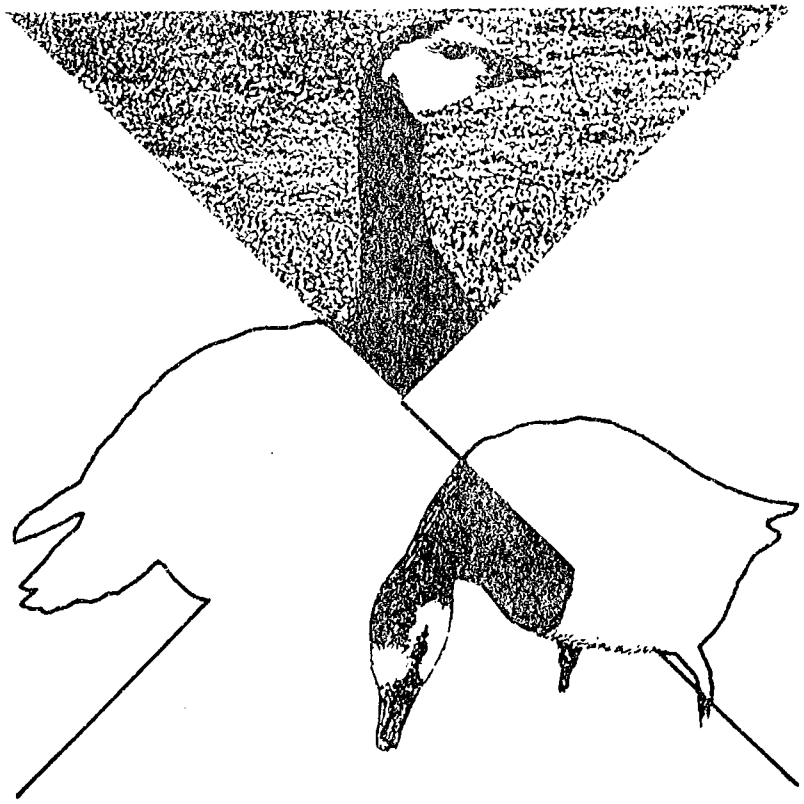
Frans Greven

The relation between diet and familysize of the Barnacle Goose during the summer on Spitsbergen

Branta leucopsis



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The relation between diet and familysize of the Barnacle Goose *Branta leucopsis* during the summer on Spitsbergen

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Student report
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Summary

During the summer of 1990 droppings of a population of Barnacle Goose *Branta leucopsis* were collected that could be attributed to observed geese.
The observations revealed whether droppings were produced by males, females and young and to which family they belonged. In the zoological laboratory in Haren of the Rijksuniversiteit Groningen faecal analyses of the droppings of 10 selected families were executed during 1993. The diet composition of the geese were deduced by means of the data thus deduced.
Subsequently several questions were examined with the aid of computational models of plant-ecology.
The questions whether there are differences between the composition of the diets of males,females and juveniles was confirmed. Juveniles eat far more horsetail than the adults do. This difference was so big that it was even significant for the period of 3 July up to 17 August whereas this difference was actually solely caused by the difference in the period of 3 July up to 12 July. Juveniles eat on the contrary less Mosses than the adults do.
The second question whether there is a trend in the course of time is also positively answered. The percentage of Salix decreases for adults and young,the percentage of Mosses decreases for adults and the percentage of Equisetum decreases for young. The percentages of Graminoids and the Rest group increases over the season for young,and the percentage of Graminoids for adults is highest at the end of July.
The third question was if there is a difference between the diets of large families and the diet of small families. The adults in small families eat far more Mosses than the adults in the larger families do. The juveniles of the large families eat much more of the rest group than the juveniles of the small families. Both differences seem to be of benefit for the geese.

-January 1994-

Acknowledgements

First of all I would like to thank Maarten Loonen,who,although always very busy,helped me to get insight in the problems of this project, infected me with enthousiasm,gave the project the right direction and always participated intensively. When he could not be there,he saw to it that somebody else could help. René van der Wal helped me in this stage to get insight in the possibilities of analyzing data.
During this project I got help from Johan van Rhijn of the Open Universiteit,who also introduced me at the Animal Ecology department of the Rijks Universiteit Groningen,where I worked on this project.
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Further I would like to thank Prof.Drent for the facility to find a subject to work on.

I would like to thank a friend,Cees van Gorkom for making the cover illustration.
My wife,Els helped me with the tedious job to put more than 12,000 data in a database computer program. She also helped me to look beyond the very crowded schedule of last year.

Introduction

In this study we examined the relation between the brood size and the diet composition of the Barnacle Goose *Branta leucopsis* during the summer on Spitsbergen.
Barnacle geese have a limited period to raise their young,because the arctic summer on Spitsbergen is very short(about six weeks). Besides that,the area in which they pass the summer is limited,firstly because the young can not fly before the end of the summer and secondly because the adults loose their ability to fly in the moulting period. Foraging has to be done walking and therefore takes place in a limited area(Prop et al.,1979). The vegetation that is present is heavily grazed. The individual capacities of the geese to obtain the best food differ. Individuals differ in intake rate and individuals falling below the median intake rate for a specific date invariably fail to complete incubation(Prop et al., 1984).
Further survival is related to the age of the goslings(and therefore hatch-date) and to the weight of the goslings. Only 20% of the young weighing under 600 g on 1 August arrived in Scotland,compared with more than 70% of those over 700 g (Owen & Black 1989).
Those females returning to Scotland with broods were heavier than those that had nested (brood patch present)but had no young in winter. Losses on autumn migration probably represent a substantial proportion of first-year mortality in those species that undertake long migrations without the opportunity of feeding in transit(Owen & Black 1989).
This is the case with the barnacle goose population that migrates between Spitsbergen in the summer and the Solway Firth in Scotland where they winter exclusively(fig.1). The distance between these two places is 3000 km and is covered non-stop in two days (Owen 1990).

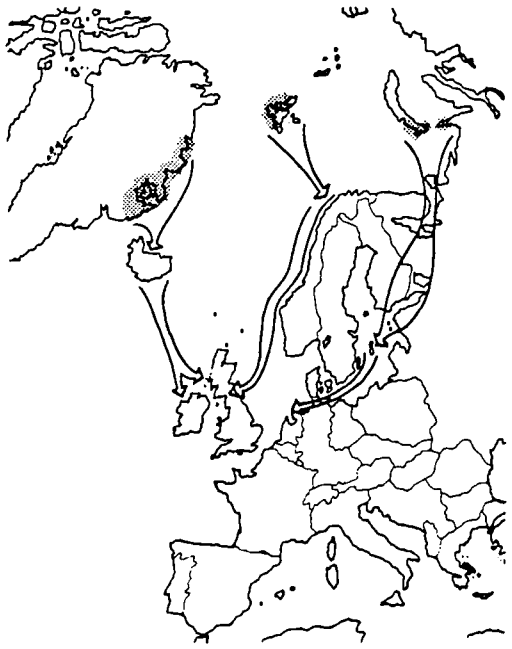


Figure 1:Map of the breeding areas,migration routes and wintering areas of the three populations.

Dominance in agonistic behaviour is positively correlated with the time spend in areas with the highest plant biomass. The dominance rank was predominantly determined by the familysize and to a lesser extent by the size and age of an individual.
The order is as follows:large families beat small families,small families beat paired adults,and paired adults beat single birds. Investment in aggressive behaviour is related to the amount of energetic pay-off (food and time saved) that could be won by a particular group(Black & Owen 1989).
In the study area of Ny Ålesund the geese differ in the use of plots. Plots were rated best,medium and marginal based on the familysize of the families visiting. The next analysis was based on families with an equal number of goslings minimizing the effect of familysize. By comparing usage of plots by families with three or four goslings which are complete when arriving in Scotland with families with three or four goslings which have at least lost one gosling it was found that the most successful families are seen more often in the plots most frequently visited by the largest families. Plots where the larger families are seen give better opportunities to the geese(Loonen & Drent unpublished).
Different types of areas have been distinguished. The best type consists of three areas:1.village centre/

weather station,2.triangular mossy area surrounded by roads near the harbour(Thiisbukta),3.village area around old sawmill(Sagbruk). The medium type consists of two areas:1.Thiisbukta,2.Storvatnet. The marginal type consists of three areas:1.Solvatnet,2.Maanevatnet,3.area around the tower of Amundsens Zeppelin.
When at least one goose of a brood was seen once in a certain area this was a score. So for the family in which all geese survived,the maximum score in the best areas is 8x3=24 and in the medium areas 8x2=16. In these cases the score was respectively 17 and 13 and the percentages respectively 70% and 81%. It is clear that the families in which all survive are seen more often in the better areas(table 1).

	All survive 8 broods	Partial loss 6 broods
A:Best(3)	17/24=70%	2/18=11%
B:Medium(2)	13/16=81%	3/12=25%
C:Marginal(3)	24/24=100%	18/18=100%

Table 1:The percentages of observations of geese in two categories (all broods consist of three or four goslings and category 1 has no losses when they arrive in the wintering grounds in Caerlaverock,Scotland and in category 2 at least one young did not arrive in the wintering grounds) that visit the different types of areas.

When the time spent in these areas is also taken into account it is clear that the families in which all juveniles survive are not only visiting more often the better places,but they are also staying there for a longer period (figure 2).

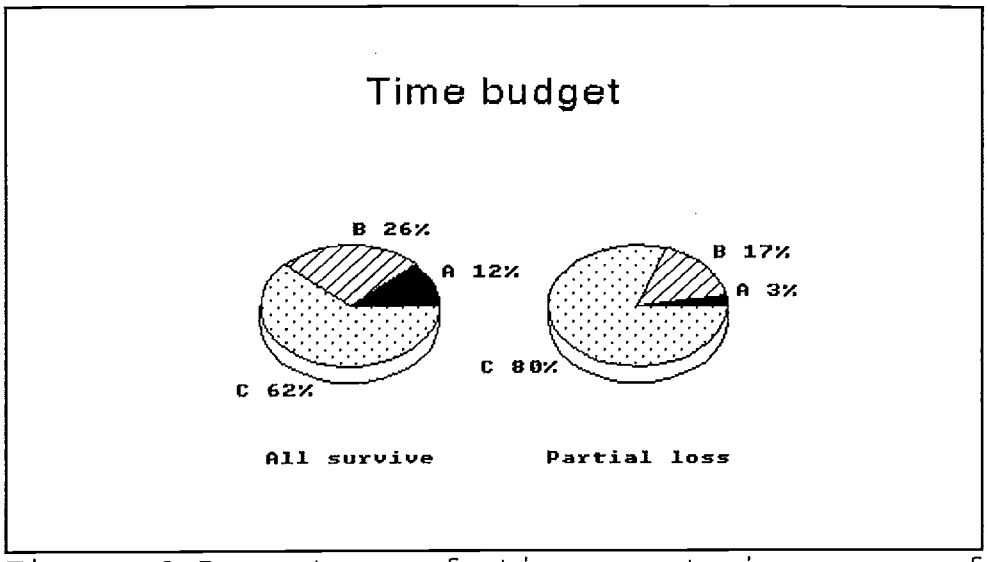


Figure 2:Percentage of time spent in areas of different quality by families that arrive completely in the wintering grounds and families that suffer partial loss before arriving in the wintering grounds in Scotland.

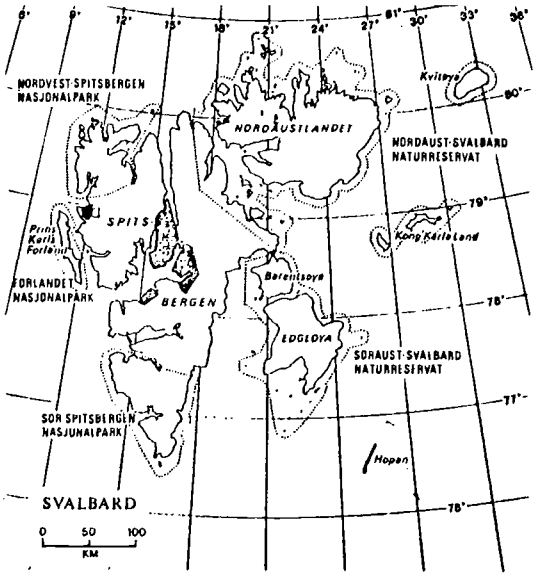
Food depletion is a common phenomenon in nature. It is the rule rather than the exception. The first birds of a flock that arrive in an area make a different selection of the plants on offer compared with birds further back in the flock,even in a single visit(Prop & Loonen 1989). Research on the Brent goose show that acquisition of food is dependent on the dominance rank of the animals. A male with a high competitive status provides better feeding opportunities for the mate,predominantly because they get access to better sources of vegetation before it is exhausted by other members of the flock and the risk of being supplanted during foraging is minimized. Preference for certain types of food is clearly related to both biomass and protein content,but these factors could not be torn apart. The birds with the highest reproductive success are characterized by the relatively high number of aggressive interactions of the male,a low step rate in the favourable areas and the longest defecation intervals. Females that had reproductive success had a much greater proportion *Triglochin maritima*(31 %) in their diet than females that had no reproductive success(6 %)(Teunissen et al.1985). A research on Schiermonnikoog(Prop et Deerenberg,1991) also showed a direct link between success of the Brent Goose and the diet composition. *Plantago* and *Triglochin* increased in importance in supplying the geese with components with which to build their body reserves and these species were mostly obtained by dominant pairs within the flock. With this in mind (the dominance of the bigger families,the relation between success and diet composition)the question to be examined is: What is the relation between the diet and the familysize of the Barnacle Goose during the moult-period on Spitsbergen?

Materials and methods

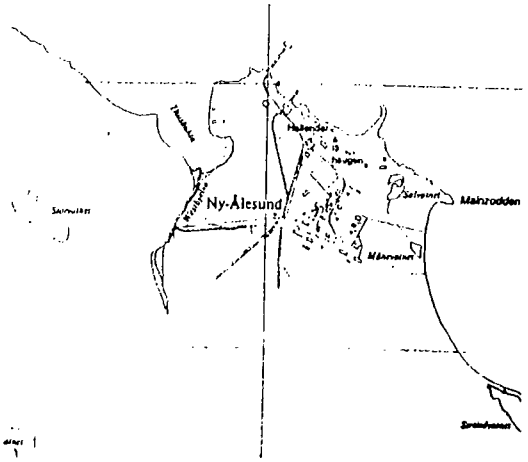
2.1 Materials

2.1.1 Study area

All the droppings used for the microscopical faecal analysis were collected in 1990 near Solvatnet a lake,close to the village of Ny Ålesund. Ny Ålesund is the most northern village of the world(79°N 12°E) in a bay along the west coast of Spitsbergen. Solvatnet is a little lake in between the village and the coast were the geese are foraging during day and nighttime. The vegetation around Solvatnet consists predominantly of a wet mosscarpet with Dupontia(for the description of the plantspecies see Appendix A).
While only the more dominant geese visit the village,all geese are seen in the territory of Solvatnet. The vegetation of the village consists mainly of dry moss on gravel with clumps of Deschampsia and Poa in between.



1a.



1b.

Figure 1a:Spitsbergen(Svalbard). Ny Ålesund is marked by a dot.
Figure 1b:The environment of Ny Ålesund.

Solvatnet is a sleeping place,where almost all geese that were foraging to the north-east of the village go sleeping. Because almost every goose has the opportunity to choose from the same scale of feeding places this area is a good study area.
In the summer of 1990 field observations have been carried out in the environment of Ny Ålesund,Spitsbergen on the Barnacle Geese that were present at that time(1 july-20 august). During these observations droppings have been collected,dried and weighted. These droppings could be attributed to an individual goose,because the geese that were producing droppings,whilst resting could be identified by means of their engraved coloured rings. The geese have regular bouts of alternating periods of foraging and periods of resting(Prop et al.,1979).
The interval between two droppings shows a variation throughout the year. During moult(July-August) the dropping interval is about 8 minutes (Prop & Vulink,1992).
During resting their respective resting places have been drawn on a map. After they went foraging the droppings were collected and given a code(one code per amount of droppings at the same place,at the same time per individual).
The droppings were subsequently dried at 60 degrees Celsius for about 48 hours until they had reached a constant weight and weighted.

2.1.2 Microscopical analysis of the faeces

The reason why diet composition is determinable is that geese have a relatively inefficient digestive tract,that will leave many of the cellwall-structures of the eaten plants intact. Specific characteristics of the epidermis like the size,form and position of the cells and stomata,the structure of the edge of the leaf and the presence of hairs,if any, and their structure, will therefore remain recognisable (see Appendix A).
Of all droppings selected for the research,one dropping per code was taken and cut in four pieces. There was an equal amount of material scraped of three cutting planes. This material was moisted for a few minutes in water. Spreaded on an object-glass this sample could be examined by means of a stereo-microscope.In one of the oculars an ocular-micrometer was fitted.

This ocular-micrometer was not used to determine the absolute size of a plantfragment,but to determine the relative size as compared with other fragments. The sizes given in the results are therefore portions of the scale. The samples have been examined at a magnification of eighty times.
The qualitative examination of the faecal samples consisted of recognising the cuticles. This was trained by comparing the faecal samples with drawings and photographs of cuticles of already known plants and with reference samples of plants(Zettel,1974;Metcalfe,1960;Storr,1960; Stewart,1967).
In the quantitative method we wanted to find a trustworthy way to be able to determine the proportion of a plant species in the diet of the geese. The quantitative method was the so-called line-intercept method according to an article of Seber and Pemberton(Seber & Pemberton, 1979). This method consists of measuring the lengths of intercept of all the cuticles that intercept the line of the ocular-micrometer(fig.1).

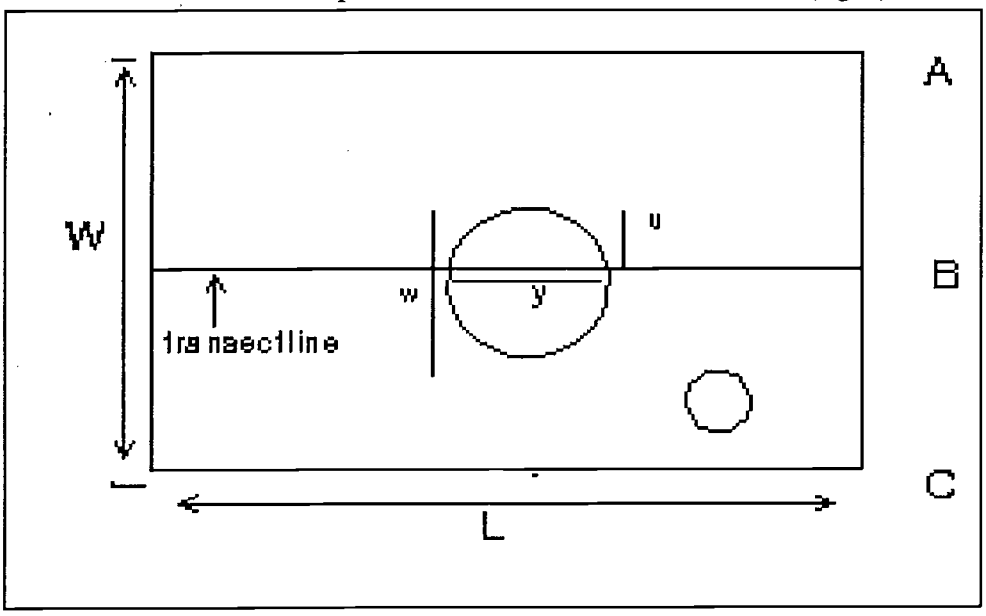


Figure 1:A random line transect intersecting the *i*th cuticle.The point B is chosen at random on AC.

In this way a line transect of length L was selected by choosing a point at random on the side of the rectangle of width W and then drawing a chord or the rectangle through the point perpendicular to the side. For simplicity,suppose there are only two species in the sample.

Then n and n' are the numbers of cuticles of each species that intersect the line and y_i and y'_j are the lengths of the chords of intersection of the two species($i=1,2,\ldots,n; j=1,2,\ldots,n'$). Define $Y=\sum_i Y_i$ and $Y'=\sum_j y'_j$. Then, irrespective of the shape and the orientation of the cuticles, we find that $\mu_y=E[Y]=Na/W$, and an estimate of the proportion π is $p=Y/(Y+Y')$. So by summation of the lengths of a particular species and dividing it by the total length of all species in the sample we are working with a simple calculation to find the proportion of that species. The advantage of this type of measurement is that it takes into account the fragmentation size of a species.
In practice this method is hardly more difficult or tedious to do than the most simple quantitative method of counting the cuticles that intersect the line.

The fragmentation size of a certain species differs between males, females and juveniles and while with other species it doesn't differ.

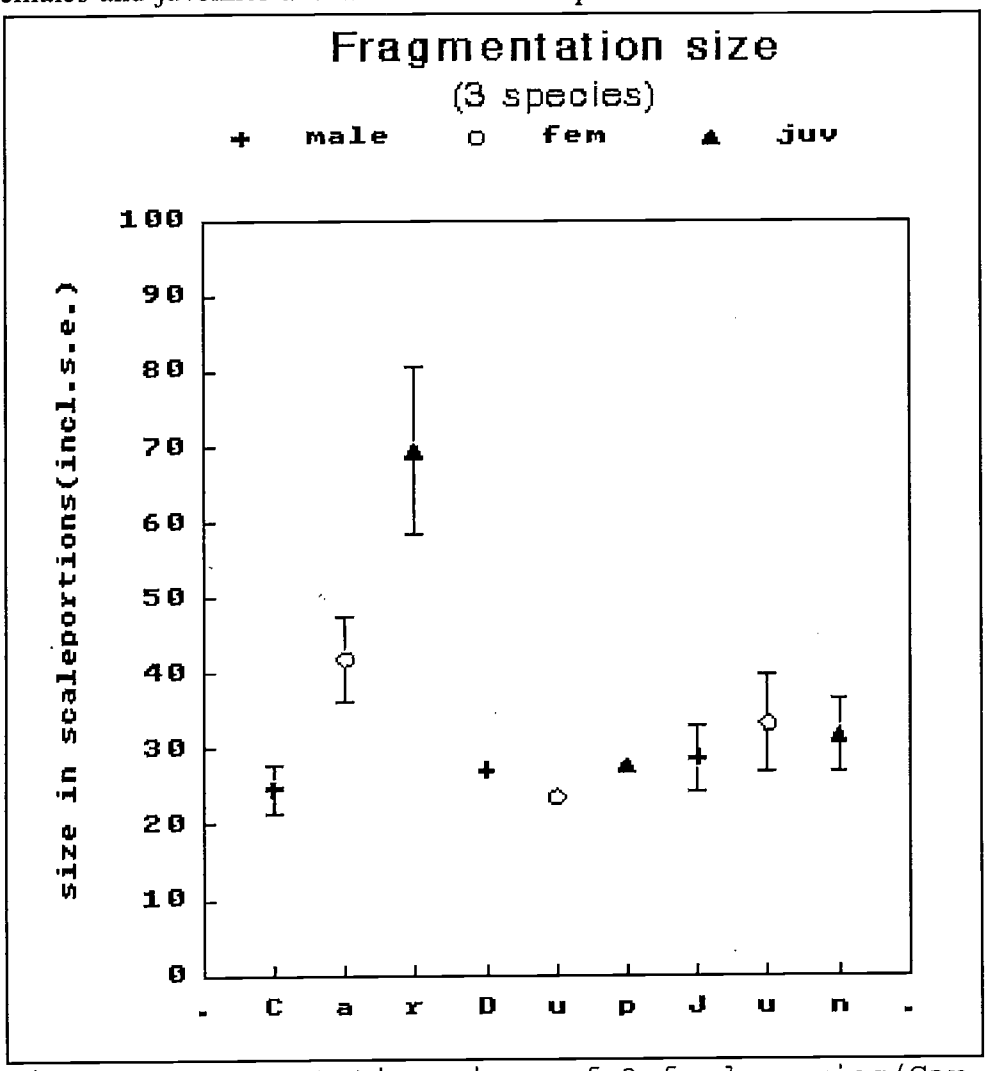


Figure 2:Fragmentation sizes of 3 food species(Carex subpathacea,Dupontia fisherii,Juncus bufonius) for males,females and goslings.-Standard errors of the fragmentation sizes is very small for Dupontia.

Because there is no constant ratio between the species considering their fragmentation it is not possible to correct the number of a certain species by multiplying it by a certain factor(for instance:if the size of species *a* is two times the size of species *b* multiply the number of species *a* by two). Comparing both methods a substantial difference was found(fig.3).

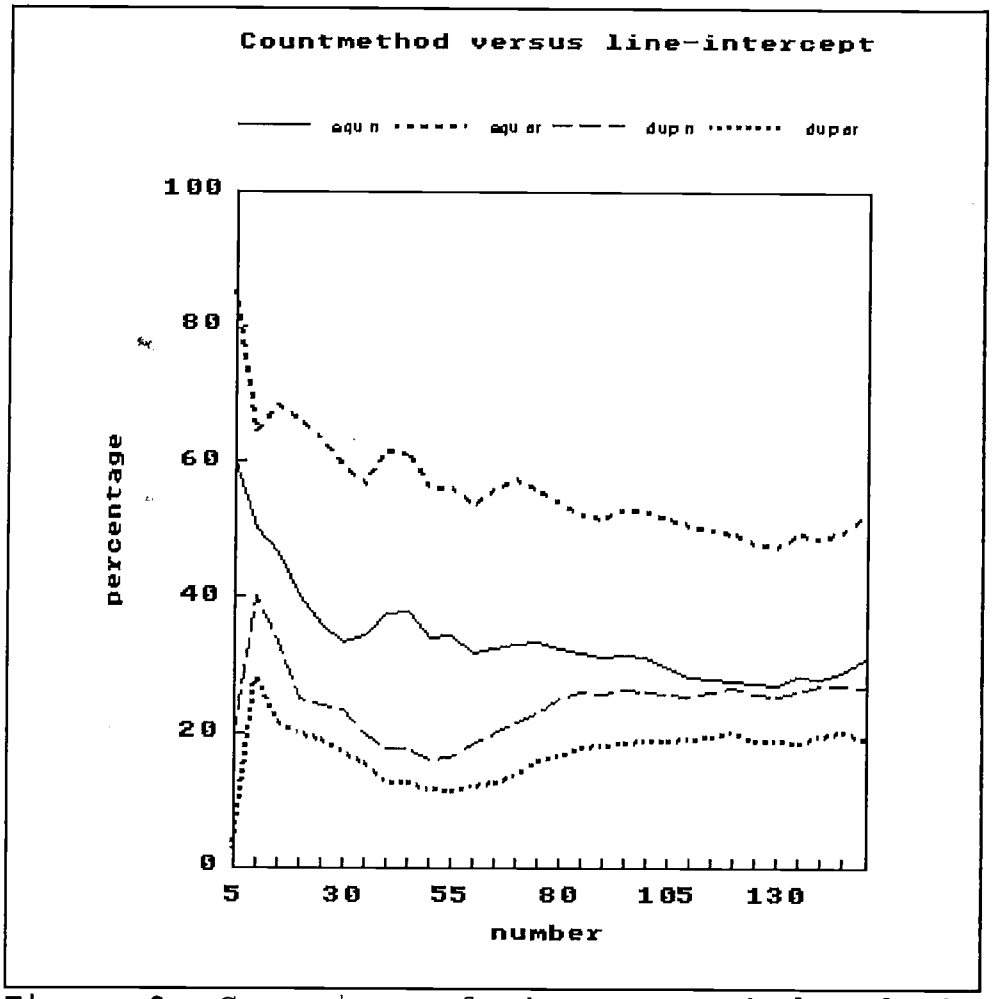


Figure 3: Comparison of the countmethod and the line-intercept method analysing a faecal sample (equ n= % Equisetum according to the count-method equ ar= % Equisetum according to the line-intercept method.

The number of determinations per sample was found empirically. Up to 100 determinations per sample the proportion of a certain species fluctuated and beyond 100 the fluctuations decreased (fig.4). Therefore 150 determinations per sample were chosen.

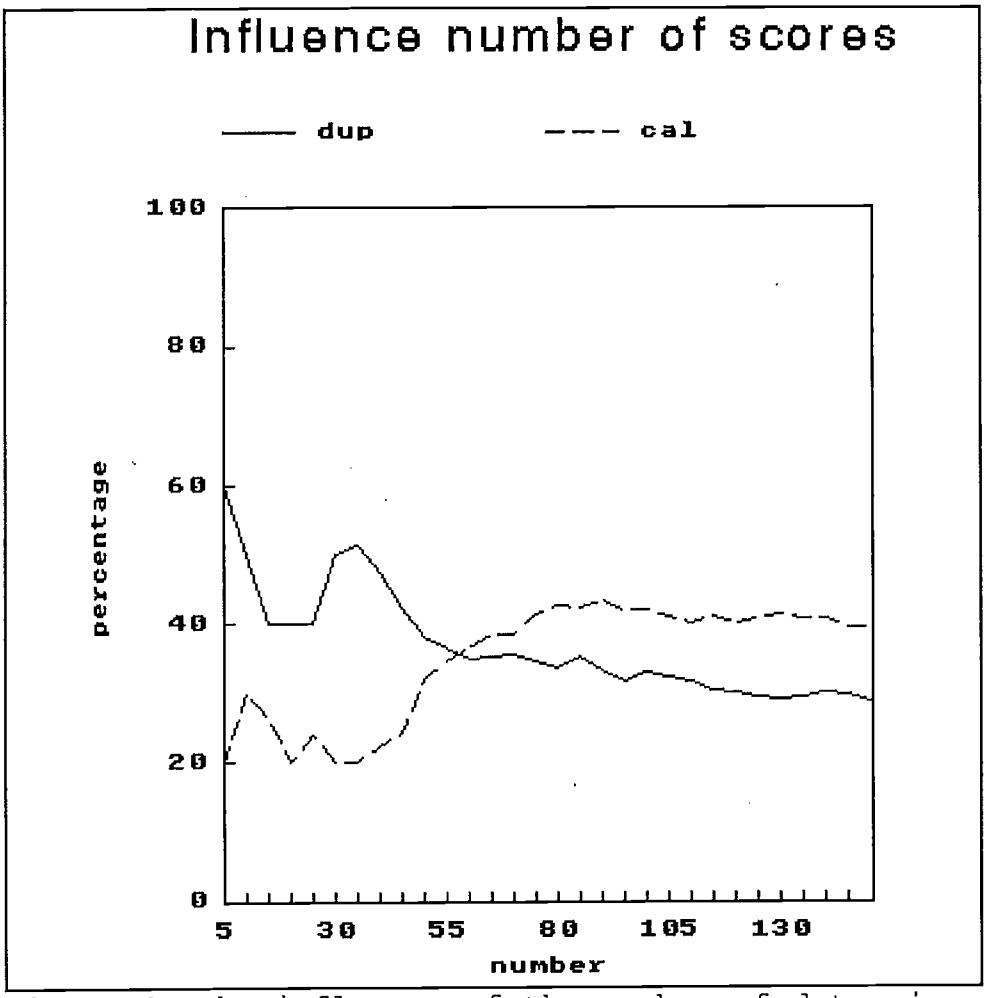


Figure 4: The influence of the number of determinations per sample.

2.1.3 Selection of the samples

To plan an experiment it is ideal,when looking for a variable that is dependent on another variable,that all other influencing factors are constant. To examine whether the diet composition of the barnacle goose is dependent on the familysize it is best to exclude,as far as possible,interfering circumstances. A selection was made of all the collected droppings (about 2400) by taking those families that differed in familysize but foraged in the same area,at the same time and their young had to be hatched at more or less the same time,because the young develop physiologically very fast. In a few weeks after hatching the juveniles grow fast. The length of the gut will increase and absolutely and relatively. In the first days after hatching the juveniles are therefore not able to deal with the food the adults or older juveniles deal with. By taking into account these limiting conditions 78 faecal samples,spread over five comparisons of two families each,remained to be examined(table 1). Note!-A sample in table 1 actually is a group of samples,*viz.* samples of a family on the same spot at the same time.

julydays	BZL3-YSLC7	BTF2-YSIC5	YVPZ2-YVSP4	GAAY3-YLYJ5	YEDK1-GAAX4
1				H	
			H	X	
5	H	H			
		H		H	H H
	H		O	X	X
	X X				
10					H
15					
		M			
				M	
			M	M	M
220					M
	M M	M			X
25		O	O		X M
	X X				X
	X X				
30	X X	O			
			O		
		X	X		
35					
40					
	O O				
45					
		X	X		
50					

Table 1:Overview of the examined faecal samples collected in Solvatnet,near Ny Ålesund,Spitsbergen in the summer of 1990. Above the ringcode of the female of a family followed by the number of juveniles.H=hatch-date,M=date of start of moult,X=complete sample of male and female and juvenile, O=incomplete sample.Left the julydays.

2.2 Methods

2.2.1 Mathematical methods

For processing the data collected according to the above-mentioned method,methods of plant-ecology were used.Ordination methods have been used to make an arrangement of samples in relation to each other in terms of similarity (or dissimilarity) of species composition and their associated environmental controls(Kent & Coker,1992;Bakker & Fresco,1993). In plant-ecology similar datasets have to be analyzed and therefore different methods have been developed. In these,in such a manner generated dissimilarity matrices,the samples will be plotted.
It is possible to bring all the identified species in such an ordination or define bigger categories to get a better insight in the complex matter.
In the ordination five categories were used:graminoids,mosses,equisetum,salix and a rest category. In the computer program **Vegrow** the following computations and plots were generated.In the subprogram **Dimat** a square root datatransformation has been applied. This has been done because the following aspects of a diet are important:1.whether a species has been eaten or not,2.how much of a certain species has been eaten. Both aspects of the diet are better expressed in the square root transformated data. In all other computations and programs used this square root transformation remained.
The percentage dissimilarity computed is a qualitative one(qualitative= Sørensen Appendix B).
In the next subprogram **Ordin** an ordination was made(see Appendix B).
The points that were produced in this manner were plotted in the next subprogram **J-plot**(see Appendix B).The subprogram **Curve** generated curves through the datapoints(see Appendix B)(Fresco 1991).
Several statistic methods have been used to find significant differences between the samples. Examples are analysis of variance,Student-Newman-Keuls test,regression,covariate regression,Kruskal-Wallis test.All statistical tests were performed using SPSS.
Three different relations were examined:
1).What is the relation between the period and the diet composition? Is there a trend in time and if so,what is the trend?
2)What is the diet composition of a juvenile,a male and a female? Are there differences and if so,what are the differences?
3).What is the relation between familysize and the diet composition?

Results

3.1 Average diet

Of all samples an average diet of a juvenile,a male and a female was deduced. This is done in Solvatnet for the whole period(1 july-20 august) and for four separated periods(period 1:3-12;period 3[1]:23-32; period 4:33-42;period 5:43-52 numbers are julydays).
An average diet has been determined for both the five plantgroups(graminoids,mosses,Equisetum,Salix and a rest group) and all the 18 identified plantspecies. Some of the results are shown in tables 1 up to 3 inclusive(for detailed information see Appendix C).

Males	period 1	period 3	period 4	period 5
Samplesize	6	12	2	2
Graminoids	17.0 (3.7)	59.4 (8.9)	51.0 (14.5)	25.2 (17.8)
Mosses	45.6 (7.0)	15.8 (7.7)	16.7 (6.5)	7.5 (0.1)
Equisetum	4.2 (2.1)	5.6 (5.4)	1.9 (1.3)	3.2 (1.0)
Salix	10.8 (6.6)	0.0 (0.0)	0.0 (0.0)	38.3 (27.1)
Rest	14.9 (7.1)	16.1 (5.3)	27.4 (7.8)	21.2 (9.0)

Table 1:Average diet as percentages (standard error between brackets) of a male per period.

[1] Period 2 consists of 2 successive periods of 10 days of which the first has no data.

Females	period 1	period 3	period 4	period 5
Samplesize	5	13	2	2
Graminoids	32.9 (8.0)	67.1 (7.6)	74.9 (10.3)	9.4 (6.6)
Mosses	30.2 (3.6)	10.4 (5.5)	13.8 (9.5)	51.7 (29.1)
Equisetum	6.1 (4.7)	0.5 (0.4)	0.0 (0.0)	6.1 (4.3)
Salix	19.0 (9.3)	0.3 (0.2)	0.0 (0.0)	20.0 (14.1)
Rest	8.4 (2.3)	19.6 (5.6)	10.5 (1.3)	9.5 (3.5)

Table 2:Average diet as percentages (standard error between brackets) of a female per period.

Goslings	period 1	period 3	period 4	period 5
Samplesize	6	9	2	4
Graminoids	16.0 (6.6)	59.4 (9.3)	51.2 (15.1)	51.8 (12.0)
Mosses	14.1 (3.9)	17.1 (8.8)	21.6 (2.7)	7.6 (3.9)
Equisetum	41.8 (12.0)	5.5 (4.5)	1.3 (0.9)	3.8 (3.0)
Salix	4.1 (1.8)	0.2 (0.1)	0.7 (0.5)	0.6 (0.3)
Rest	20.6 (5.8)	15.5 (3.6)	22.0 (9.5)	33.1 (6.5)

Table 3:Average diet as percentages (standard error between brackets) of a gosling per period.

The differences between the three groups(male,female,juvenile) have also been tested with an analysis of variance(ANOVA). The Student-Newman-Keuls test has to determine which groups differ significantly when ANOVA shows significant differences in any group.
For the whole period of examination a significant difference has been found for Equisetum($p=0.0407, F_{2,64}=3.3721$. This difference is mainly caused by the difference in period 1(see further).
Per group of food species its average share in the diet of the males,females and goslings is marked in the figures 1 up to 5 inclusive. Besides the averages the standard errors are also indicated.Comparing these values it is striking that there are always differences(no overlap of the average values $\pm$ standard errors) between juveniles and/or males and/or females in period 1(=3-12 july 1990). In period 5(julydays 43-52) there are very often differences(except for the Equisetum group). In the two intermediate periods 3 and 4 (julydays 23-42; there are no data of period 2) the differences are smaller in such a way that there is always overlap(except for the Rest-group in period 4).

Looking at the Graminoids-group it can be seen that the averages of the juveniles and the males in the periods 1,3 and 4 are almost the same and that they diverge in period 5. But including the standard error in this view,the difference in period 5 is that small that there is overlap of the error bars.

In period 1 the female eats more graminoids than the males and juveniles do and in period 5 the females eat less graminoids than the juveniles do (figure 1).
However these observations are only qualitative. To test significance a nonparametric statistical test,viz.the Kruskal-Wallis one-way analysis of variance,has been applied(Siegel & Castellan,1988).
In the Graminoids-group there was no significant difference between the sexes in any period according to the Kruskal-Wallistest(period 1: p=0.3508;period 3:p=0.6467;period 4:p=0.6347;period 5:p=0.2046).

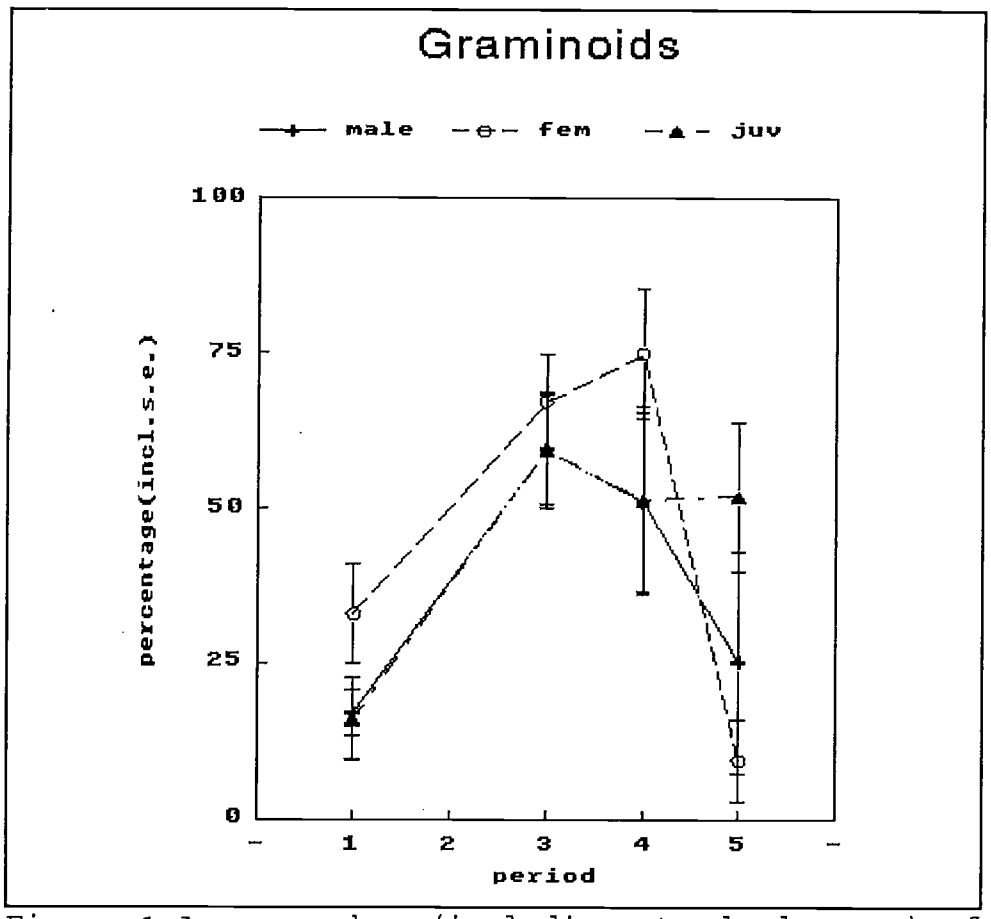


Figure 1:Average share(including standard error) of graminoids in the diet of the males,females and juveniles per period.

In the first period the males eat more mosses than the females and the juveniles eat less mosses. In period 5 the females eat more mosses than males and juveniles do (figure 2).
Again these differences are solely notations of no overlap of the averages with errorbars. The obtained values of the Kruskal-Wallis test are,except for period 1,not significant(period 1:p=0.0121;period 3: p=0.6044;period 4:p=0.9639;period 5:p=0.3064). In period 1 the males eat significant more Mosses than the juveniles do(Appendix B). According to the Student-Newman-Keulstest there appear to be significantly different groups for the Mosses.
The goslings eat less Mosses than the adults do($F_{2,16}$=9.1469, p=0.0029).
Mean Juveniles:3.34%
Females :7.23%
Males :11.10%

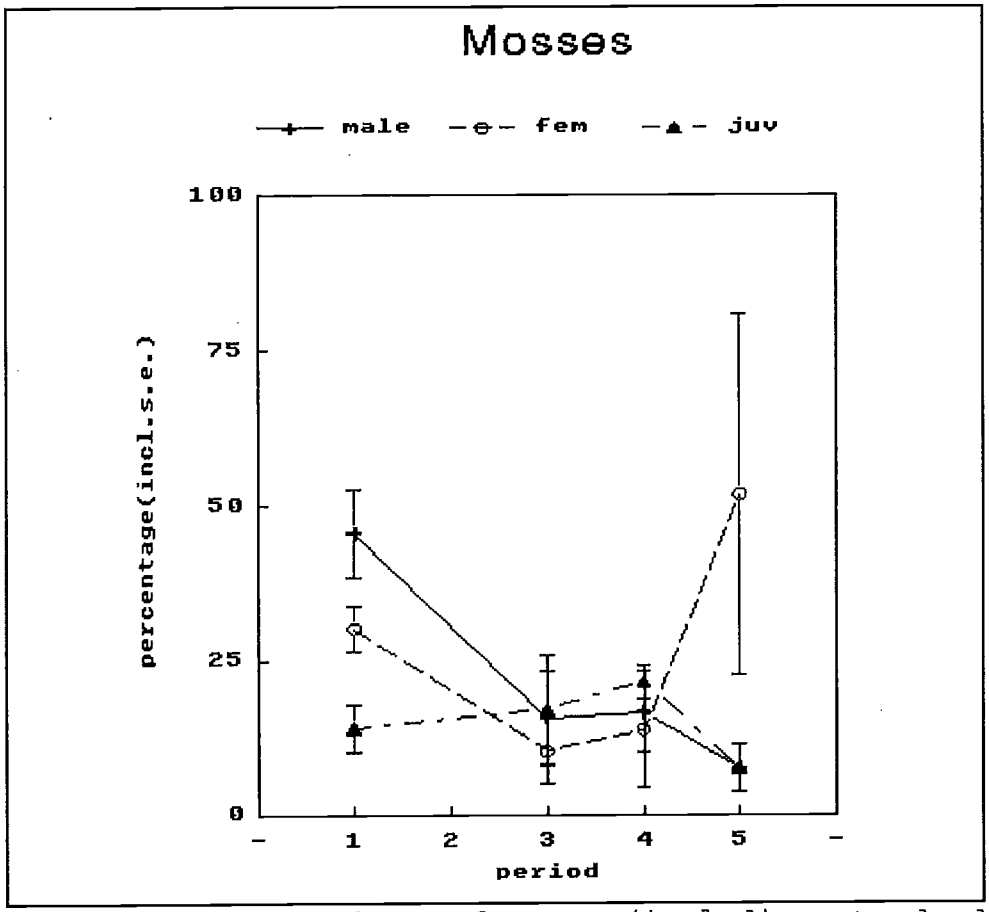


Figure 2:Average share of mosses(including standard error) in the diet of males,females and juveniles per period.

In period 1 there is a big difference between the share of Equisetum in the diet of goslings(41.8%) and in the diet of males(4.2%) and of females(6.1%) (figure 3).This difference turns out to be significant according to the Kruskal-Wallis test for the first period (period 1: p=0.0443;period 3:p=0.6930;period 4:p=0.5220;period 5:p=0.7691). According to the Student-Newman-Keulstest there are significant differences for Equisetum for the period 1.
The goslings eat more of this group than the adults do ($F_{2,16}$=5.6568, p=0.0158).
Mean Juveniles:32.73%
Females :2.51%
Males :1.99%

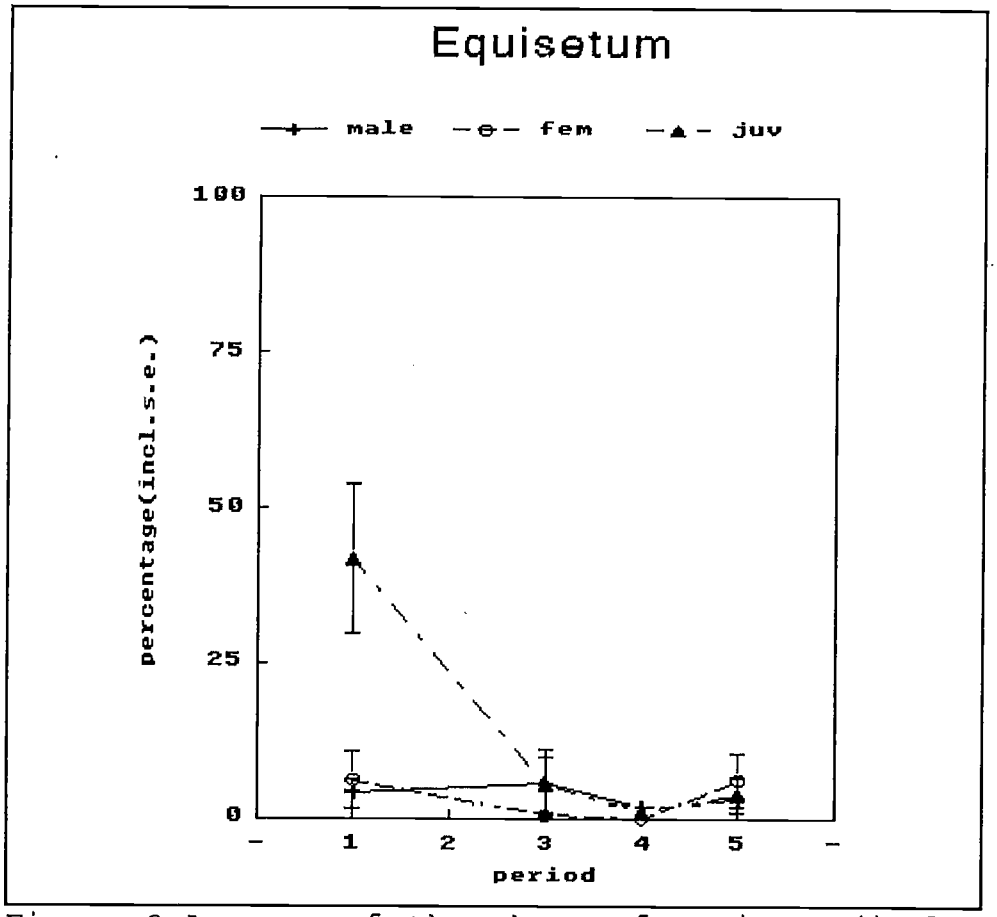


Figure 3:Average of the share of Equisetum(including standard error) in the diet of males,females and juveniles per period.

In period 1 the juveniles eat less Salix than the females do and in period 5 the juveniles eat less Salix than the males and the females do (figure 4).
Neither of these differences however appear to be significant in the Kruskal-Wallis test(period 1:p=0.5351;period 3:p=0.2786;period 4: p=0.0.3679;period 5:p=0.8059).

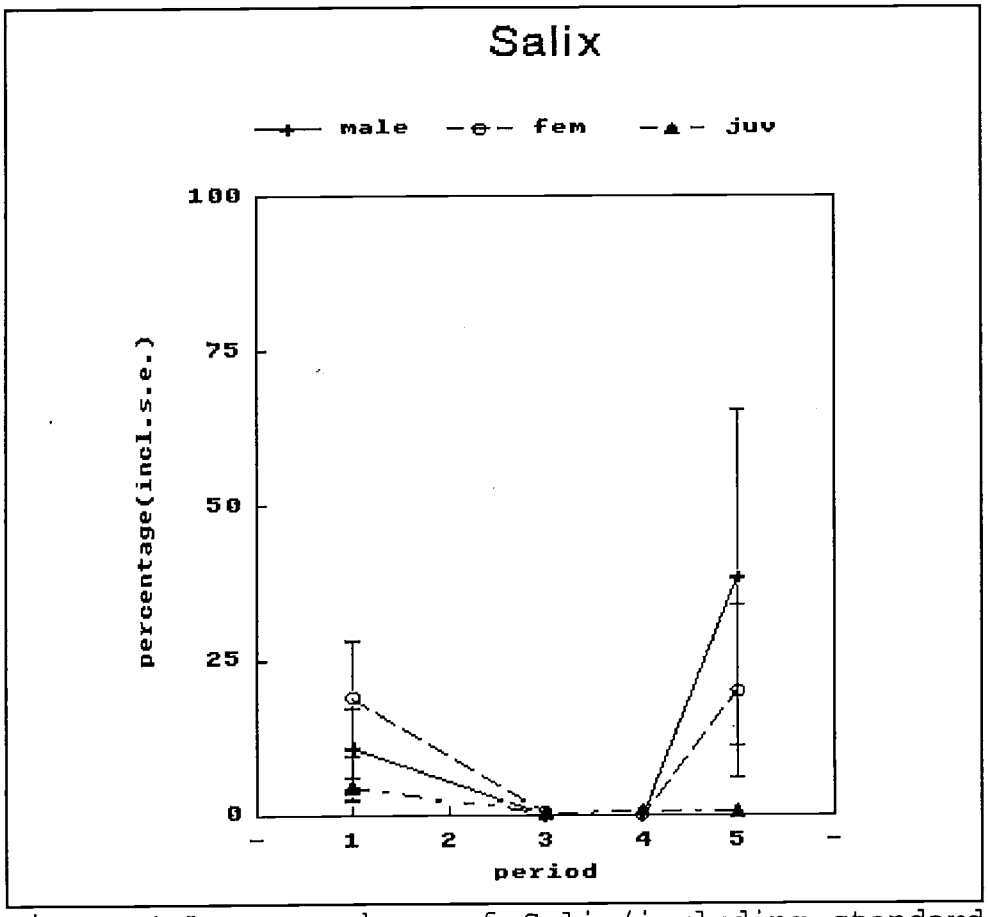


Figure 4:Average share of Salix(including standard error) in the diet of the males,females and juveniles per period.

The females eat less of the Rest-group than the juveniles do in the periods 1 and 5 and also less than the juveniles and males do in period 4 (figure 5). Neither of these differences appear to be significant according to the Kruskal-Wallis test(period 1:p=0.6518;period 3:p=0.9224; period 4:p=0.2342;period 5:p=0.2157).

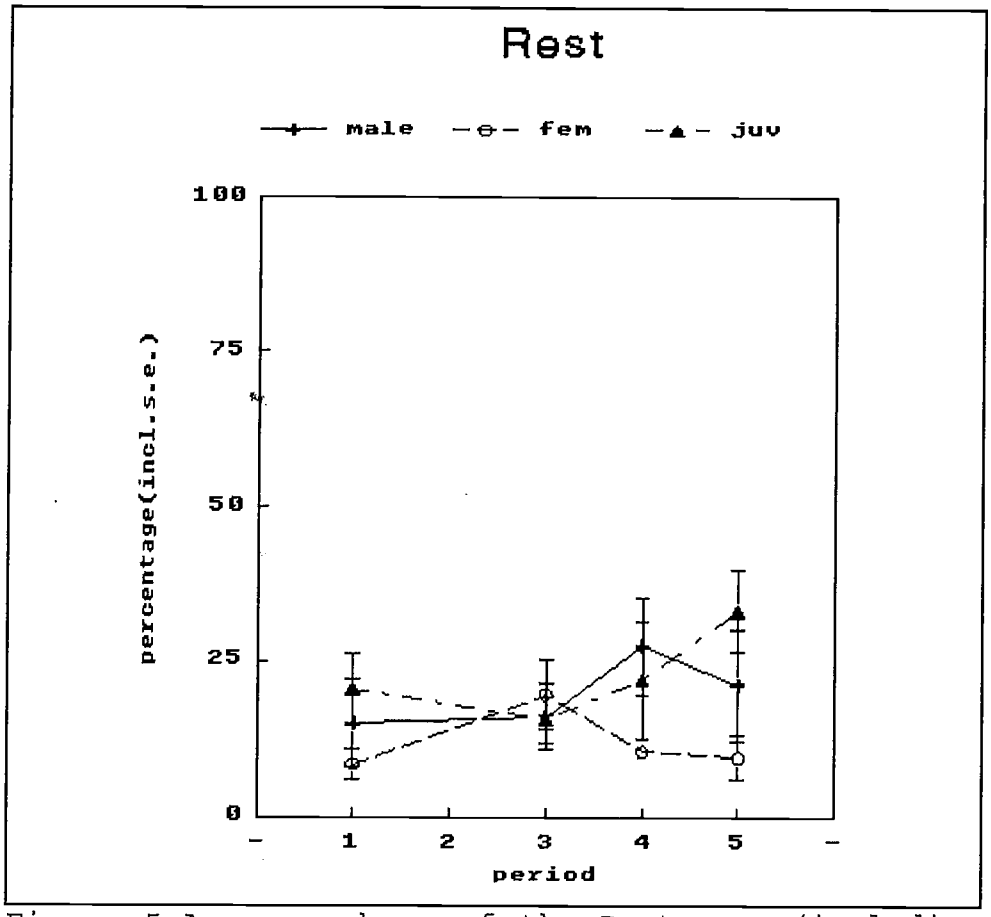


Figure 5:Average share of the Rest-group(including standard error) in the diet of the males,females and goslings per period.

All members of a family are feeding together at the same site. One would expect large overlap in the diet of all members of a family. In the next section the difference among the families will be examined. First the difference between male-female and gosling,secondly differences among goslings.
In the subprogram Dimat of the program Vegrow dissimilarities are calculated(based on the 18 species diet;all other dissimilarities are based on the 5 groups diet). The higher the value of the dissimilarity of two samples the less these samples are alike. The dissimilarities male-female,male-juvenile and female-juvenile of the samples in each family per daynumber have been calculated and plotted in the figures 6 and 7.

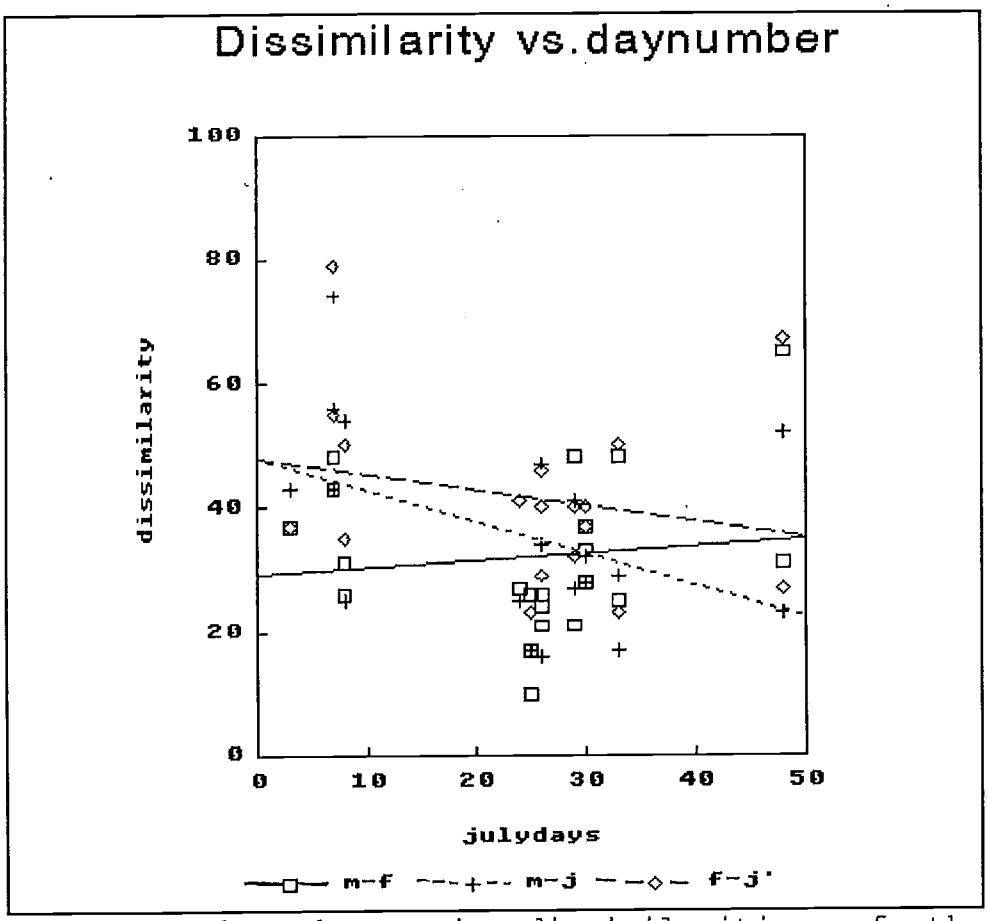


Figure 6:The change in dissimilarities of the faecal analysis between male-female,male-juvenile and female-juvenile.

A line fit has been calculated for each category of dissimilarities(male-juvenile,female-juvenile,female-male) which is also plotted in the figure. In figure 6 all samples were used for these calculations. It is clear that the dissimilarities of the juveniles as compared to the males and the females are in the beginning of the examination period relatively high and in the course of time they are decreasing. The decrease is highest for the dissimilarities of the juveniles as compared to the males.
For these data regressions were calculated. The change in dissimilarities between males and females over this period was not significant ($r^2=0.01193, F_{1,20}=0.22931, p=0.6375$). Also the changes in dissimilarities between males and juveniles and between females and juveniles versus daynumber were not significant(male-juvenile:$r^2=0.19106, F_{1,18}=4.01512, p=0.0613$ and female-juvenile:$r^2=0.05352, F_{1,17}=0.90466, p=0.3557$),when $p<0.05$ is considered to be significant.
When day 48 was excluded for these multiple regressions some changes in dissimilarities turned out to be significant(male-juvenile:$r^2=0.39609, F_{1,16}=9.83829, p=0.0068$ and adult-juvenile:$r^2=0.29505, F_{1,32}=12.97499, p=0.0011$). Although the change in dissimilarities between female and juvenile was not significant it was almost the case(female-juvenile:$r^2=0.22611, F_{1,15}=4.09035, p=0.0627$). The changes in differences in dissimilarities between male and female were even in the shortened period not significant(male-female:$r^2=0.06077, F_{1,18}=1.09990, p=0.3090$)(figure 7).

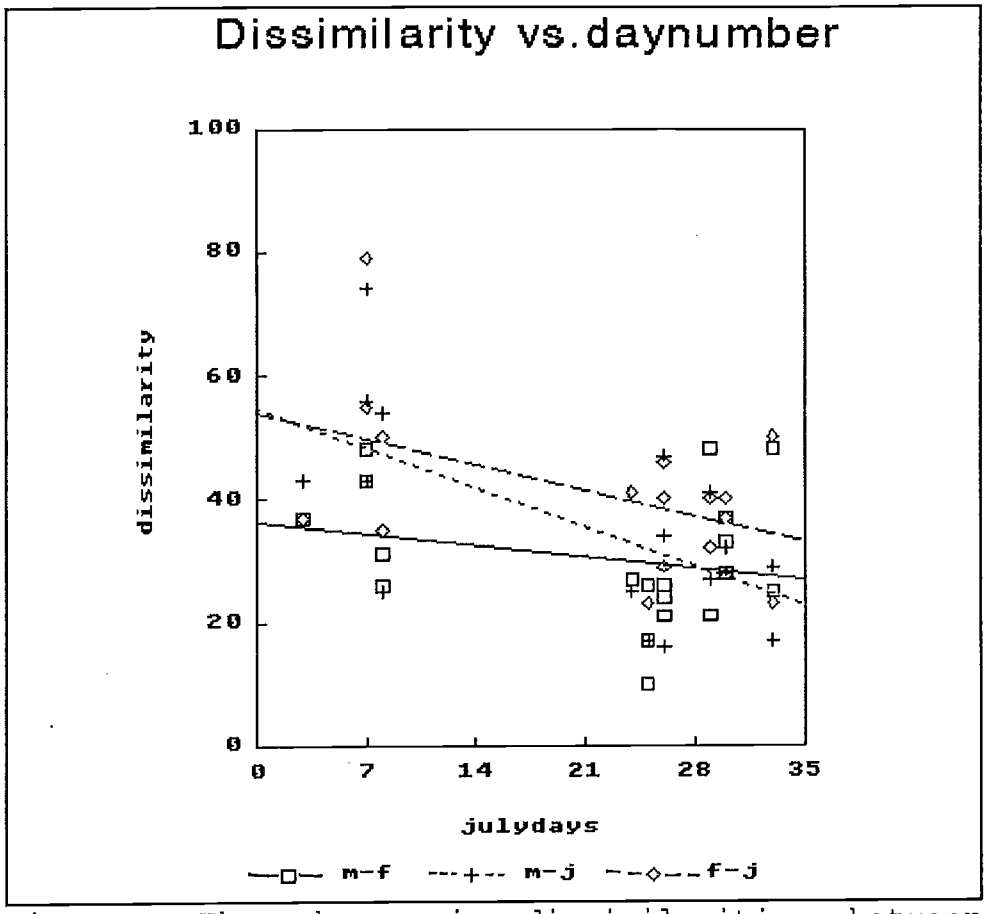


Figure 7:The change in dissimilarities between males,females and juveniles in a shortened period.

The reason for excluding day 48 is that the data for this day are somewhat peculiar. A possible reason for this deviation is that the behaviour of the geese changes because they can almost (maybe already) fly and do not stick that much together as in the previous time. A different explanation is that the partners were mixed up. The engraved coloured ring with the mark BTF could easily be mistaken for BTG and vice versa. In this way the droppings could be attributed to the partner.

The differences among gosling will be examined now. These differences are of the same magnitude or smaller as compared to the differences between goslings and males and between goslings and females. These data have been examined in two families(YSICxYSICP; BTFxBTG).

	F-J	M-J	J-J
YSICxYSICP+5 juveniles	33	54	27
BTFxBTG8+2 juveniles	69	22	24

Table 4:The average values of the dissimilarity index of comparisons in two families.

These results are plotted in the figures 8 and 9.

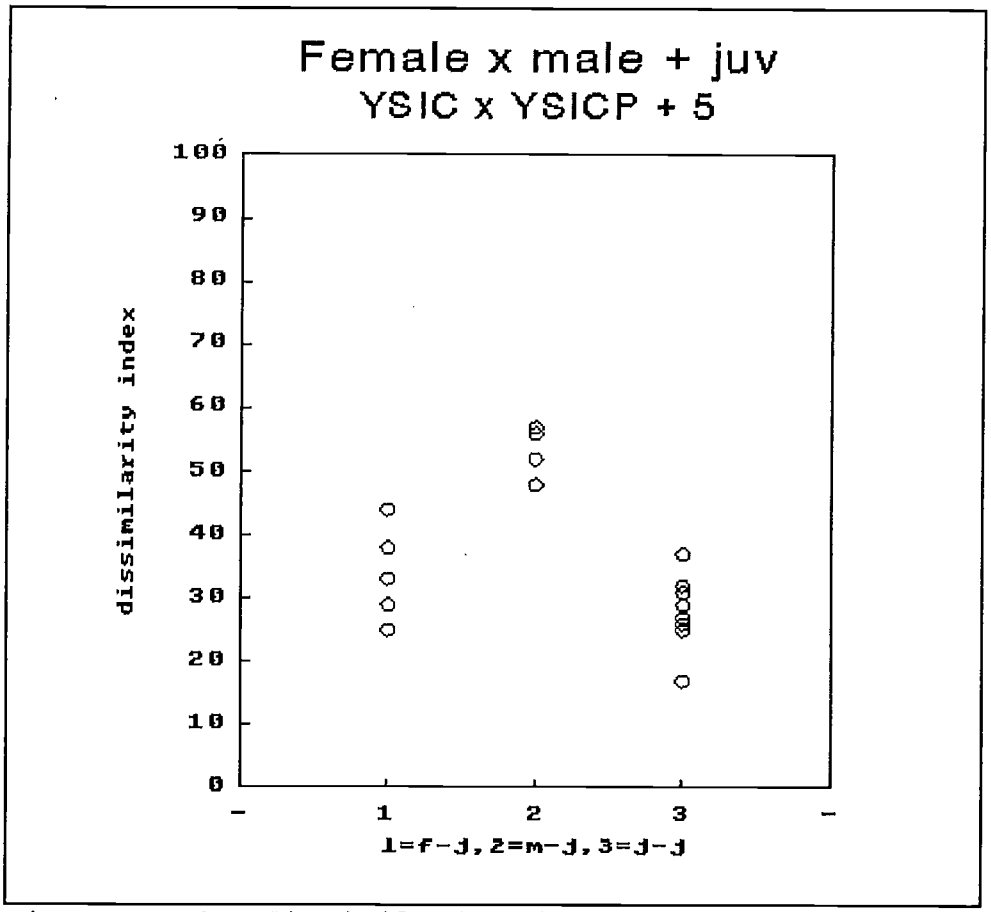


Figure 8:The dissimilarity indexes of female-juvenile,male-juvenile and juvenile-juvenile in the family YSICxYSICP.

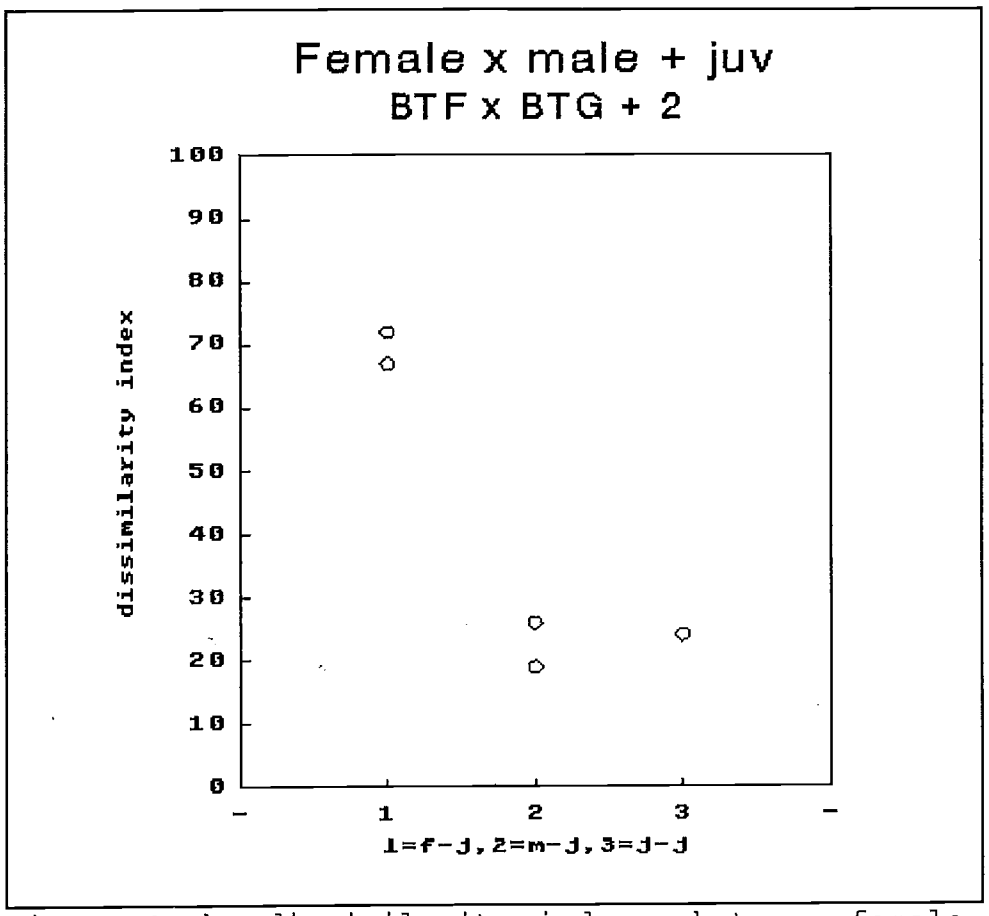


Figure 9:The dissimilarity indexes between female-juvenile,male-juvenile and juvenile-juvenile of the family BTFxBTG.

Figure 9 shows the dissimilarity within the family BTFxBTG. The partners are possibly mixed up. If so then these data are in accordance with the other data.

3.2 Diet in the course of time

In the subprogram Curve of the program Vegrow a hierarchical set of models are applicated to the percentages of a food species in the faecal samples. The models are fitted to the observations by means of logistic and non-linear regression techniques(Huisman et al.,1993). The in this way deduced equations for these models are presented in Appendix B. In figure 10 the changes of the shares of the different species are plotted versus the daynumber. Note that the percentages have been square root transformed. This has been done because the following aspects of a diet are important:1.whether a species has been eaten or not,2.how much of a certain species has been eaten. Both aspects of the diet are better expressed in the square root transformed data. Taking all samples into account the groups of Mosses,Equisetum and Salix start with maxima at day 3 (the shares of these groups decrease in order of appearance) and decrease to less than 1% at day 25 (all three groups). For Cerastium and the Rest-group the shares at day 3 show a minimum and increase up to about 10% at day 10 and stabilize after that date (Note that Cerastium is a part of the Rest-group). The Graminoids start at day 3 with about 10% and increase to $\pm$ 90% at day 48.
It is important to be aware of the fact that all the food species have been classed in the five groups(Cerastium has been analyzed as the quantitatively most important component of the Rest-group).The sum of these five groups must be 100% at any time. Sometimes the sum will be more or less than 100% because the model chosen by the subprogram Curve per group is always a simplification of the reality and is fitted in such a way that the data of the other four groups have not been taken into account. So the value per curve might differ from the input data.

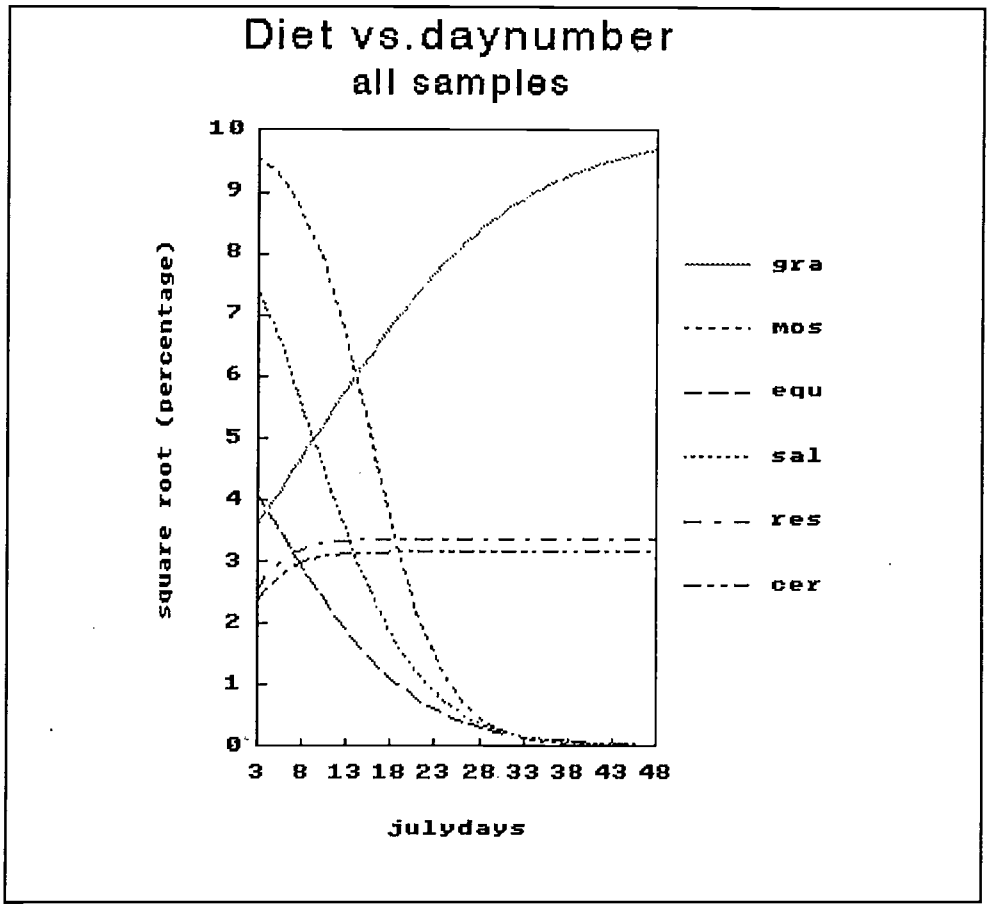


Figure 10:Share of plantspecies in the diet of all the geese versus the daynumber.

When only the samples of adults are used for calculating the curves the results for Mosses and Salix are almost the same. There is no trend in time for Equisetum,Rest and Cerastium. The share of Graminoids is increasing from day 3 up to day 30 and then decreasing until day 48. The percentage of the Graminoids is at the optimum about 50%(figure 11).

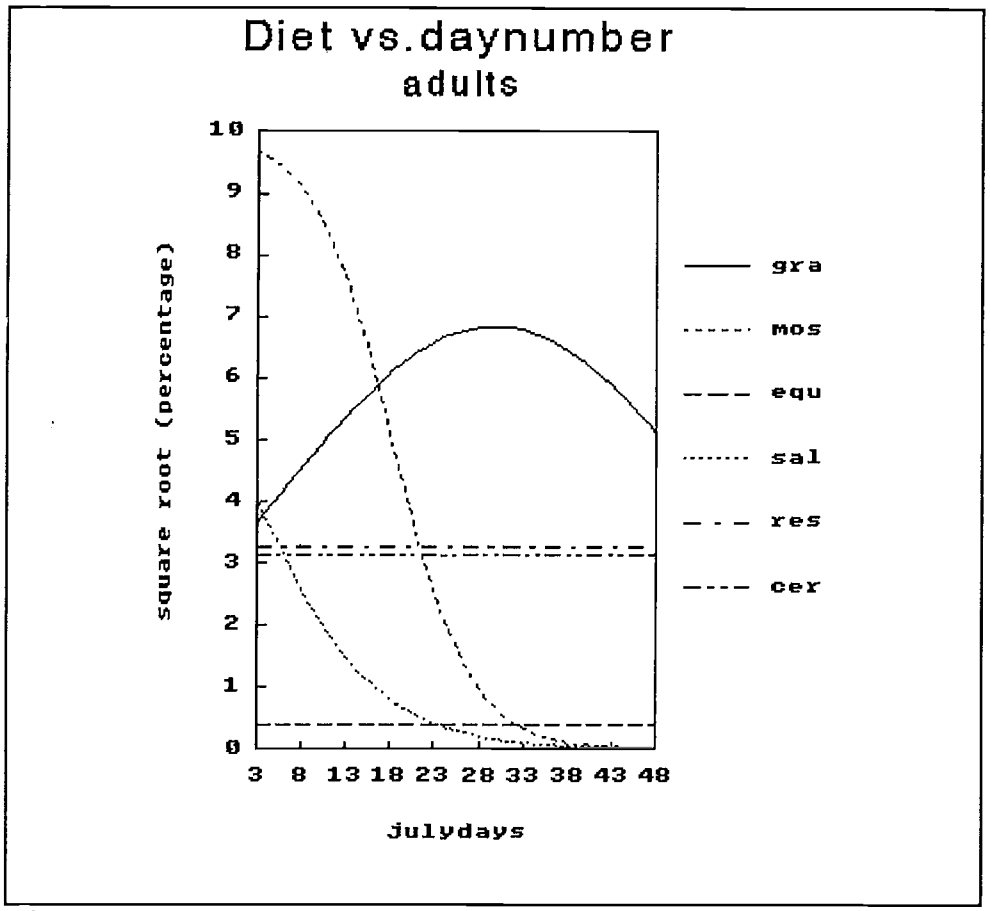


Figure 11:Share of the food species in the diet of the adults versus daynumber.

The shares of Salix in the diet of the juveniles show the same decreasing trend in time as these shares do in the diet of the adults. There is however a difference in the rate of decrease and the initial values. There is no trend in time as for Mosses,Rest and Cerastium. The share of Graminoids is increasing from 14% at day 3 up to more than 50% at day 48. A big difference between the juveniles and the adults is that the juveniles eat far more Equisetum in the beginning than the adults do (figure 12).

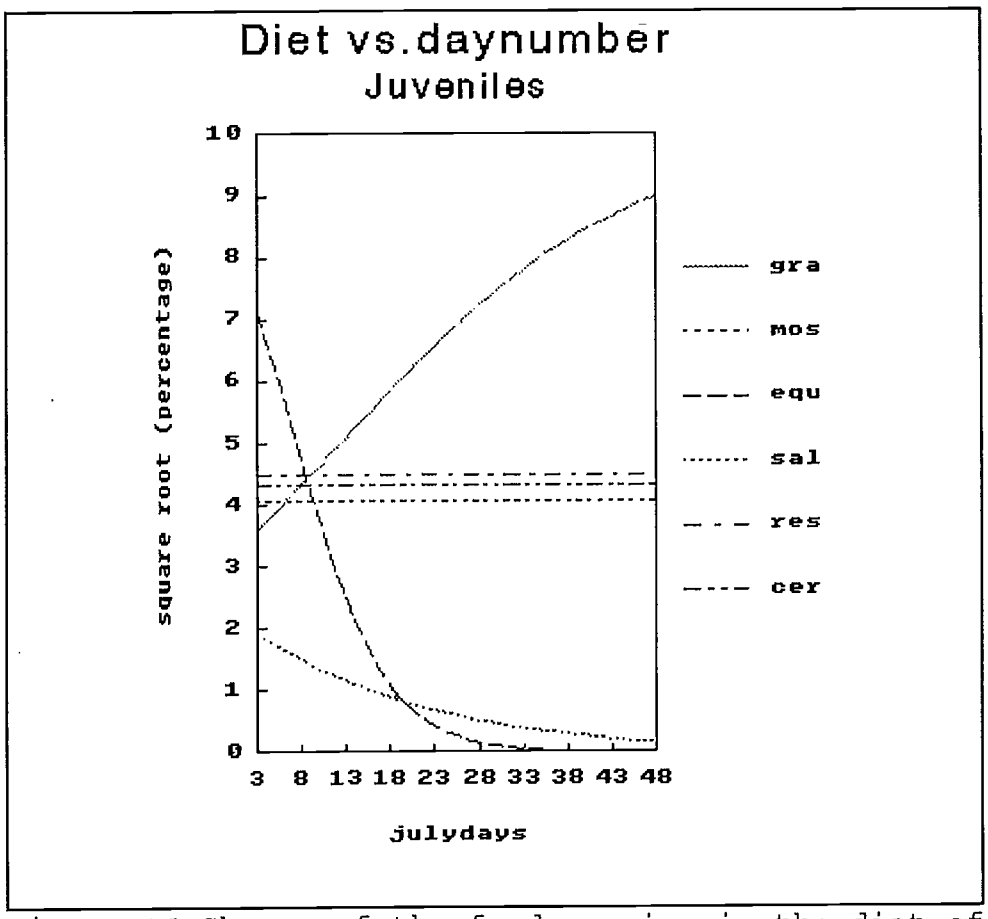


Figure 16:Shares of the food species in the diet of the juveniles versus daynumber.

3.3 Diet and brood size

The calculations done for diet versus daynumber were also done for diet versus brood size. Looking at all samples there is no trend for Graminoids,Mosses and Equisetum. For Salix a trend was found that a family with four goslings eat the most. For Rest and Cerastium it was found that an increase in brood size is accompanied by an increase in the amount of these food species(figure 13).

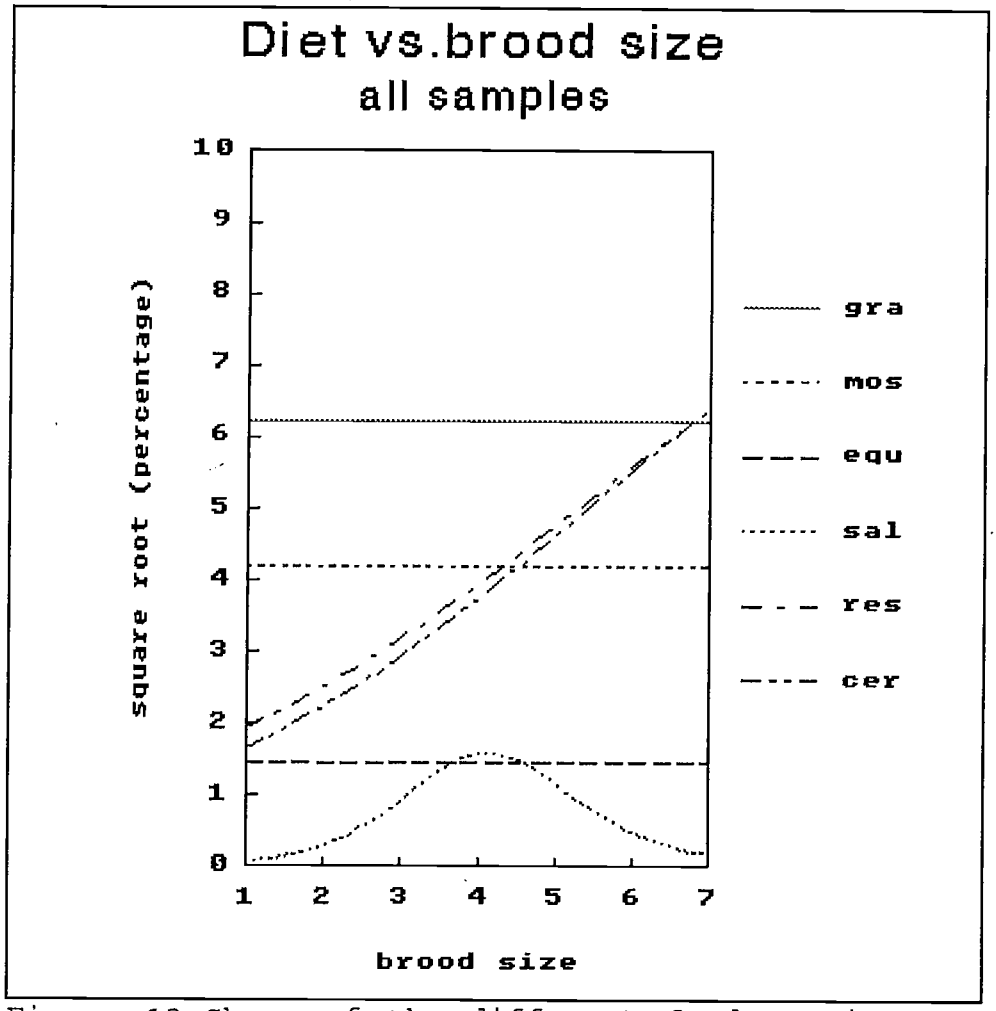


Figure 13:Share of the different food species for all samples versus the brood size of the geese.

An analysis the results of the diet of the adults versus brood size shows that there are only two trends. The trend in Salix is almost the same for adults as for all samples. But whereas there was no trend for Mosses for all samples together there is a clear trend for adults. The adults of a family with one gosling eat a substantial amount of Mosses and larger families eat hardly any Mosses (figure 14).

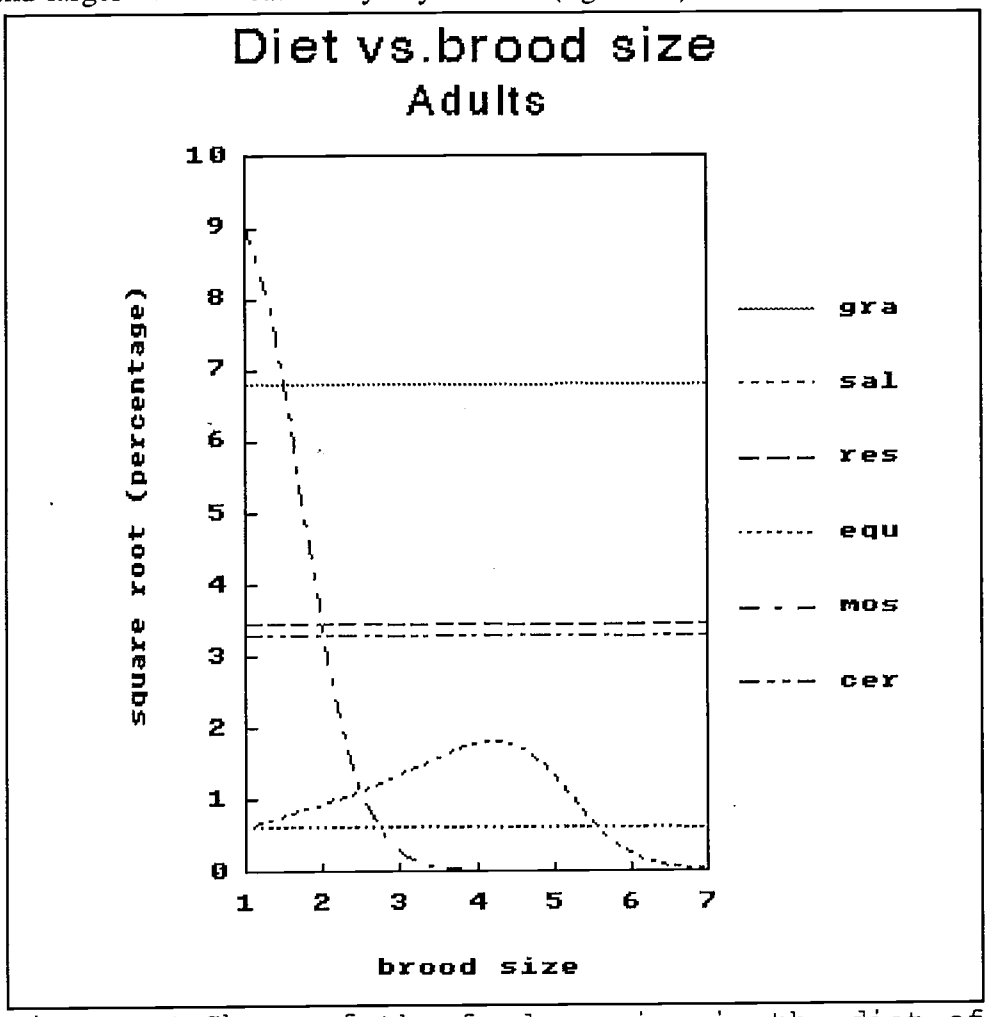


Figure 14:Share of the food species in the diet of the adults versus brood size.

The trends in the diet of the juveniles differ much from the trends in the diet of the adults. Graminoids,Mosses and Equisetum show no trend. The trend for Salix is that goslings of the families with more than two goslings eat about 1% and the goslings of the families with 1 or 2 gosling eat almost no Salix. The clearest trend is found for Rest and Cerastium. Whereas goslings of families with few goslings eat hardly any Cerastium,the goslings of families with more than three goslings eat more of this species than of any other species(figure 15).

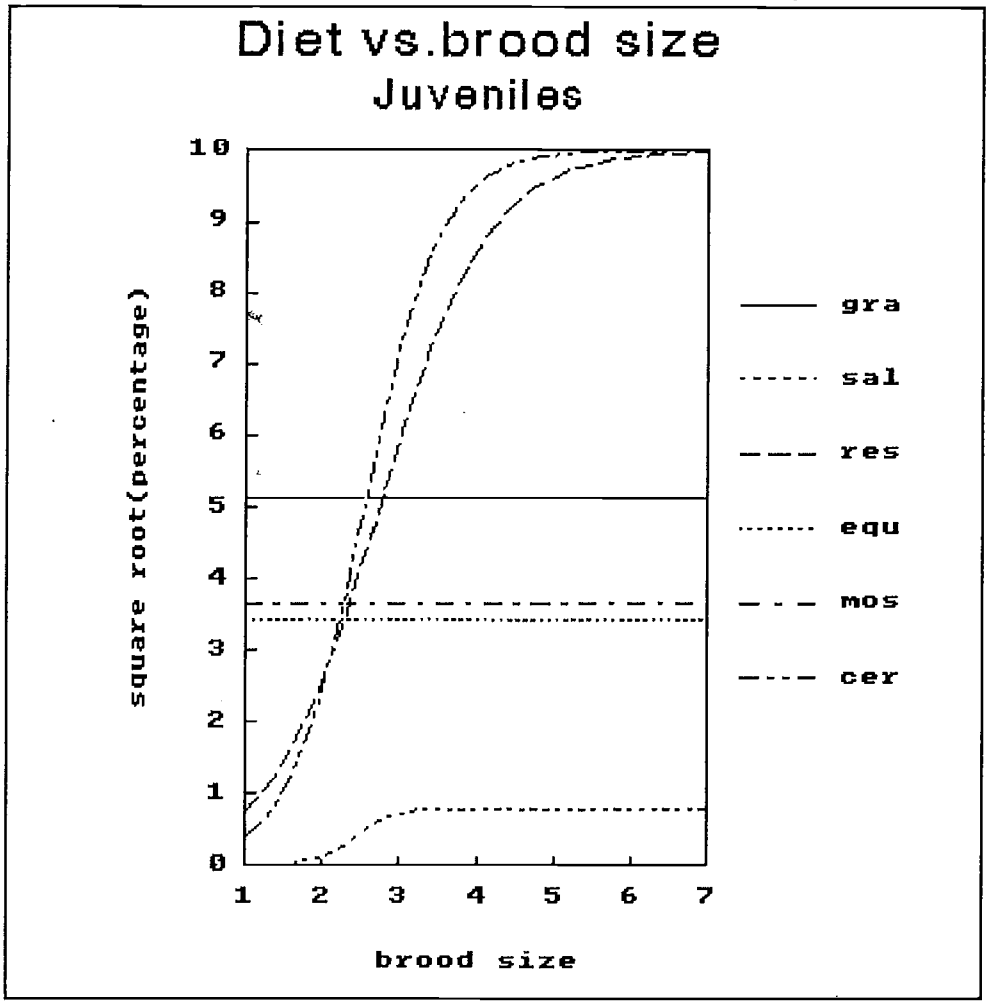


Figure 15:Shares of the food species in the diet of the juveniles versus the brood size.

The Kruskal-Wallis tests show the following differences:In families with less than 4 goslings and goslings and males and females differ significantly from the two others as for the Mosses($F_{2,7}$=64.7264, p=0.0003)
Mean Juveniles:2.31%
Females :7.42%
Males :12.33%
For Salix there is also a difference in which females eat significantly more than males and juveniles do($F_{2,7}$=14.8303,p=0.0079).
Mean Juveniles:0.00%
Females :36.13%
Males :5.48%

In families with more than three goslings there appears to be a significant greater share of Graminoids in the diet of females than in the diet of males and juveniles($F_{2,8}$=7.9513,p=0.0206).
Mean Juveniles:1.55%
Females :5.59%
Males :1.91%

Subsequently a comparison has been made between males,females and juveniles of the small families(less than four goslings) on the one hand and the same groups of large families(more than three goslings). The Mann-Whitney U-test shows that the juveniles of the small families eat in period 1 significantly less Salix than the juveniles of the large families do(p=0.0369). For the whole period it is not significant(p-0.0738). Although it is not significant an opposite trend was found with the Mann-Whitney U-test for females,that is females of small families eat more Salix than females of large families do(p=0.0756).

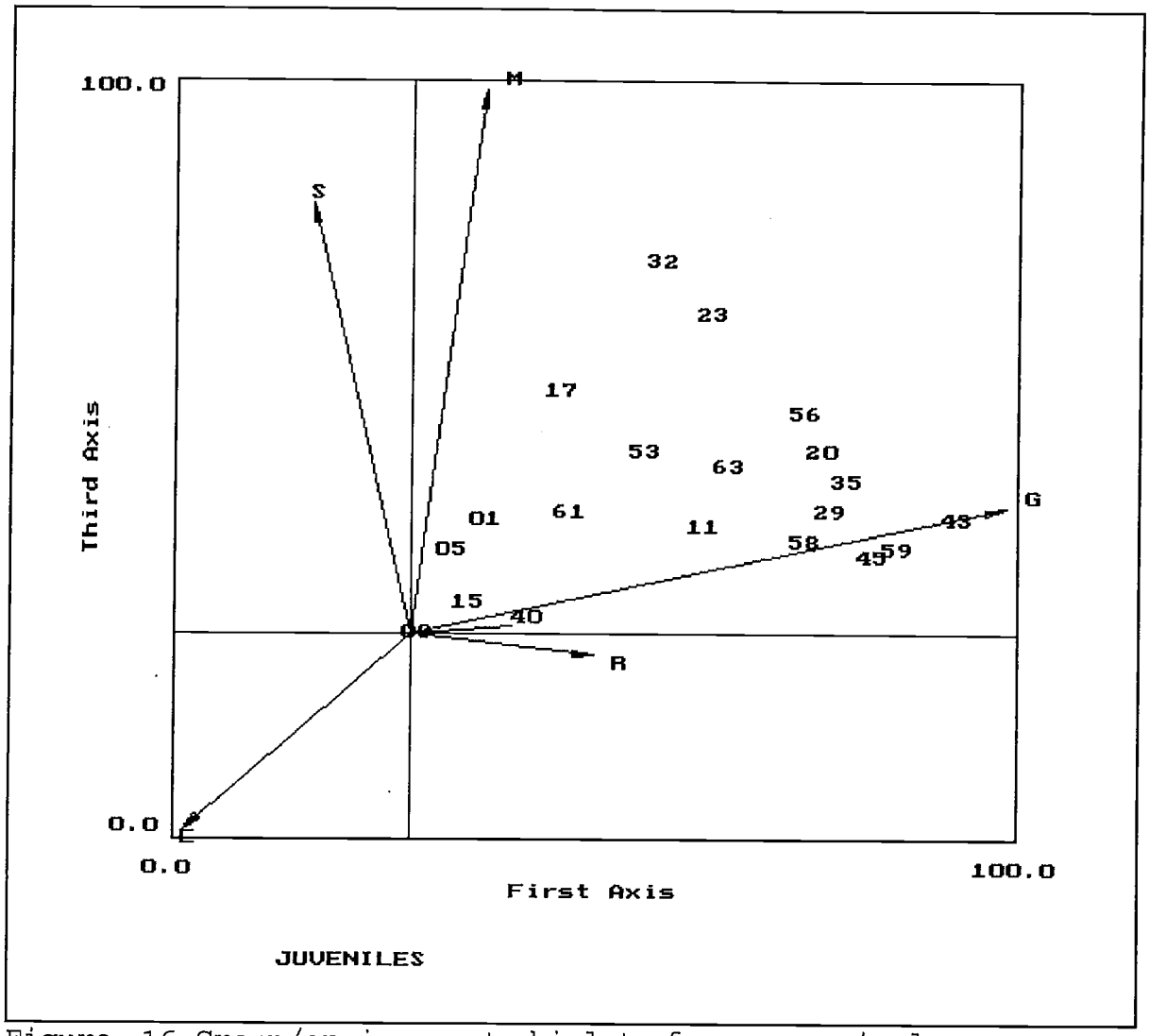


Figure 16:Group/environment biplot from canonical correspondence analysis(CANOCO) of the data of the faecal samples of the juveniles. The numbers are the samples.G=Graminoids,M= Mosses,E=Equisetum,S=Salix,R=Rest.

The data analyzed by a canonical correspondence analysis(CCA) are plotted in the subprogram J-Plot(see Appendix B).
Figures 16 and 17 show the results. The CCA doesn't give more information than the other analyses have already done. The numbers in figure 16 represent the analyzed samples and the one character symbols represent the five groups(G=Graminoids,M=Mosses,E=Equisetum, S=Salix,R=Rest). A great share of Graminoids in a sample will place it in the right corner of the figure. Figure 17 is another representation of the data plotted in figure 16. The dashed lines show the influence of the different groups. The longer the line the greater the influence. The solid lines show the influence of the environmental factors,daynumber and brood size(DA=daynumber,FA=brood size).There is a slight influence of brood size and daynumber in the direction of Graminoids and Rest visible of which the influence of daynumber is the largest.

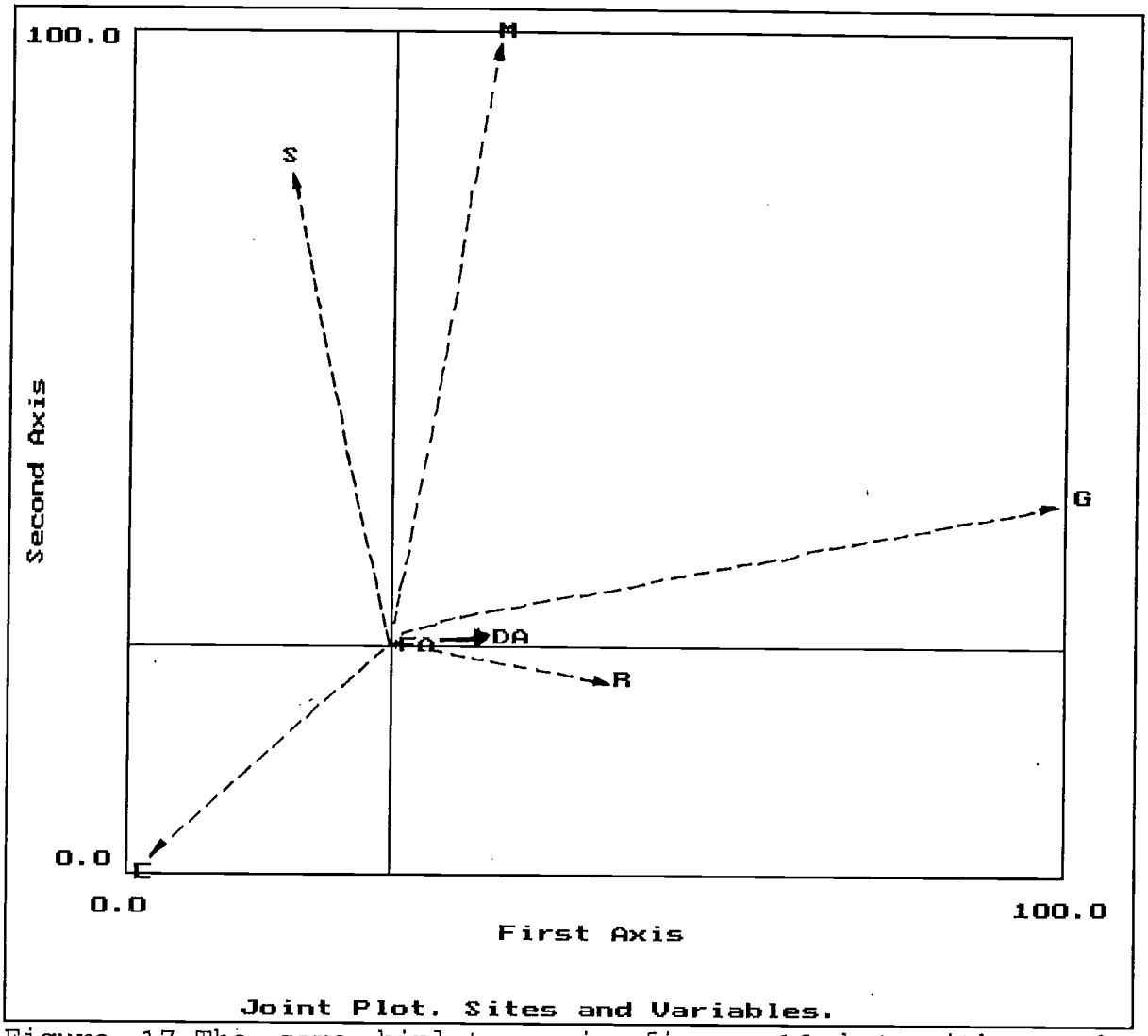


Figure 17:The same biplot as in figure 16 but without the individual samples.Here FA is visible which is not the case in figure 16 although FA is present there.

Discussion

4.1 Food items

To understand the diet of the Barnacle Goose some information on the several food items is necessary. The different components in the diet are evaluated both based on nutritional and abundance using literature data.
A quality ranking is possible between the different food species. It is known for instance that Equisetum contains much minerals like sodium (Na),potassium(K),calcium(Ca),phosphorus(P),magnesium(Mg) and also much protein(Øritsland,1986;Thomas & Prevett,1982). The digestibility of Equisetum is high as compared with the digestibility of mosses(figure 1)(Prop & Vulink,1992). Equisetum is available as soon as the snow has dissappeared.

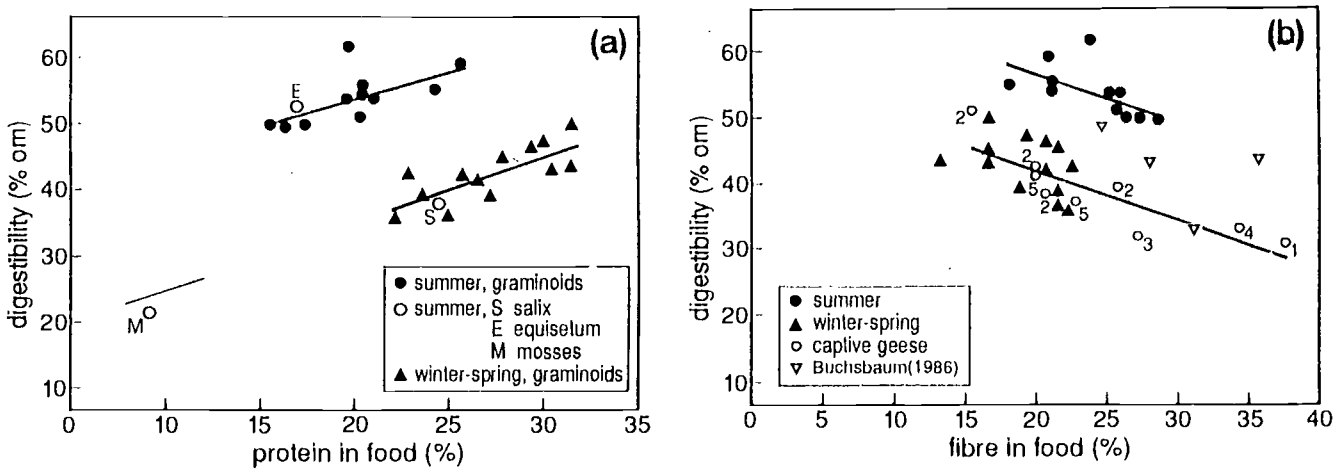


Figure 1:Relationship between organic matter digestibility and a.the protein in the food and b.the fibre in the food(Prop & Vulink,1992).

Graminoids are characterized by high protein levels,intermediate levels of cell content,and low in lignin. They are not immediately after the snow has melted and therefore the share of Graminoids in the diet of the geese will not have its optimum in the beginning of the period after the eggs have hatched(Prop & Vulink,1992).

Mosses are generally low in protein content and have also a low digestibility. The restgroup are all dicotyledons and have moderate protein levels,a high lignin content and a high cell content. The Mosses are among the most common and widespread plants in the Arctic and unlike Graminoids available throughout the summer(Prop & Vulink,1992). The buds are the only parts of Salix that can be exploited and only for a short time. Later in the season the leaves are very unattractive because of high fibre content and the incorporation of secondary compounds which lowers digestibility. The availability of good Salix parts is therefore limited to the beginning of the summer(Prop et al.,1984; Prop & Vulink,1992).Cerastium regelii which is the main species of the Rest-group,increases in biomass throughout the summer. Table 1 shows important characteristics of the food items.

	Cell content	Protein	Lignin	Digestability	Remarks
Graminoids	intermediate	high	low	high	optimum not immediately after snowmelt
Mosses	low	low	high	low	present throughout the year
Equisetum	high	moderate	low	high	minerals
Salix	high	high	high	moderate	buds
Rest	high	moderate	high	low	

Table 1:Characteristics of the five food items during post-hatching period and moult.

4.2 Behaviour and physiology

Besides collecting the droppings of the geese in 1992 on Spitsbergen other data were collected under which the development of the weight of the geese during the summer. It was found that the weight of females decreased during incubation until they are nearly starved at hatch followed by a recovery between hatch and the onset of moult. During moult the weight of the females remained constant and in the pre-migration period there was a clear increase. The weight of the males remained constant during incubation,post-hatching and moult and it showed the same increase during the pre-migration period as the weight of the females (figure 2)(Loonen,unpubl.).

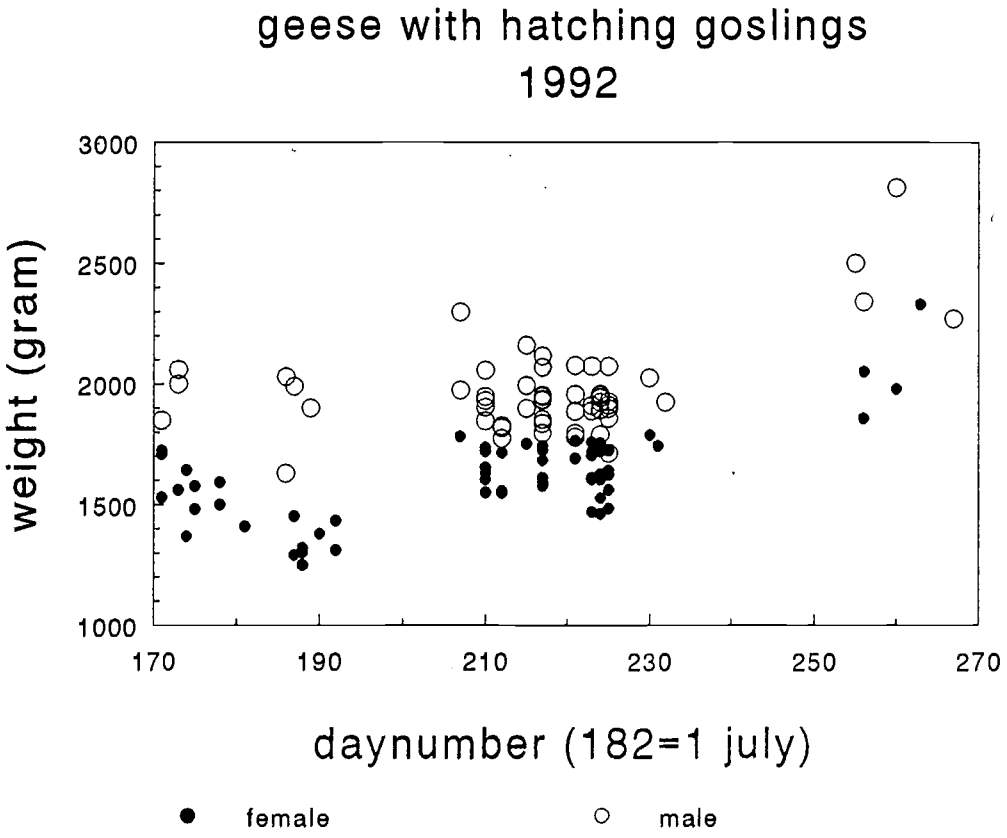


Figure 2:The development of the weights of the adults during the summer of 1992 on Spitsbergen.

Because the juveniles are growing animals their weight is increasing during the whole period. Besides that the juveniles develop during the summer longer guts. The behaviour of goslings show that there is an alternating pattern of foraging and nonforaging,which might implicate that rate of processing limits rate of food intake because a relatively constant period of time is regularly required to empty the oesophagus before foraging can be resumed. The restriction of food intake by digestive processes increase the importance of dietary nutrient concentrations because low nutrient concentrations can not be compensated for by higher rates of food intake(Sedinger & Raveling,1988).Parental behaviour of different geese species shows that the post-hatching period differs between the sexes. The males spend less time grazing than the females do and the females spend less time being vigilant(Bregnballe & Madsen,1990;Sedinger & Raveling,1990;Stroud,1982). Direct evidence of benefit derived from the male's parental effort during rearing of goslings in a monogamous,precocial bird species was found. Goslings of paired females spend more time grazing and survive with a higher probability(Schneider & Lamprecht,1990). Also positive correlations between alert and aggressive behaviours and brood size,and negative correlations between foraging time and brood size have been found (Schindler & Lamprecht,1987;Sedinger & Raveling,1990). In a recent study on the Barnacle Goose the intensity of vigilance was positively related to brood size in males,females and pairs,and also to the maximum observed distance between parents and young. The intensity of vigilance was probably directly dependent on brood size,rather than the other way around,because parents immediately decreased their vigilance when brood size decreased. The results are contrary to the prediction that vigilance should be unrelated to brood size in nidifugous bird species which do not feed their young(Forslund,1993).

4.3 Results as expected?

Firstly the analyses show that there are differences between the diets of juveniles,males and females. On average juveniles eat less Mosses and far more Equisetum than adults do. This is explicable because juveniles are growing and have therefore higher demands of the food used. Mosses are inferior in food quality as compared to other food species. On the other hand is Equisetum of a much higher quality and as for digestibility as for nutrients such as calcium,magnesium,potassium and phosphorus(Prop & Vulink,1992,Thomas & Prevett,1982).

The contrast in the Mosses share in the diet is higher in families with less than four gosling and in these families the females eat far more Salix than the rest does. When there are more goslings a family gets a higher dominance rank and therefore it will get acquisition to the better foraging places. This benefit compensates for the higher costs of the dominant behaviour. There is evidence for this because and the juveniles and the females in artificially enlarged families weigh more than other juveniles and females(Loonen & Bruinzeel,in press,Limosa).
In the larger families females eat more Graminoids,which is good because the females have to recover from a state that is close to starvation. For some of the foodcategories a trend in time has been found. There is a decreasing trend for Salix for both adults and juveniles,for Mosses for adults and for Equisetum for juveniles. For Graminoids there is an increasing trend visible for both adults and juveniles,which is decreasing again for the adults after day 30.
There are also some trends when diet is compared versus brood size. Juveniles and adults differ in these aspects considerably. The adults in small families eat far more Mosses than the adults in the larger families..The juveniles in the large families eat much more of the Rest-group (predominantly Cerastium) than the smaller families.

4.4 Problems

In this study there are some problems which have to be noted. The first is the large variation that is present in the diet within the family. Therefore differences between the families are not always easy recognisable. The second problem,the small samplesize,strengthens the first, because the large variation requires a large samplesize for significance. The differences that are present are then hard to become significant.
The third problem is that of adoption of juveniles by other families. Using the brood size in our data as an independent variable with equal distances between 1 and 2 as between 5 and 6 goslings might be questionable,because there are no nests found with more than 5 eggs. So the families with 6 or 7 goslings are families which have adopted other juveniles. In a recent examination DNA fingerprinting analysis was used to reveal cases of intraspecific nest parasitism and adoption of a foreign young. Adoption appears to be common shortly after juveniles have hatched and has been assumed to result from accidental brood mixing when parent-offspring recognition is not yet fully developed. But in this examination it was found that adoptions occur in juveniles as old as 4-12 weeks,when both parents and offspring are capable of recognizing each other,suggesting that accidental mixing alone can not explain this phenomenon(Choudhury *et al.*,1993). Do these families be-

have exactly according to the dominance rank as found when comparing single geese,couples,small and large families or do they on the contrary behave somewhat awkwardly.
The fourth problem are the possible field mistakes. In the examination of dissimilarity versus daynumber comparisons were also made excluding day 48. The data of this day were somewhat peculiar. The reason could be that the behaviour of the geese changed because they were able to fly by then. A different explanation could be that the adults were changed during observation. The engraved coloured ring with the mark BTF could easily be mistaken for BTG and vice versa. In this way the droppings could be abusively attributed to the partner.

4.5 Final conclusions

The question of the relation between brood size and diet has not been exhaustively treated in this examination. Before this examination was executed some expectations,among which the expectation that larger families would eat more of the high-quality food such as graminoids, were present. The results found in this study were in accordance with these expectations,although the differences found were not that clear as we had expected. Females in families with more than three goslings eat more Graminoids than the juveniles and males do.

4.6 Suggestions for further research

The most important suggestion is to continue this examination with more collected data,because there is a large variation within the families. More data can be collected by including more families(in this examination there are 10) in the examination. Another possibility to examine more samples of a family.
Especially the first period(3-12 july) showed significant differences, whereas the period of mid July until mid August showed no differences. When looking at smaller differences period 1 appears to be even more important.
Because the rate of changes within a juvenile is highest in the first two weeks and the juveniles compared show differences in hatch-data it might be interesting to examine the diet in relation to the hatch-data instead of julydays.

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Appendix A:Description of the plant species

In total 18 plant species have been identified in the faecal samples. All the species are grouped in five categories:Graminoids,Mosses,Salix, Equisetum and a Rest group (table 1). This grouping has been done to make comparisons more easy to do,while a certain degree of homogeneity within the groups is still guaranteed.

GRAMINOIDS	MOSSES	SALIX	EQUISETUM	REST
1.Alopecurus alpinus	1.Aulacomnium turgidum	1.Salix polaris	1.Equisetum variegetum	1.Cerastium regelii
2.Carex subpathacea	2.Calliergon			2.Draba alpina
3.Deschampsia alpina	3.Drepanocladus uncinatus			3.Minuartia biflora
4.Dupontia fisherii	4.Oncophorus wahlenbergii			4.Ranunculus pygmaeus
5.Juncus bufonius				5.Saxifraga
6.Luzula arctica				
7.Poa alpina				

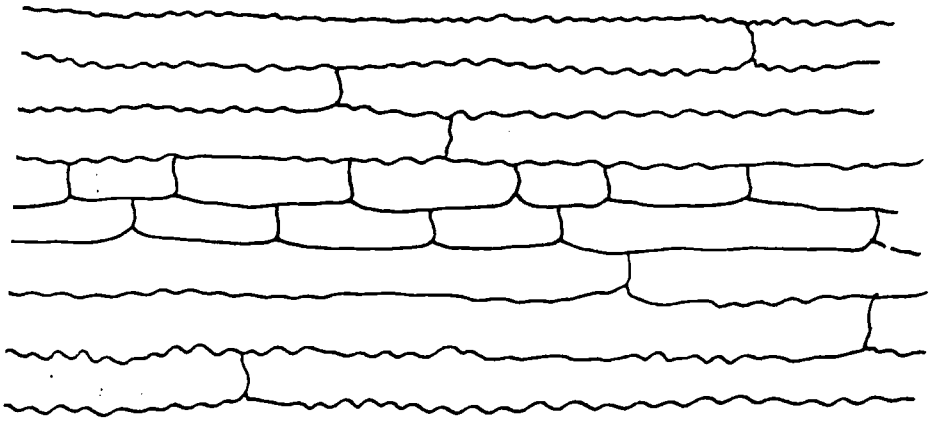
Table 1: All species that have been identified in the faecal samples.

There are also some fragments that have not been identified,but they appeared only a few times in the samples and will statistically not play a dominant role in the comparisons.

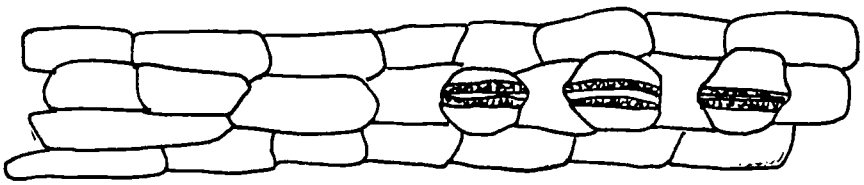
Description of the cuticles

GRAMINOIDS:

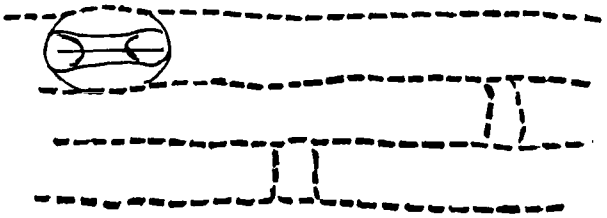
1.*Alopecurus alpinus*. Apart from the resemblances the cells are tinier than *Dupontia fisherii*(see Graminoids nr.4).



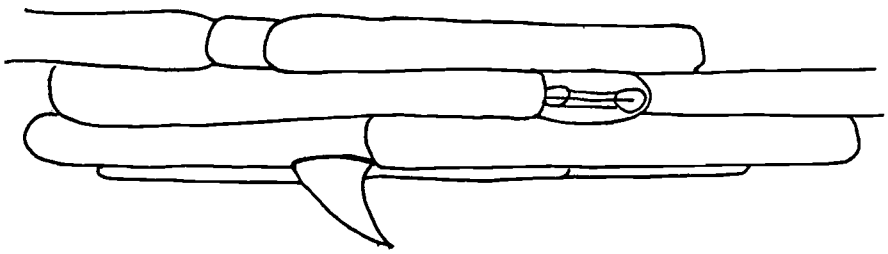
2.*Carex subpathacea*. The cells are more or less rectangular and big. Compared to the stomata of grasses(see Graminoids nrs.3,4,7)they are rounder. The cellwalls can be thin or thick.



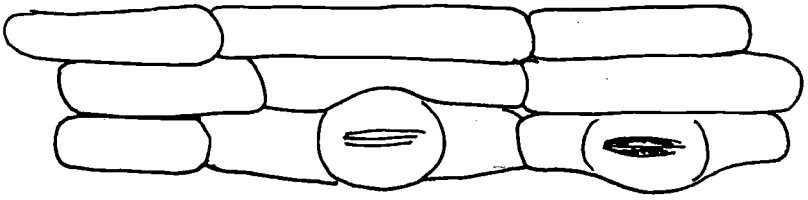
3.*Deschampsia alpina*.Lower epidermis:Clear cells with parallel cellwalls longitudinally. The cells are mostly long,now and then replaced by a short one. The stomata in the 'grass'-species are almost indistinguishable(see drawings). The cellwall is quite thick and gives the impression of being build up with 'loose bricks'. Upper epidermis: Spindle-shaped cells with smooth cellwalls.



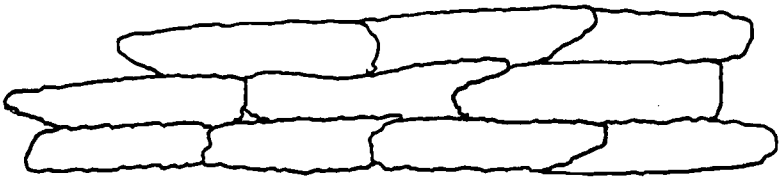
4.*Dupontia fisherii*.Lower epidermis:The cells strongly resemble those of *Deschampsia alpina*(see Graminoids nr.3). The most remarkable difference is that the cellwalls are a bit ridgy and the 'loose brick' structure is less prominently present.
The edge of the leaf often shows spines. Despite these differences it is sometimes hard to distinguish the fragments. This applies even more for the upper epidermis.



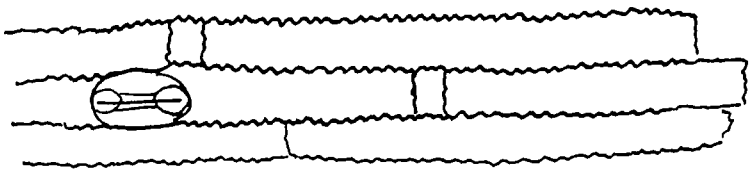
5.*Juncus bufonius*. In the slides these cells were very clear with thin cellwalls. The stomata resemble the stomata of *Carex subpathacea*(see Graminoids nr.2).



6.*Luzula arctica*. The celltypes are like the longitudinal cells of *Cerastium*(see Rest nr.1),but the cellwalls are instead of being smooth, wobbly.

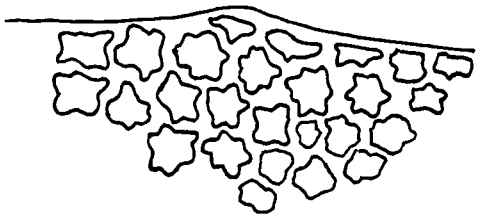


7.*Poa alpina var.viviparum*.Resembles *Dupontia fisherii* (see Graminoids nr.4)with the difference of a meandering cellwall.

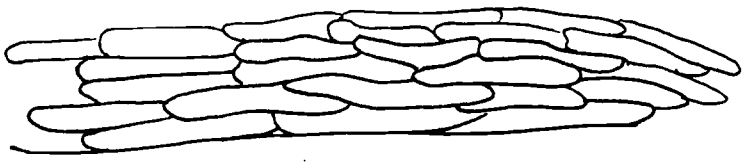


MOSSES:

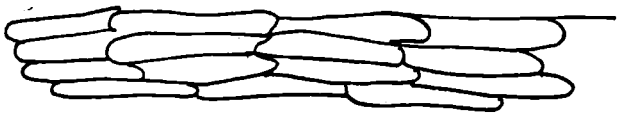
1.*Aulacomnium turgidum*.Small,irregular,clear cells that variate from squares to hexagons.The cellwall is very characteristic(sometimes thin sometimes thick).



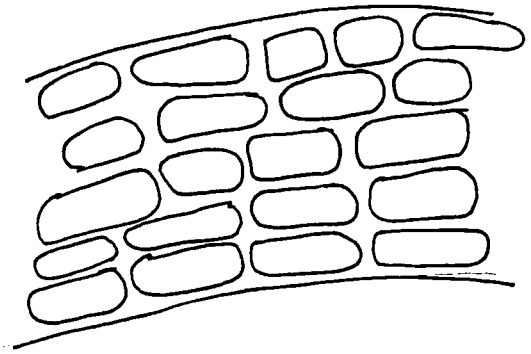
2. *Calliergon*. This genus consists of a few species that have clear,easily recognisable cells.



3. *Drepanocladus uncinatus*. This species strongly resembles the genus *Calliergon*(see Moss nr.2),but can be distinguished because at the edge the cells stick out a little. Because the fragments in the droppings do not always have an edge,the two species are lumped together and called *Calliergon*.

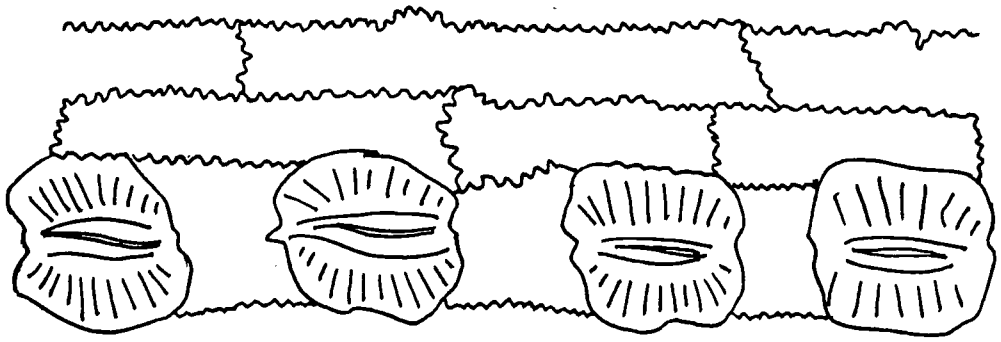


4.*Oncophorus wahlenbergii*. This species can sometimes be mixed up with *Calliergon*(see Moss nr.2),but can often be distinguished,because the form of the cells is rounder and the cellwalls are often thicker.



EQUISETUM:

1.*Equisetum variegetum*. The cells are big and coarse with thick wobbly cellwalls. The stomata are very characteristic with radial lines.

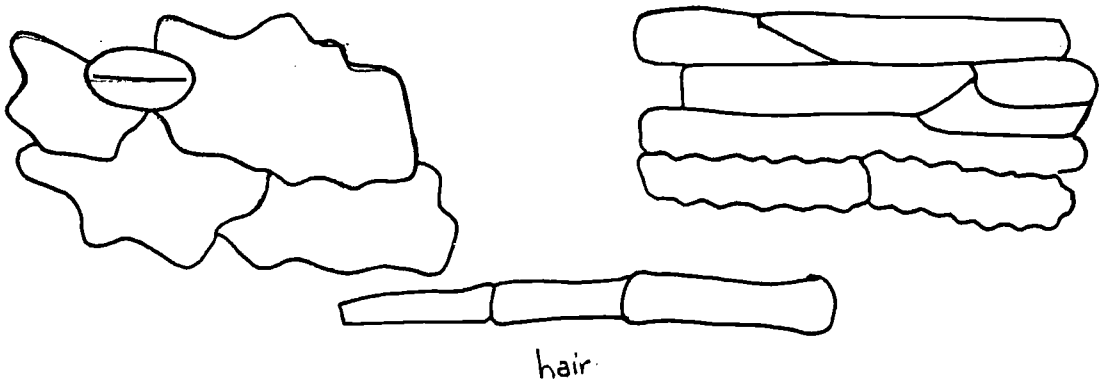


SALIX:

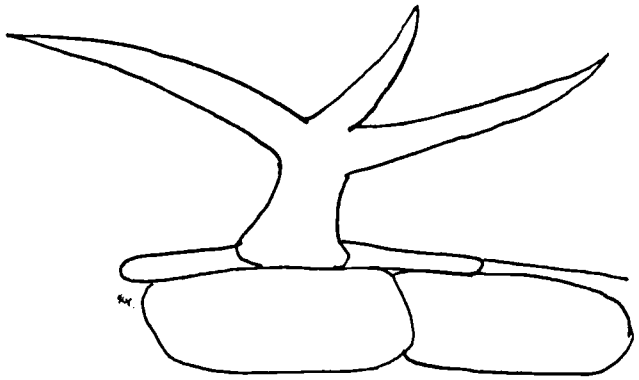
1.*Salix polaris*. Small cells that are square,rectangular or polygonic. Hairs,flexible and consisting of one part.

REST:

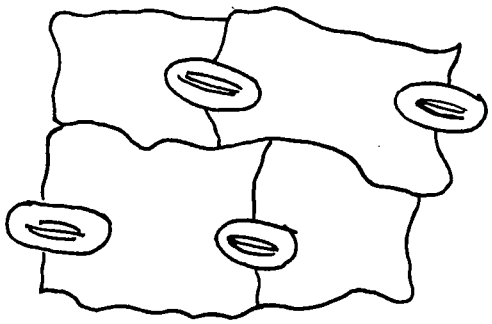
1.*Cerastium regelii*. In the fragments *Cerastium* has different appearances. Sometimes irregular,polygonic cells with thin cellwalls are found with stomata in between. Sometimes the cells in a fragment are longitudinal-shaped. Mostly the cellwalls are smooth and thin,but now and then there are meandering cellwalls. The hairs are jointed and characteristic.



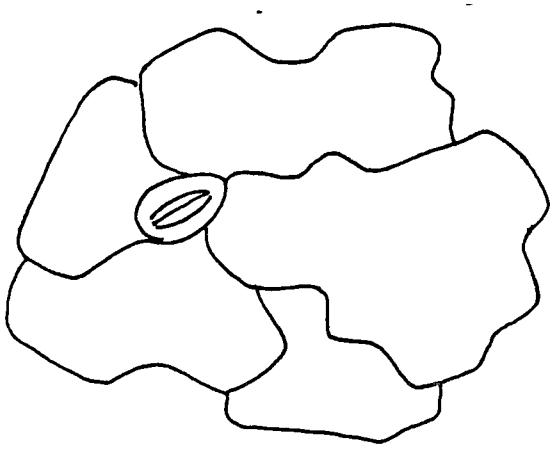
2.*Draba alpina*. The cells resemble the longitudinal and the polygonic cells of *Cerastium*(see Rest nr.1) and are sometimes very big with very thin cellwalls. When spines are present mistakes are almost impossible to make. They consist of one part with mostly two or three pointy branches.



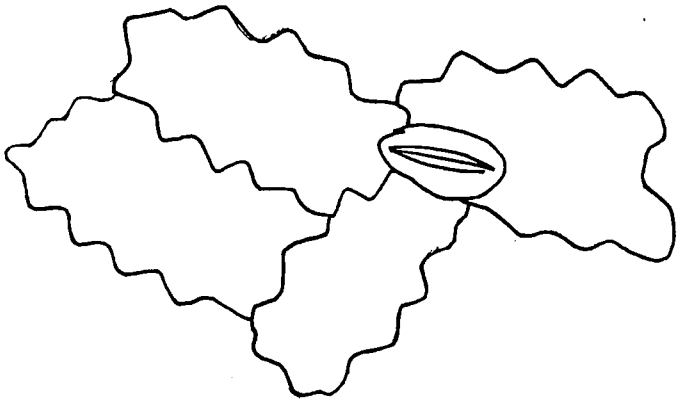
3.*Minuartia biflora*. The cells are irregular and the stomata have a characteristic position. The position is often perpendicular on the interface of two cells.



4.*Ranunculus pygmaeus*. The cells resemble the irregular,polygonic cells of *Cerastium*(see Rest nr.1). The stomata are slightly different (compare the figures).



5.*Saxifraga*. This genus has a few species. The cells are irregular polygonic,like those of *Cerastium*(see Rest nr.1),but sometimes more angular (this is probably *Saxifraga hieracifolia*). As a whole very transparent,there is nearly no contrast. There are always coloured patches with the shape of a cell within the cells.



Except for these 18 identified plantspecies there are also some unidentified fragments in the faecal samples. This can be caused by different factors. Sometimes there is dirt in the fragments and parts of them are in those cases not visible. Sometimes the fragmentation is in such a way that,although some cells are visible,the ultrastructure of the fragment is lost.
In these cases differentiation between two species that have resembling cells is impossible to do. Thirdly there are some fragments that don't fit in the description of one of the identified species and remain unknown. However all these unidentified fragments are few as compared to the identified species and are therefore statistically insignificant.

Appendix B

Mathematical specifications

1.Percentage dissimilarity (qualitative=Sørensen).

Note that the percentages have been square root transformed. This has been done because the following aspects of a diet are important:1.whether a species has been eaten or not,2.how much of a certain species has been eaten. Both aspects of the diet are better expressed in the square root transformed data. In all the following procedures the square root transformation of the data remained.
The percentage dissimilarity is used in the module **Dimat** to generate a dissimilarity-matrix,which in turn will be in the module **Ordin** to make an ordination. The equations are below(Sørensen,1948):

Sørensen coefficient: $S_s = \frac{2a}{2a+b+c}$

Dissimilarity: $D_s = \frac{b+c}{2a+b+c}$ or $1.0 - S_s$

a=number of species common to both samples
b=number of species in sample 1
c=number of species in sample 2

In this case the species are the five groups that consist of one or more species.

2.Ordin.

Polar analysis is a technique which gives a visual insight in the dissimilarities of the samples. Along the axis the samples that differ the most- and have therefore the greatest dissimilarity with respect to each other- will be placed at both extremes. All the data were square root transformed. The values at the beginning and the data at the end of an axis then will be stretched out and the middle will be compressed. This square root data transformation has been done to get more easily interpretation.

An ordination was made using two axes. The axes were standardized transformed(0-100). The program selected the reference points and an indirect analysis was done.

3.J-Plot.

In J-plot the samples were plotted according the ordination done in Ordin. The categorial plots used relative values,the percentage of the maximum *per variable*. Five classes can be distinguished:

Class 0: 0%
Class 1: ≤10%
Class 2: ≤25%
Class 3: ≤65%
Class 4: ≥65%

The data analyzed by a canonical correspondence analysis(CCA) are plotted in the subprogram J-plot.
CCA is an ordination technique which incorporates the correlation and regression between the data of the species in the diet(18) and the environmental factors(in this case brood size and daynumber) within the ordination analysis itself. The resulting ordination diagram thus expresses not only patterns of variation in species composition in the diet but also demonstrates the principal relationships between the species and each of the environmental variables(Kent & Coker 1992).

4.The Kruskal-Wallis one-way analysis of variance by ranks

This test is useful for deciding whether k independent samples(in this case k=3:1=male,2=female,3=juvenile)are from different populations.
When a significant Kruskal-Wallis value has been found,it indicates that at least one of the groups is different from at least one of the others. It does not tell which ones are different,nor does it tell how many of the groups are different from each other. We can test the significance of individual pairs of differences by using the following inequality.

If

$$|\bar{R}_u - \bar{R}_v| \geq z_{\alpha/k(k-1)} \sqrt{\frac{N(N+1)}{12}\left(\frac{1}{n_u}+\frac{1}{n_v}\right)}$$

-where k=number of groups
N=number of cases in the combined groups
R_u=average of the ranks in the *u*th group
n_u=number of cases in the *u*th group
$z_{\alpha/k(k-1)}$=abscissa value from the unit normal distribution above which lies $\alpha/k(k-1)$ percent of the distribution-then we may reject the hypothesis H_0 that there is no difference.
In period 1 for the Mosses k=3,N=17,R_1=13.00,R_2=9.80, R_3=4.33,n_1=6,n_2=5,n_3=6.

The row entries (#c) are the number of comparisons. When there are k groups,there are k(k-1)/2 comparisons possible. So for 3 groups there are 3*2/2=3 comparisons possible. For a two-tailed test with $p<0.05$ and three row entries the value of z is 2.394. The result is that when comparing group 2 with group 1 or group 3 the righthand of the inequality is $2.394*(9.35)^{0.5}=7.320$ and $|R_1-R_2| = |13.00-9.80| = 3.20$ and $|R_2-R_3| = |9.80-4.33| = 5.47$.
These differences are both smaller than 7.320 and are therefore not significant.
When comparing group 1 with group 3 the righthand of the inequality will be $2.394*(8.50)^{0.5}=6.980$ and $|R_1-R_3| = |13.00-4.33| = 8.67$.
This difference is larger than 6.980 and is significant. So males eat significant more Mosses than juveniles do(Siegel,S. & Castellan,Jr.N., 1988).

5.Curve.

In the subset Curve of the program Vegrow five models are generated that are ranked according to the increasing complexity of the biological information contained.

Model 1: no significant trend in space or time;
Model 2: an increasing or decreasing trend where the maximum is equal to the upper bound M;
Model 3: an increasing or decreasing trend where the maximum is below the upper bound M;
Model 4: increase and decrease by the same rate: symmetrical response curve;
Model 5: increase and decrease by different rates: skewed response curve.

The following consistent set of logistic equations can be used for positive data with an upper bound M:

Model 1: $y=M*(1+\exp(b))^{-1}$

Model 2: $y=M*(1+\exp(a*x+b))^{-1}$

Model 3: $y=M*(1+\exp(a*x+b))^{-1}*(1+\exp(d))^{-1}$

Model 4: $y=M*(1+\exp(a*x+b))^{-1}*(1+\exp(a*x+c))^{-1}$

Model 5: $y=M*(1+\exp(a*x+b))^{-1}*(1+\exp(d*x+c))^{-1}$

The figures 8 up to 13 inclusive in the chapter 'Results' have been generated with these equations. The upper bound M equals 10 in these cases because the percentages have been square root transformed(the square root of 100 equals 10).
The x-values have been standardized according to this equation: $(X-X_{min})/(X_{max}-X_{min})$. So in the case of comparing the diet to the day-number((x-3)/45) is filled in where in the general formulas x is found. And in the same way ((x-1)/6) is used when the diet was compared to the brood size.

The values of the exponents in the equations:

All samples,daynumber:Graminoids model 2 a=-3.982, b=0.571;Mosses model 2 a=10.972,b=-3.114;Equisetum model 2 a=6.072,b=0.444;Salix model 2 a=7.665, b=-1.069;Rest model 3 a=15.285,b=-1.164,d=0.676;Cerastium model 3 a=-15.283,b=-1.063,d=0.773.

Adults,daynumber:Graminoids model 4 a=-3.497,b=0.509, c=3.497,d=-3.642;Mosses model 2 a=10.134,b=-3.415; Equisetum model 1 b=3.141;Salix model 2 a=6.146, b=0.374;Rest model 1 b=0.721;Cerastium model 1 b=0.782.

Juveniles,daynumber:Graminoids model 2 a=-2.762, b=0.578;Mosses model 1 b=0.383;Equisetum model 2 a=9.050,b=-0.901;Salix model 2 a=2.665,b=1.431;Rest model 1 b=0.211;Cerastium model 1 b=0.278.

All samples,brood size:Graminoids model 1 b=-0.502; Mosses model 1 b=0.326;Equisetum model 1 b=1.772;Salix model 5 a=6.858,b=-2.822,c=-9.358,d=4.875;Rest model 2 a=-2.000,b=1.426;Cerastium model 2 a=-2.194,b=1.609.

Adults,brood size:Graminoids model 1 b=-0.747;Mosses model 2 a=17.167,b=-2.216;Equisetum model 1 b=2.696; Salix model 5 a=15.168,b=-10.111,c=-2.511,d=2.686;Rest model 1 b=0.644;Cerastium model 1 b=0.709.

Juveniles,brood size:Graminoids model 1 b=-0.047;Mosses model 1 b=0.550;Equisetum model 1 b=0.650;Salix model 3 a=-9.796,b=4.015,d=2.442;Rest model 2 a=-3.951, b=1.442;Cerastium model 2 a=-5.259,b=2.066.

Appendix C

Average diet(percentages)

MALES

per species

	CC 03 M4 12	DD 07 M5 6	C- 07 M2 7	D- 07 M3 9	AA 08 M7 12	A- 08 M3 16	EE 24 M4 18	BB 25 M5 22	E- 25 M1 25	B- 25 M2 26	A- 26 M3 30	EE 26 M4 33	AA 26 M7 34	AA 29 M7 37	A- 29 M3 41	AA 30 M7 46	A- 30 M3 47	B- 30 M2 50	BB 33 M5 52	B- 33 M2 54	BB 48 M5 62	B- 48 M2 65
ALO	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUL	1	0	4	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CAL	22	75	45	44	27	49	12	3	75	1	0	74	1	0	1	0	0	4	23	7	7	7
CAR	0	0	0	2	0	0	6	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1
CER	3	0	6	12	52	11	15	23	2	8	6	3	64	1	8	11	9	9	38	16	8	33
DES	1	0	0	0	0	0	11	0	3	0	2	3	0	0	0	0	0	8	0	0	0	0
DRA	3	0	2	1	0	0	1	1	0	0	0	2	9	0	1	4	11	6	0	0	1	1
DUP	3	24	9	10	17	32	50	58	17	85	89	14	16	97	8	76	73	56	28	72	0	43
EQU	14	0	9	3	0	0	0	0	0	0	0	0	0	0	67	0	0	0	4	0	2	5
JUN	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
LAR	0	1	0	0	0	0	0	2	0	0	2	0	0	0	9	0	4	1	2	0	0	7
MIN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MOS	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	0	0	0
ONC	0	0	0	3	1	0	1	0	1	0	0	0	6	0	2	5	0	0	3	0	1	0
POA	1	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0	0	10	0	0	0	0
RAN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SAL	45	0	13	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	77	0
SAX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
X	7	0	13	21	2	2	4	5	2	4	1	4	3	2	2	4	3	2	1	5	6	4

all males		period 1 males		period 2 males		period 3 males		period 4 males	
avg	ste	avg	ste	avg	ste	avg	ste	avg	ste
0.1	0.1	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0
0.3	0.2	1.2	0.2	0.2	0.2	0.0	0.0	0.0	0.0
21.7	5.5	42.6	5.5	23.3	11.7	19.1	15.8	6.9	2.7
0.6	0.3	0.4	0.3	1.1	0.8	0.1	0.1	0.6	0.3
15.4	3.5	14.7	3.5	10.9	2.7	18.8	13.0	17.7	4.4
1.3	0.6	0.2	0.6	2.7	1.6	0.7	0.6	1.1	1.0
1.9	0.6	0.9	0.6	0.4	0.2	3.1	1.8	3.2	1.4
39.7	6.5	12.3	6.5	55.2	10.7	33.7	18.3	49.5	9.8
4.7	3.0	5.1	3.0	0.0	0.0	16.8	14.5	1.4	0.7
0.1	0.1	0.0	0.1	0.5	0.3	0.0	0.0	0.0	0.0
1.3	0.5	0.2	0.5	0.7	0.4	2.4	2.0	1.9	0.9
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.3	0.1	0.2	0.1	0.0	0.0	0.4	0.2	0.5	0.3
1.0	0.3	0.8	0.3	0.2	0.1	2.0	1.1	1.2	0.6
0.9	0.5	0.5	0.5	1.1	0.9	0.0	0.0	1.4	1.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6.4	3.9	12.2	3.9	0.7	0.6	0.0	0.0	10.9	10.1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4.4	0.9	8.5	0.9	3.0	0.7	3.0	0.4	3.5	0.5

MALES

	CC 03 M4 2	DD 07 M5 6	C- 07 M2 7	D- 07 M3 9	AA 08 M7 12	A- 08 M3 16	EE 24 M4 18	BB 25 M5 22	E- 25 M1 25	B- 25 M2 26	A- 26 M3 30	EE 26 M4 33	AA 26 M7 34	AA 29 M7 37	A- 29 M3 41	AA 30 M7 46	A- 30 M3 47	B- 30 M2 50	BB 33 M5 52	B- 33 M2 54	BB 48 M5 62	B- 48 M2 65	all males avg	all males ste	period 1 males avg	period 1 males ste	period 2 males avg	period 2 males ste	period 3 males avg	period 3 males ste	period 4 males avg	period 4 males ste
per group(without X=unidentified fragments)																															
MOS	23	75	49	49	28	50	13	3	76	1	0	74	8	1	4	5	1	6	26	7	8	7	23.3	5.5	44.7	5.5	23.7	11.8	21.6	15.2	8.5	2.8
GRA	6	24	9	13	17	32	67	68	20	88	93	17	16	97	18	76	77	77	30	72	0	50	44.0	6.7	17.0	3.7	59.4	8.9	51.0	14.5	25.2	17.8
SAL	45	0	13	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	77	0	6.4	3.9	10.8	6.6	0.0	0.0	0.0	0.0	38.3	27.1
RES	5	0	8	13	52	11	16	33	4	14	8	9	76	3	21	20	27	21	42	21	91	45	17.3	3.7	14.9	7.1	16.1	5.3	27.4	7.8	21.1	9.0
EQU	14	0	9	3	0	0	0	0	0	0	0	0	0	0	67	0	0	0	4	0	2	5	4.7	3.0	5.1	3.0	0.0	0.0	16.8	14.5	1.4	0.7

Average diet(percentages)
FEMALES

	CC 03 F4 1	DD 07 F5 4	D- 07 F3 10	AA 08 F7 13	A- 08 F3 14	EE 24 F4 19	BB 25 F5 21	E- 25 F1 24	B- 25 F2 27	A- 26 F3 28	EE 26 F4 31	AA 26 F7 36	AA 29 F7 38	A- 29 F3 42	AA 30 F7 44	A- 30 F3 48	B- 30 F2 49	BB 31 F5 51	B- 33 F2 55	BB 33 F5 57	BB 48 F5 60	B- 48 F2 64	all females		period 1 females		period 2 females		period 3 females		period 4 females	
per species																							avg	ste	avg	ste	avg	ste	avg	ste	avg	ste
ALO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AUL	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.1	0.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0
CAL	17	37	30	31	22	2	3	40	0	0	63	2	2	10	0	2	2	0	27	0	4	92	17.5	5.0	27.1	3.2	9.7	5.2	13.6	9.4	48.2	31.3
CAR	0	1	0	0	0	1	1	0	1	1	2	5	0	0	0	3	0	0	1	0	4	0	0.9	0.3	0.2	0.1	1.0	0.4	0.6	0.4	2.0	1.4
CER	2	13	0	12	6	7	16	7	6	6	0	53	10	60	2	39	19	5	12	9	13	5	13.6	3.4	6.6	2.3	17.5	5.3	10.5	1.3	8.6	2.9
DES	1	8	0	1	0	40	0	9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2.8	1.8	2.1	1.4	3.9	3.0	0.0	0.0	0.0	0.0
DRA	0	0	0	1	0	1	0	0	0	0	8	10	0	1	0	0	0	0	0	0	2	0	1.1	0.5	0.2	0.2	1.6	0.9	0.0	0.0	0.9	0.6
DUP	50	35	0	24	43	39	65	27	87	71	22	14	88	22	96	55	73	88	56	78	14	0	47.5	6.3	30.2	7.8	57.3	7.8	67.2	7.8	7.1	5.0
EQU	3	0	0	27	1	0	0	1	0	0	0	0	0	6	0	0	0	0	0	0	12	0	2.3	1.3	6.1	4.7	0.5	0.4	0.0	0.0	6.1	4.3
JUN	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0.2	0.1	0.0	0.0	0.2	0.1	0.5	0.4	0.0	0.0
LAR	0	0	0	0	0	0	3	0	0	15	0	0	0	0	0	0	0	2	0	6	1	0	1.2	0.7	0.0	0.0	1.5	1.1	2.8	2.0	0.4	0.3
MIN	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0
MOS	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.0	0.3	0.1	0.0	0.0	0.0	0.0	0.2	0.1
ONC	1	2	6	1	1	0	0	8	0	0	0	2	0	0	0	0	0	0	0	0	7	0	1.2	0.5	2.1	1.0	0.7	0.6	0.2	0.1	3.4	2.4
POA	1	0	2	0	0	0	8	0	3	7	3	12	0	0	0	0	7	2	3	5	0	0	2.3	0.7	0.4	0.3	3.2	1.1	3.8	0.6	0.0	0.0
RAN	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.3	0.0	0.0	0.5	0.5	0.0	0.0	0.0	0.0
SAL	18	0	57	0	21	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	40	0	6.3	3.1	19.0	9.3	0.3	0.2	0.0	0.0	20.0	14.1
SAX	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.2	1.1	0.7	0.0	0.0	0.0	0.0	0.0	0.0
X	5	4	4	3	1	4	4	5	1	1	2	4	0	1	2	1	0	4	0	2	4	3	2.4	0.3	3.4	0.6	2.1	0.5	0.9	0.6	3.5	0.6

FEMALES

	CC 03 F4 1	DD 07 F5 4	D- 07 F3 10	AA 08 F7 13	A- 08 F3 14	EE 24 F4 19	BB 25 F5 21	E- 25 F1 24	B- 25 F2 27	A- 26 F3 28	EE 26 F4 31	AA 26 F7 36	AA 29 F7 38	A- 29 F3 42	AA 30 F7 44	A- 30 F3 48	B- 30 F2 49	BB 31 F5 51	B- 33 F2 55	BB 33 F5 57	BB 48 F5 60	B- 48 F2 64	all females avg	all females ste	period 1 females avg	period 1 females ste	period 2 females avg	period 2 females ste	period 3 females avg	period 3 females ste	period 4 females avg	period 4 females ste
per group(without X=unidentified fragments)																																
MOS18	39	37	33	24	2	3	48	0	0	63	3	2	10	0	2	2	0	27	0	11	93		19.0	5.2	30.2	3.6	10.4	5.5	13.8	9.5	51.7	29.1
GRA52	44	2	25	43	79	77	36	92	93	27	31	88	22	96	58	80	92	60	89	19	0		54.8	6.6	32.9	8.0	67.1	7.6	74.9	10.3	9.4	6.6
SAL18	0	57	0	21	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	40	0		6.3	3.1	19.0	9.3	0.3	0.2	0.0	0.0	20.0	14.1
RES	5	13	0	13	11	14	16	7	7	6	8	62	10	61	2	39	19	5	12	9	14	5	15.3	3.5	8.4	2.3	19.6	5.6	10.5	1.3	9.5	3.5
EQU	3	0	0	27	1	0	0	1	0	0	0	0	0	6	0	0	0	0	0	0	12	0	2.3	1.3	6.1	4.7	0.5	0.4	0.0	0.0	6.1	4.3

Average diet (percentages)
JUVENILES

	CC 03 J4 3	DD 07 J5 5	C- 07 J2 8	D- 07 J3 11	A- 08 J3 15	AA 08 J7 17	EE 24 J4 20	E- 25 J1 23	A- 26 J3 29	EE 26 J4 32	AA 26 J7 35	AA 29 J7 39	A- 29 J3 40	A- 30 J3 43	AA 30 J7 45	BB 33 J5 53	B- 33 J2 56	AA 44 J7 58	A- 44 J3 59	BB 48 J5 61	B- 48 J2 63	all juv.		period 1 juv.		period 2 juv.		period 3 juv.		period 4 juv.	
per species																						avg	ste	avg	ste	avg	ste	avg	ste	avg	ste
ALO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AUL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0.0	0.0	0.1	0.0	0.0	0.0	0.3	0.2	0.0	0.0
CAL	10	7	6	7	7	34	5	56	1	73	1	6	1	0	0	21	15	1	0	9	8	12.8	4.1	11.9	4.1	16.0	8.8	18.2	2.1	4.4	2.0
CAR	0	0	0	1	0	0	2	0	0	0	2	1	8	13	1	2	0	14	15	1	2	2.9	1.0	0.1	0.1	2.9	1.4	1.2	0.8	7.8	3.3
CER	3	26	11	33	6	39	12	2	18	2	7	17	35	4	22	34	9	42	17	48	22	19.4	3.0	19.4	5.6	13.4	3.4	21.1	8.8	32.3	6.6
DES	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	1	0	1	0.3	0.3	0.0	0.0	0.6	0.6	0.0	0.0	0.3	0.2
DRA	1	0	0	1	1	1	1	3	3	0	3	1	0	0	2	2	0	1	0	0	2	1.1	0.2	0.9	0.2	1.4	0.4	0.8	0.6	0.9	0.4
DUP	19	5	4	43	11	6	66	26	69	17	85	63	8	69	65	24	60	22	27	13	46	35.6	5.6	14.8	5.6	51.9	8.6	41.7	12.8	27.1	6.0
EQU	53	47	77	5	69	1	0	0	0	0	0	7	43	0	0	3	0	0	0	14	1	15.1	5.4	41.8	12.0	5.5	4.5	1.3	0.9	3.8	3.0
JUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0.4	0.3	0.0	0.0	0.0	0.0	3.9	2.5	0.0	0.0
LAR	0	0	0	7	0	0	7	0	0	0	0	0	3	14	1	1	0	15	39	0	1	4.3	2.0	1.1	1.0	2.8	1.5	0.7	0.5	14.0	7.9
MIN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
MOS	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0.2	0.1	0.3	0.1	0.1	0.1	0.2	0.2	0.1	0.1
ONC	5	0	2	0	4	1	5	0	1	2	0	1	0	0	0	4	2	0	0	9	3	1.8	0.5	1.8	0.7	1.0	0.5	2.8	0.6	3.1	1.9
POA	0	0	0	0	0	0	0	0	0	0	0	2	0	0	9	2	5	1	0	0	8	1.3	0.6	0.0	0.0	1.2	0.9	3.7	1.1	2.4	1.7
RAN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SAL	6	10	0	0	0	9	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1.5	0.7	4.3	1.8	0.2	0.1	0.7	0.5	0.6	0.3
SAX	0	0	0	0	0	2	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0.3	0.3	0.3	0.7	0.6	0.0	0.0	0.0	0.0
X	4	4	0	4	1	8	2	7	1	6	1	2	1	0	0	6	1	3	2	3	4	2.9	0.5	3.4	1.0	2.3	0.8	3.4	1.5	3.1	0.4

JUVENILES

	CC 03 J4 3	DD 07 J5 5	C- 07 J2 8	D- 07 J3 11	A- 08 J3 15	AA 08 J7 17	EE 24 J4 20	E- 25 J1 23	A- 26 J3 29	EE 26 J4 32	AA 26 J7 35	AA 29 J7 39	A- 29 J3 40	A- 30 J3 43	AA 30 J7 45	BB 33 J5 53	B- 33 J2 56	AA 44 J7 58	A- 44 J3 59	BB 48 J5 61	B- 48 J2 63	all juveniles avg	all juveniles ste	period 1 juv. avg	period 1 juv. ste	period 2 juv. avg	period 2 juv. ste	period 3 juv. avg	period 3 juv. ste	period 4 juv. avg	period 4 juv. ste
per group (without X=unidentified fragments)																																
MOS	15	8	9	7	11	35	10	56	2	75	1	7	2	0	0	25	18	1	0	19	11	14.8	4.1	14.1	3.9	17.1	8.8	21.6	2.7	7.6	3.9
GRA	19	5	4	50	11	6	75	32	69	17	87	66	18	96	75	30	73	53	82	15	58	44.8	6.6	16.0	6.6	59.4	9.3	51.2	15.1	51.8	12.0
SAL	6	10	0	0	0	9	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1.5	0.7	4.3	1.8	0.2	0.1	0.7	0.5	0.6	0.3
RES	4	26	11	34	7	42	13	5	27	2	10	18	35	4	25	35	9	43	17	48	24	20.9	3.1	20.6	5.8	15.5	3.6	22.0	9.5	33.1	6.5
EQU	53	47	77	5	69	1	0	0	0	0	0	7	43	0	0	3	0	0	0	14	1	15.1	5.4	41.8	12.0	5.5	4.5	1.3	0.9	3.8	3.0