can also be a learning process, in which the geese have learned over years by experience that the areas outside the village are dangerous; so they avoid them even though in some years the most important predator is not present.

There is an interesting difference between the results from the diet analysis in this study and the results from two other studies that were performed in the same area. In the study of Prop & Vulink 1992, the proportion of graminoids found in the diet increased in the period June-August from 26 to 50%. The proportion of mosses in the diet decreased from 43% to 17% in the same period. It was argued that early in the season there are hardly any grasses present and the biomass of grasses increases in the season, resulting in more graminoids in the diet.

In the second study performed by Frans Greven in 1994, there also was an increase in the proportion of graminoids and a decrease in the proportion of mosses in the season. How is it possible that an opposit trend of both food categories is found in this study.

The droppings in these studies were collected in 1990 and 1992. At that time the population of Barnacle geese in the Kongsfjord area was at a much lower level. In 1990 the number was approximately 200 and in 1992 about 480 individuals (Loonen et al. 1997b). The present population level is between 700 and 800 individuals. The compitition for food is likely to be much higher nowadays than it was in '90-'92. Because of the higher goose grazing intensity the most attractive food plants (graminoids) are depleted to a higher extend much earlier in the season. The geese are forced to feed on alternative food plants, like mosses. Evidence for longterm changes due to an increasing goose population are well known from other studies (Gadallah & Jefferies 1995a and 1995b, Cooch et al. 1991). In this study is shown that there is a decline in the gosling weight the last decade. This is attributed to the decrease of preferred foodplants due to goose grazing and the use of alternative foodplants which have a lower nutrient content. A long-term decline in the gosling size has also been documented for this Barnacle goose population in the Kongsfjord (Loonen et al. 1997c)

In this study samples of droppings were collected on different habitats. If these droppings were produced by males, females or juveniles was not known. In the study of Frans Greve is shown that there are differences in the diet between adults and juveniles. Juveniles eat on average less mosses and far more horsetail (*Equisetum variegetum*). However there was only a big difference early in the season (3-12 July). There was a decreasing trend of dissimilarity between the diets of parents and juveniles. Especially early in the season directly after hatching the diets of adults and goslings differed and they resembled each other more and more as the season progressed. In the period when the diets differed between the adults and juveniles, no droppings were collected in this research. The first dropping samples were collected later when the diets of adults and juvenile resembled each other to a large extend. In the research of Greve no big differences between the adult diet and juvenile diet were found in this period. So the diets that were constructed from the dropping analysis are representative for both adults and juveniles.

The areas where the droppings were collected, were especially visited by families. Non breeders only visited these areas during a short period early in the season. Only moss area 1 was an exception, the density of non breeders was much higher than the density of families. This means that the majority of the droppings that are collected are from families. The diets that are found on the different areas are the diets of families except for moss area 1 which is the diet of non breeders. Non breeders could have a different diet because they don't need to have such a high quality diet as the growing goslings do.

4.3 Hatch date effects

There is hardly any difference in the habitat choice between early and late families. They show the same distribution pattern. They start grazing in the moss areas and later shift to the grass and tundra areas. The youngest goslings are therefore found on the moss areas and the oldest on the tundra. The early and late families shift in the same period from moss to the grass and tundra. In the end of the season the early and late hatched families are on the tundra area. However the late families are still more observed on the moss and grass habitat. The difference between the early and late families is in the first day that they visit each habitat. The early families visit each area as the first ones. The late families visit all the areas 7-9 days later. On the moss areas this is due to the later hatching dates of the later families, they are not all present at the same time. But the later arrival is consistent on the other habitats as wel. The manipulated families (delayed in hatch) show the same pattern as the late families, they always arrive later than the early families and most of the time later than the unmanipulated late families. It is plausible that the families that hatch early have parents with the best condition. High quality birds are likely to be dominant and should visit the best feeding areas as the first ones. The manipulated families have the same quality of parents as the early families. So a possible effect of parental quality can be ruled out.
The early families are always the first ones to arrive in a certain area, this means that the early hatching goslings visit the areas when there is a higher biomass of graminoids and the areas are less depleted. They graze away the food of the later arriving late families.
A seasonal decline in both the quantity and quality of he preferred foodplants of geese in high arctic environment has been illustrated in several studies (Gadalah & Jefferies 1995a and 1995b, Lindholm et al. 1994, Sedinger & Raveling 1986, Lepage 1997). In this study is also shown that the biomass declines rapidly due to grazing by geese and due to natural leaf death. Goslings are faced with a deteriorating food supply. Goslings that hatch early are exposed to a higher biomass of grasses (Munneke 1997), and the quality of their food will be better. There is a change in diets in the season. There is a shift in the diet from preferred to alternative, less attractive food plants (with a lower quality). These diet changes vary between different areas. The most intensively grazed areas show the most dramatic changes in the diet. Non breeding adults can probably handle with a deteriorating diet, for example by increasing there retention time of ingested food as is illustrated in Prop & Vulink 1992. Families with growing goslings need a high quality food and show a shift during the season towards areas which are less intensively grazed, and with a higher biomass of grasses. Families that hatch early are always the first ones that make the shift so they are always having the best feeding opportunities, both in respect to biomass and the occurrence of preferred food plants.

Why do the late families make the same shift to the areas already used by the early families. It would be more adaptive if they dispersed more and used different areas which have not been grazed so intensively. In Cooch et al. 1993 this behaviour is adressed to philopatry, the tendency of individuals to exhibit long-term use of certain areas. Philopatry might become maladaptive if these areas deteriorate. In Cooch et al. 1993 shown that families which use alternative brood rearing areas had goslings that were heavier and bigger. The most likely cause for this larger size was a greater per capita availability of preferred food plants. If goslings that are raised in non traditional feeding areas are bigger than the ones raised in the traditional areas in our research area is not known, and special attention should be paid for that. In our study area we hypothesize that the geese are forced in their shifts. The youngest goslings are found on the moss areas close to the water. As the goslings grow older they disperse more and more. Young goslings are especially vulnerable for predation. The moss areas are the most save places with respect to predators. Geese can run to open water which always present in these habitats. When the goslings grow older their need for food increases and they shift to other habitats. The goslings that hatch early are able to leave the save places much earlier in the season and can benefit from the higher biomass in the areas outside the intensively used village. There can also be a possible effect of the digestion efficiency on the habitat choice of families with differnt hatchdates. Young goslings have a short digestive tract and are inefficient digesters. In this way they can benefit from the possitive effects of grazing on the intensively grazed sites. Their inefficient digestion might make it impossible to graze on the areas outside the village where the quality of the food plants is likely to be different (there are no data about this and futher research is recommended). So the late hatched goslings are forced to stay in the save places in the village which have already been used by the early families and the non-breeders. Habitat selection can be restricted in this way by both predation and by the quality of the vegetation.

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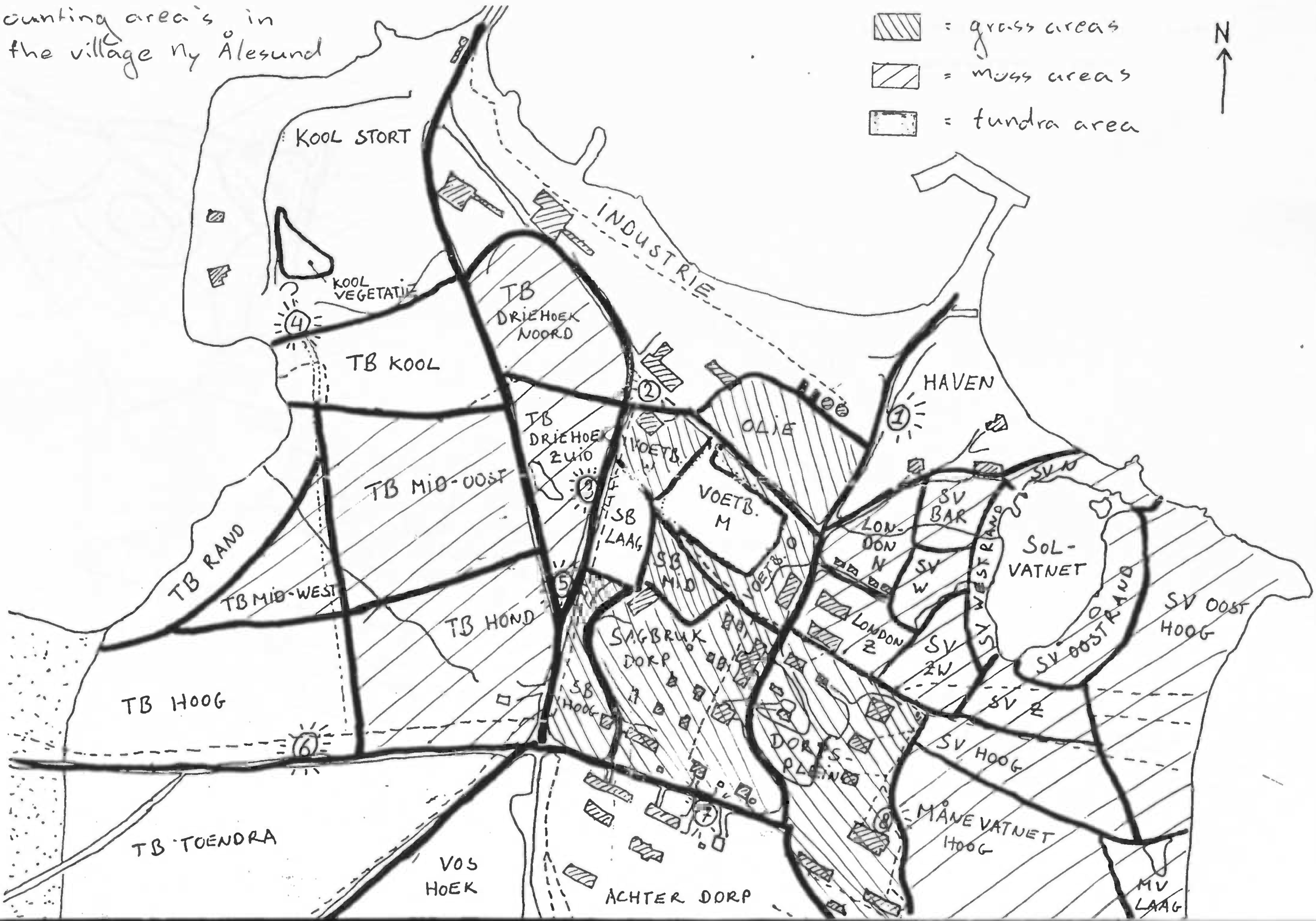
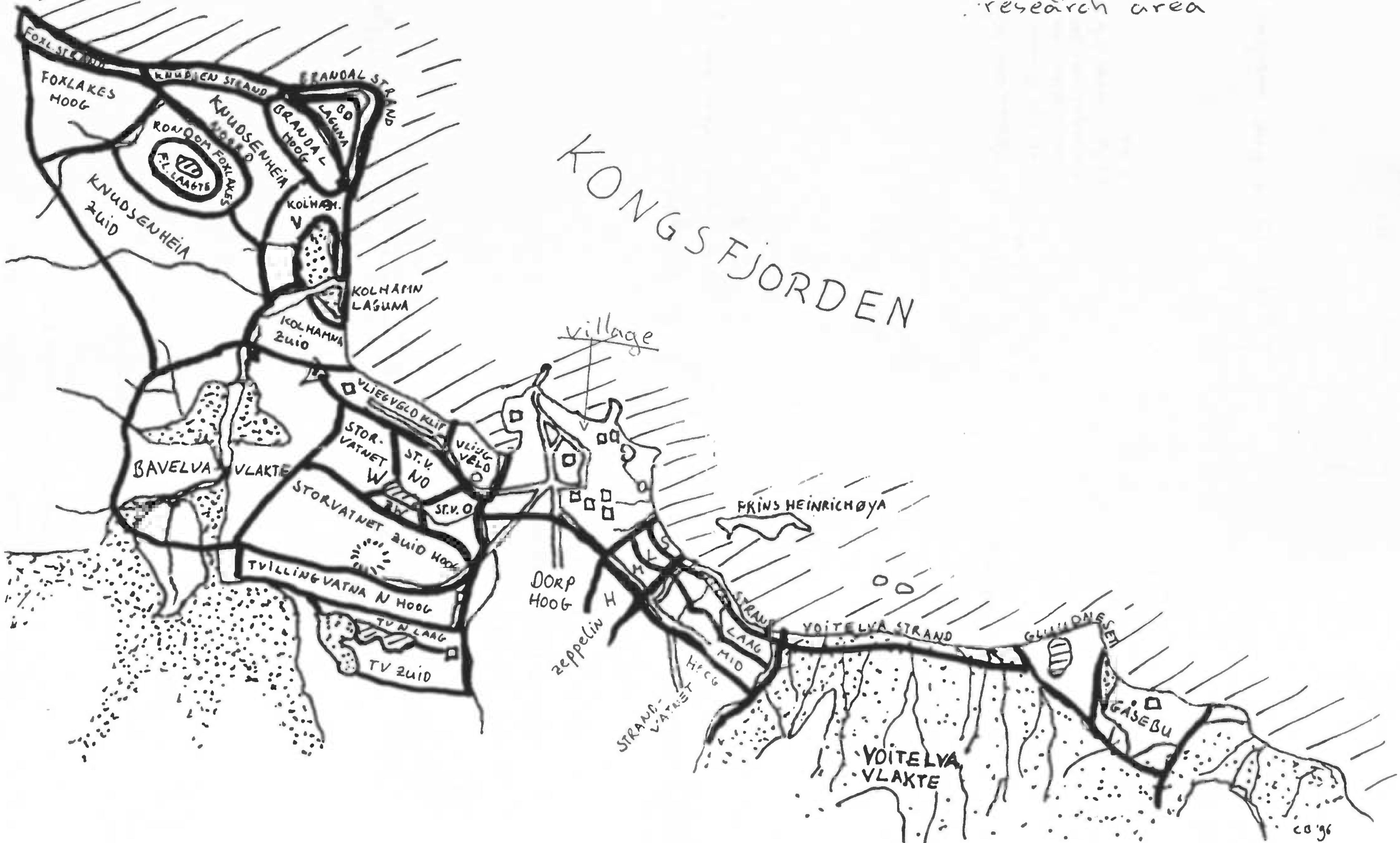
Appendix

Counting area's in the village Ny Ålesund

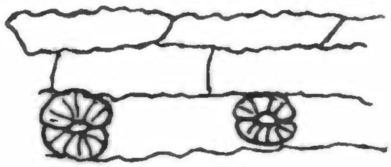




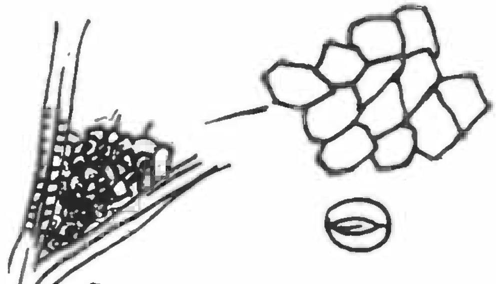
Counting areas of total research area

referentie - collectie
8 x 10 x

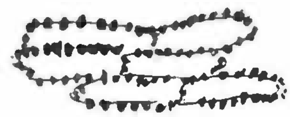
planten Spitsbergen
faeces - analyse



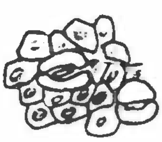
① Equisetum arvense



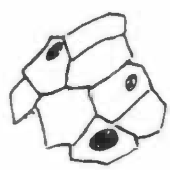
③ Salix polaris
dunne gladde celwand



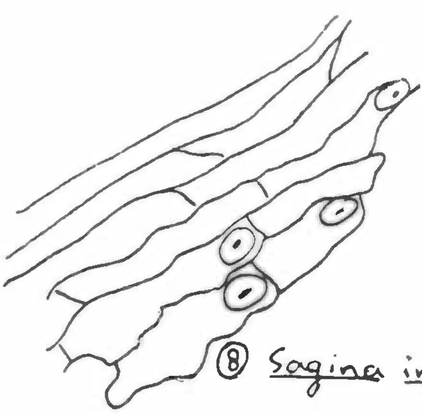
⑤ Oxyria digyna



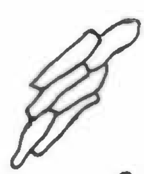
⑥ koenigia



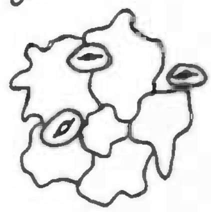
⑦ polygonum
cellen groter dan koenigia, hoekig



⑧ Sagina intermedia

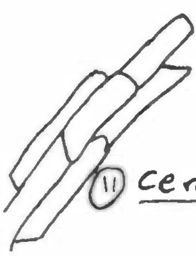


bloem

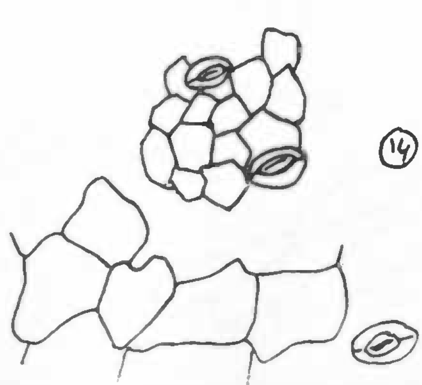


blad

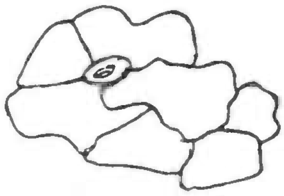
⑩ Minuartia biflora
lijkt op Ranunculus maar cellen veel onregelmatiger
cellen moeilijk te zien



⑪ Cerastium regelii

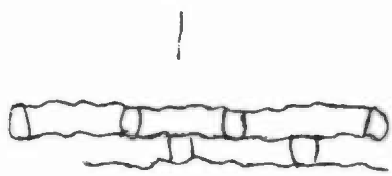


⑭ Silene uralensis

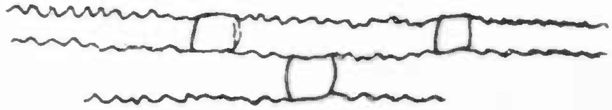


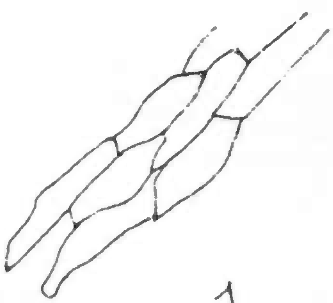
Ranunculus pygmaeus.

Festuca hyperborea

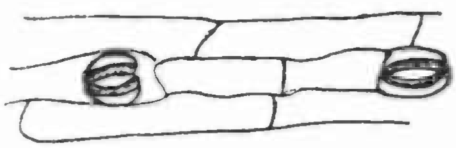


Festuca rubra (niet gevonden in preparaten)

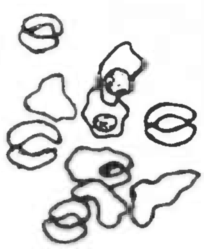




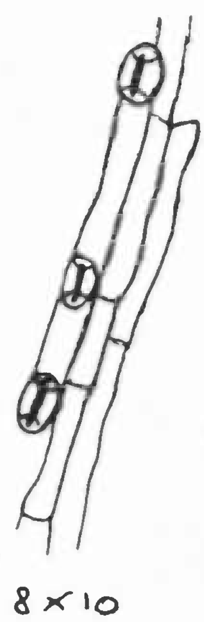
Juncus biglumis

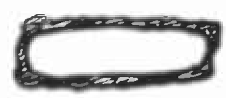


Juncus confusa



(24) S. oppositifolia (saxifraga)
celwanden vaak nauwelijks
te zien, "coloured patch" in cell

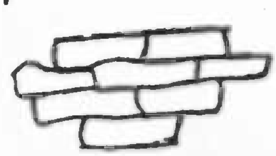


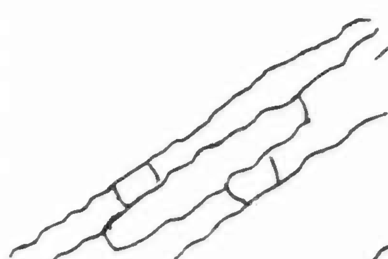


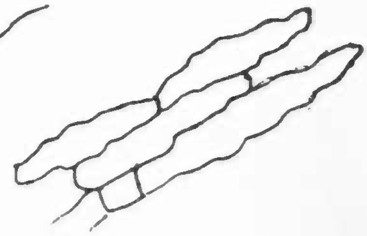
8x40

8 x 10

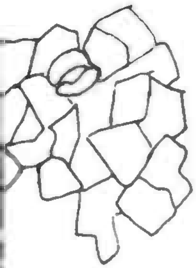
Poa arctica







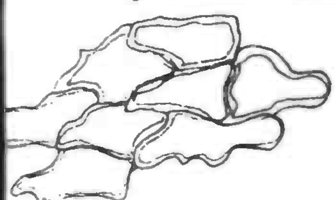
Salix polaris

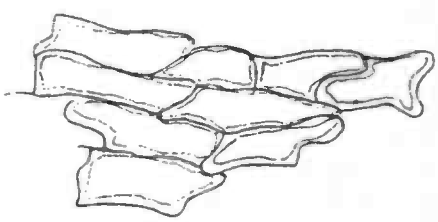


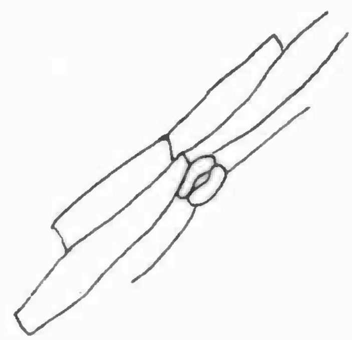
onregelmatige, hoekige cellen
niet in een patroon

axifraga cespitosa

dikke celwand
doorns aan bladrand

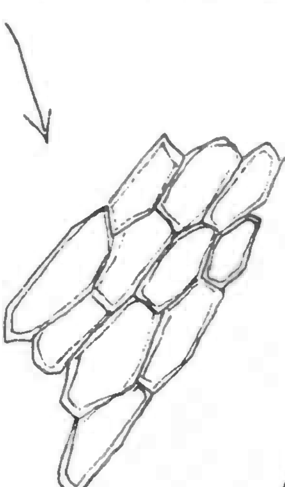




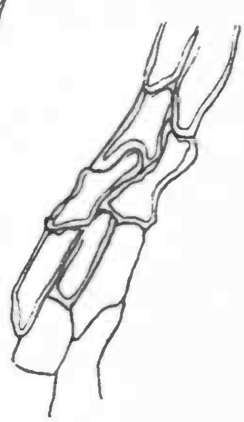


Alopecurus lijkt op Poa, andere
huidmondjes

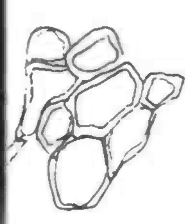
xifraga oppositifolia

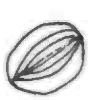


dikke celwanden, zoals cespitosa
doorns aan bladrand

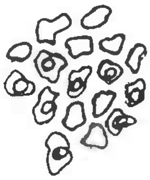


kompasplant

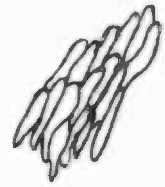




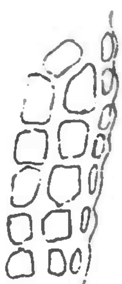
Mossen



Aulacomnium turgidum
8 x 10



Caliergon trifarium
8 x 10

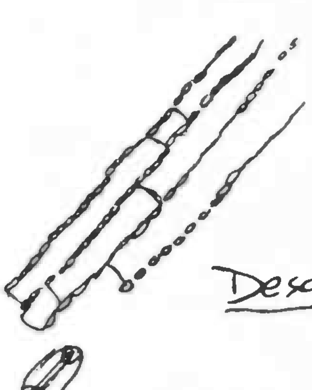


Oncophorus virens

Grassen eigen preparaten

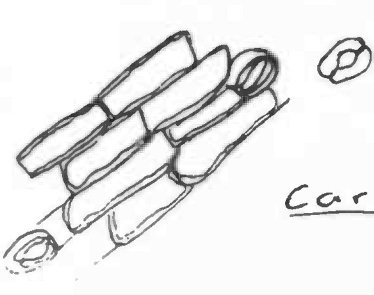
Poa arctica

meanderende celwanden,
normaal rechthoekig,
soms ook "opgeblazen"
lange cellen afgewisseld
met een korte cel.
stomata smal en dun,
(halter-stomata)



Deschampsia alpina

Lijkt soms sterk op Poa,
Heeft celwanden als losse
bakstenen, soms meanderen
cellen rechthoekig.
(halter-stomata)



Carex (voshoek)

Licht meanderende celwanden,
cellen niet zo langgerekt maar
zoals een baksteen, geen korte
cellen tussen de lange cellen,
stomata ronder, met "mondje"
(ronde stomata)