Spring migration strategies and stop-over ecology of pink-footed geese

Results of field work in Norway, 1996

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Summary

The spring fattening and ecology of pink-footed geese *Anser brachyrhynchus* at stopover sites in Trondheimsfjord, Trøndelag and Vesterålen in Norway was studied in 1996. The first geese arrived from Denmark to Trøndelag in mid April; numbers peaked with up to 17,400 geese during 7-17 May, and the last geese departed around 24 May. In Vesterålen, the first geese arrived in early May; numbers peaked during 18-21 May at 6,500 geese, and the last geese departed around 24 May. From resightings of neckbanded birds it is estimated that 20,500-24,200 individuals stopped in Trøndelag and 15,600-18,500 in Vesterålen, but because of rapid turnover, these were never all counted at any one time. At least 69% of the individuals observed in Trøndelag were subsequently recorded in Vesterålen. The spring migration was probably delayed due to severe winter conditions and late spring in the winter quarters in Denmark, the Netherlands and Belgium and this may explain the late arrival in Vesterålen compared to other years; however, the observations confirm the patterns seen in previous seasons, namely that the geese are making increasing use of Trøndelag and decreasing use of Vesterålen.

To analyse the possible consequences of choice of different spring staging strategy for spring fattening (assessed by abdominal profile index API), individually neckbanded adult females were grouped into five categories of strategies according to their timing of migration and use of stopover sites in Norway. The highest rates of increase in API's were observed in Vesterålen; in Trøndelag, the rates of increase were high during mid May, but low during late April-early May. Hence, females departing early from Denmark (before 5 May), staging in Trøndelag and only stopping briefly in Vesterålen around 20 May increased their API scores and departed from Vesterålen towards Svalbard in poor condition. Females departing late from Denmark, staging in Trøndelag as well as Vesterålen were intermediate in final API's, while geese departing late from Denmark and flying directly to Vesterålen showed the highest API's at departure. In autumn 1996, the breeding success of the individuals was recorded in Denmark and the Netherlands. Comparing the five categories of spring migration strategies in marked females, there was a significant relationship between final departure API's in Vesterålen and the subsequent breeding success. A similar pattern was found in unmarked females, paired to marked males for which the migration strategy and subsequent breeding success were known. Thus, in 1996 there was a penalty attached to early arrival in Trøndelag, whereas there was a premium attached to making extensive use of Vesterålen.

In Trøndelag, the foraging day-length in late April was approximately 16 hours; however, due to farming activity and other human-induced disturbance during the day, the geese were restricted to feed mainly during mornings and evenings. They spent on average 34% of the 24 hours feeding. Because of a rapidly increasing day-length, the geese increased the foraging day to approximately 22 hours by mid May and

spent on average 53% of the 24 hours feeding. The first arriving geese foraged on stubble, unharvested cereal fields and pastures; during May the geese made increasing use of newly sown cereal fields. In late April, there was little grass growth; this growth increased during May, and the nitrogen content of grass blades peaked during mid May. Furthermore, the newly sown fields provided the geese with a food source which is highly digestible and energy-rich. The combination of these factors probably explains the difference in the rates of increase of API's in Trøndelag.

The results show that the choice of migration strategy can have repercussions on spring fattening and breeding success. The increasing use of the Trondheimsfjord staging area apparently conflicts with the consequence of using this area as measured by individual API's. However, the year-to-year consequences of using different migration strategies need to be assessed in a range of different seasonal conditions before the individual fitness consequences of choice of migration strategy can be evaluated over the lifetime of individual birds. The use of the Trondheimsfjord area is still changing and if the geese can accommodate the effects of human activities (by local habituation), there is scope for an improved usage by the geese and for improving spring fattening rates. Snow cover and frost set a limit on the time of arrival (around early April at the earliest). The increasing use of the Trondheimsfjord area has reduced the agricultural conflict in Vesterålen; however, it not only moves the conflict southwards in Norway but from a national perspective, it may lead to an overall exacerbation of the problem.

1 Introduction

During spring migration, the pink-footed geese *Anser brachyrhynchus* from the Svalbard breeding population migrate from spring staging areas in Denmark via stopover sites in Norway to the breeding grounds. Until recently, the geese departed from Denmark during the first half of May, to stop in Vesterålen in north Norway during approximately 7-20 May (Rikardsen 1982, Madsen 1987). However, since the late 1980s, the geese have started to use the Trondheimsfjord area as an additional stopover, positioned almost exactly half way between Denmark and Vesterålen. The numbers of geese using the intermediate stopover have increased dramatically and, furthermore, first arrival dates have advanced from around 5 May in the late 1980s to mid April in the mid 1990s (P.I. Nicolaisen and J. Madsen unpubl.). Furthermore, since the 1970s, the dates of first arrivals in Vesterålen have advanced by approximately one week, whereas the timing of departure has not changed.

As a consequence of the increasing use by the geese of both Vesterålen and the Trondheimsfjord area, there has been increasing conflict between agriculture and geese. In Vesterålen, farmers in 1993-94 organised a campaign to scare the pink-footed geese off grasslands used for sheep grazing in spring. Because of the frequent scaring, geese in disturbed sites were unable to feed effectively and did not put on sufficient nutrient reserves to breed as successfully as geese from areas without scaring. Goose numbers in Vesterålen were reduced, however, with a demonstrable impact on fecundity of a large proportion of the breeding population (Madsen 1994, unpubl.).

In order to create a common understanding of the need for reducing conflicts and to establish safe limits for sustainable goose populations, the Norwegian Directorate for Nature Management (DN) in 1996 produced a national management plan for geese (Direktoratet for naturforvaltning 1996). The recent developments in the use of Norwegian stopover sites by pink-footed geese was of major concern because, at the time of writing the plan, the conflict was escalating.

During 1991-1994, the National Environmental Research Institute (NERI), Denmark studied the spring migration ecology of pink-footed geese in Norway, partly with the aim of describing the importance of the Norwegian stopover sites for the build-up of body stores as a prelude to breeding, and partly to analyse the fitness consequences of the choice of migration strategy by marked individuals. In 1996, DN contracted NERI to study the stopover ecology of pink-footed geese in both the Trondheimsfjord area and Vesterålen. The purpose of the study was to describe the body condition build-up by pink-footed geese during spring in Norway and to assess if there were any detectable constraints on numbers and the period of stay. If such knowledge could be established, it would feed into the predictions of the future goose damage conflict and its possible solution.

2 Acknowledgements

This work was co-financed by NERI and DN (study contract L 26/96). We are grateful to the many dedicated birdwatchers who contributed goose counts and reading of neckbands. A special thanks to Vesterålen fugleforening (part of the Norwegian Ornithological Society) and their coordinator of the goose inventories, Tor Bønes, and to Steinkjer fugleforening (also part of the Norwegian Ornithological Society) and their coordinator of the goose inventories, Per Ivar Nicolaisen. Niels Ulrik Pedersen, Erik Overlund and others are thanked for watching the geese in west Jutland, Denmark, while we were in Norway. Thanks to Mære Landbruksskole in Trøndelag and to farmer Tommy Jonsen, Vik in Vesterålen, for allowing us to use their land for vegetation measurements. The Norwegian Meteorological Institute is thanked for supplying weather data.

3 Study areas

3.1 Habitats

The Trondheimsfjord staging area, Trøndelag: Extends from Gaulosen near Trondheim in the south to Snåsavatnet north of Steinkjer in the north (Fig. 1). The geese roost on the coast in sheltered bays or on lakes (Snåsavatnet, Leksdalsvatnet) and feed on the adjacent farmlands. The farmland is composed mainly of pasture and spring-sown cereals as well as rough pasture. In spring, stubble remains from the previous season, as well as cereal fields which were not harvested. Sowing of spring cereals commences from early May; in 1996 sowing started in late April (on dry soils) but continued through to late May. There is generally very little salt marsh on the coast.

The Vesterålen staging area, Nordland: Extends from Hadseløya, Langøya, Hinnøya in the south to Andøya in the north (Fig. 1). In addition, flocks occasionally occur on Gimsøya on Lofoton. The geese roost on the coast and feed on the adjacent farmlands which are situated in the lowlands (below 100 m altitude) close to the coasts. All the farmland is artificial grassland used for sheep or cattle grazing and hay cutting. Along some of the coast line, areas of salt marsh remain; however, most are overgrown through lack of summer grazing by livestock.

The Danish staging areas were described by Madsen (1996).

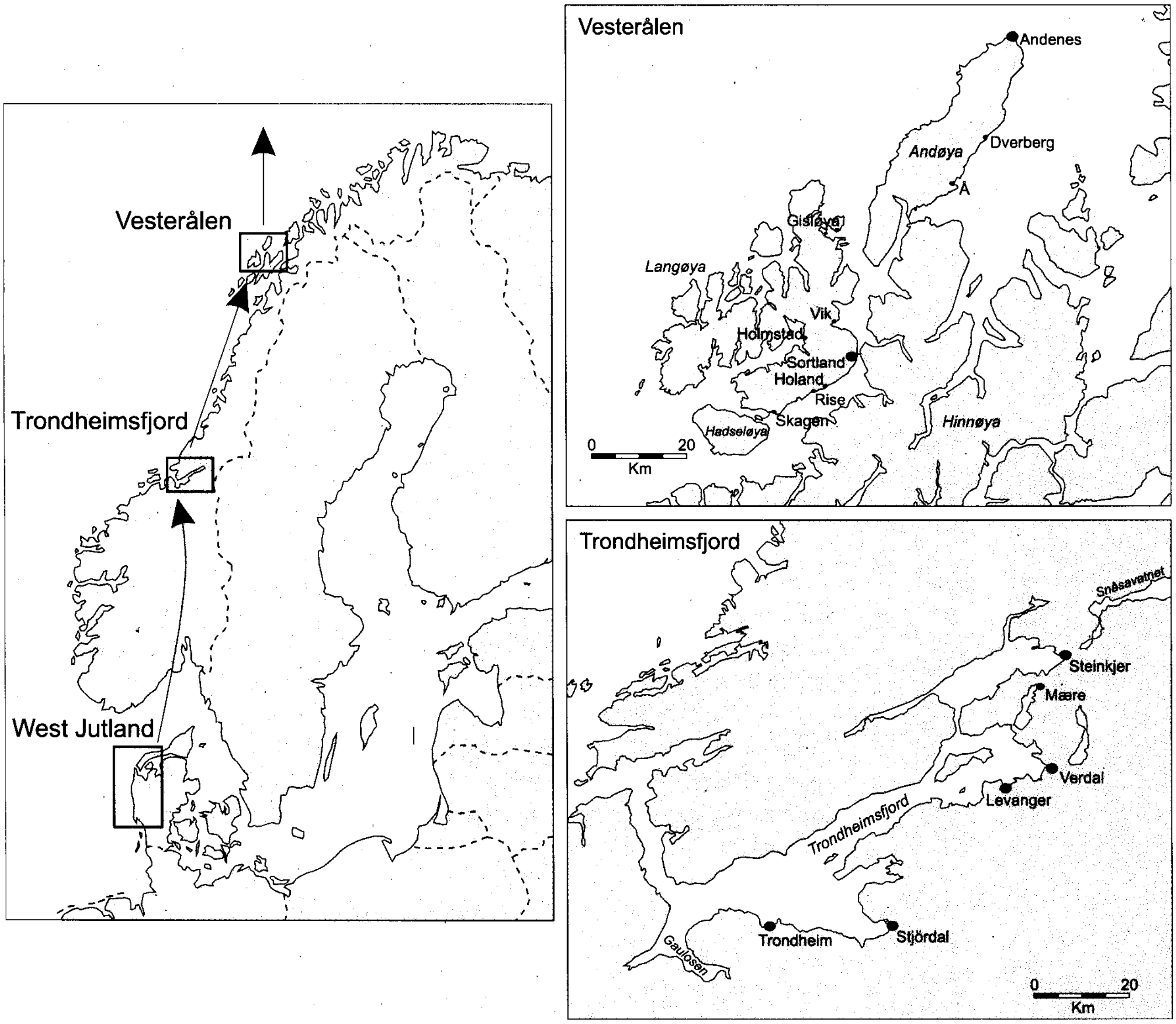


Figure 1. The Norwegian and Danish study areas used by pink-footed geese during spring. Arrows show the spring migration route. Site names mentioned in the text are shown on the two insert maps.

3.2 Weather

Daily temperatures are recorded at the Verdal weather station which is central to the Trondheimsfjord area and at the Sortland weather station which is central to the Vesterålen staging area.

Verdal: During 15 April to 20 May, i.e. the goose staging period, daily temperatures ranged from -5 to 15°C (Fig. 2), increasing during the period. In the second half of April, mean maximum and minimum temperatures were above the average of the preceding six years, whereas in May, both mean maximum and minimum temperatures were below the average (Table 1, Fig. 2). In mid April, many fields were still snow covered; however, on south facing slopes, the thaw was progressing and this quickly advanced during the second half of April.

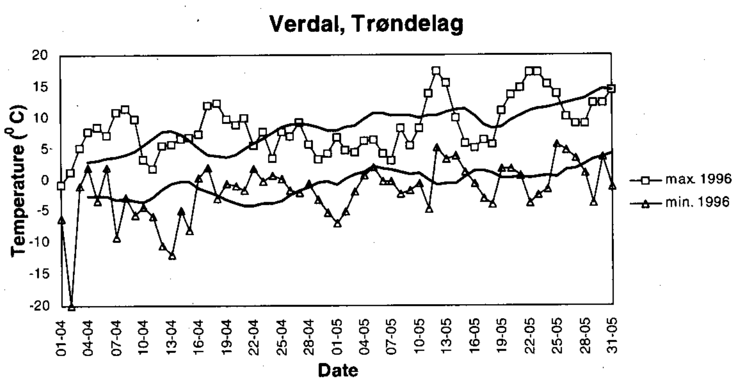
Sortland: During 15 April to 20 May, daily temperatures ranged from -

Table 1. Maximum and minimum temperatures (°C) during the period of presence of pink-footed geese in the Trondheimsfjord area (Verdal weather station) and in Vesterålen (Sortland weather station), in 1996 and 1990-95, respectively. Source: Norwegian Meteorological Institute.

Verdal	April 15-30		May 1-20	
	avg 90-95	1996	avg 90-95	1996
Max	6.59	7.56	10.07	8.12
Min	-2.37	-1.45	0.68	-0.61

Sortland	April 15-30		May 1-20	
	avg 90-95	1996	avg 90-95	1996
Max	5.97	4.50	7.66	4.98
Min	0.17	0.59	2.24	0.31

4 to 8°C, increasing during the period (Fig. 2). During the second half of April, the mean maximum temperature was below the average of the preceding six years, whereas the mean minimum was above average. In May, both mean maximum and minimum temperatures were below the average (Table 1, Fig. 2). In the first days of May, most of the pastures were still snow covered, but south facing slopes were becoming free of snow. By the middle of May, almost all snow had thawed.



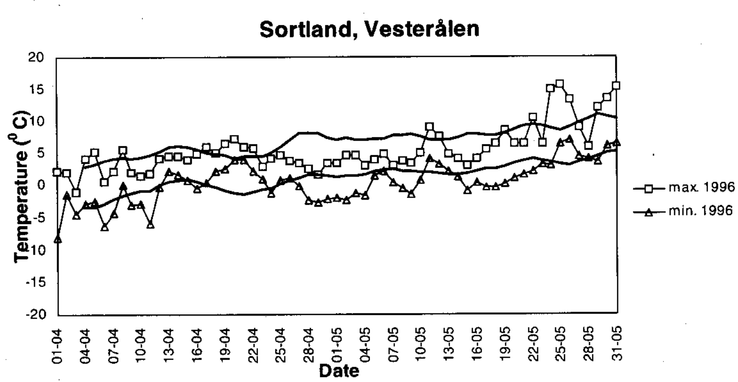


Figure 2. Maximum and minimum temperatures at Verdal in Trøndelag and Sortland in Vesterålen, April and May 1996, and averages (4-day moving averages) for 1990-1995. Source: The Norwegian Meteorological Institute.

4 Methods

4.1 Field work

The Trondheimsfjord area was visited by Flemming Hansen during 20 April to 22 May. Local birdwatchers assisted with counts and reading of neckbands (coordinated by Per Ivar Nicolaisen, Steinkjer fugleforening).

Vesterålen was visited by Jan Bolding Kristensen and Hugh Boyd from 1 to 21 May and by Jesper Madsen from 6-10 May and 17-21 May. JBK and HB organised daily counts, reading neckbands and scoring abdominal profiles; JM was primarily collecting geese for carcass analysis of fat and protein deposition (not reported here). Local birdwatchers assisted with counts and reading of neckbands on Langøya (coordinated by Tor Bønes, Vesterålens fugleforening).

4.2 Counting of geese

Because of the large size of the area and a high degree of unpredictability in goose numbers, the Trondheimsfjord area could not be covered on a daily basis, but core areas were visited almost daily or at approximately two day intervals. In Vesterålen, observations were made daily on Langøya, while Andøya was visited at two day intervals.

Counting of geese was mostly done from cars using telescopes or binoculars. The position of flocks was recorded at site level. Site boundaries were defined on maps. Feeding habitat of each flock and the time of observation were recorded.

4.3 Behavioural observations

In Vesterålen, activity budgets of pink-footed geese have been described in previous seasons and this was not given priority in 1996. In the Trondheimsfjord area, observations of activity were carried out to establish a crude activity budget. However, it turned out to be extremely difficult to follow a specific flock throughout a day because the geese flew from the roosts to feeding grounds which were difficult to find. Consequently, FH drove through the study area at various times throughout the 24 hour cycle and recorded the number of geese present on the roosts and the feeding grounds, respectively. Activities of flocks on the roosts and in the fields were sampled by scan observations, recording the number of individuals engaged in various activities (foraging, resting, flying, aggression, alertness) at 10 minute intervals. Rather than following a single flock for several hours, the activity of several different flocks was scored once or twice when the geese were encountered and not disturbed by the observer. Hence, by this method, the proportion of geese on the feeding grounds and on the roosts was established on a diurnal basis; knowing the activity budgets in the fields and on the roosts, respectively, the diurnal time spent feeding could then be calculated.

To obtain a measure of the tolerance of flocks of pink-footed geese towards human activity, the escape flight distance in response to approaching cars was estimated.

4.4 Sightings of neckbands and scoring of abdominal profiles

During 1990-1995, 610 pink-footed geese have been caught and marked with plastic neckbands on the spring staging grounds in west Jutland in Denmark (NERI). Neckbands are blue with white three-digit inscriptions. With the aid of a telescope, the neckbands can be read at a distance of up to 600-900 m, depending on weather conditions. In spring 1996, approximately 1% of the total population was carrying neckbands.

In all goose flocks encountered, it was attempted to read all neckbands. In the Trondheimsfjord area this often proved difficult, because many flocks were observed while roosting on the coast when neckband reading is often impossible.

Abdominal profiles (API's) of marked birds were scored when birds were observed as active in the fields and only in situations when it was reasonable to assume that the geese had been foraging for at least two hours in advance, so that they had filled their guts. Seven categories of abdominal profiles indexes are used (Fig. 3). Observations of profiles are scored when the geese stand with their heads in upright position. The observations were only made by experienced observers (FH, JBK, HB and JM), who were inter-calibrated in their scoring. Previous experience shows that there is a high inter-observer consistency in scoring (tested by independent scoring of the same individuals)(J. Madsen and H. Boyd, unpubl.). Furthermore, a preliminary analysis shows, that there is a significant linear relationship between abdominal profile indexes and body weight (based on birds which were caught, marked and weighed and subsequently observed in the field within the following two days) (J. Madsen unpubl.).

4.5 Measurements of vegetation growth

To achieve a measure of grass productivity rates, the rate of blade length increment and death was measured on individual shoots. Grass blade length increment does not correspond directly to biomass increment; however, because the geese are selectively picking the new

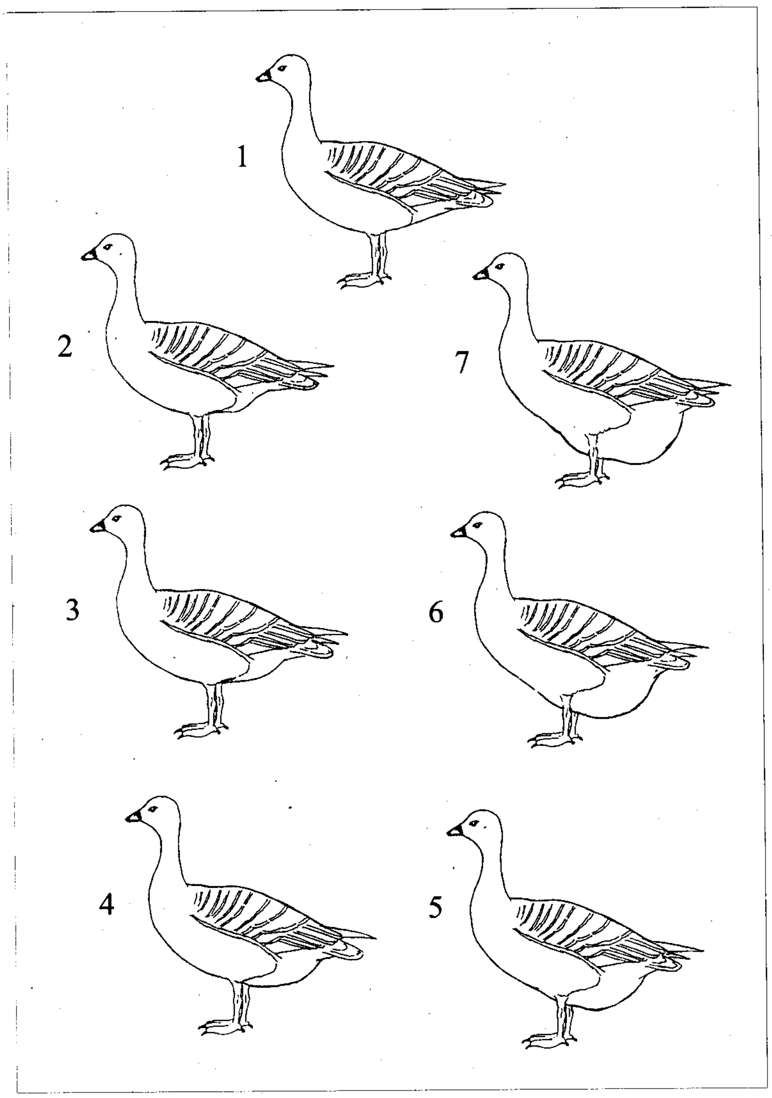


Figure 3. Abdominal profiles indexes (1-7) used for scoring condition of pink-footed geese in the field.

blades with the highest nutrient contents (Fox 1993, Madsen unpubl.), it is more relevant to measure the blade lengths rather than the biomass which includes older as well as new blades.

In the Trondheimsfjord area trials were set up on 22 April in a pasture at Mære, which had been reseeded three years ago and was composed primarily of a mixture of *Poa pratense*, *Phleum pratense* and *Festuca pratensis*. The field had no slope and was partly free from snow on 22 April. In Vesterålen, trials were set up on 3 May in a pasture at Vik. The field had been reseeded two years ago and was composed of the same grass species as in the Mære field. The field faces south with a slight slope and was partly free from snow on 2 May.

In both study fields, four 60 cm diameter exclosure plots were set up, fenced with plastic chicken wire. In each plot, 16 randomly selected shoots were marked with 1-2 rings (made of pieces of plastic straw), giving a total of 64 marked shoots in each study area. At 4-5 day intervals, the length of each blade of each marked tiller was measured with a ruler. Each blade was given a code: A, the most recent blade at the

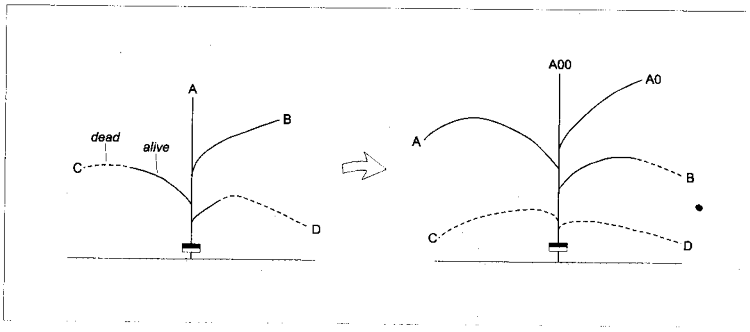


Figure 4. Schematic grass shoot marked at two stages of development with blade categories used in blade increment/death measurements.

start of the trial; B, second blade (older); C, third blade; D, fourth blade; A0, new blade emerging after start of trial and, A00, new blade emerging after A0. For blades with dead tips, the length of the live and the dead part was measured separately. The principle behind the measurements and the turnover of blades is shown in Fig. 4. All marked shoots were *Poa pratense,* except for four shoots of *Phleum.* Since the growth rates of the two species did not differ, they have been pooled.

At weekly intervals in the Mære field and at 4-5 day intervals in the Vik field, samples of grass blades (new blades) were collected for ni trogen analysis (Kjelldahl). Analyses were made by the Central Laboratory of the Danish Institute of Agricultural Sciences.

4.6 Assessment of breeding success

In the autumn of 1996, when the population of pink-footed geese returns from the Svalbard breeding grounds to autumn staging grounds in west Jutland, Denmark and in Friesland, the Netherlands, FH assessed the breeding success of marked individuals by observation of the brood sizes (i.e. the number of juvenile geese) and mating status (paired/unattached) of marked birds. FH observed the geese during 22 September to 19 October in west Jutland and during 29 October to 13 November in Friesland. Of a total of 237 different neckbanded individuals observed, the breeding status was recorded for 227 (96%). Because the pink-footed geese often congregate in large and dense flocks, it can be difficult to determine the exact number of juveniles in the broods. For the purpose of this analysis, it has only been entered whether a bird bred successfully or not.

5 Results

5.1 Goose numbers and distribution

In the Trondheimsfjord area, the first pink-footed geese (18 individuals) were observed on 16 April; numbers remained low until 8 May, when more than 4,000 birds were counted (Fig. 5). Numbers peaked

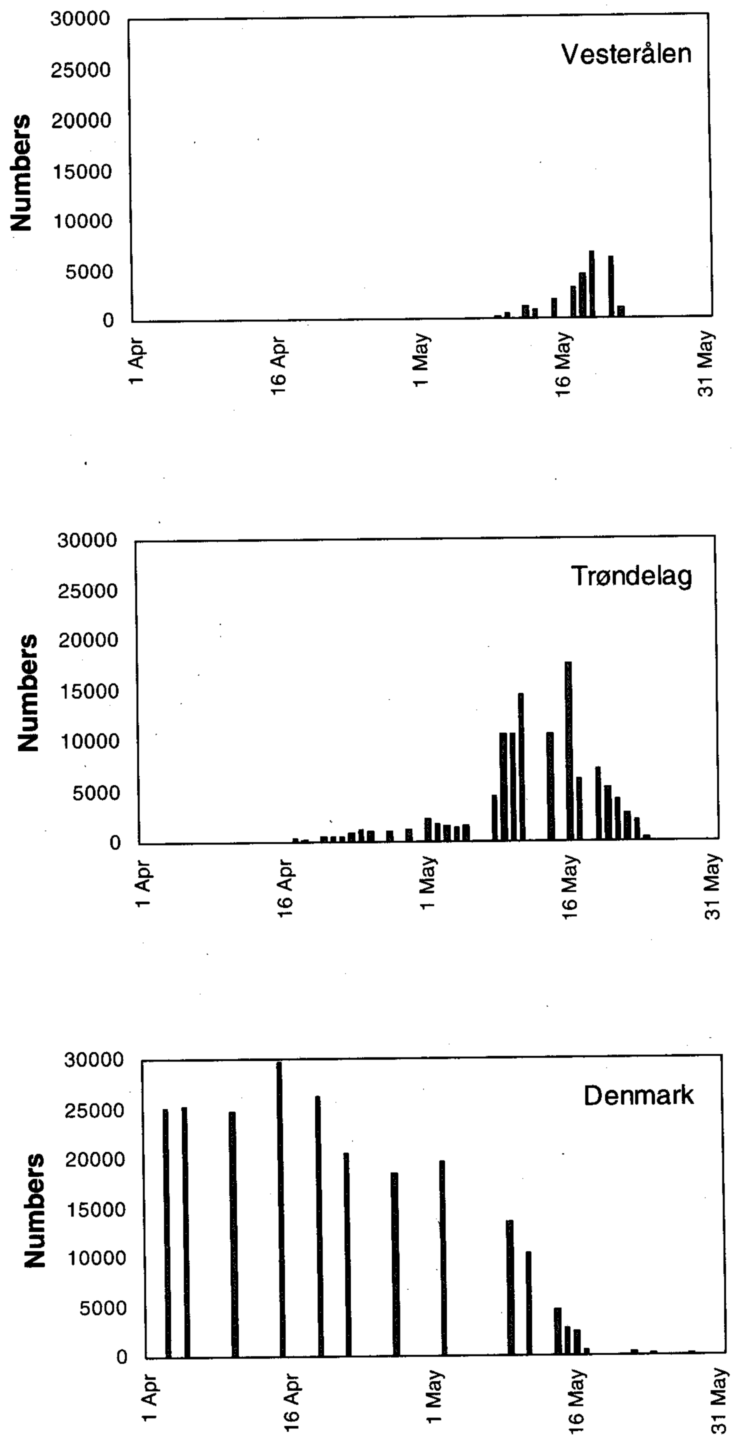


Figure 5. Number of pink-footed geese counted in the three study areas during April and May 1996.

with 17,400 on 16 May; thereafter numbers declined. The last 300 geese were observed on 24 May.

In Vesterålen, the first pink-footed geese (2) were observed on 2 May. Numbers slowly increased; however it was not until 12 May that numbers exceeded 1,000 birds. Numbers peaked with 6,500 on 19 May. The majority of geese had left on 22 May (Fig. 5).

In west Jutland, up to 30,000 pink-footed geese were counted on 15 April. During the last 10 days of April numbers declined to approximately 20,000, and after 1 May, there was a gradual decline (Fig. 5). On 17 May, almost all geese had departed. When numbers are added up for west Jutland, Trøndelag and Vesterålen, it appears that approximately 6,000-8,000 geese were not seen during the last 10 days of April and at least 5,000 were not seen during May. The highest total number summed for the three regions was 26,000 on 10-11 May.

In the Trondheimsfjord area, the centre of gravity in the distribution was along the coast from Levanger to Steinkjer, in the north up to Snåsavatnet (Fig. 6). The most intensively used area was the surroundings of Mære, with up to 7,000 geese during 10-11 May. In the Verdal area, up to 4,400 geese were recorded on 14 May, in Klingsundet at Snåsavatnet up to 4,000 on 16 May, and in Ulven/Föling just west of Snåsavatnet up til 3,500 on 11 May. Ulven/Föling was only discovered by observers in 1996, and according to local farmers, the geese have been using the site for several years now. Gaulosen, which has in previous years been an important site, was only little used by the pink-footed geese in 1996.

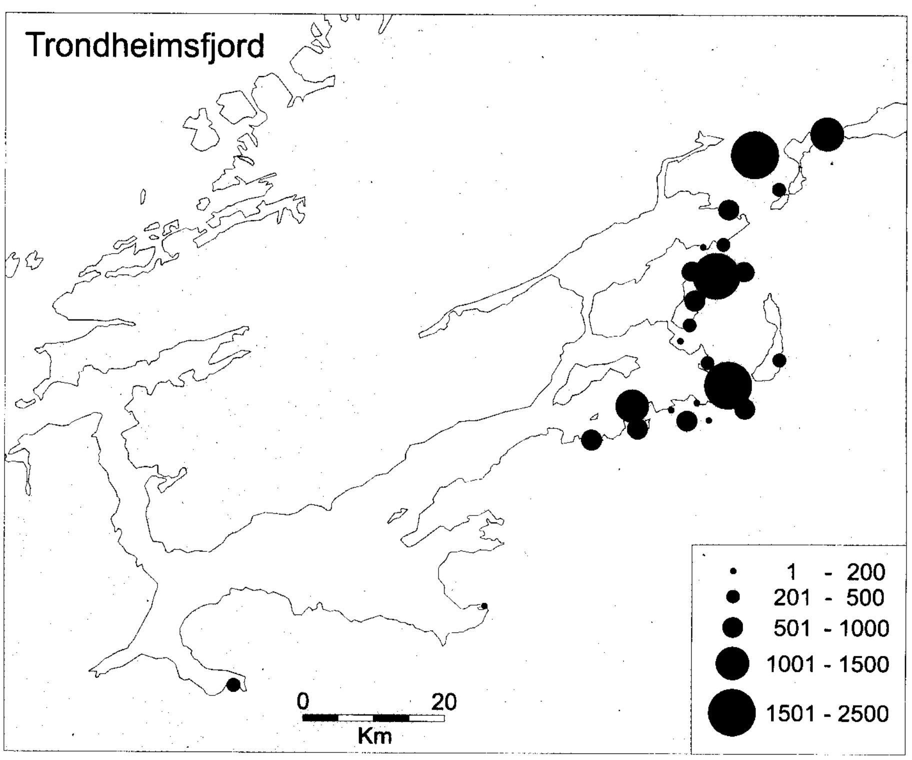


Figure 6. Distribution of pink-footed geese in the Trondheimsfjord area, expressed by the average number recorded per site during 1-20 May 1996.

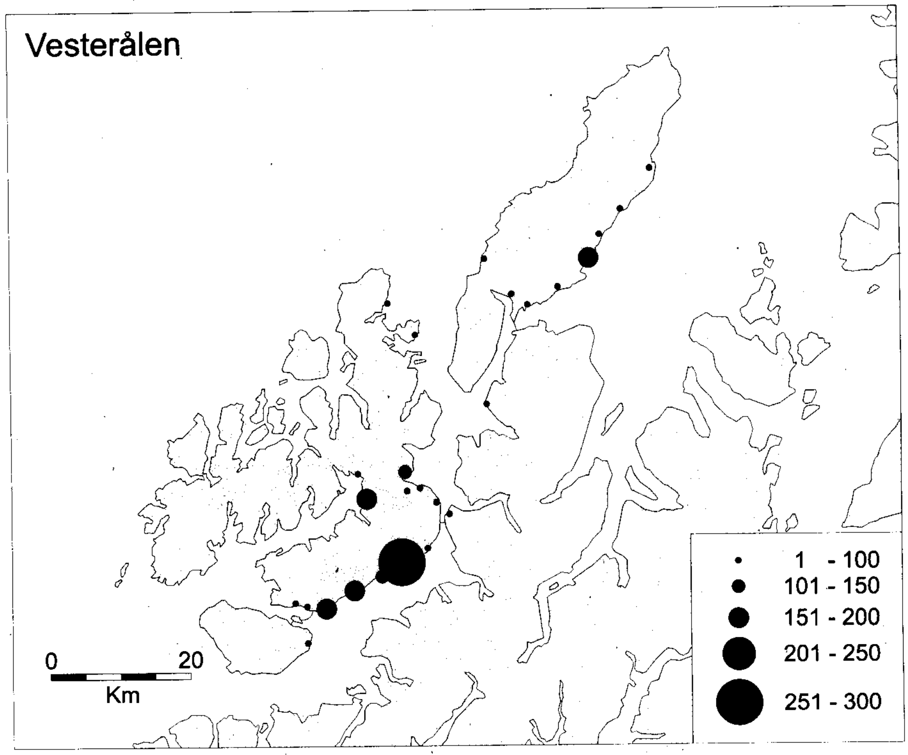


Figure 7. Distribution of pink-footed geese in Vesterålen, expressed by the average number recorded per site during 1-20 May 1996.

In Vesterålen, the centre of gravity in distribution of pink-footed geese was the east coast of Langøya from Vik to Skagen and on the east coast of Andøya from Å to Dverberg (Fig. 7). The most important sites were Holand-Kleiva (up to 1,070 on 19 May), Haukenes-Grytting (up to 1,390 on 21 May), Å (up to 500) and Holmstad (up to 2,050 on 21 May). The numbers seen in 1996 were considerably lower than in previous years.

5.2 Exchange of marked individuals

A total of 1,372 sightings of 292 different neckbanded individuals was made in Norway in April-May 1996. In total, 345 neckbanded individuals were known to be alive in spring 1996; hence, 85% were observed at least once in Norway. Undoubtedly, the 15% geese which were not recorded have stopped in Norway but have escaped observation. The majority of these 'missing' geese were observed in Denmark for the last time between 5-15 May, and it is highly unlikely that they have migrated directly to Svalbard.

In the Trondheimsfjord area, a total of 832 sightings was made of 236 different individuals, and in Vesterålen 540 sightings of 180 different individuals. Of the 180 individuals observed in Vesterålen, 124 (69%) had also been observed in the Trondheimsfjord area.

The day-to-day probability of resighting an individual can be estimated for neckbanded birds which are known to have spent more than one day in an area, e.g. observed in Vesterålen on one day and subsequently resighted in the same area two days later (as it has never been observed that an individual migrates southwards during spring it can be assumed that the bird was still in Vesterålen on the day in between observations). For west Jutland as a whole, the day-to-day resighting probability of a marked bird in 1996 was 0.27 (from 1 April onwards), for the Trondheimsfjord 0.44 and for Vesterålen 0.79. Based on these probabilities, it seems most likely, that the missing birds escaped detection in the Trondheimsfjord area. This calculation does not take into account the fact that there may be completely unknown staging areas used by birds exclusively or only briefly visiting known and monitored areas. As in the Trondheimsfjord area, new sites are still being discovered, and it is likely that as yet unknown sites represent part of the explanation for the missing birds.

Under the assumption of a random distribution of marked individuals in the population during spring migration, the total number of geese stopping in the Trondheimsfjord and Vesterålen can be estimated. The assumption of random mixing is regarded as valid at the regional level since the ratios of marked to unmarked individuals in the two areas were very similar, 0.77 and 0.79, respectively (at local level, the distribution of marked individuals is not random because they are clumped due to marking of paired individuals). The total spring population was estimated at 30,000 individuals (peak count in Denmark in early April). A conservative estimate of the numbers stopping over (for a shorter or longer period) in the Trondheimsfjord is thus (236/345)*30,000 = 20,522, and for Vesterålen (180/345)*30,000 = 15,653. This estimate does, however, not take into account the differences in resighting probabilities between areas. A more realistic, yet conservative estimate is that (236/292)*30,000 = 24,247 individuals stopped in the Trondheimsfjord and (180/292)*30,000 = 18,493 individuals in Vesterålen. Because of a continuous immigration and emigration of individuals, those numbers were never counted at one time.

5.3 Habitat use by geese

In the Trondheimsfjord, the first arriving geese fed on stubble, unharvested cereal, undersown stubble and pastures. After the commencement of sowing (and ploughing of stubble) from late April onwards, the geese increasingly foraged in newly sown cereal fields and decreasingly on stubble and undersown stubble. Throughout the staging period, pasture was an important feeding habitat (Fig. 8). The geese were recorded feeding in fields up to five km inland from the roosts and at altitudes up to 600-700 m. In Vesterålen, 98% of all marked birds observed on the feeding grounds (n=332) were recorded feeding on pasture; the remaining 2% were observed feeding on salt marsh.

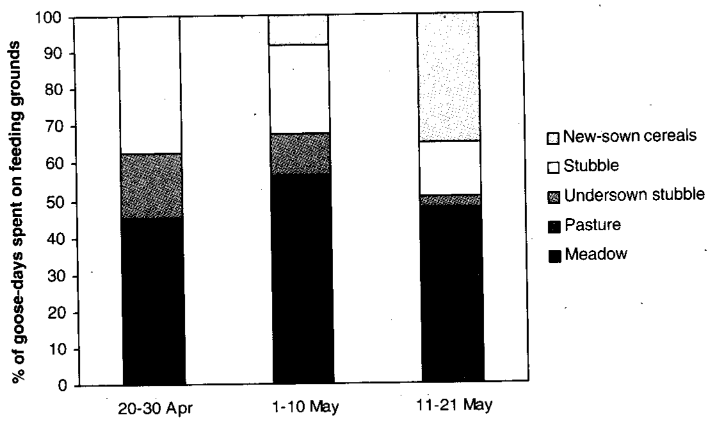
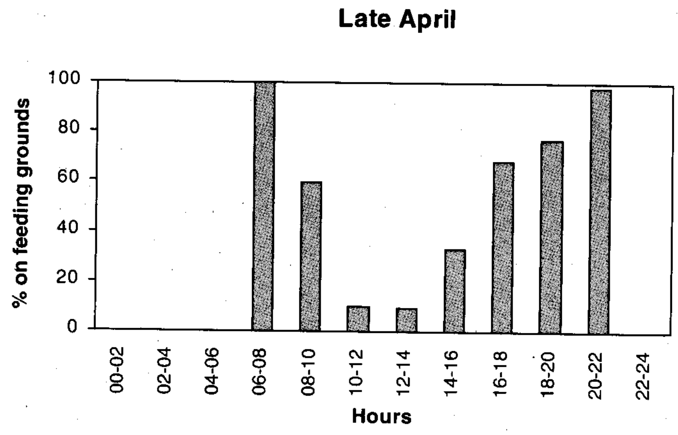


Figure 8. The feeding habitat distribution of pink-footed geese in the Trondheimsfjord area during three 10-day periods, April-May 1996, expressed as the proportion of goose-days spent in each habitat type.

5.4 Activity budgets and reactions to human activity

In late April in the Trondheimsfjord area, the sun sets at around 21.15 hrs and rises at 05.15 hrs and in the middle of May, at 22.20 hrs and 04.10 hrs, respectively. In late April, it grew dark after sunset, whereas in mid May, there was twilight in the hours around midnight. Consequently, during late April and early May, the geese only foraged during the daytime and flew to the roosts at night. In contrast, during mid May, the geese stayed on the feeding grounds almost all night and only spent short time on the roosts around midnight (Fig. 9). The foraging day thus increased from approximately 16 hours to 22 hours.

During the middle of the day, there was considerable farming activity in the fields (ploughing, sowing etc.) as well as diffuse disturbance from road traffic, and hence, geese were frequently disturbed. Most geese flew to the roosts and stayed there until the late afternoon. As a result of this, feeding activity was bimodally distributed during the 24 hrs; however, because of the increasing night feeding which occurred during mid May, the proportion of the 24 hours spent on the feeding grounds increased from 38% to 58%. Furthermore, the intensity of foraging activity while on the feeding grounds, was higher on the new-sown fields compared to pastures and stubble (Table 2). On the roosts, the geese mainly roosted and preened; low levels of feeding occurred on salt marsh or meadow. Combining the data on feeding day length with the habitat-specific feeding frequencies, it is calculated that in late April, the geese spent on average 8.4 (35%) of the 24 hours feeding, compared to 12.7 hrs (53%) in mid May.



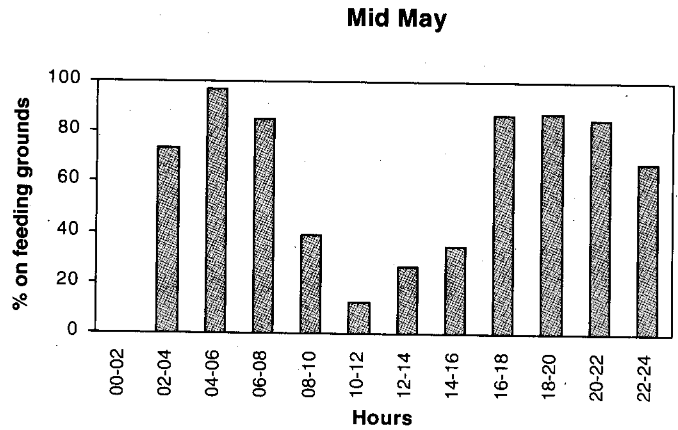


Figure 9. Diurnal feeding activity pattern of pink-footed geese in the Trondheimsfjord area in late April and mid May, respectively, expressed by the proportion of geese observed on the feeding grounds as opposed to the roosts.

On pastures, the escape flight distance in relation to approaching cars was on average 116 m ± 47 (95% c.l.)(n=8); in newly sown cereal fields the escape flight distance was on average 273 m ± 92 (n=8) (two-tailed student's t-test, $P<0.05$). As the confidence limits indicate, there was a large variation in response.

Table 2. Foraging activity of pink-footed geese in three habitat types in the Trondheimsfjord area, expressed as the percentage of individuals in a flock observed foraging (by scan observations).

	Stubble	Pasture	New-sown cereals
Average (%)	85.2	78.2	94.3
n (no. of scans)	17	19	35
95% conf. limits	14.4	9.9	3.9

5.5 Vegetation development

In late April in the Trondheimsfjord field, there was a low but positive growth of grass blades which exceeded death rate even at low temperatures (around 0°C at screen height). The growth rate increased in early May (Fig. 10) and was primarily caused by the shoots developing new blades (so-called A0's, A00's...), whereas it was only the older blades which died.

In Vesterålen, growth also exceeded death rate even at low temperatures (around 0°C). However, it was not until the second half of May that the growth rate increased (Fig. 10). There too, the growth was caused by the development of new blades while it was the older blades which died.

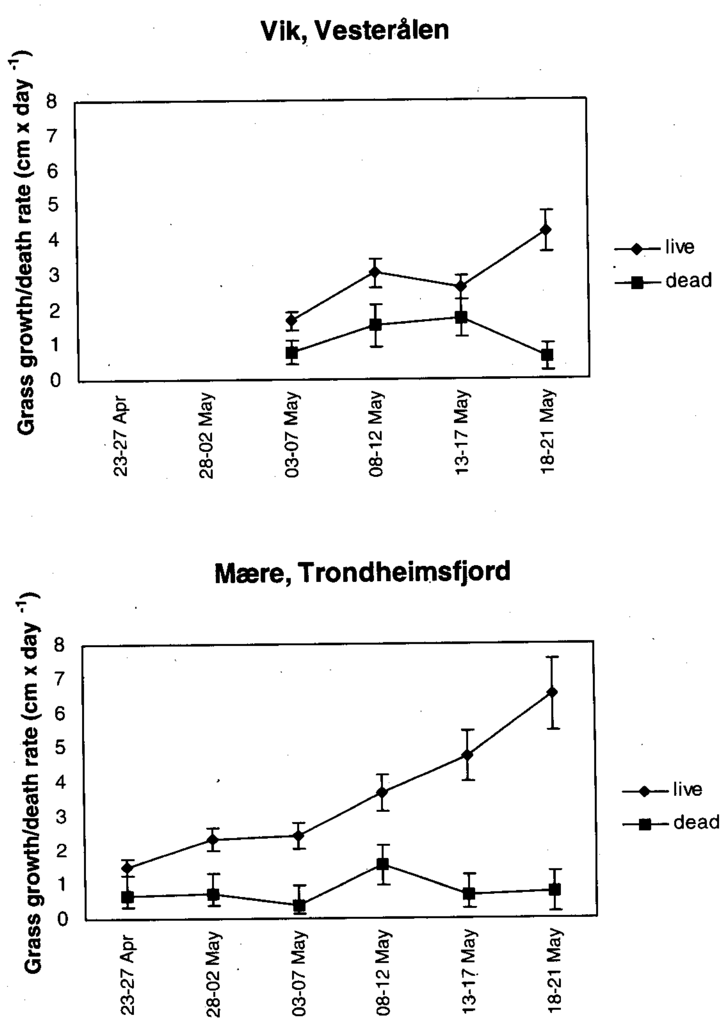


Figure 10. Grass blade increment and death rates per shoot of *Poa pratense* in artificial grasslands in Vesterålen and Trøndelag, April-May 1996. In both areas, trials were started immediately after snow clearance of the fields. Bars show 95% confidence limits.

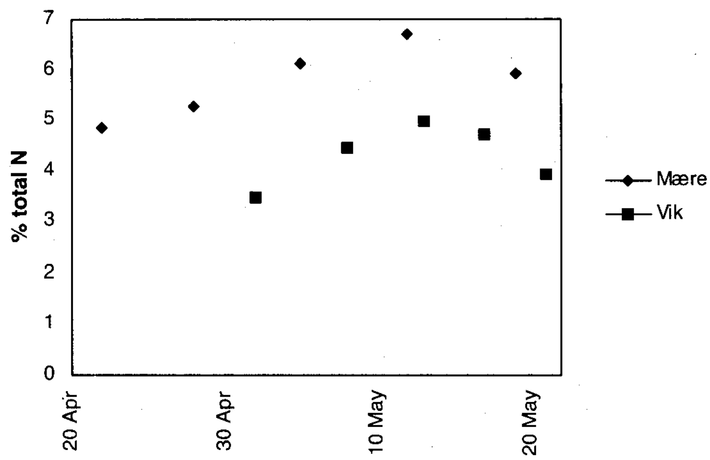


Figure 11. Nitrogen contents in green grass blades (mainly *Poa pratense*) in artificial grasslands in Vik in Vesterålen and Mære in Trøndelag, respectively, during April-May 1996. In both areas, collection of grass was started immediately after snow clearance of the fields. Each data point represents one grass sample.

In both areas, the nitrogen content of the blades increased to reach a peak around mid May (Fig. 11); the few data available suggest that the nitrogen content in both areas started to decrease after that.

5.6 Condition and subsequent breeding success

In order to analyse the consequences of choice of spring migration strategies for the build-up of condition, the migration strategies by individual birds with reasonably good resighting records have been grouped into five categories (Fig. 12). First, the period of emigration from west Jutland was divided into two halves; birds leaving in the first half (before 5 May) were categorised as early departers, birds leaving in the second half as late departers. Second, birds were categorised according to the length of stay in the Norwegian stopover

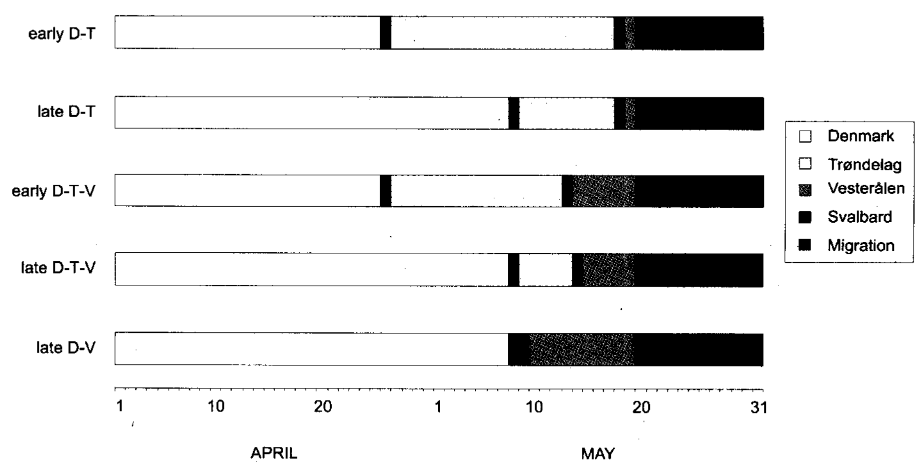


Figure 12. Schematic outline of five migration strategies used by pink-footed geese during north migration, spring 1996.

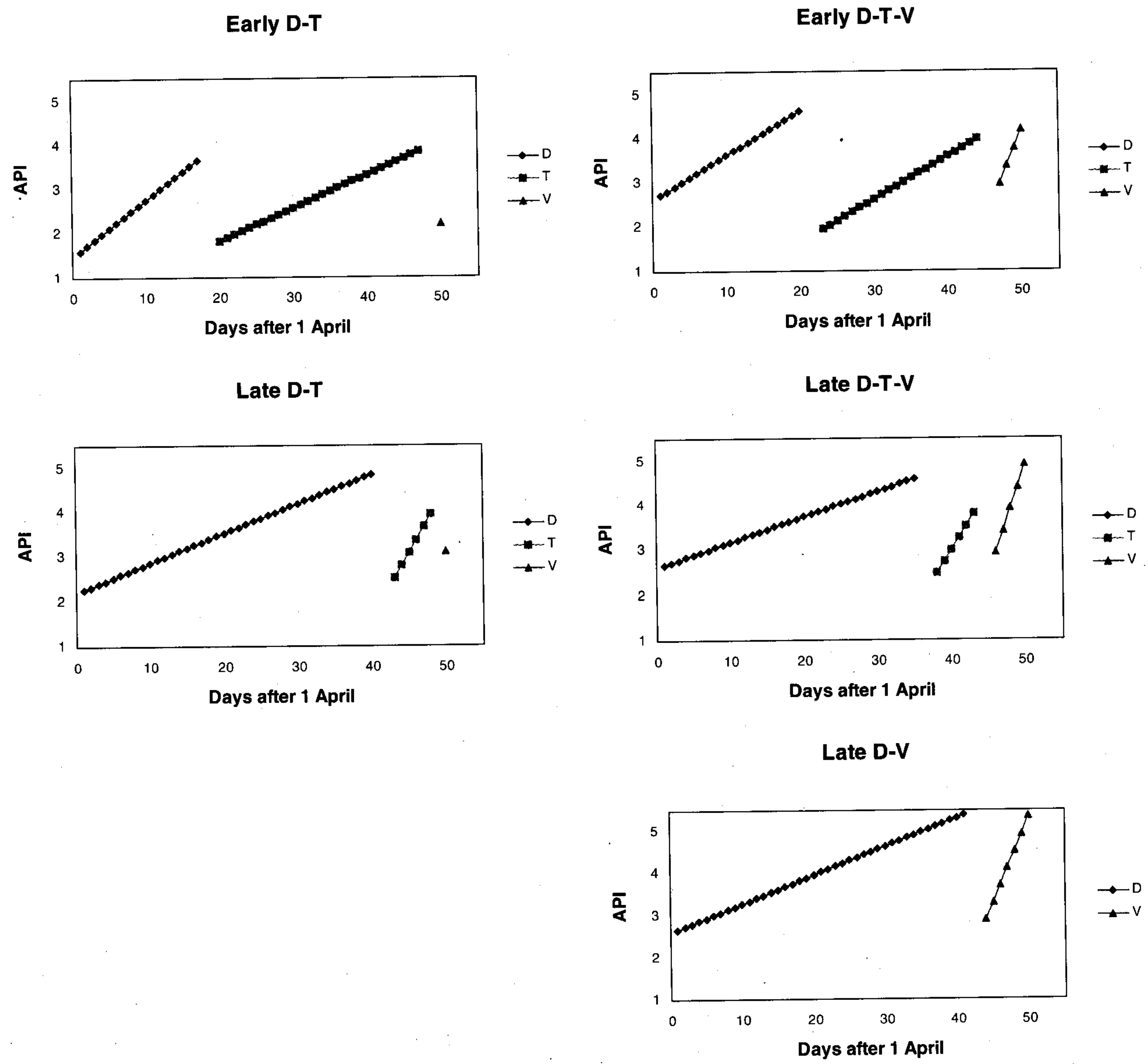


Figure 13. Rates of increments in abdominal profiles in adult females of pink-footed geese using different migration strategies, spring 1996. The shown rates of increment represent the average rates of increment by all females using a certain category of migration strategy. For all five categories, the abdominal profiles have been extrapolated back to 1 April and forward to 20 May (for the categories 'early D-T' and 'late D-T', the data for 20 May are observed average values).

sites. Birds spending less than three days in Vesterålen were categorised as not exploiting that area since 1-2 days was too short a time to significantly improve the condition. The analysis has been restricted to adult females, since they have the highest reproductive costs and consequently the highest need for building up nutrient stores.

The daily rate of increase in abdominal profiles by the females using the five migration strategies have been summarised in Fig. 13 and in Table 3. Since the abdominal profiles were not scored every day, the starting point for all females, arbitrarily defined as 1 April, has been extrapolated from the individually observed rates of increase during April in Denmark. For each of the five groups, the average daily rate of increase was calculated; using this, the initial condition on 1 April

Table 3. Migration strategies by individually marked females, their initial abdominal profile index (API) in Denmark before migration, rates of increase in API's in the three staging areas, the final API's at the time of final migration to the Svalbard breeding grounds and, the subsequent breeding success as observed during the subsequent autumn in Denmark and The Netherlands. The categories of migration strategies are described in the text. The API's on 1 April is extrapolated from rates of increase within each category of migration strategy. The API's on 20 May are observed value. The category of unmarked females represents birds which were paired to marked males, for which the migration strategy and the subsequent breeding success were known.

Migration strategy	No. of females	API on 1 April	Increase of API (day^{-1})			Final API around 20 May	% breeding successfully		
		Denmark	Denmark	Trøndelag	Vesterålen	Vesterålen	Marked females	Unmarked females	Overall
	n	Avg (95% c.l.)	Avg (95% c.l.)	Avg (95% c.l.)	Avg (95% c.l.)	Avg (95% c.l.; n)	% (n)	% (n)	% (n)
Early D-T	13	1.6 (0.4)	0.13 (0.06)	0.08 (0.05)	-	2.2 (0.4; 9)	10.0 (10)	14.3 (7)	11.8 (17)
Late D-T	68	2.2 (0.2)	0.07 (0.01)	0.29 (0.09)	-	3.1 (0.4; 25)	18.4 (49)	19.4 (36)	18.8 (85)
Early D-T-V	9	2.7 (0.9)	0.10 (0.11)	0.10 (0.08)	0.41 (0.18)	4.0 (0.6; 6)	20.0 (5)	50.0 (2)	28.6 (7)
Late D-T-V	21	2.7 (0.3)	0.06 (0.02)	0.27 (0.14)	0.49 (0.20)	4.7 (0.4; 16)	38.9 (18)	66.7 (9)	48.2 (27)
Late D-V	10	2.7 (0.3)	0.07 (0.07)	-	0.41 (0.08)	4.9 (0.6; 10)	50.0 (8)	50.0 (2)	50.0 (10)

has been backwards extrapolated from the date of the first scoring in April. On 1 April, the group of females which were subsequently departing early and staging in Trøndelag only ('early D-T'), had lower API's than the other categories of females. Rates of increase in Denmark were comparable to rates of increase in Trøndelag during the early phase; however, the rate of increase in Trøndelag significantly increased from the early to the late departing birds. This was also the case in females which stayed in Trøndelag from late April to around 15 May; in these the rate increased from 0.03 API day^{-1} before 5 May to 0.27 API day^{-1} after that date. Throughout, the highest rates of increase were observed in Vesterålen. The flight cost of migration equates to the decline in API between areas. On average, females lost 2.2 scores between Denmark and Trøndelag, 1.1 scores between Trøndelag and Vesterålen and, birds flying directly from Denmark to Vesterålen, lost on average 2.5 scores.

The proportion of females using the various strategies is reflected by the sample size in each category. Thus, the majority of females (56%) were late-departing and stopping in Trøndelag and only for 1-2 days in Vesterålen ('late D-T'), followed by late-departing females stopping in both Trøndelag and Vesterålen (17%) ('late D-T-V'). However, a group of late-departing females (n=13) were not observed in Norway at all. Probably they stayed in a site not monitored or poorly monitored in Trøndelag (see chapter 5.2) and hence probably have to be added to the category 'late D-T'.

Around 20 May, just before the final migration from Vesterålen to Svalbard, there was a marked difference in condition between females using the various strategies. Hence, birds departing early and spending the longest time in Trøndelag hardly improved their condition compared to that in early April, and birds departing later but only stopping shortly in Vesterålen also did relatively poorly. Birds stopping in both Trøndelag and Vesterålen showed moderate accumulation of stores, while birds departing late, bypassing Trøndelag and staging for around a week in Vesterålen, showed the greatest acquisition of stores. Thus, there was a penalty attached to arriving early in Trøndelag, and a premium for using Vesterålen.

In autumn 1996, the breeding success of both marked females as well as unmarked females paired to marked males using the various strategies, expressed as the proportion of females bringing juveniles back to the autumn staging areas, was correlated with the average ultimate abdominal profile observed in Vesterålen (Table 3; r_s one-tailed = 1.000; P=0.025). Hence, in females departing early from Denmark and spending long time in Trøndelag, only two out of 17 bred successfully, whereas in females departing late from Denmark and flying direct to Vesterålen, five out of 10 (50%) bred successfully.

6 Discussion

The winter of 1995/96 was severe throughout the winter range of pink-footed geese in northwest Europe, and by the end of the winter the pink-footed geese were in poor condition compared to previous mild winters (J. Madsen unpubl.). Because the spring was relatively cold as well, the geese were also in poor condition well into the spring. The spring migration towards Norway started as early as in previous years, but the last geese left Denmark more than a week later than usual. The geese also arrived unusually late in Vesterålen. This could be a consequence of the delayed migration from Denmark but could also be related to the fact that the geese make increasing use of Trøndelag, at the expense of Vesterålen. In the previous two years, there had been a decreasing use of Vesterålen (Tor Bønes, pers. comm., J. Madsen unpubl.) and possibly, 1996 saw a continuation of that tendency.

In 1996, the Trondheimsfjord area was used by the majority of the pink-footed geese; many geese just made a short stop in Vesterålen, and that group of geese depended on the Trondheimsfjord as the area for spring fattening. As demonstrated above it turned out to be the "wrong" strategy in 1996 in terms of both spring fattening and, subsequently, fecundity. The birds arriving early at the Trondheimsfjord met conditions which were unfavourable for spring fattening: low grass production and disturbance from farming activity which reduced the diurnal window of time available for feeding. Consequently, early arrivers only slowly gained body stores, and it was not until May that light conditions and food stocks enabled more rapid fattening. As in west Jutland, the geese were feeding intensively on newly sown cereal, which is an energy-rich food supply with high digestibility (Madsen 1985). Furthermore, during May the grass increased its growth and peaked in nutrient content.

From previous field seasons (J. Madsen unpubl.) it has been shown that in May in Vesterålen, the pink-footed geese feed throughout the 24 hour period (diurnally, 18-19 hours are spent feeding under undisturbed conditions); they are highly tolerant of human activity which enables them to fully exploit the resources (e.g. during night feeding along roads and even in gardens), and they exploit a nutrient-rich pasture vegetation. The combination of these three factors explains why the geese can rapidly accumulate stores there. In 1996, the rate of increase of abdominal profiles exceeded that observed in the Trondheimsfjord during mid May. The explanation could be that because of disturbance effects, the geese had less time available for foraging in Trøndelag compared to Vesterålen. In 1993 and 1994, the organised scaring of geese in Vesterålen caused a reduction in the feeding time by the geese and an increase in energetically costly activities such as flying. There too, the condition build-up was hampered by disturbance.

In the Trondheimsfjord area, geese were less tolerant towards human activity than in Vesterålen, which is expressed by their escape flight distance towards approaching cars. Hence, in the Trondheimsfjord area, the geese flew at an average distance of 116 m (on pastures) and 273 m (on newly sown cereals) whereas in Vesterålen, they flew at an average distance of 17 m (J. Madsen unpubl.). The habitat-related differences observed in Trøndelag were probably reflecting the fact that farmers scared the geese away from the newly sown fields which increased the wariness of the geese there. The difference between habitats and areas suggests that the geese learn (by habituation) where they are safe and where they are not. It is remarkable that the same geese which are highly wary in Trøndelag fly on to Vesterålen where they become highly tolerant. This difference suggests that because the use of Trøndelag is of such recent origin, the geese are still in a period of learning about local predation risks (since in this context, disturbance can be regarded as a predation risk to the geese). The net result is that the disturbance restricts both the diurnal use and the area used in Trøndelag. It is possible that within a few years, the geese will have habituated to the local conditions and then can make a more full use of the area.

The observed relationship between choice of migration strategy, condition build-up and ultimate breeding success represents the first case study which suggests that there are fitness consequences of decision-making in migration strategies in birds. Of course, it is premature to evaluate fitness consequences based on a single year. Obviously, in 1996 it did not pay off to arrive early and stay late in Trøndelag; however, in other years, e.g. with early spring growth of vegetation and early sowing, it may represent a strategy with a greater pay off. The next step in future analysis will be to analyse existing information collected from 1991 to 1994, to assess the annual profitability of using various strategies and individual between-year variation in choice and subsequent breeding outcome.

It must be assumed that there is a strong natural selection on migration strategies in long-distance migrants like the arctic nesting geese (e.g. Alerstam 1981). However, hitting optimal timing and a path enhancing fitness is a dynamic process, especially in the light of the rapidly changing environmental conditions (e.g. changes in farming practises). The rapid increase in numbers of pink-footed geese using Trøndelag and their progressively earlier arrival indicate that the geese are still developing and sampling the site(s). In this process, the geese are bound to meet environmental limits with negative fitness consequences, and, assuming that the development is based on individuals gaining experience, this is likely to be an iterative process over a period of time until an evolutionary stable equilibrium is reached (if such a state exits). One proximate limitation in Trøndelag is climatic conditions (snow cover, temperatures below the freezing point) which seems, at the moment, to set a limit for the arrival around early to mid April. Another possible constraint is the behavioural plasticity of the geese which will determine their exploitation capacity of the local resources.

Before 1990, the pink-footed geese flew over the Trondheimsfjord on their migration towards Vesterålen. They occasionally stopped to rest but the majority just passed over (Frengen 1977, Bollingmo 1981). Why had the geese not discovered the area long before, and what made the sudden change? One possible explanation is that during the 1980s the pink-footed geese spring-staging in Denmark dramatically expanded their exploitation of newly sown cereal fields (Madsen 1987, unpubl.) and, possibly, a group of geese accidentally discovered similar fields in Trøndelag. The rapid development in numbers shows that this has been a 'cultural shift' with an increasing number of geese being drawn into the area. It is still an open question as to what kind of individuals established this. It is puzzling that in 1996 it was actually females in poor condition which departed earliest for Trøndelag. Are these birds with low social status (poor competitive abilities) or birds which have specific nutrient requirements which can more easily be met in Trøndelag (e.g. a need for nitrogen-rich food which can be obtained from the early growth stages of grass)? An analysis of data from previous seasons may provide some insight to this.

To sum up, there is evidence that the choice of migration strategy can have repercussions on spring fattening and breeding success. The 1996 data show that the use of the Trondheimsfjord area is, in some seasons, disadvantageous. The increasing use of the Trondheimsfjord staging area apparently conflicts with the consequence of using this area as measured by individual API's. However, the year-to-year consequences of using different migration strategies need to be assessed in a range of different seasonal conditions before the individual fitness consequences of choice of migration strategy can be evaluated over the lifetime of individual birds. The use of the Trondheimsfjord area is still changing and if the geese can accommodate the effects of human activities (by local habituation), there is scope for an improved usage by the geese and for improving spring fattening rates. Snow cover and frost set a limit on the time of arrival (around early April at the earliest).

The management implication of the increasing use of the Trondheimsfjord area is that it has reduced the agricultural conflict in Vesterålen; however, it not only moves the conflict southwards in Norway but, from a national perspective, it may lead to an overall exacerbation of the problem.

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