#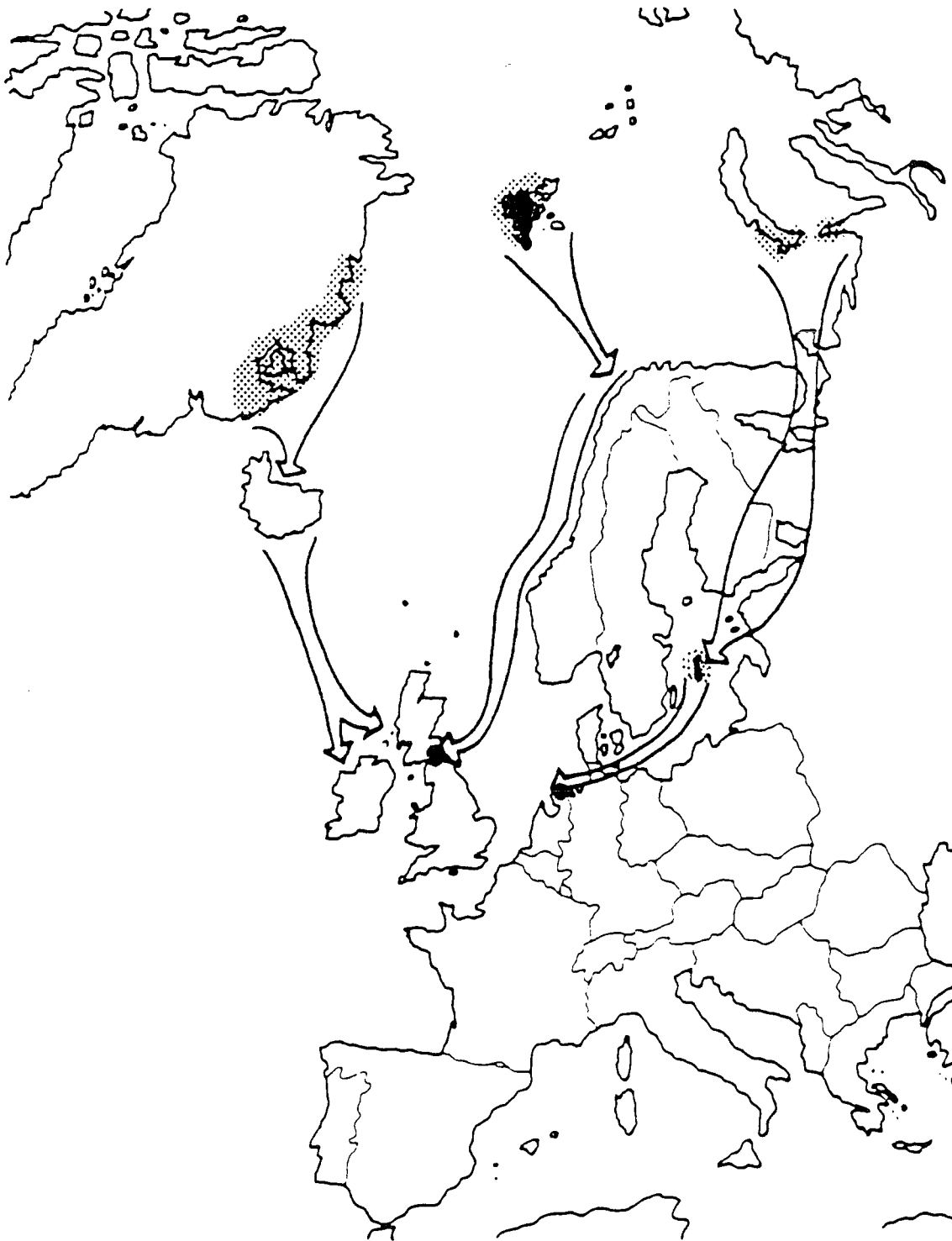 Temperate breeding in Barnacle Geese (*Branta leucopsis*): factors affecting growth and quality of food on Gotland, Sweden.

Ineke van der Veen, Student report, University of Groningen, The Netherlands.

Temperate breeding in Barnacle Geese (*Branta leucopsis*): factors affecting growth and quality of food on Gotland, Sweden.

Student report, "doctoraal verslag subfase III".

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April 1994, University of Groningen, The Netherlands.

Abstract

In this report the phenology of food plants of Barnacle Geese breeding on Gotland (temperate zone) is investigated. Both study seasons (1992 and 1993) were very dry and grass growth was found to be inhibited by the lack of rain. Not all investigated species reacted in the same way to the lack of water. *Agrostis stolonifera* and *Festuca rubra* showed a comparable and strong reaction while *Puccinellia maritima* showed little reaction to the lack of rain. *Puccinellia* is growing closer to the sea and has probably better access to seawater. A watering experiment on the *Festuca* dominated vegetation showed that the decrease in production was slowed down when there was extra water.

Not only production, but also nitrogen content of *Festuca* and *Agrostis* was decreasing during the season. The nitrogen content of *Puccinellia* increased during the season. At the end of the season, in the pre-migration period, the nitrogen content of *Festuca* and *Agrostis* increased again, after periods with rain. This seems to indicate that growth on this saltmarsh is primarily limited by water and not by nitrogen, as is the case in most arctic breeding areas. When there was sufficient water, nitrogen content was high, even late in the season.

As the nitrogen content on the *Festuca* dominated vegetation decreased, the grazing pressure on this vegetation type also decreased.

On Gotland, goose grazing had a stimulating effect on grass growth through the whole season. The increase in growth could not be accomplished by fertilization through goose droppings alone, as fertilization with droppings showed no effect.

Nitrogen contents of food plants in the moulting period on Gotland were in the same order as those found by others on Spitsbergen (arctic zone). Also the observed total feeding time per day was in the same order as found on Spitsbergen. However, the Gotlandic geese seemed to have a lower digestion efficiency. In this respect the Gotlandic geese might be at a disadvantage on the breeding grounds compared to arctic breeding geese.

Acknowledgements

Contents

1 Introduction

Geese are herbivores. They are totally dependent on the quality of some plant species, because of their limited capacity to digest plants (Drent & Prins 1987). Differences in food quality can affect body condition (Coleman & Boag 1987), which can affect different life history parameters (Sedinger & Raveling 1984).

For example, the geese that are the heaviest after spring fattening, have the highest chance to come back with young in the next winter (Ebbinge & Spaans 1992). Females depend on their body reserves during incubation (Ankney 1977), and depletion of body reserves is the underlying cause of reproductive failure in geese (Prop & De Vries 1993). Also moult is a nutrient-costly (Owen 1980) and energetic expensive process for geese. Geese can not maintain high body weight during wing moult (Van der Wal 1992).

For goslings good food quality is even more important, because they have to synthesize all their feathers, a skeleton and muscles in a short period (Ankney 1979). The nutritive value of the gosling diet is affecting gosling growth (Cooch et al. 1991, Larsson & Forslund 1991), and seasonal decline in gosling growth rates is resulting from seasonal variation in food quality or availability (Sedinger 1986, Cooch et al. 1991, Sedinger & Flint 1991). The underlying cause of gosling mortality may often be competition for food which, for example, may make goslings more vulnerable to predation, chilling and diseases (Forslund 1993, Williams et al. 1993, Larsson & Forslund 1995).

Differences in growth rate of goslings may affect their fitness in two ways: slower growing birds may have lower recruitment probabilities into the breeding population (Cooke et al. 1984, Sedinger & Raveling 1984, Cooch et al. 1991, Prop & De Vries 1993) and low growth rate affects final adult body size (Cooch et al. 1991, Larsson & Forslund 1991), and that may influence fecundity or adult survival (Sedinger & Raveling 1984, Cooch et al. 1989, Cooch et al. 1991, Williams et al. 1993). Therefore it is important for geese to select for high quality food.

A lot of grass species show a seasonal decline in growth rate (Thorvaldsson 1987a). Rate of growth, decrease in crude protein content and decline in digestibility of grass are affected by many external factors, such as temperature, solar radiation, water supply, nitrogen mineralization and fertilizer application. Genetic factors are also of importance. All these factors cause a variation between years and places in growth and nutritional value of grass (Thorvaldsson & Andersson 1986). Differences in weather cause differences in nutritive value of the food, which causes difference in survival of goslings (Larsson & Forslund 1991).

Increased temperature accelerates the rate of development of grass, especially the rate of leaf production (Thorvaldsson 1987b, Pruis 1992) and the phenologic development (Thorvaldsson 1987b). Also the amount of ammonia volatilization increases with increasing ambient temperature (Ruess et al. 1989), diminishing the nitrogen availability in the soil.

Water deficiency tends to increase the rate of morphological development, but also the rate of decline in leaf proportion (Thorvaldsson 1987b). Too much rain has the effect of washing

soluble nitrogen from droppings (Bazely & Jefferies 1985), and thus diminishing the nitrogen availability.

Some studies have shown that water is the limiting factor for growth, by experimental treatment of the vegetation (Prins 1988, Georgiadis *et al.* 1989). However, those experiments were done on dry savanna grassland vegetation in Africa. When water is limiting, rainfall has, through its influence on primary production, an influence on the built up of animal populations (Prins & Loth 1988, Bayliss 1989).

In chapter 3 I will study the growth of three different grass species from the saltmarsh used by the Gotlandic Barnacle Geese to raise their young. The influence of weather parameters on the growth of those grass species will be investigated, and the results of a watering experiment will be described. The significance of the effects of water for the geese will be discussed.

In a lot of studies the effect of grazing on vegetation has been investigated and a lot of different effects were found.

One important effect is that grazing influences the species composition of the vegetation (Bazely & Jefferies 1986, Bakker 1987, Milchunas & Lauenroth 1993). Grazing or clipping can increase the nitrogen level of grass (Ydenberg & Prins 1981, Day & Detling 1990) or the production of the vegetation (McNaughton 1976, Prins *et al.* 1980, Cargill & Jefferies 1984b, Sedinger & Raveling 1986, Kotanen & Jefferies 1987, Bazely & Jefferies 1989b, Day & Detling 1990, Hik & Jefferies 1990, Bergeron & Jodoin 1993). Those effects can still be noticed in the following season (Bergeron & Jodoin 1993). On the other hand, in other studies no effect of grazing or clipping on the nitrogen content (Bergeron & Jodoin 1993) and the production (Bédard *et al.* 1986, Abdul Jalil & Patterson 1989, Faber 1989, Madsen 1989, Hik *et al.* 1991, Prop 1991) could be detected. It was shown that the effect of grazing depends on the length of the grazing period (Prins *et al.* 1980, Hik & Jefferies 1990).

Nitrogen levels can not only be increased by grazing or clipping, but the period in which nitrogen levels are high can also be prolonged (Ydenberg & Prins 1981, Cargill & Jefferies 1984b, Sedinger & Raveling 1986, Hik & Jefferies 1990), or high production (Cargill & Jefferies 1984b, Kotanen & Jefferies 1987). It has been experimentally shown that clipping increases the nitrogen uptake of a plant (Wallace & Macko 1993).

The results of all these studies emphasize that plant production responses to defoliation can vary widely (Georgiadis *et al.* 1989).

There are different observed or proposed mechanisms for increased primary production after grazing: (1) increased photosynthetic rates in tissue remaining or produced after grazing, (2) increased proportion of photosynthate allocated to production of new leaf area, (3) increased tillering or lateral bud growth from either removal of apical dominance or opening of the canopy and increasing light penetration, (4) conservation of soil moisture by reducing transpirational leaf area (Hilbert *et al.* 1981) and (5) enhanced production of vegetative propaluges. Large numbers of

leaves, shoots and rooted tillers are released into the environment and some of these can establish in soft sediment (Chou *et al.* 1992).

It is proposed that grasses exhibit adaptations that suggest mutualism with grazers, like high palatability, vegetative reproduction and basal meristem position (Owen & Wiegert 1981), which is not destroyed when a shoot is grazed (Kotanen & Jefferies 1987). Another proposed adaptation is that salvia of animals stimulates grass growth, but a lot of controversy has arisen over this subject (Owen & Wiegert 1981).

Grazing can probably stimulate primary production by accelerating N cycling (Cargill & Jefferies 1984b). An extra effect in this is that grazing creates more open space, from which cyano bacteria can benefit, which results in higher nitrogen fixation (Bazely & Jefferies 1989a). The rapid recycling of nitrogen in a soluble form appears to be essential to maintain the growth rate of the forage specie on a sub-arctic saltmarsh (Bazely & Jefferies 1985).

Another way in which herbivores can influence the vegetation is through fertilization by their droppings. A lot of experiments have been done to asses the effect of fertilization on the vegetation. Those studies show that fertilization can influence species composition (Jefferies & Perkins 1977), increase nitrogen content (Bazely & Jefferies 1985), and production (Fletcher & Shaver 1983, Balkenhol *et al.* 1984, Day & Detling 1990, Manseau & Gauthier 1993). However, a lot of those experiments have been done with amounts of fertilizers that do not reflect the natural amounts accomplished by grazing. Natural amounts of goose droppings can either stimulate (Bazely & Jefferies 1985, Madsen 1989), or have no effect on production (Wiersma 1991), depending on the geographical location, time of year and limitations of the system.

It has been shown that areas which were fertilized, what enhances the food quality, were used more intensively by geese than unfertilized areas (Percival 1993). In some areas, shifts in diet and habitat have been reported, because of depletion of high quality food. This reduced the nutritional quality of the diet as brood rearing progressed (Sedinger & Raveling 1986, Cooch *et al.* 1991, Sedinger & Flint 1991, Prop & Vulink 1992).

By field observations it has been shown that after grazing, utilization of an area increases, either by other herbivorous species (McNaughton 1976), or by the same species. For Barnacle Geese on their wintering grounds it has been shown that this occurs with very regular intervals (Prins *et al.* 1980, H. van der Jeugd unpubl. data), which is said to accomplish the highest regrowth of the plant (Prins *et al.* 1980).

In chapter 4 I will study the effect of grazing by geese and fertilization by droppings on the vegetation of the saltmarsh used by . The effects of grazing will be studied in different periods of growth of the goslings.

2 Methods

Study population

Since the seventies there has been an increase in the numbers of arctic breeding geese that winter in Europe (Ebbinge et al. 1975, Ebbinge 1985). One of those arctic breeding species is the Barnacle goose (*Branta leucopsis*). There are three populations of Barnacle Geese distinguishable by their breeding and wintering areas. The Greenland population breeds on Greenland and winters in northwest Ireland and Scotland, the Spitsbergen population breeds on Spitsbergen and winters in southwest Scotland, the Russian population breeds on Novya Zemlya and winters in the Netherlands and Germany (Owen 1980, Madsen 1991).

While migrating from their wintering grounds in the Waddensea area to their breeding grounds in arctic Russia, the Russian Geese stopover in the Baltic area (fig 1). The geese are using Gotland (Sweden) to gain fat storage for the rest of their migration flight to arctic Russia (Owen 1980).
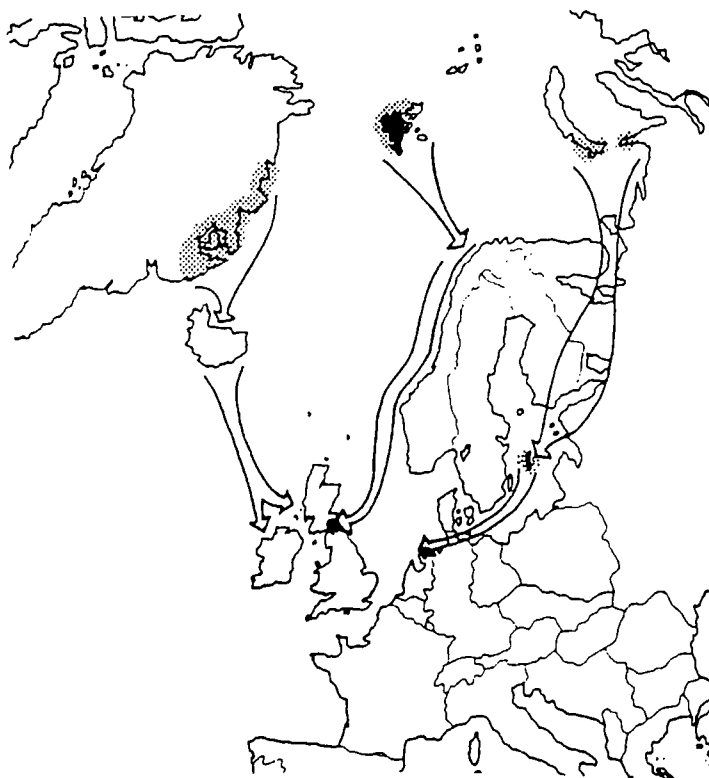
Figure 1 Breeding areas and migration routes of different Barnacle Geese populations.

Since 1971 breeding Barnacle Geese have been observed on Gotland. The Barnacle Geese breeding on Gotland probably descend from the Russian Barnacle Geese population (Larsson et al. 1988). Both the Russian and the Gotlandic Barnacle Geese use the same wintering areas and mixing of the two populations takes place in winter in the Wadden sea area (Ebbinge & Van Biezen 1987, Van der Jeugd in prep.) and in spring on Gotland (pers obs.). In Sweden, the

7

Barnacle Geese breed on small islands around Gotland and Öland in three different colonies: Rone Ytterholme, Kåreholm/Sillgrund and the main colony, Laus holmar (Forslund 1992, Larsson 1992). During the late seventies the number of breeding pairs of Barnacle Geese started to increase from 1 (1971) to about 2000 pairs (1993) (Larsson et al. 1988, Forslund & Larsson 1991, Larsson & Forslund 1995). Presently, since the enormous increase in breeding numbers, one might add this Gotlandic population as the fourth Barnacle Geese population.

Site description

Most of the geese breeding on Laus holmar (57°17'N, 18°45'E) take their young to the peninsula Närsholmen (fig 2), a few days after hatching (Larsson 1992). Here the geese mainly feed on a narrow strip of saltmarsh at the edges of the peninsula. This is an old *Festuca* dominated saltmarsh, consisting mainly of the grass species *Festuca rubra* and *Agrostis stolonifera*. There is also some *Poa trivialis*, *Juncus gerardii*, *Potentilla anserina* and *Plantago maritima* abundant, but all in smaller quantities (fig 3). *Puccinellia maritima* is growing on a small strip along the coastline. Later in summer the geese take their young also to the middle part of the peninsula, to feed on seeds of many different plant species, mainly *Graminea* and *Carex* species.

The peninsula has been grazed extensively by cows for many years. Every year the cows are moved into the area at the beginning of June and are removed in September. The cows have free access to the whole peninsula, but they mainly use the middle part of the peninsula and hardly ever graze on the saltmarsh (pers. obs.).
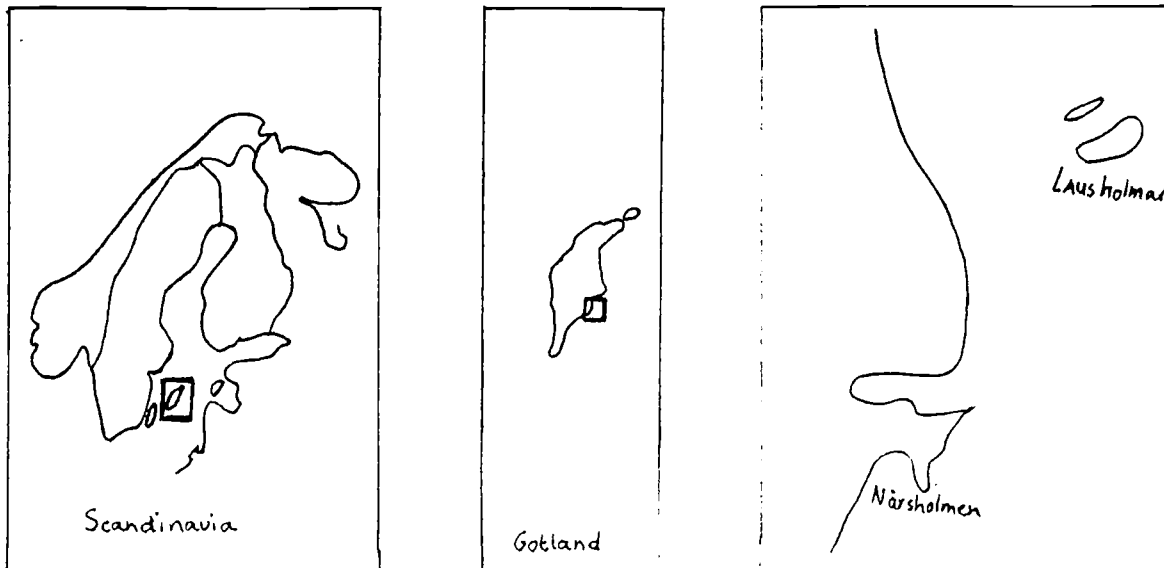

Figure 2 Map of areas used by the studied Barnacle Geese population on Gotland.
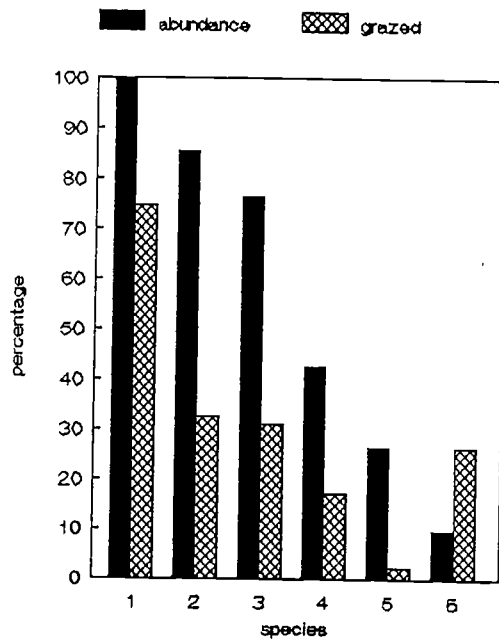
Figure 3 Abundance of species on *Festuca* dominated saltmarsh. Abundance was calculated as the percentage of squares of about 6 cm² in which a specie was abundant. Grazed percentage was calculated as the percentage of the squares in which a specie was abundant. 1 is *Festuca rubra*, 2 is *Agrostis stolonifera*, 3 is *Juncus gerardii*, 4 is *Poa trivialis*, 5 is other dicotyledons and 6 is *Plantago maritima*.

Grass growth measurements

Growth was measured as total leaf prolongation of individually marked shoots in millimetres per shoot per day. For the growth measurements three different grass species were used; *Festuca rubra*, *Agrostis stolonifera* and *Puccinellia maritima*, further referred to as *Festuca*, *Agrostis* and *Puccinellia*. From each species 16 shoots were measured in a small exclosure. Measurements were done from 3-6-92 until 23-7-92 and from 28-3-93 until 26-7-93 (table 1). In 1992, the *Festuca* and *Agrostis* shoots were in one exclosure on N3 and the *Puccinellia* was measured on N4 and N1-Fyr (fig 4). In 1993 all the measurements were done on N3, with again *Festuca* and *Agrostis* in the same exclosure at about the same place on the saltmarsh as in 1992. *Puccinellia* was measured near the edge of the beach on N3.

The shoots were chosen randomly, with a distance of approximately 10 cm. in between. The shoots were marked with small plastic rings around the stems. When a shoot lost its plastic ring, because of removal by either human, cattle or ants, and became unrecognizable a new shoot was chosen. When the *Puccinellia* exclosure on N4 was destroyed on 7-7-92, a new exclosure on N1-Fyr was made, and new shoots were marked.

On 28 June 1993 (Aprilday 89) the *Puccinellia* exclosure had been submerged because of the high sea level. On 12 July 1993 this exclosure was flushed by the sea again and stayed under water until 15 July 1993. This made measuring of the shoots impossible and thus there are no *Puccinellia* data available after 6 July 1993 (Aprilday 97).

9

The leaves were measured from the point where they left the stem to the top of the leaf, in one millimetres interval. A note was made when a leave was grazed, dead or scenescing. In 1992 only the mother shoot was measured throughout the season. In 1993 both mother and axillary shoots were measured. In 1992 shoots were measured twice a week. In 1993 shoots were measured about once a week.

The total length alive of the species was computed only with shoots that were measured from the start until the end of the measurement period. In 1992, no data for *Puccinellia* were available, following this criterium.
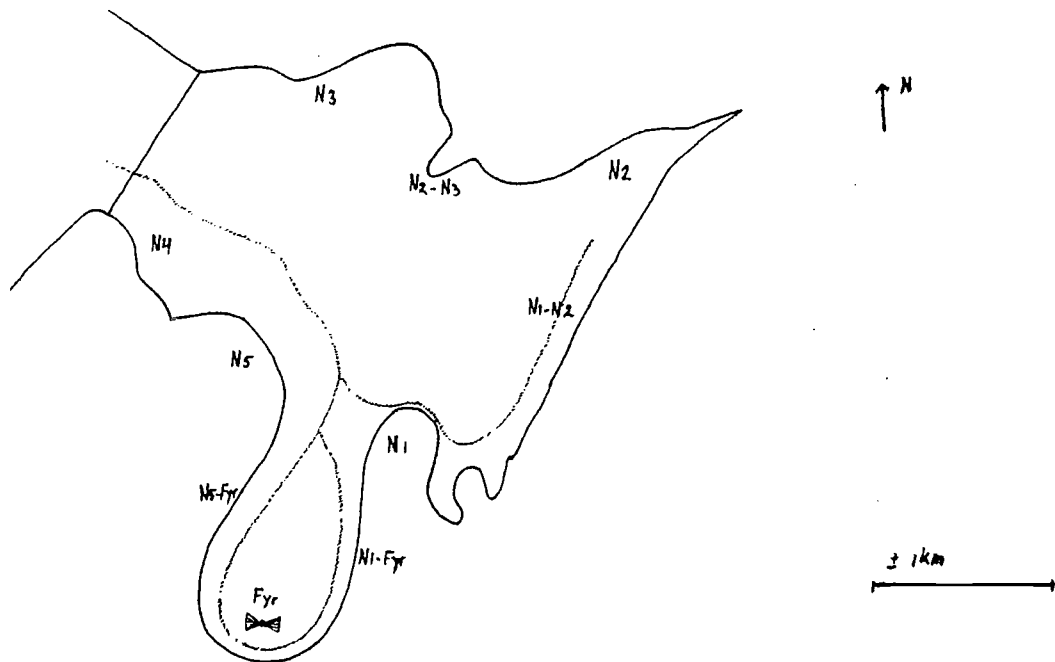
Figure 4 Map of Närsholmen, the peninsula to which the geese take their young just after hatch.

The weather data used to examine the effect of rain on grass growth, were collected by the weather station in Herrvik, on the coastline of Gotland, 22 km north and 11 km east of Närsholmen. The precipitation in an interval between two growth measurements was counted from the day of the first measurement until the day before the second measurement of an interval.

Effect of grazing

In 1993 all three grass species were measured as described above in permanent and in temporary exclosures. The permanent exclosures were put on the saltmarsh on the first measurement day (28-3-93). The first temporary exclosures were put on the saltmarsh on the same day, but were moved to a nearby grazed part of the saltmarsh about every three weeks (table 1). When the temporary exclosures were moved, new, grazed shoots were marked and measured during the following three weeks.

10

Table 1 The dates on which the exclosures for measuring shoots of *Festuca rubra*, *Agrostis stolonifera* and *Puccinellia maritima* were put on the saltmarsh and removed again in 1992 and 1993, with Aprildays between brackets.

	start	removed
1992	3 June (63)	23 July (114)
1993 ungrazed	28 April (28)	26 July (117)
1993 grazed 1	28 April (28)	24 May (54)
1993 grazed 2	24 May (54)	13 June (74)
1993 grazed 3	13 June (74)	6 July (97)
1993 grazed 4	6 July (97)	26 July (117)

Since *Agrostis* and *Puccinellia* produce axillary shoots an adjustment had to be made to make the grazed and ungrazed plots comparable. Each time an exclosure was moved to another location, the growth rate of a shoot in the permanent exclosure was calculated by using the mother and the axillary shoots produced from that moment on. The axillary shoots that were already there were neglected in the comparison between the grazed and ungrazed vegetation.

Festuca did not produce any axillary shoots, so the presented growth rates are the total growth rates in the plots.

Watering experiment

In 1992 a watering experiment was performed at about the same place as 1993 (see below, effects of droppings). The plots were harvested twice, around 28-6-92 and around 16-7-92, and no grazing occurred in the exclosure between the first and the second harvest, but grazing occurred in the exclosure before the first harvest. Therefor the watering effect can only be studied by comparing the first and the second harvest.

One plot got 0.5 litre water twice a week and one plot did not get any extra water. Each plot was a squares of 0.5 by 0.5 metre. Round the experiment a fence (ca. 1 metre high) was build to exclose geese and cows from the experimental plots. Between the squares and the wire there was an open space of 0.5 metre on each side of the experimental plots.

Harvesting was done by taking three samples from the plots, by cutting squares of 5 by 5 cm. The standing crop was cut off just above the soil. The vegetation was sorted in the following categories: dead material, grasses (*Festuca rubra, Agrostis stolonifera, Juncus gerardii, Poa trivialis*), dicotyledons and mosses. All sorted categories were put in paper bags and within a week they were put in an oven to dry for two days at 60 degrees Celsius. After that they were put in plastic bags. In the lab in Haren they were weighed to the nearest 0.001 gram.

To asses the effect of watering the differences between the first and second harvest were tested for the water and no water treated plot. Because the samples were taken randomly from a plot, all the differences between all samples in both plots per treatment were used for testing (pers comm. M. Björklund). This resulted in nine differences for each treatment. When this is tested with a t-test, the degrees of freedom are 16 (n_1+n_2-2). However, because the original data consisted only of two times three samples, the degrees of freedom for this test must be 4.

Fertilization experiment

Natural dropping densities were used as an indication for the amount of droppings per plot in the fertilization experiment. Dropping densities during the season were also used as a measure for grazing pressure (Ydenberg & Prins 1981) on the *Festuca* dominated salt marsh. On N3 (fig 4) droppings were counted in four circles with a surface area of two square metres each. After counting, all droppings were removed from the counted area. In 1992, counts were made without a regular interval and in 1993 approximately once a week. In the regression analyses of the dropping data only data after the first count in June were used, because during the first week in June not all geese had arrived with their young on Närsholmen yet.

On 4-6-1993 a fertilization experiment was started on the *Festuca* dominated saltmarsh on N3. In this experiment three different treatments were compared in biomass produced in the brood rearing period. Two exclosures of 0.5 by 0.5 metre were placed on the saltmarsh, about 1.5 metre apart. One got 100 droppings per square metre at the start of the experiment, which is about the double of the natural dropping density found on the same vegetation type. The other got no further treatment, but was exclosed from grazing. The third treatment was natural grazing, the geese had free access to the plot.

Harvesting was done from 29-6-93 to 3-7-93, by taking three samples from each of the three treatments. At the start of the experiment on 4-6-93, three samples from the grazed vegetation were taken. Harvesting was done as described above (see watering experiment). The different categories were put in paper bags and dried in the sun. In the lab in Haren they were dried in an oven at 60°C for two days and then weighed to the nearest 0.001 gram.

Another measurement for the effect of fertilization on the production of the vegetation could be the shoot density on the plots. From the 5 by 5 cm samples described above all alive and dead shoots were counted.

Nitrogen content

Quality of the grass was measured as the amount of total nitrogen per gram grass. In 1992 samples were clipped on three different vegetation types: *Festuca rubra* dominated vegetation on N3, *Puccinellia maritima* on N4 and *Agrostis stolonifera* on N4 (fig 4). An extra sample was taken of *Juncus gerardii* on N1-N2 and a mixed seed sample from the higher part of the peninsula on N2-N3. Clipping was done by hand, trying to simulate geese bites. After clipping, the dead material was removed and the samples were dried in an oven for two days at 60 °C. After drying, the samples were put in plastic bags and taken to Haren, where they were ground with a 1 mm. sieve. Again the samples were dried for two days in an oven at 60 °C. The total amount of Nitrogen was measured by the Kjelldahl method.

Digestion rates

In chapter 6 a comparison is made between geese breeding on Spitsbergen and geese breeding on Gotland. One of the proposed differences between the geese in the two areas might be their digestion efficiency. As measurement for digestion rates of geese the time interval between two droppings of an individual goose was measured (Prop & Vulink 1992). To do this a goose was followed with the aid of a telescope. If possible, the chosen goose was followed until five droppings were seen. Dropping intervals were noted in seconds.

All statistical analysis in this report were done using the statistical programm SPSS (Norusis 1988). A list of Aprildays and real dates is given in Appendix 1.

Above some of the figures the different stages of the geese through the season are indicated. In this scheme the peak of nesting, hatch and fledging are indicated and also the peak of departure of the Russian geese. Those dates are a rough indication, because they differ between years.

3 Growth of different grass species

Results

Axillary shoot production

In 1993 all leaves of individual shoots were followed through the season. If a shoot (mother) produced and axillary shoot, this shoot was also followed through the season. *Festuca* did not produce any axillary shoots. *Agrostis* produced axillary shoots mainly early in the season (fig 5). After 24 May (Aprilday 54) the 16 *Agrostis* shoots produced only two more axillary shoots. *Puccinellia* produced axillary shoots during the whole period (fig 5).
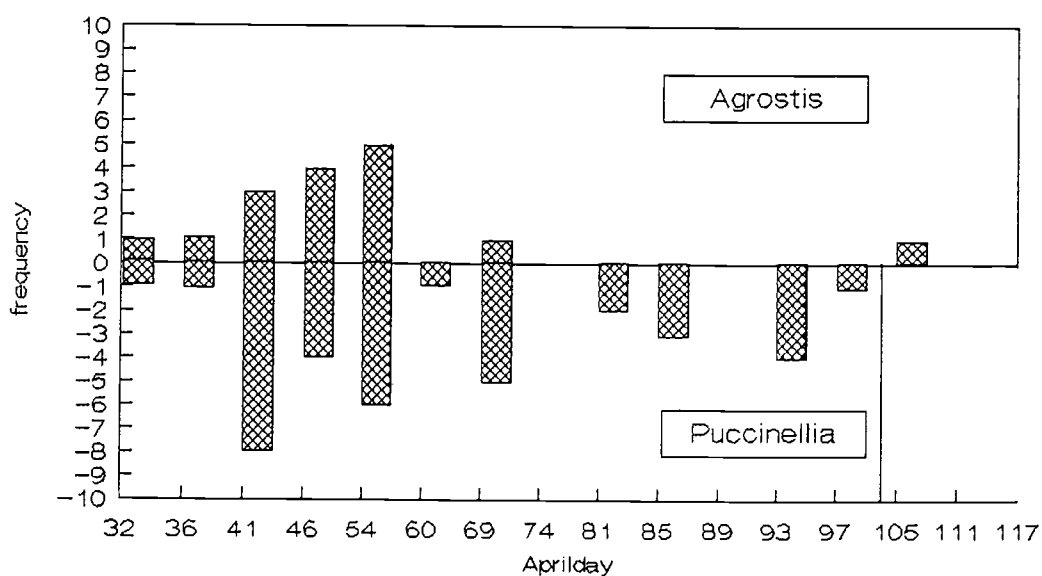
Figure 5 Number of axillary shoots produced throughout the season for 16 *Agrostis stolonifera* and 16 *Puccinellia maritima* shoots in 1993.

Growth rate of mother shoot and total (i.e., mother plus axillary) shoot differed during the season. For *Agrostis* (fig 6a), the difference decreased almost to zero on 20 June (Aprilday 81), when growth almost stopped. The growth rates of mother and total of *Puccinellia* (fig 6b) differed until the end of the season. For both *Agrostis* and *Puccinellia*, growth rate of mother and total showed the same pattern during season, but at a different level.

14
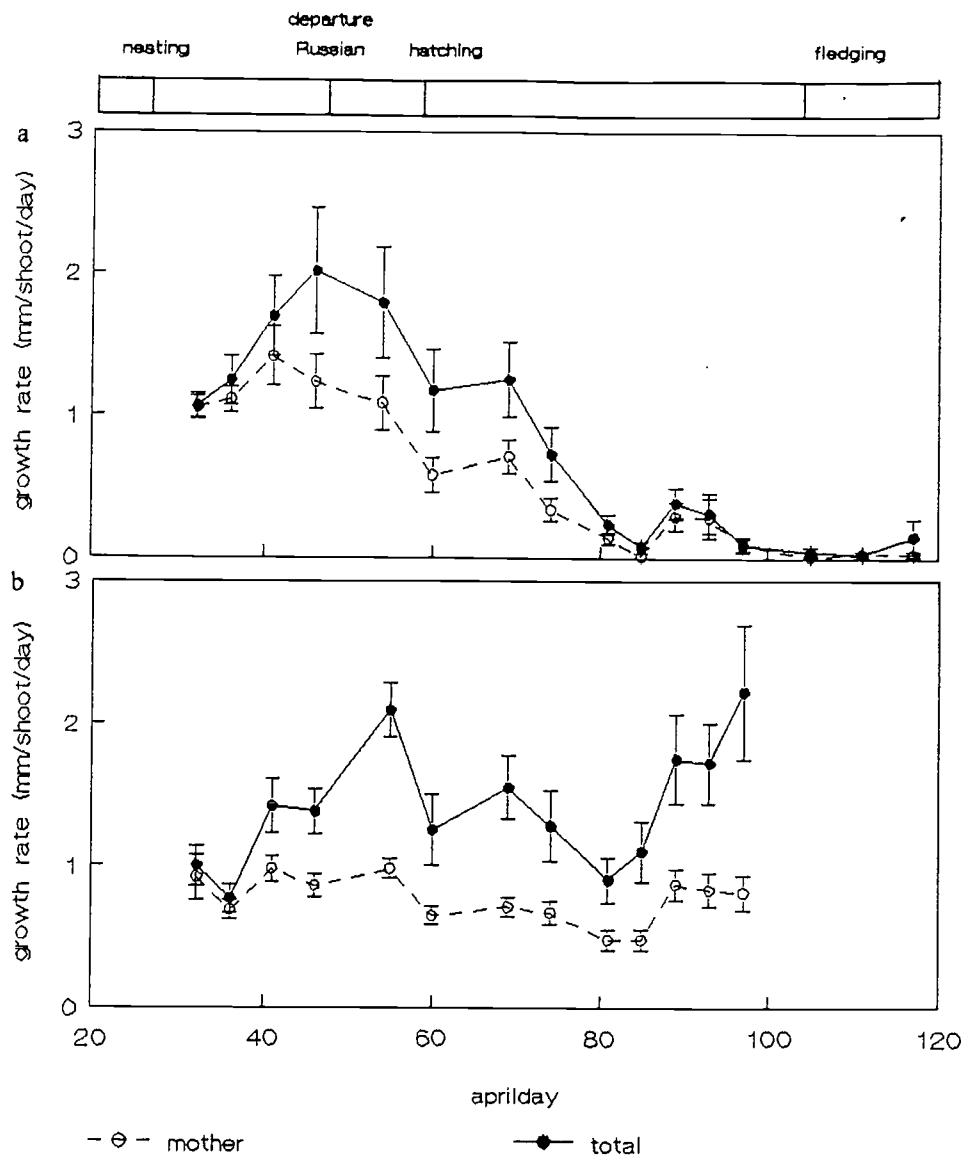
Figure 6 Growth rate of mother shoot and total shoot (=mother+axillary shoot) of *Agrostis stolonifera* (a) and *Puccinellia maritima* (b).

Differences between years

For comparison between years, only growth rates of mother shoots were used, because in 1992 no axillary shoots were measured.

The *Festuca* growth rate (fig 7a) decreased during the brood rearing season to zero in 1992. In 1993 there was no peak in growth rate of *Festuca* and growth rate was lower than in 1992. Also in 1993 growth rate decreased to zero in the middle of the brood rearing period.

In 1992, *Festuca* showed a peak in total length alive per shoot (fig 8a) around 20 June (Aprilday 81), in the middle of the brood rearing period. Festuca did not show a peak in total length alive in 1993.

The data of *Agrostis* (fig 7b) show almost the same pattern as *Festuca*. Growth rate decreased to zero in the middle of the brood rearing season in 1992 and 1993. In 1993 maximum growth rate occurred three weeks for the peak in hatching, just before departure of the Russian geese.

15

In 1992, *Agrostis* had a peak in total length alive per shoot around 20 June (Aprilday 81) (fig 8b), which is in the middle of the brood rearing period. In 1993 there was no peak in leaf length.

Also for *Puccinellia* growth rates were lower in 1993. In 1993 there was no peak in the growth of the mother (fig 7c).
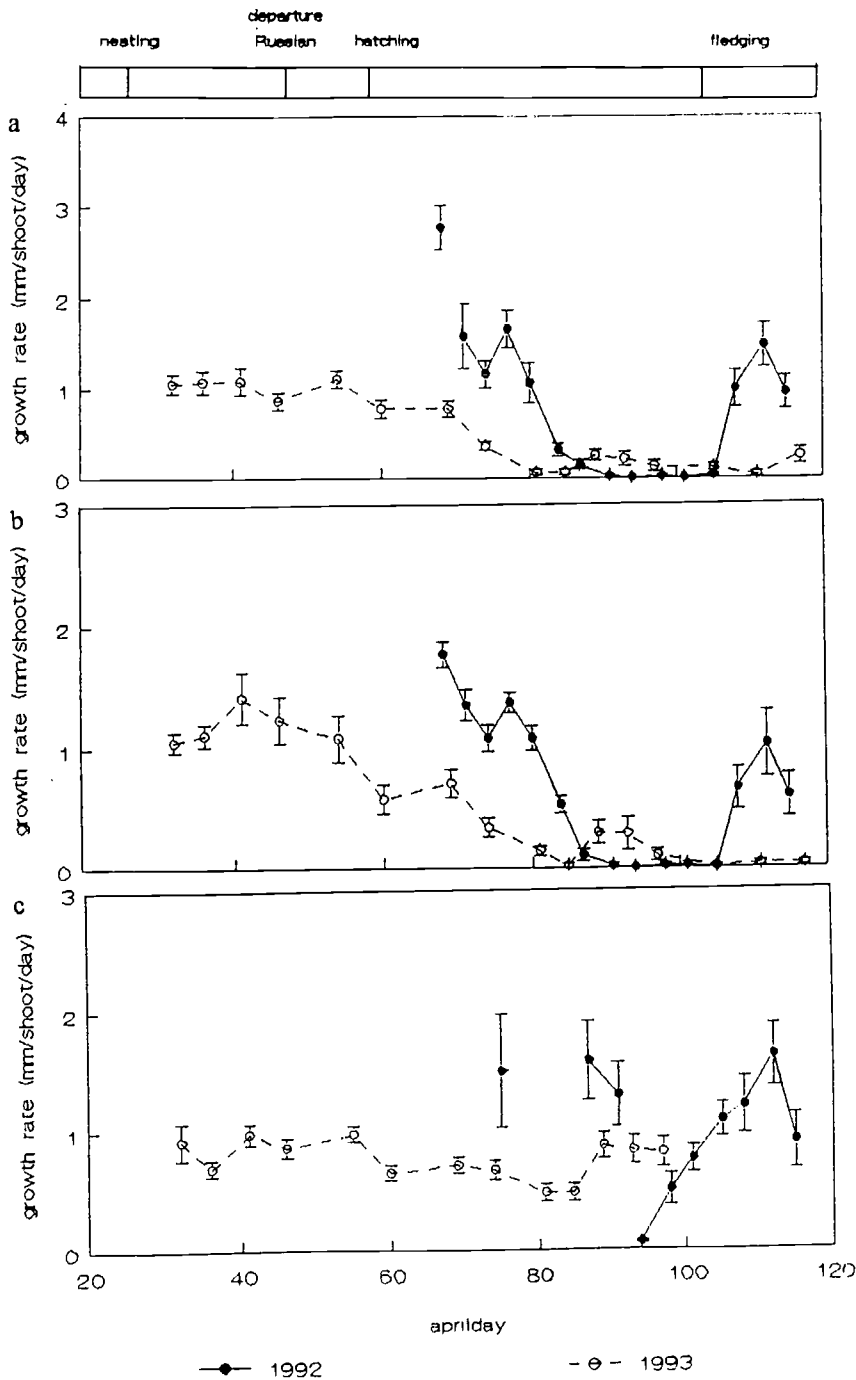
Figure 7 Growth rates of Festuca rubra (a), Agrostis stolonifera (b) and Puccinellia maritima (c) in 1992 and 1993.

16
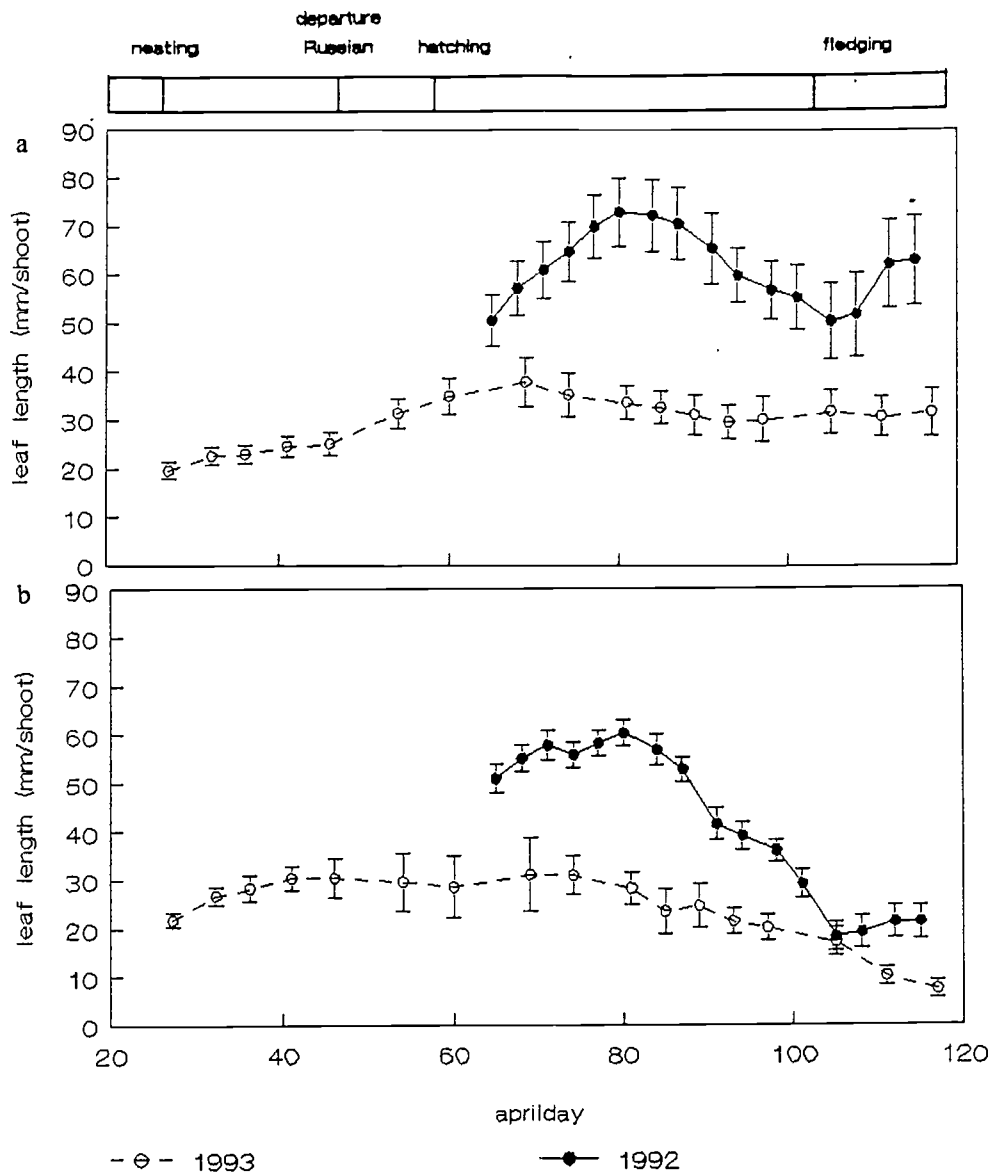
Figure 8 Total leaf length per shoot during the season in 1992 and 1993 for Festuca rubra (a) and Agrostis stolonifera (b).

The weather on Gotland

It was very wet in April 1992, but in May and June it was much drier than normal (table 2). The lack of rainfall was accompanied by high temperatures. In 1993 it was very dry much earlier in the season, but after that period it was wetter than normal. In 1993 the temperature was high early in season, but later (from June onwards) it was normal.

Table 2 The average temperature (5 metre above ground) and precipitation per month in 1992, 1993 and the average of 1961 until 1990 measured in Herrvik, 22 km north, 11 km east of Närsholmen.

month	temperature (°C)			precipitation (mm)		
	1992	1993	1961-1990	1992	1993	1961-1990
March		2.4	0.5		24	31
April	3.9	4.8	3.6	45	19	28
May	10.9	11.5	8.2	10	12	29
June	16.2	13.3	13.4	14	39	33
July	17.2	15.4	15.9	58	51	47
August	16.5		15.9	52		47

In both 1992 and 1993 the temperature showed a slow and fluctuating increase in the course of the season (fig 9a). In both years the temperature was about 3°C around the first of April and increased to about 17°C in 1992 and 15°C in 1993.

The precipitation was not equally divided over the season in both years (fig 9b). In 1992 a dry period started on 13 May (Aprilday 43) that lasted for 29 days. After this dry period there were some days with rain again. In 1993 a dry period started on 21 April that lasted to 24 May (Aprilday 54), with only one small shower with 1 mm rain on 5 May (Aprilday 35). So there had been almost no rain for 33 days in a row. After this long dry period there were some days with rain, after which there was a dry period again, that lasted for two weeks.

Effect of precipitation on grass growth

To study the effect of precipitation on growth rate, the change in growth rate between two measurements (interval) was compared for intervals in which it had rained and intervals in which it had not rained. In 1992 there was a significant effect of rain on growth change of the three species together (MWU p<0.0001), with rain growth rates showed an increase, and without rain growth rate was decreasing (fig 10a). In 1993, there was no significant effect of rain on change in growth rates. When the season was split in two parts, one before hatching of the young (April and May) and one after hatching (June and July, same period as 1992), both periods showed a difference between intervals with and without rain for the three grass species together (MWU-test before p<0.001; after p<0.0001). Before hatch growth rate was decreasing when it rained and increasing when it did not rain. After hatching the growth rate decreased in both intervals, but decreased significantly more when it did not rain (fig 10a).
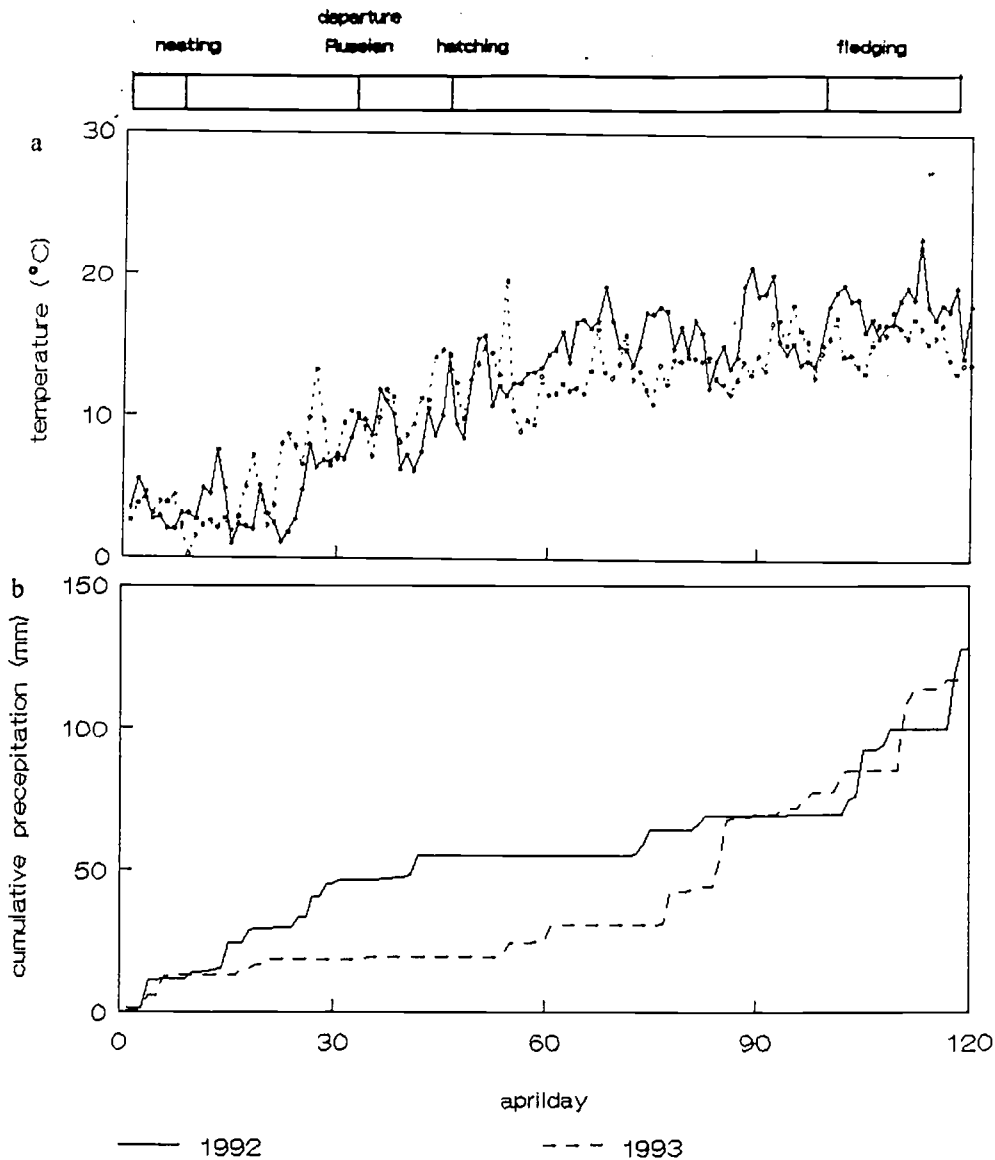
Figure 9 Temperature (a) and precipitation (b) during the season in 1992 and 1993.

For *Festuca* (fig 10b), change in growth rate was significantly higher when it had rained than when it had not rained in 1992 (MWU p<0.0001). When it rained there was an increase in growth rate and when it did not rain growth rate was decreasing. In 1993 before hatch, rain had a negative influence on growth rate of *Festuca*, when it did not rain growth rate was significantly higher (MWU p<0.05). In the period after hatch, when the Gotlandic breeding geese start to use the study area, for both rain and no rain there was a decrease in growth rate. Intervals without rain had a significant larger decrease in growth rate (MWU p<0.0001).

In 1992 *Agrostis* (fig 10c) showed an increase in growth rate when it rained and a significantly lower, negative change in growth rate when it did not rain (MWU p<0.0001). In 1993 in the period before hatch there was no significant difference between intervals with and without rain. After hatch, change in growth rate was significantly more negative when it had not rained (MWU p< 0.0001).

19
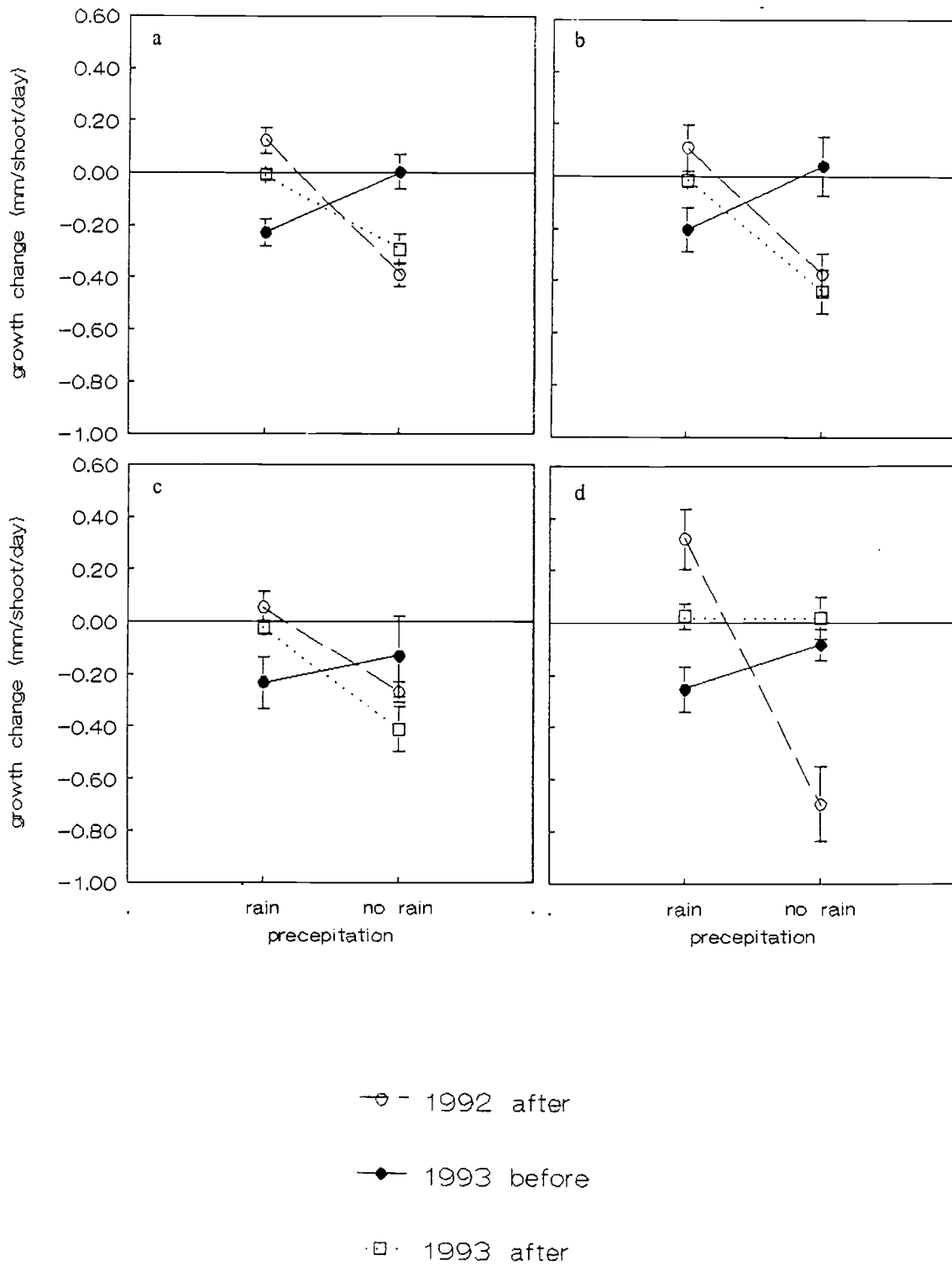
Figure 10 Average change in growth rate of all three grass species (a), *Festuca rubra* (b), *Agrostis stolonifera* (c) and *Puccinellia maritima* (d) in intervals with and without precipitation. Before means before hatch (April, May) and after means after hatch (June, July).

Puccinellia (fig 10d) growth rate in 1992 was significantly different between intervals with and without rain. With rain growth rate increased and without rain growth rate decreased (MWU p<0.0001). In 1993 in the period before hatch, change in growth rate was negative, both in intervals with and without rain, but when it rained the change was significantly more negative (MWU p<0.01). After hatch, growth rate was in both intervals positive and not significantly different.

In 1992 there was a difference in change of growth rate among the three species, both for rain and no rain (Kruskal-Wallis, rain: p<0.05, no rain: p<0.05). With rain, *Puccinellia* had a larger increase in growth rate (MWU p<0.05). The other species did not differ from each other. When there was no rain, *Puccinellia* had a larger decrease in growth rate than *Festuca* and *Agrostis* (MWU resp. p<0.05 and p<0.01). *Agrostis* and *Festuca* did not differ significantly in intervals without rain.

In 1993 before hatch there were no differences in change in growth rate between the three species. After hatch there were no differences between the species in intervals with rain, but in intervals without rain *Festuca* and *Agrostis* had a decrease in growth rate and *Puccinellia* a significantly higher increase growth rate (MWU both p<0.01).

So, in 1992 *Puccinellia* was more sensitive to rain than the other two species. When it rained, it grew faster and when it did not rain, it grew slower. In 1993 after hatch *Puccinellia* suffered less from the lack of rain than the other two species.

Watering experiment

A watering experiment was preformed to asses the effect of (lack of) water on the biomass. Only data between 28-6-92 and 17-7-92, in the middle of the period between hatch and fledge of the juveniles, are available, In the plot that was watered there was a significant smaller decrease in biomass in this period than in the not watered plot (table 3: t-test p<0.025). There were no significant differences for dead material.

Table 3 The difference between 28-6-92 and 17-6-92 in biomass of grasses plus dicotyledons and dead material for watered and not watered plots, with standard errors between brackets (for method of testing see method).

	water	no water	t-test
grass+dicotyledons	-0.084 (0.03)	-0.198 (0.03)	p<0.025
dead	0.238 (0.03)	0.265 (0.02)	NS

Discussion

During the shoot measurements in 1992, the axillary shoots were neglected. Before a comparison between the two years in growth rates of the grass can be made, the influence of the production of axillary shoots should be evaluated.

Festuca did not produce any axillary shoots, both in 1992 and in 1993. *Agrostis* produced axillary shoots mainly early in season, before hatching, and *Puccinellia* produced axillary shoots the whole breeding season (fig 5).

In 1992 measurements started in the period that *Agrostis* produced almost no axillary shoots anymore in 1993. In that period, the difference in growth between mother shoot and total shoot was not very large. When considering the real (= total) growth of an *Agrostis* shoot, the interpretation of the 1992 data remain almost the same. The 1992 growth of *Puccinellia*, which had a larger difference between mother shoot and total growth, could be higher than shown in the data (fig 7c). To make an accurate comparison between the growth in 1992 and 1993, for both *Agrostis* and *Puccinellia*, only the mother shoots should be compared.

Both *Festuca* and *Agrostis* showed the same kind of growth rate pattern over the seasons. Those two species were measured at the same site on the peninsula. *Puccinellia* showed a quit different growth pattern. The *Puccinellia* was measured on a lower part of the peninsula, closer to the sea. The exclosure in which the *Puccinellia* was measured in 1992, was destroyed and a new exclosure had to be made and new shoots had to be measured. Those new shoots were grazed until the new exclosures were made, so they were grazed for a longer period then the *Agrostis* and *Festuca* shoots measured on the same date. This makes comparisons between species, season and years difficult considering *Puccinellia*.

For the three species there were quit big differences between the two years (fig 7). For all three species the growth rates were much lower in 1993 than in 1992. The data of 1992 seemed to suggest a peak in growth just before the measurements were started. In 1993 however no such growth peak was found for either of the three species.

To explain how these differences in growth rates were accomplished, the weather data of the two years were compared (table 2). Gotland has a temperate climate, and the summers are warm and dry. The summers of 1992 and 1993 were even warmer and dryer than normal. Not only the total amount of rain is important, but also the way in which it is distributed over the days can have a great influence on the growth rate of the grass and that can influence the growth of goslings (Sedinger 1986, Cooch *et al.* 1991, Sedinger & Flint 1991). Both in 1992 and 1993 there were long dry periods during the breeding season.

Not only the lack of precipitation was an important factor for grass growth, but because of the high temperature, the evaporation was also increasing. Also because of this the ground was very dry and the small amounts of rain that were falling on the ground, were evaporating before they could cause an effect on grass growth.

During the season growth rate of grass was declining, which has also been reported in other studies (Cargill & Jefferies 1984a, Prop *et al*. 1980). In 1992 lack of rain had a negative effect on growth rate of grass, but the measurements only started after hatch. In 1993, considering the whole season, there was no effect of rain on grass growth. Before hatch, rain had an inhibiting effect on the growth rate of grass (fig 10). After hatch, when the geese with their young actually use the area, lack of rain had a stronger negative effect on the grass growth than abundance of rain.

When the vegetation was regularly watered, in the last part of the brood rearing period, the biomass was less decreasing over time. Adding water had a positive effect on the vegetation by slowing down the retardation of the vegetation.

Not all species reacted on rain in the same way. In the period after hatch (both 1992 and 1993) *Festuca* and *Agrostis* showed a similar reaction. When it did not rain there was an inhibiting effect on the growth rate of those species. *Puccinellia* showed a very strong effect on lack of rain in 1992, but in 1993 *Puccinellia* showed an increase in growth rate, both for rain and no rain. Those differences between years might be caused by the poor data of Puccinellia in 1992. Puccinellia was measured at different places and not the whole period through, this might have influenced the measurements. The different reaction of *Puccinellia* compared to the other species in 1993, might be caused by the fact that *Puccinellia* grew much closer to the sea than the other two species. Therefor *Puccinellia* probably had better access to water. The Baltic sea is not too salt to be used and therefor *Puccinellia* was less sensitive to drought.

This difference in response is very important for the geese, especially in periods with low grass growth rates. Geese can select for good quality food (Sedinger & Raveling 1984, Bazely *et al*. 1991, Laing & Raveling 1993). However, *Puccinellia* is not as abundant as *Festuca* and *Agrostis* (pers. obs.), so the geese will have to compete for *Puccinellia* spots. And only the dominant families can benefit from those better food patches (Prop *et al*. 1984).

In the period the Russian geese use Närsholmen, before hatch, rain has an inhibiting effect on the grass growth. The Russian geese need good quality food, to store fat before moving on to their breeding area in arctic Russia. Rain can have a negative influence on this spring fattening, which influences the reproductive success of the geese (Ebbinge & Spaans 1992).

In the period the Gotlandic geese take their young to feed on Närsholmen, lack of rain is becoming an important factor for the grass growth and thus for the protein content of the grass. One of the biggest problems the Gotlandic geese have to cope with during the breeding season is drought, which I have never seen reported for arctic breeding geese. However, drought is reported to be limiting grass growth on temperate salt marshes (De Leeuw *et al*. 1990). In arctic breeding geese food availability and quality is limiting the growth of goslings (Sedinger 1986, Cooch *et al*. 1991, Larsson & Forslund 1991, Sedinger & Flint 1991), but the factor that limited the grass growth in arctic areas was nitrogen (Cargill & Jefferies 1984a, Bazely & Jefferies 1985, Fletcher & Shaver 1983, Hik & Jefferies 1990, Hik *et al*. 1991, Manseau & Gauthier 1993, M. Loonen unpubl. data). In a very dry summer like the two study years, drought can have severe effects on the vegetation and thus on the geese, but on the other hand, in wet years, the geese can benefit

23

from the high food availability (pers. comm. K. Larsson). While in arctic breeding areas, nitrogen is a constant limiting factor for grass growth, on Gotland geese are breeding in a very fluctuating environment.

4 Effects of geese on the vegetation

Results

Relation growth rate and shoot length

The total shoot length can be different in grazed and ungrazed shoots. Therefore analyses were done to investigate the relation between shoot length and growth rate of a shoot.

As shown in chapter 3, growth rate of grass species is changing over season. To make a comparison between growth rate and length of a shoot, an adjustment has to be made for this seasonal effect. Therefore, the average growth rate and average shoot length of all shoots per specie were calculated on every measurement day. For each shoot the deviation from the mean was expressed in standard deviations of the mean.

For *Festuca* in the ungrazed situation there was a significant positive regression between shoot length and growth rate, with a R^2 of 0.225 (fig 11a, F=39.67, p<0.0001). Also in the grazed situation a significant positive regression was found, with a R^2 of 0.098 (fig 11b, F=22.25, p<0.0001). There was no significant difference between the slopes of the regressions for the grazed and ungrazed *Festuca*.
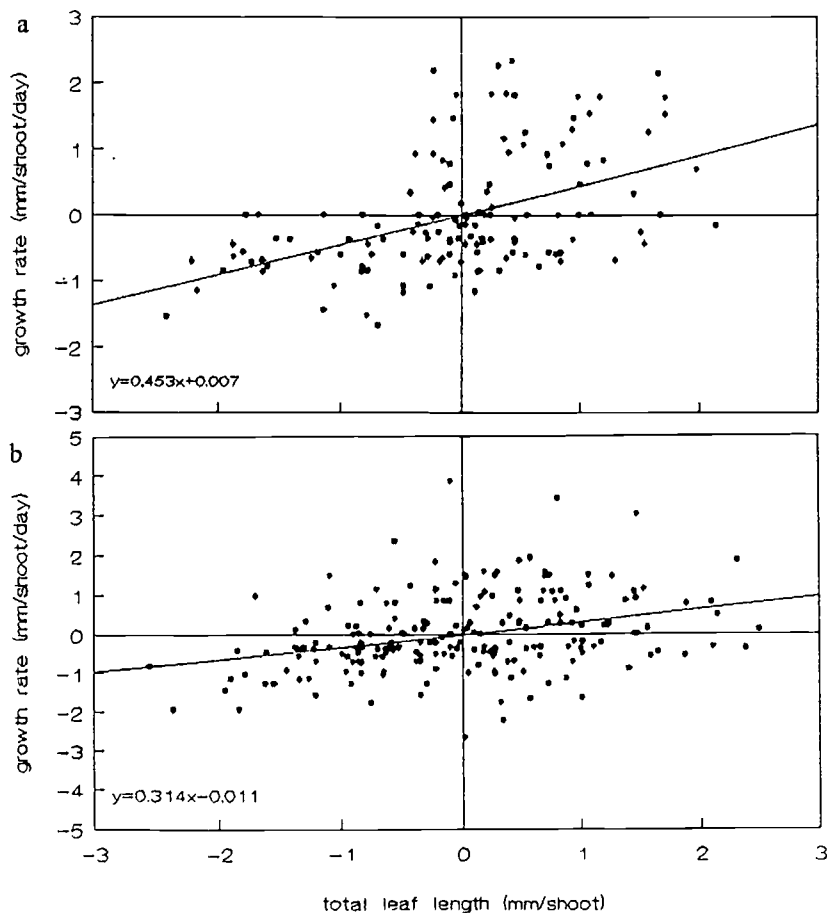
Figure 11 Leaf length per shoot and growth rates of Festuca expressed in deviation from the mean per day, in ungrazed (a) and grazed (b) situation.
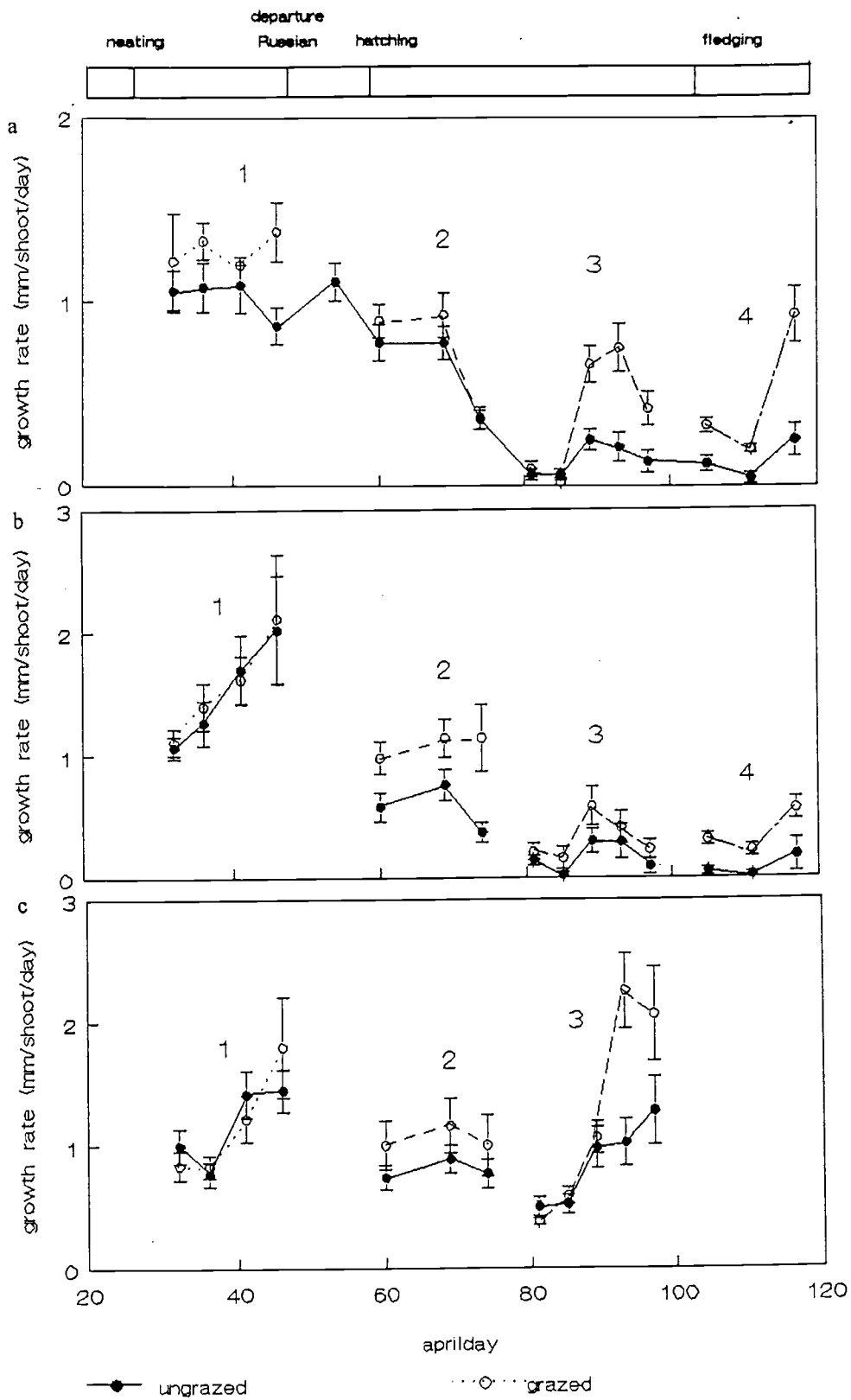
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Figure 12 Growth rate of *Festuca rubra* (a), *Agrostis stolonifera* (b) and *Puccinellia maritima* (c) in grazed and ungrazed situation.

26

Effect of grazing

For *Festuca* (fig 12a) growth in the temporary exclosure was significantly higher than in the permanent exclosure in the first grazing period (table 4: ANOVA $p < 0.05$). In the second grazing period, around hatch, *Festuca* showed no significant difference between grazed and ungrazed. The third and forth period had significant higher growth rates in the grazed exclosures (table 4: ANOVA both $p < 0.0001$).

For *Agrostis* (fig 12b) the periods 2, 3 and 4 had a significant higher growth rate in the grazed exclosures (ANOVA resp. $p < 0.001$, $p < 0.05$ and $p < 0.0001$).

The second period *Puccinellia* had no significant difference in growth rate between grazed and ungrazed, but there seemed a trend that the grazed shoots had a higher growth rate (fig 12c). In period three growth rate in the grazed exclosure was significantly higher than in the ungrazed situation (table 4: ANOVA $p < 0.05$).

Table 4 The levels of significance resulting from an ANOVA for differences in growth rate between grazed and ungrazed shoots. Period 1 is from 28 April to 16 May, period 2 is from 24 May to 13 June, period 3 is from 13 June to 6 July and period 4 is from 6 July to 26 July.

	period 1	period 2	period 3	period 4
Festuca rubra	$p < 0.05$	NS	$p < 0.0001$	$p < 0.0001$
Agrostis stolonifera	NS	$p < 0.001$	$p < 0.05$	$p < 0.0001$
Puccinellia maritima	NS	NS	$p < 0.05$	

Effect of droppings

In 1993 there were no significant differences in total material, dead material, alive biomass and grass+dicotyledons between the treatments grazed, control and droppings (table 5, fig 13 and 14). In the control plot there was significantly more moss than in the fertilized plot (table 5: ANOVA $p < 0.05$, fig 14).

There were no significant differences in any of the categories, total, dead, alive, grass+dicotyledons and moss between the start biomass and any of the treatments, except for the dead material. The amount of dead material increased on the grazed vegetation between start and end of the experiment (t-test $p < 0.05$; fig 13).

Table 5 The biomass (g/25cm²) and results of ANOVAs in the different categories for the different treatments, with standard errors between brackets. The plot "droppings" was treated with 100 droppings per square metre and like "control" it was exclosed from grazing.

	grazed	control	droppings	ANOVA
total	0.91 (0.09)	1.00 (0.04)	0.90 (0.07)	NS
dead	0.44 (0.02)	0.32 (0.05)	0.40 (0.02)	NS
alive	0.48 (0.07)	0.68 (0.02)	0.50 (0.05)	NS
grass+dicotyledons	0.27 (0.02)	0.34 (0.04)	0.39 (0.03)	NS
moss	0.21 (0.06)	0.34 (0.05)	0.11 (0.02)	p<0.05
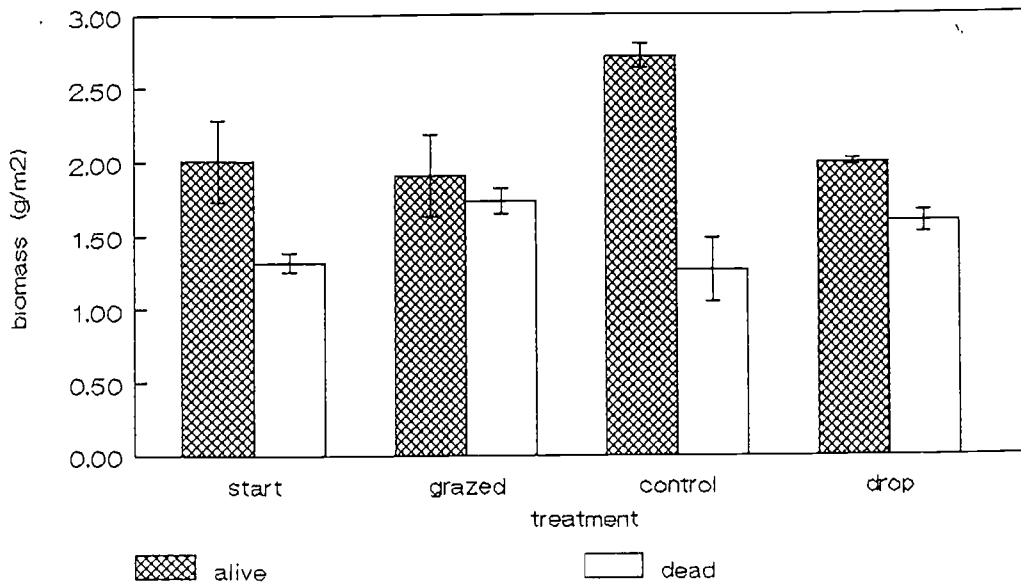
Figure 13 Biomass of alive and dead material in four different treatments at the end of the experimental period.
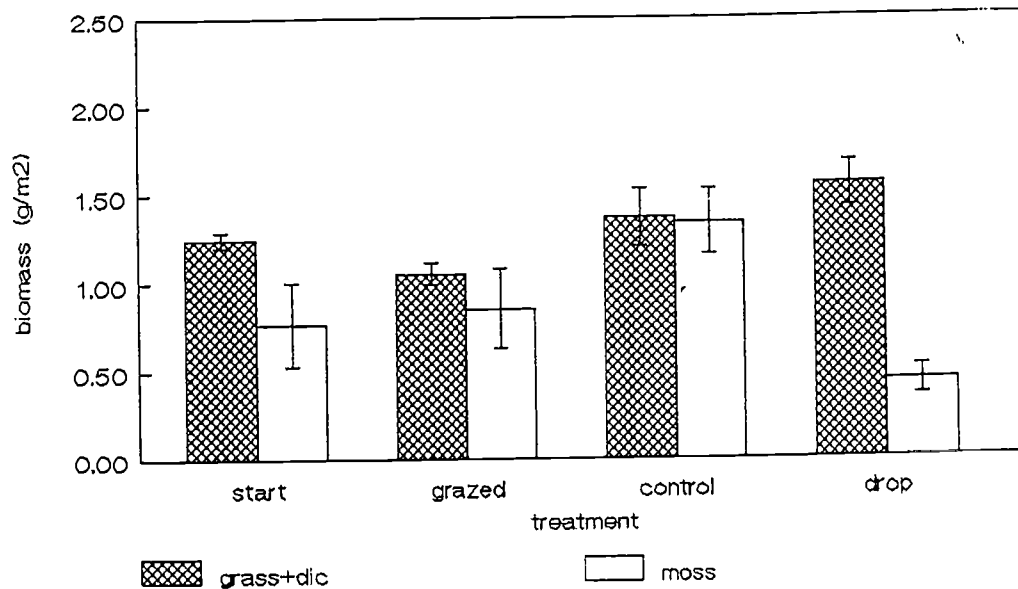
Figure 14 Biomass of moss and grasses plus dicotyledons in four different treatments at the end of the experimental period.

There was no effect of treatment on the alive shoot density in the plots, but there was for dead shoot density (table 6: $p<0.05$). The grazed vegetation had a significantly higher dead shoot density than the control and droppings treatment (table 6: t-test both $p<0.05$).

There were no differences in both alive and dead shoot density between the start and any of the treatments.

Table 6 The shoot densities (shoots/25cm^2) and results of ANOVAs in alive and dead for the different treatments, with standard errors between brackets. The plot "droppings" was treated with 100 droppings per square metre.

	grazed	control	droppings	ANOVA
alive	148.0 (11.0)	118.0 (15.0)	176.0 (14.1)	NS
dead	9.3 (1.5)	2.0 (2.0)	1.0 (0.6)	$p<0.05$

Table 7 The Pearson correlation coefficient, linear regression between dropping densities (droppings/m²/day) an date and their levels of significance on N3 in 1992 and 1993. Only data after the first count in June were included (see text). In the regression equation y is droppings per day and x is Aprilday.

	correlation	regression
1992	-0.621 (NS)	y=2.81-0.021x (p<0.05)
1993	-0.642 (p<0.001)	y=3.47-0.025x (p<0.001)

Grazing pressure

To investigate what the natural dropping density is on the saltmarsh, and how this fluctuates, droppings were counted through the season. The dropping density showed an increase between the first and second count in 1992, early in June (fig 15a). In 1993 there was also an increase in dropping density in the same period (fig 15b).
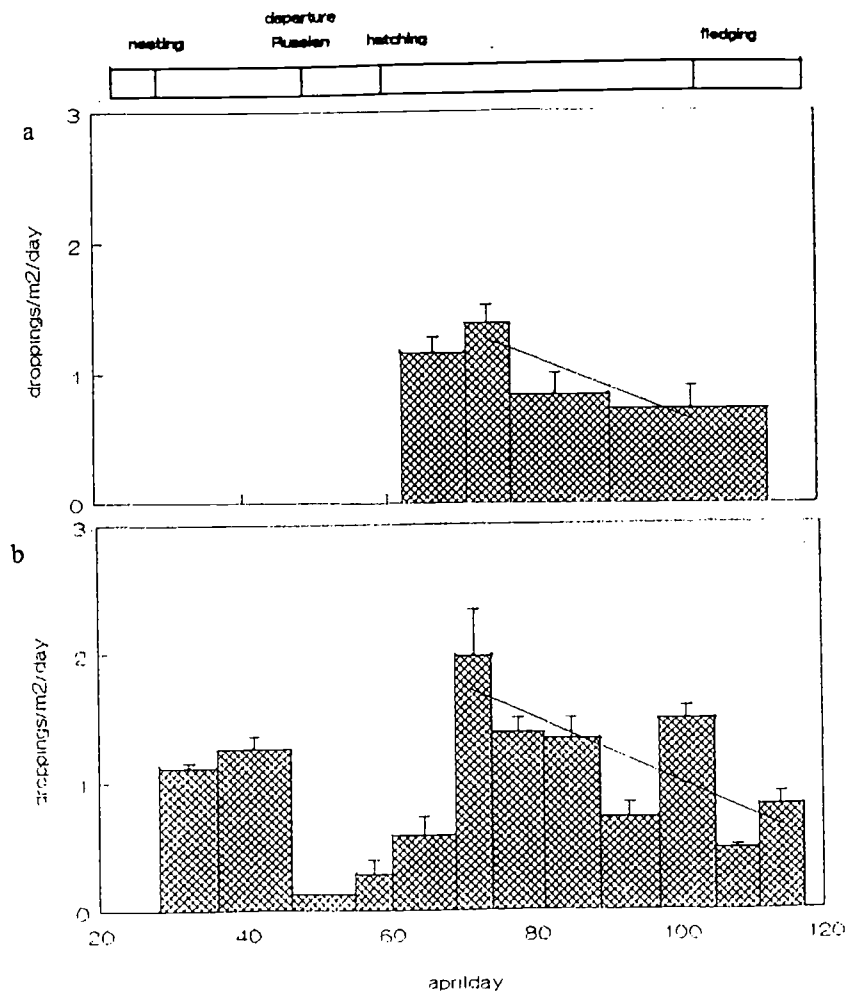
Figure 15 Dropping density in 1992 (a) and 1993 (b) on N3 during the season, with the regression line started after the first measurement in June (see text).

30

In 1993 counting started in the period that the saltmarsh was used by the Russian Barnacle Geese. After 16 May (Aprilday 46) most of the Russian geese had left Gotland. In that period there was a decrease in dropping density (fig 15b). Peak of hatch was around 28 May and after that the peninsula was used by the Gotlandic breeding geese and their young. In that period the dropping density increased again.

There was a significant negative correlation between dropping density and Aprilday after the first count in June 1993 (table 7: $p<0.001$). The regression indicates also a significant decrease in the course of the season (fig 15b, table 7: $p<0.001$; $R^2=0.42$). In 1992 the correlation was not significant, but the regression indicates a decrease in dropping density during the season (fig 15a, table 7: $p<0.05$; $R^2=0.40$).

Discussion

Effect of grazing

Before the effect of grazing on growth of grass can be evaluated a better look should be taken at which internal factors determine growth of grass. Is growth of grass dependent on the length of a shoot? The problem with this question is that growth, as shown before is also dependent on other things, rain for example. From the results of chapter 3 we see that the effect of water on the growth is not equal trough the whole season, therefor the data had to be corrected for seasonal influences.

In figure 11 was shown that growth rate of a shoot is dependent on the total length of a shoot. Large shoots have a higher growth rate. This relation was significant, but this relation explains only a small part of the existing variance (fig 11a R^2=0.225). For the grazed vegetation a same relation was found between shoot length and growth rate. The expectation was that this relation was based on the original shoot length. In the grazed situation this original shoot length is manipulated by the geese, so no relation would be expected. However, there is only a small amount of the leaves grazed. This might be the reason for the fact that there is still a relation between shoot length and growth rate in the grazed situation. This relation explains even less of the total variation (fig 12b, R^2=0.098). In both grazed and ungrazed there is a relation found, but this relation explains only a small amount of the existing variation. There must be some other factors influencing growth, which were not measured in this experiment.

In this experiment there was an significant effect of grazing on the growth of all three grass species (table 4). Grazing stimulated growth rate of the three grass species. There should not have been a significant difference between the permanent and the temporary exclosure in the first period, because the exclosures were put close to each other in the same vegetation type and on the same day. The difference found for *Festuca* (fig 12a, table 4) was probably caused by small differences in height on the saltmarsh. The saltmarsh consists of regular tiny hills, hardly visible in the beginning of the season. Later in the season, when the lack of rain is showing its influence on the vegetation, small differences become visible. The parts that are a little bit lower stay longer green, because water and probably also nutrients accumulate in those lower parts.

During the whole season there was a significant effect of grazing on the three grass species, while on a sub-arctic saltmarsh the ability to recover from grazing decreased over season (Hik & Jefferies 1990). According to Hilbert *et al.* (1981) stressed plants are better able to compensate after grazing, it might be that because of drought stress this grass has a higher ability for compensation.

All three species showed a compensating effect to grazing. Stoloniferous and non stoloniferous grass species have a different mechanism for compensation. Stoloniferous species produce axillary shoots, but non stoloniferous species enhance growth of the existing shoot as a reaction to grazing (Kotanen & Jefferies 1987, Bazely & Jefferies 1989b).

Effect of droppings

In the 1993 fertilization experiment, there was no effect of droppings on the total, dead, alive and grass+dicotyledons biomass, only moss biomass increased after fertilization (fig 13, 14). So twice the normal density of droppings did not increase the amount of grass and dicotyledons.

There was no effect of treatment on alive shoot density. The grazed vegetation had a higher dead shoot density than the exclosed plots (table 6).

In other temperate areas also no effect of droppings on production was found (Marriott 1973, Jefferies & Perkins 1977, Wiersma 1991). The explanations for this poor response to fertilization were that the grass was well adapted to the presence of summer drought and hypersaline conditions (Jefferies & Perkins 1977) and temperate salt marsh plants do not poses same plasticity as sub-arctic plants. Water is needed for nitrogen transport from dropping to shoot, so if water is limiting there is less nitrogen available from the droppings (Wiersma 1991). Also because of high temperatures in temperate summer, droppings are drying very quickly in the sun. With the same interval between production of a dropping and application on an experimental plot, a dropping in warmer areas is dryer and will thus have a lower fertilizing effect.

Another explanation for no effect of droppings in temperate areas might be that because of human activity there is a lot more nitrogen available in temperate areas compared to (sub-)arctic areas. So addition of droppings in natural amounts had no effect, because this amount of nitrogen is negligible compared to what comes into the system through other ways (for example acid rain).

Grazing pressure

The total amount of droppings per square meter produced on the saltmarsh during the season was about half the applied amount on the experimental plots. However on the plots the application is at one moment in the season, while the geese spread this over the whole season.

There was an increase in dropping density between the first and second count in 1992. In the same period in 1993 there was also an increase in dropping density. In this period not all the young had hatched yet. The increase can be subscribed to the increase in number of geese that graze with their young on the saltmarsh. In the correlation and regression analyses was only dealt with the period in which all juveniles had hatched, after the first count in June.

The dropping densities indicate a decrease in the use of the *Festuca* dominated vegetation. The young goslings need good quality food (Ankney 1979). The decrease in nitrogen content forces the geese to switch to better quality food, probably to high energy food (Sedinger & Raveling 1984, Prop & Vulink 1992).

From our observations is known that the use of the middle part of the peninsula is increasing during the season. The geese take their young there to feed on seeds, diet change to seeds is also shown in other studies (Sedinger & Raveling 1984, Sedinger & Flint 1991, Prop & Vulink 1992, Laing & Raveling 1993). Seeds have a very low nitrogen content (table 8, chapter

5), but have a high energy content (Sedinger & Raveling 1984, Prop & Vulink 1992).

The geese take higher risk while grazing in the middle part of the peninsula in tall vegetation (Laing & Raveling 1993). Because of the tall vegetation it is harder to get sight of predators, and the area is much further away from the water, which the geese need as a refuge place in case of danger. Choosing for energy rich food can include taking higher predation risk. When the goslings are older, the predation risk probably becomes smaller. Then the goslings are too big to be taken by gulls and there are hardly any records of foxes on the peninsula. In that period it might be worthwhile to take advantage of the high energy seeds.

Conclusion

Since the used amount of droppings was twice the natural occurring dropping density, the geese on Närsholmen could not have a stimulating effect on the biomass through their droppings alone, within one breeding season. In this research the effect of grazing on the growth of grass cannot be separated from the dropping effect, because when the geese were grazing the plots, they were also depositing there faeces on the plots. Although no effect of droppings was found, the two things might enhance each other. So in this temperate system there was a significant stimulating effect of grazing within a season, that could not be accomplished by fertilization through droppings alone.

5 Comparison with arctic breeding areas

The Barnacle Geese breeding on Gotland probably descend from the Russian breeding population (Larsson et al. 1988). Arctic breeding demands different adaptations of geese than breeding in temperate areas, and geese breeding in temperate areas might therefore meet other constraints.

The statement that the quality of the food was higher at higher latitudes (Owen 1980, Manseau & Gauthier 1993) has been used as an explanation for arctic breeding in geese (Owen 1980). According to Larsson et al. (1988), Owens nitrogen story needs amplification. Since the Gotlandic population is increasing (Larsson et al. 1988, Forslund & Larsson 1991, Larsson & Forslund 1995), the nitrogen content at least seems adequate to breed on Gotland in the temperate zone. Therefore I want to make a comparison between nitrogen contents of the foraging species on Spitsbergen and Gotland.

For arctic breeding geese it has been reported that food quality already starts to decline just prior to or during hatching (Raveling 1978, Sedinger & Raveling 1986, Manseau & Gauthier 1993). And the food quality and availability continues to decline during season (Cargill & Jefferies 1984a, Prop et al. 1984, Sedinger & Raveling 1984, Sedinger & Raveling 1986, Thorvaldsson & Andersson 1987, Cooch et al. 1991, Larsson & Forslund 1991, Prop & Vulink 1992, Prop & De Vries 1993) and thus late hatching goslings have lower amounts of nutrients available (Sedinger & Raveling 1986, Cooch et al. 1991).

Agrostis, *Festuca* and *Puccinellia* were sampled three times during the season (table 8). Both *Festuca* and *Agrostis* were declining in nitrogen content in the first half of the season (the brood rearing period). The nitrogen contents were equally high at the end of the season (after moulting) as at the beginning of the season. This is in accordance with the 1992 growth data in chapter 3. The growth of *Festuca* and *Agrostis* decreased to zero in the middle of the season and showed an increase at the end.

Juncus gerardii had a nitrogen content between *Festuca* and *Agrostis* in period two (table 8). The sample of the seeds had a nitrogen content lower than all the other samples.

The nitrogen content of *Puccinellia* increased from the beginning to the end of the season. *Puccinellia* had during the whole season a higher Nitrogen content than the two other species. In 1993 growth of *Puccinellia* did not decrease during the season (fig 7c), and the nitrogen content in 1992 did even increase during the season. The nitrogen content of *Puccinellia* was higher than *Festuca* and *Agrostis*. It seems that *Puccinellia* is the most attractive plant specie for the geese, concerning the nitrogen. However, *Puccinellia* is very scarce on Närsholmen, it grows only on some small strips along the coastline. The geese will have to compete for this high quality, but low abundant food. And only the dominant families can benefit from those better food patches (Prop et al. 1984).

The seasonal decline in nitrogen of *Festuca* and *Agrostis* is in accordance with other studies (Sedinger & Raveling 1986, Thorvaldsson 1987a, Thorvaldsson & Andersson 1987, Larsson & Forslund 1991, Prop & Vulink 1992). This decline might have been steepened by the lack of precipitation (Thorvaldsson 1987a, Pruis 1992). The plants take up the bulk of the nitrogen early in the season, which results in high crude protein content. As the amount of available N in the soil decreases, the plants rate of uptake cannot keep pace with their rate of growth. This results in dilution of available protein over a greater amount of dry matter, resulting in decreased protein content (Thorvaldsson & Andersson 1987).

Table 8 The nitrogen content in % of the dry matter (N) and the sampling date (date) of the different vegetation types. Period 1 is the period from hatching of the young until moulting of the parents. Period 2 is the period in which the parents moult their primaries. Period 3 is the period after the moult and the fledging period of the juveniles.

| | period 1 | | period 2 | | period 3 | |
sample	N	date	N	date	N	date
Agrostis stolonifera	3.809	2-6	2.972	24-6	3.902	30-7
Festuca rubra	2.780	11-6	2.091	5-7	3.285	25-7
Puccinellia maritima	3.919	2-6	4.776	24-6	5.440	29-7
Juncus gerardii			2.325	24-6		
seeds			1.920	16-7		

Table 9 Nitrogen content (%) during different periods of the breeding season of Barnacle Geese on Spitsbergen and Gotland (Spitsbergen data from Prop & Vulink 1992).

| | | Spitsbergen | | Gotland | |
period	sample	months	N	months	N
pre incubation	moss	May	2.2		
incubation	grass	June-July	3.8	April-May	3.5*
moulting	grass	July-Aug	3.2	June-July	3.3
pre migration	grass	Aug-Sept	4.5	July-Aug	4.2

* this sample was taken just after the incubation period.

When the 1992 data are compared with earlier data they are in between the nitrogen contents measured by Larsson and Forslund (fig 16) in 1987 and 1988. 1992 seems to be an average year. In 1987 there had been a lot of rain and the young were very big at the end of the season. In 1988 it was very dry and the young were very light at the end of the season (pers. comm. K. Larsson). Comparing those data with 1992, one should be cautious, because Larsson and Forslund used a C:H:N-analyzer to determine nitrogen contents (Larsson & Forslund 1991) and in this study analyses were done with the Kjelldahl method. All three years showed a decrease of nitrogen content during the season.
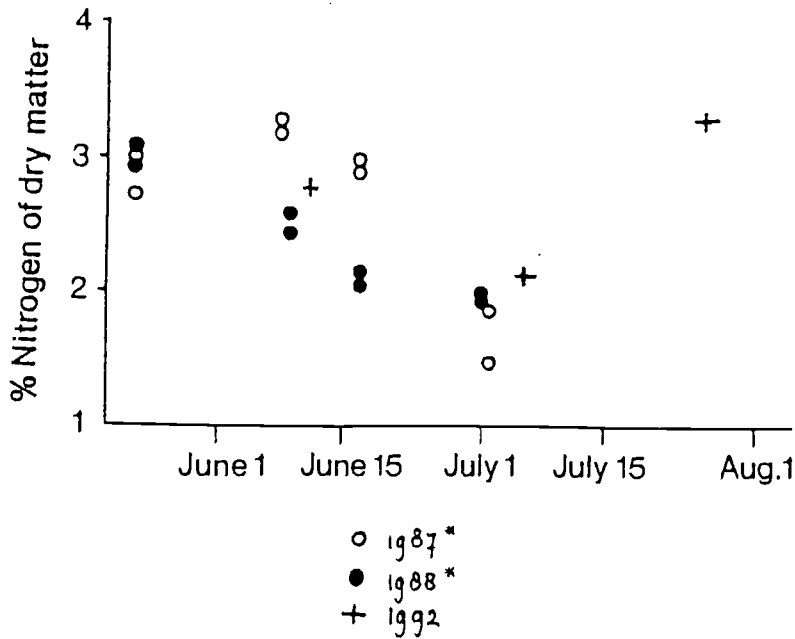

Figure 16 Nitrogen content of Festuca rubra in 1987, 1988 and 1992 during the season (data from 1987 and 1988 from Larsson & Forslund 1991)

From table 9 we see that during the moulting period, the period in which the goslings are growing, the nitrogen content is in the same range on Gotland and on Spitsbergen. In the period the geese have to raise their young, they face the same quality of food, concerning the nitrogen content. In the incubation period and the pre migration period, the nitrogen contents of both places are also comparable.

There is one important thing in this subject, it is not known if there has been a change in nitrogen levels on Gotland. It might be that nitrogen levels in the temperate zone were much lower than they are now. But on Gotland fertilizers have never been used on the area used by the geese and there is also no evidence for recent changes in grazing pressures (Larsson et al. 1988)

The nitrogen content of the grass is not the only important factor for geese. Also the time they have available to spend grazing and the efficiency in which they can digest their food are important factors that might differ between Gotland and the Arctic. At higher latitudes, the number

of daylight hours increases. Geese can benefit of longer daylight by spending more time feeding (Prop & Vulink 1992) and investing more time in the digestion of their food (Ebbinge & Ebbinge-Dallmeijer 1975, Prop & Vulink 1992).

On Gotland the geese spent 51 % of the 20 hours daylight feeding, while on Spitsbergen they spent 41 % of the 24 hours daylight on feeding (after Ten Bolscher 1992). In total feeding hours per day this is on Spitsbergen 10.0 hours (Prop & Vulink 1992) and on Gotland 10.2 hours (table 10).

Table 10 Hours daylight, dropping intervals (with standard deviation between brackets) and feeding hours per day for Barnacle Geese in different periods of the year. All data from Prop & Vulink (1992), except the Gotland data.

period	daylight (h)	interval (min)	n	feeding (h)
winter (Jan-Feb)	9	3.5 (1.2)	38	7.4
autumn (Oct)	11	4.0 (1.2)	90	8.7
spring (April)	12	4.4 (1.3)	82	9.0
spring (May)	19	4.9 (1.2)	160	12.9
pre migration (Aug-Sept)	20	5.8 (2.1)	71	11.5
Gotland moult (June-July)	20	7.1 (3.5)	307	10.2
Spitsbergen moult (July-Aug)	24	8.2 (3.2)	278	10.0
Spitsbergen Incubation (June-July)	24	15.0 (14.2)	101	1.4

By increasing their digestion, geese can minimizing their feeding time (Prop & Vulink 1992). As a measure for digestion, the dropping interval was measured, which is related to the retention time of the food in the digestive track. With increasing daylight hours, Barnacle Geese are increasing their retention time and thus their digestion (table 10). The data from Gotland fit quit well in this table from Prop & Vulink (1992). In the Arctic geese can optimize their digestion because they are able to keep a constant feeding-resting rhythm during the day (Prop et al 1980, Prop & Vulink 1992). On Gotland the geese have to go to a sleeping place to lower their predation risk during the dark period (Prop & Vulink 1992). While doing this, the geese have to break their feeding rhythm for several hours, which decreases their digestion efficiency.

So geese on Gotland have the same food quality, and spent equal time on feeding, but have a lower digestion efficiency. This lower digestion might result in a slower growth rate of goslings. On Gotland the goslings take about 8 weeks from hatch until fledging, while on Spitsbergen fledging already takes place after 6 weeks. Preliminary results seem to indicate that goslings on Gotland grow slower than goslings on Spitsbergen (I. van der Veen, K. Larsson & M. Loonen unpubl. data).

Literature

Abdul Jalil, S. & I.J. Patterson (1989). Effect of simulated goose grazing on yield of autumn-sown barley in north-east Scotland. Journal of Applied Ecology 26: 897-912.

Ankney, D.C. (1977). The use of nutrient reserves by breeding male Lesser Snow Geese *Chen caerulescens caerulescens*. Canadian Journal of Zoology 55: 1984-1987.

Ankney, D.C. (1979). Does the wing moult cause nutritional stress in Lesser Snow Geese? The Auk 96: 68-72.

Bakker, J.P. (1987). Diversiteit in de vegetatie door begrazing. In: S. de Bie, W. Joenje & S.E. van Wieren (eds.) Begrazing in de natuur. Pudoc, Wageningen.

Balkenhol, B., H-H. Bergmann, R. Holländer & M. Stock (1984). Über den Einfluß von Gänsekot auf die Vegetation von Grünflächen (On the impact of wild goose faeces on meadow vegetation). Ökologie der Vögel 6, Heft 2.

Bayliss, P. (1989). Population dynamics of Magpie Geese in relation to rainfall and density: implications for harvest models in a fluctuating environment. Journal of Applied Ecology 26: 913-924.

Bazely, D.R., P.J. Ewins & R.H. McCleery (1991). Possible effects of local enrichment by gulls on feeding-site selection by wintering Barnacle Geese *Branta leucopsis*. Ibis 133:111-114.

Bazely, D.R. & R.L. Jefferies (1985). Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology 22: 693-703.

Bazely, D.R. & R.L. Jefferies (1986). Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. Journal of Ecology 74: 693-706.

Bazely, D.R. & R.L. Jefferies (1989a). Lesser Snow Geese and the nitrogen economy of a grazed salt marsh. Journal of Ecology 77: 24-34.

Bazely, D.R. & R.L. Jefferies (1989b). Leaf and shoot demography of an arctic stoloniferous grass, *Puccinellia phryganodes*, in response to grazing. Journal of Ecology 77: 811-822.

Bédard, J., A. Nadeau & G. Gauthier (1986). Effects of spring grazing by Greater Snow Geese on hay production. Journal of Applied Ecology 23: 65-75.

Bergeron, J.-M. & L. Jodoin (1993). Intense grazing by voles (*Microtus pennsylvanicus*) and its effect on habitat quality. Canadian Journal of Zoology 71: 1823-1830.

Bolscher, F.H. (1992). Activiteits-budget & dagritmiek van de brandgans (*Branta leucopsis*), Gotland 1992. (Activity budget & daily rythm of the Barnacle Goose (*Branta leucopsis*), Gotland 1992. Student report, University of Groningen.

Cargill, S.M. & R.L. Jefferies (1984a). Nutrient limitation of primary production in a sub-arctic salt marsh. Journal of Applied Ecology 21: 657-668.

Cargill, S.M. & R.L. Jefferies (1984b). The effects of grazing by Lesser Snow Geese on the vegetation of a sub-arctic salt marsh. Journal of Applied Ecology 21: 669-686.

Chou, R., C. Vardy & R.L. Jefferies (1992). Establishment from leaves and other plant fragments by the foraging activities of geese. Functional Ecology 6: 297-301.

Coleman, T.S. & D.A. Boag (1987). Canada Goose foods: their significance to weight gain. Wildfowl 38: 82-88.

Cooch, E.G., D.B. Lank, R.F. Rockwell & F. Cooke. (1991). Long-term decline in body size in a Lesser Snow Goose population: evidence of environmental degradation? Journal of Animal Ecology 60: 483-496.

Cooke, F., C.S. Findlay & R.F. Rockwell (1984). Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). The Auk 101: 451-458.

Day, T.A. & J.K. Detling (1990). Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71: 180-188.

Drent, R.H. & H.H.T. Prins (1987). The herbivore as a prisoner of its food supply. In: Disturbance in Grasslands. J. van Andel *et al.* (eds.). Dordrecht, The Netherlands.

Ebbinge, B.S. (1985). Factors determining the population size of arctic-breeding geese, wintering in western Europe. Ardea 73: 121-128.

Ebbinge B.S. & J.B. van Biezen (1987). Estimation of annual survival rates using resightings of individually marked barnacle geese *Branta leucopsis* wintering in the Netherlands and northern Germany. Acta Ornithologica 23: 101-114.

Ebbinge, B.S., K. Canters & R. Drent (1975). Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. Wildfowl 26: 5-19.

Ebbinge, B. & D. Ebbinge-Dallmeijer (1975). Barnacle Geese (*Branta leucopsis*) in the Arctic summer - a reconnaissance trip to Svalbard. Norsk Polarinst. Årbok 1975: 119-138.

Ebbinge, B.S. & B. Spaans (1992). The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding of Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. Manuscript in: Population limitation in arctic-breeding geese. B.S. Ebbinge, dissertation, University of Groningen, Groningen 1992.

Faber, J. (1989). The effects of grazing by Barnacle Geese on the growth of red fescue. Manuscript, University of Groningen.

Fletcher, N. & G.R. Shaver (1983). Life histories of tillers of *Eriophorum vaginatum* in relation to tundra disturbance. Journal of Ecology 71: 131-147.

Forslund, P. (1992). Effects of reproductive tactics and population density on breeding success in the Barnacle Goose *Branta leucopsis*. Dissertation Uppsala University, Uppsala, Sweden.

Forslund P. (1993). Vigilance in relation to brood size and predator abundance in the Barnacle Goose, *Branta leucopsis*. Animal Behaviour 45: 965-973.

Forslund, P. & K. Larsson (1991). Breeding range expansion of the Barnacle Goose (*Branta leucopsis*) in the Baltic area. Ardea 79: 343-346.

Georgiadis, N.J., R.W. Ruess, S.J. McNaughton & D. Western (1989). Ecological conditions that determine when grazing stimulates grass production. Oecologia 81: 316-322.

Hik, D.S. & R.L. Jefferies (1990). Increase in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. Journal of Ecology 78: 180-195.

Hik, D.S., H.A. Sadul & R.L. Jefferies (1991). Effects of the timing of multiple grazings by geese on the net above-ground primary production of swards of *Puccinellia phryganodes*. Journal of Ecology 79: 715-730.

Hilbert, D.W., D.M. Swift, J.K. Detling & M.I. Dyer (1981). Relative growth rates and the grazing optimization hypothesis. Oecologia 31: 14-18.

Jefferies R.L. & N. Perkins (1977). The effect on the vegetation of the additions of inorganic nutrients to salt marsh soils at Stiffkey, Norfolk. Journal of Ecology 65: 867-882.

Jeugd, H.P. van der (in prep.) Increasing habitat differences between two populations of Barnacle Geese during spring staging.

Kotanen, P. & R.L. Jefferies (1987). The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. Journal of Ecology 75: 961-975.

Laing, K.K. & D.G. Raveling (1993). Habitat and food selection by Emperor Goose goslings. Condor 95: 879-888.

Larsson, K. (1992). Ecological and quantitative genetic processes in a population of the Barnacle Goose (*Branta leucopsis*). Dissertation Uppsala University, Uppsala, Sweden.

Larsson, K. & P. Forslund (1991). Environmentally induced morfological variation in the Barnacle Goose, *Branta leucopsis*. Journal of Evolutionary Biology 4 : 619-636.

Larsson, K. & P. Forslund (1995). Population dynamics of the Barnacle Goose *Branta leucopsis* in the Baltic area: density-dependent effects on reproduction. Journal of Animal Ecology (in press).

Larsson, K., P. Forslund, L. Gustafsson & B. Ebbinge (1988). From the high Arctic to the Baltic: the successful establishment of a Barnacle Goose *Branta leucopsis* population on Gotland, Sweden. Ornis Scandinavica 19: 182-189.

Leeuw, J. de, H. Olff, J.P. Bakker (1990). Year-to-year variation in peak above ground biomass of six salt-marsh angiosperm communities as related to rainfall deficit and inundation frequency. Aquatic Botany 36: 139-151.

Madsen, J. (1989). Spring feeding ecology of Brent Geese *Branta bernicla*: annual variation in saltmarsh food supplies and effects of grazing on growth of vegetation. Danish Review of Game Biology 13: 4-16.

Madsen, J. (1991). Status and trends of goose populations in the Western Palearctic in the 1980s. Ardea 79: 113-122.

Manseau, M. & G. Gauthier (1993). Interactions between Greater Snow Geese and their rearing habitat. Ecology 74: 2045-2055.

Marriott, R.W. (1973). The manurial effect of Cape Barren Goose droppings. Wildfowl 24:131-133.

McNaughton, S.J. (1976). Serengeti migratory Wildebeest: facilitation of energy flow by grazing. Science 191: 92-94.

Milchunas, D.G. & W.K. Lauenroth (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63: 327-366.

Norusis, M.J. (1988). SPSS/PC+ v2.0 Base manual. SPSS Inc., Chicago.

Owen, D.F. & R.G. Wiegert (1981). Mutualism between grasses and grazers: an evolutionary hypothesis. Oikos 36: 376-378.

Owen, M. (1980). Wild geese of the world. Batsford, London.

Percival, S.M. (1993). The effects of reseeding, fertilizer application and disturbance on the use of grasslands by , and the implications for refuge management. Journal of Applied Ecology 30: 437-443.

Prins, H.H.T. (1988). Plant phenology patterns in Lake Manyara National Park. Journal of Biogeography 15: ??-??.

Prins, H.H.T. & P.E. Loth (1988). Rainfall patterns as background to plant phenology in northern Tanzania. Journal of Biogeography 15: ??-??.

Prins, H.H.T., R.C. Ydenberg & R.H. Drent (1980). The interaction of Brent Geese *Branta bernicla* and sea plantain *Plantago maritima* during spring staging: field observations and experiments. Acta Botanica Neerlandica 29: 585-596.

Prop, J. (1991). Food exploitation patterns by Brent Geese *Branta bernicla* during spring staging. Ardea 79: 331-342.

Prop, J., M.R. van Eerden, S. Daan, R.H. Drent, J.M. Tinbergen & A.M. St. Joseph (1980). Ecology of the Barnacle goose (Branta leucopsis) during the breeding season. Proceedings of the Norwegian-Netherlands Symposium on Svalbard. Arctic Centre, Groningen.

Prop, J., M.R. van Eerden & R.H. Drent (1984). Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. Norsk Polarinstitution Skrifter 181: 87-117.

Prop, J. & J. de Vries (1993). Impact of snow and food conditions on the reproductive performance of Barnacle Geese *Branta leucopsis*. Ornis Scandinavica 24: 110-121.

Prop, J. & T. Vulink (1992). Digestion by Barnacle Geese in the annual cycle: the interplay between retention time and food quality. Functional Ecology 6: 180-189.

Pruis, J. (1992). Grazing the salt-marsh: Barnacle Goose foraging behaviour in relation to *Festuca rubra* quality and quantity. Student report, University of Groningen.

Raveling, D.G. (1978). The timing of egg laying by northern geese. The Auk 95: 294-303.

Ruess, R.W., D.S. Hik & R.L. Jefferies (1989). The role of Lesser Snow Geese as nitrogen processors in a sub-arctic salt marsh. Oecologia 79: 23-29.

Sedinger, J.S. (1986). Growth and development of Canada Goose goslings. The Condor 88: 169-180.

Sedinger, J.S. & P.L. Flint (1991). Growth rate is negatively correlated with hatch date in Black Brant. Ecology 72: 496-502.

Sedinger, J.S. & D.G. Raveling (1984). Dietary selectivity in relation to availability and quality of food for goslings of Cackling Geese. The Auk 101: 295-306.

Sedinger, J.S. & D.G. Raveling (1986). Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. Journal of Animal Ecology 55: 1083-1102.

Thorvaldsson, G. (1987a). The effects of weather on nutritional value of Timithy in northern Sweden. Acta Agric. Scand. 37: 305-319.

Thorvaldsson, G. (1987b). The morphological and phenological development of Timothy as affected by weather, and its relation to nutritional value. Manuscript in: Thorvaldsson, G. (1987). The influence of harvest date, nitrogen application and weather on development and nutritional value of Timothy (*Phleum pratense* L.) and its implication for prediction of forage quality. Dissertation, University of Agricultural Sciences of Uppsala, Uppsala, Sweden.

Thorvaldsson, G. & S. Andersson (1986). Variations in Timothy dry matter yield and nutrtional value as affected by harvest date, nitrogen fertilization, year and location in northern Sweden. Acta Agric. Scand. 36: 367-385.

Wal, R. van der (1992). The energetic costs of moult in the Greylag Goose (*Anser anser*). Student report University of Groningen.

Wallace, L.L. & S.A. Macko (1993). Nutrient acquisition by clipped plants as a measure of competative success: the effects of compensation. Functional Ecology 7: 326-331.

Wiersma, P. (1991). Spring grazing by geese on a temperate zone salt marsh: do they benefit from their droppings? Student report University of Groningen.

Williams, T.D., E.G. Cooch, R.L. Jefferies & F. Cooke (1993). Environmental degradation, food limitation and reproductive output: juvenile survival in Lesser Snow Geese. Journal of Animal Ecology 62: 766-777.

Ydenberg, R.C. & H.H.T. Prins (1981). Spring grazing and the manipulation of food quality by Barnacle Geese. Journal of Applied Ecology 18: 443-453.

Appendix 1.

Aprilday	date	Aprilday	date	Aprilday	date
1	01-04	41	11-05	81	20-06
2	02-04	42	12-05	82	21-06
3	03-04	43	13-05	83	22-06
4	04-04	44	14-05	84	23-06
5	05-04	45	15-05	85	24-06
6	06-04	46	16-05	86	25-06
7	07-04	47	17-05	87	26-06
8	08-04	48	18-05	88	27-06
9	09-04	49	19-05	89	28-06
10	10-04	50	20-05	90	29-06
11	11-04	51	21-05	91	30-06
12	12-04	52	22-05	92	01-07
13	13-04	53	23-05	93	02-07
14	14-04	54	24-05	94	03-07
15	15-04	55	25-05	95	04-07
16	16-04	56	26-05	96	05-07
17	17-04	57	27-05	97	06-07
18	18-04	58	28-05	98	07-07
19	19-04	59	29-05	99	08-07
20	20-04	60	30-05	100	09-07
21	21-04	61	31-05	101	10-07
22	22-04	62	01-06	102	11-07
23	23-04	63	02-06	103	12-07
24	24-04	64	03-06	104	13-07
25	25-04	65	04-06	105	14-07
26	26-04	66	05-06	106	15-07
27	27-04	67	06-06	107	16-07
28	28-04	68	07-06	108	17-07
29	29-04	69	08-06	109	18-07
30	30-04	70	09-06	110	19-07
31	01-05	71	10-06	111	20-07
32	02-05	72	11-06	112	21-07
33	03-05	73	12-06	113	22-07
34	04-05	74	13-06	114	23-07
35	05-05	75	14-06	115	24-07
36	06-05	76	15-06	116	25-07
37	07-05	77	16-06	117	26-07
38	08-05	78	17-06	118	27-07
39	09-05	79	18-06	119	28-07
40	10-05	80	19-06	120	29-07