Temporal changes in spring migration phenology in the Norwegian Greylag Goose *Anser anser*, 1971–2004

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Abstract

During spring, Greylag Geese *Anser anser* migrate from staging grounds in the Netherlands to breeding sites in Norway. The timing of this migration is critical as it corresponds to the most energetically expensive period in the birds' seasonal cycle, and governs the time available for breeding during the short northern summer. This paper reports how the spring migration and the subsequent breeding season of Greylag Geese nesting in Norway have gradually become earlier since 1971, by about 5–7 days per decade up to 2004. First arrival date, median arrival date and first hatching date at the most important breeding site in Norway were inversely related to spring temperatures in the Netherlands, suggesting that this trend may be a function of climate change.

Key words: Greylag Geese, Norway, spring migration, breeding phenology, climate change.

Migration routes in Arctic and temperate breeding geese tend to be fixed (Owen 1980), although changes in population size or human interference (e.g. hunting or agricultural practices) could alter these routes as the suitability of destination sites changes (van Roomen & Madsen 1992; Percival & Anderson 1998). The timing of goose migration to and from the breeding, staging and wintering sites may, however, vary by days or even weeks between years (Nilsson & Persson 1994; Madsen 2001). Temporal differences in the timing of migration in geese could be intrinsically related to body condition (Drent *et al.* 2003; Prop *et al.* 2003), but ultimately are likely to be a function of food availability, climate, hunting pressure or a combination of these.

For geese breeding at northern latitudes, spring is considered to be the most energetically demanding period in their annual cycle due to the combination of migration and breeding activities, including egg laying in females (Ebbinge & Spaans 1995; Prop & Black 1998; Madsen 2001). In addition, arctic-breeding birds, and to a lesser extent birds that breed just south of the arctic, are constrained by the short northern summers. This creates a fairly narrow window of opportunity in which to produce fledged chicks. Consequently, the spring migration and timing of arrival at the breeding site have a strong influence on breeding success and can be expected to be important in shaping the demographics of the population (Daan *et al.* 1990; Nilsson & Persson 1994; Bêty *et al.* 2003).

The Norwegian Greylag Goose *Anser anser* population is demographically distinct from the Swedish Greylag Goose population (Pistorius *et al.* in press), and has virtually no emigration of breeding birds into other Northwest European Greylag Goose populations or vice versa (Andersson *et al.* 2001). On the one hand, Norwegian Greylag Geese form an important target species for recreational hunters, and on the other their growth in numbers over the last few decades has resulted in increasing conflict with farmers (Follestad 1994a). The sustainable management of this population is therefore of considerable importance and has led to birds being marked with individual neck bands from 1986 onwards as part of the Greylag Goose Project financed by the Nordic Council for Wildlife Research. The main aim of this neck banding is to allow research into the patterns of migration and local movement. The important staging, wintering and moulting areas and the birds' movements between these and the breeding sites are now reasonably well understood (Andersson *et al.* 2001).

Andersson *et al.* (2001) provided a detailed description of migration patterns in Nordic Greylag Geese. In summary, Norwegian Greylag Geese are at their breeding grounds between April and early September, but there are some regional differences, with northern breeding birds departing from their breeding grounds later than those nesting in the southern part of the range. All individuals migrate in autumn along the Atlantic flyway to the Netherlands, which is used as a staging site, with some birds stopping over for short periods in Denmark. Although some individuals remain in the Netherlands to overwinter, the vast majority migrate further south in November to over-winter in southwestern Spain (Guadalquivir Marismas) and Villafáfila in north central Spain. The geese leave Spain in early spring for a staging period of about a month in the Netherlands, before returning to the breeding grounds.

For migratory birds, the timing of arrival at the breeding grounds is a key determinant of reproductive success, survivorship and fitness (Sedinger *et al.* 1995; Kokko 1999; Both & Visser 2001; Bêty *et al.* 2003). This study documents temporal changes in the timing of arrival of Greylag Geese at one of their primary breeding sites in Norway (Vega) after migrating from the Netherlands. More specifically, the aim of the study was to (1) document and test for trends in the date of (a) first arrival at Vega since 1971, (b) first hatching date since 1971, and (c) median arrival date from 1991 to 2004, when resighting data from marked individuals became available. In the light of the increasing evidence suggesting that climate change has the potential to alter migration phenology in birds (Both & Visser 2001; Cotton 2003), the study further aimed to (2) identify the relationship between spring temperature in the Netherlands and the above-mentioned parameters (a–c). It would be expected that there is a significant relationship between spring temperature in the Netherlands and the timing of Greylag Goose migration if climate change is indeed impacting on their migratory phenology. The final aim of the study was to (3) test whether spring temperatures in Norway influence the timing of breeding (first hatching date) in Norwegian Greylag Geese.

Methods

Study area

The study area comprised the island of Vega (65º42'N, 11º51'E) in central Norway and the surrounding archipelago on the Helgeland coast, which is one of the main breeding sites for Greylag Geese in Norway (Follestad *et al.* 1988).

The Greylag Geese breed principally on islands of grass and heather along the outermost coast (Follestad 1994a,b). The agricultural activity in this area is predominantly grass production; there is very little cereal farming in the region.

Data collection and analyses

Between 1988 and 2002, 162 breeding adults (i.e. geese with offspring), 344 goslings and 982 non-breeding birds were caught and marked at Vega and the surrounding area (Table 1). Greylag Geese were caught when they were flightless due to wing-feather moult and undeveloped wings. Most non-breeders and many families were captured in a sweep net while they were in the water after a short pursuit by boat. Some family groups were also caught by being rounded up on the grazing pastures and forced into nets. Each Greylag Goose captured received a neck band that was manufactured out of laminated plastic of a UV-resistant quality. These were uniquely coded for subsequent recognition of individual birds, and could be read with a telescope at distances of up to 600 m in good light conditions.

Daily observations were made at the study site during the Greylag Goose breeding season – remarkably, by the same observer (using a similar monitoring pattern) – throughout the duration of the study, from 1971 to 2004 inclusive. The date on which the first individual arrived at the breeding site and the first observation of a newly hatched gosling (hereafter referred to as first hatch date) were recorded. Since 1991, the identities of all marked individuals present have also been recorded. Reported dates of individual arrival and first hatching were assumed to be very close to the real dates, since there was a very high daily resighting rate.

The median arrival date of marked individuals, measured as the number of days after 1 January, was calculated as the date by which 50% of all marked individuals observed in the area during any one breeding season were observed for the first time (Table 2). Temperature estimates in the Netherlands and Norway were taken from Klein-Tank (2002) and North Atlantic Oscillation data from the National Weather Service/ Climate

Table 1. Numbers of Greylag Geese marked with neck bands at Vega and Nordland, 1988–2002.

Year	Breeding Adults	Juveniles	Non-breeding Adults	Total
1988	2	17	47	66
1989	6	23	70	99
1990	24	17	110	151
1991	5	43	105	153
1992	17	60	150	227
1993	22	33	156	211
1994	26	50	133	209
1995	13	35	44	92
1996	9	23	60	92
1997	7	18	36	61
1998	0	0	0	0
1999	0	0	0	0
2000	0	2	0	2
2001	30	15	42	87
2002	1	8	29	38
Total	**162**	**344**	**982**	**1,488**

Prediction Centre in Maryland (http://www.cpc.ncep.noaa.gov/data/teledoc/nao.html). Most Greylag Geese arrive in the Netherlands from Spain close to mid-March and depart for Norway in April (Andersson *et al.* 2001). Mean air temperature in the Netherlands in March and April (Fig. 1) therefore was used when studying the effect of spring temperatures at the staging site on the dates of arrival at the breeding grounds. To test whether first hatching date was influenced by local conditions influencing food availability at the breeding grounds, mean temperatures were similarly used for Norway in the analysis. March and April temperatures were also used here since temperatures a few weeks before arrival are likely to influence vegetative growth of the geese's food resources, which is expected to influence the duration of time spent foraging around the breeding sites before nesting. Average daily temperatures for these months were used to produce the mean estimates for each year. The influence of spring temperatures in the Netherlands on the interval between first and median arrival dates (of marked individuals) was also investigated.

A standard statistical package (SPSS version 12) was used for the analyses. Kolmogorov-Smirnof tests were used to test that the data did not differ significantly from a normal distribution. To avoid autocorrelation in our time-series data, autoregression models were used and tests were made for significant effects of year, spring temperatures and NAO index on first and median arrival dates and first hatching dates of Greylag Geese at Vega. Most time-series data have some trend (positive or negative) and any two trending series will correlate simply because of the trends, regardless of whether or not they are causally related. Use of the autoregression approach permitted the removal of the potential autocorrelation inherent in the time series data, and any statistically significant relationships between the dependent

Table 2. Number of neck-banded Greylag Geese resighted on the breeding grounds at Vega, 1991–2004.

Year	No. of individuals
1991	40
1992	36
1993	57
1994	83
1995	82
1996	74
1997	76
1998	63
1999	38
2000	22
2001	20
2002	20
2003	9
2004	11
Total	631

variables and candidate regressors could be ascertained. If autocorrelation in the data was not significant, an autocorrelation coefficient was still maintained in the models to account for the limited potential bias. An *a priori* set of models was constructed (Burnham & Anderson 1998) that included variations of the abovementioned covariates to describe patterns in arrival and first hatching dates. Although many variants of these models could be applied, four to five basic models representing the most likely array of plausible biological hypotheses were chosen. The Akaike Information Criterion (AIC) was used to select the most parsimonious autoregression model that adequately described the data. Other models with an AIC difference of less than two were also considered useful in describing the data (Burnham & Anderson 1998).

Results

First and median arrival and first hatching dates were distributed normally (P = 0.871, 0.935, 0.629). A year effect was present in first arrival, first hatching and median arrival dates at Vega (Tables 3 & 4). Between 1971 and 2004, first arrival and first hatching dates of Greylag Geese at Vega varied between 14 March and 10 April (mean: 29 March) and 12 May and 4 June (mean: 25 May) respectively, with a significant negative linear trend in both parameters evident over this period (y = 2093.76 - 1.212x, R^2 = 0.621, P < 0.001 and y = 2121.24 - 0.922x, R^2 = 0.562, P < 0.001; Figs. 1a,c). A similar relationship for median arrival date was apparent for years where these data existed, i.e. since 1991 (y = 2052.88 - 0.531x, R^2 = 0.318, P = 0.036), ranging between 5 April and 21 April (mean =14 April; Fig. 1b).

On average, first arrival date was nine days earlier in the second half of the study (1988–2004), relative to the first half (1971–1987). The average first arrival date was 3 April for the period 1971-1981, 29 March for 1982-1992, and 23 March for 1993-1994. A substantial shift of 11 days in the latter

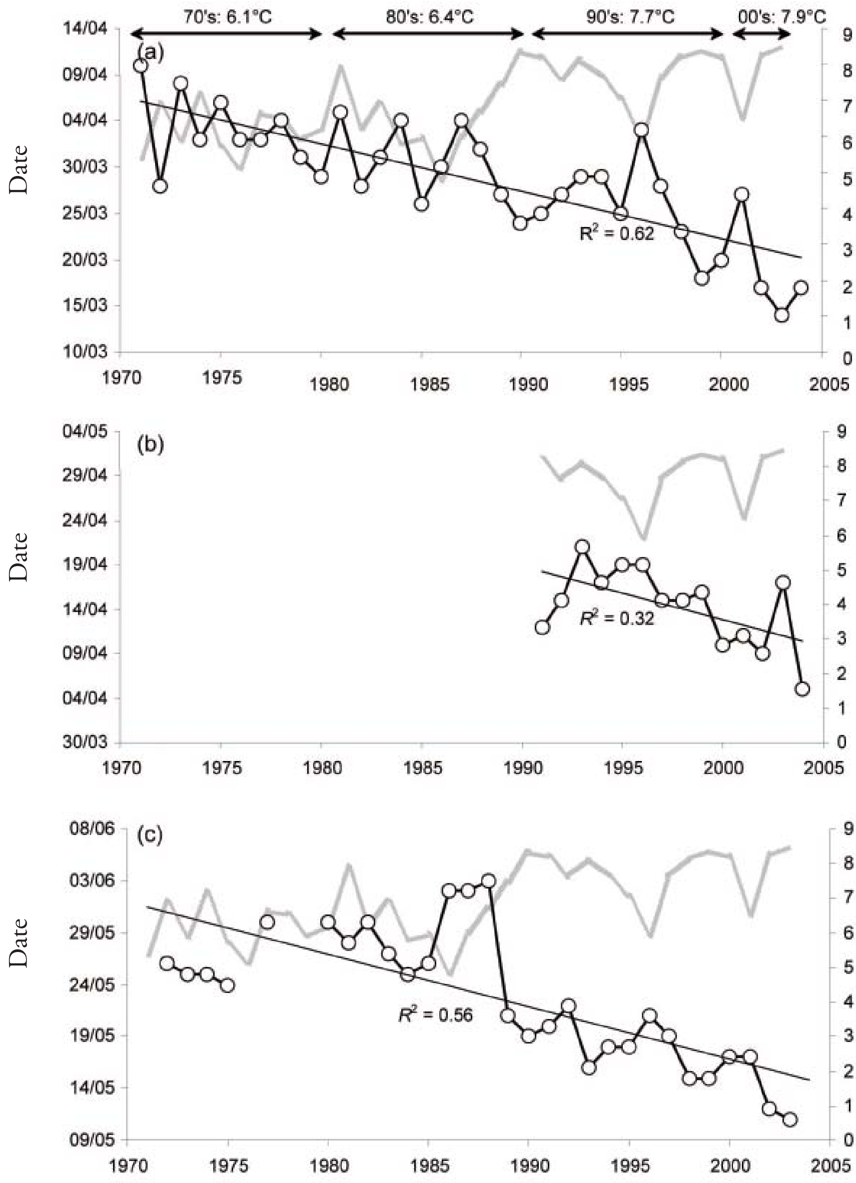

Figure 1. Time series of (a) date of first arrival of Greylag Geese at Vega; (b) date of arrival of 50% of neck-banded birds; and (c) date of first hatching (black lines), in relation to the average daily temperature for March and April in the Netherlands (grey line).

Table 3. Akaike information criterion (AIC) values for the autoregression models used to assess changes in first arrival date, first hatching date and median arrival date of Greylag Geese at Vega. Abbreviated parameters are autocorrelation coefficient (AR), year (yr), spring North Atlantic Oscillation index (NAO), spring temperatures in the Netherlands (Temp (D)) and spring temperatures in Norway (Temp (N)).

Model	AIC
First arrival date (FAD)	
$FAD_{AR,\ yr,\ Temp\ (D)}$	169.539
$FAD_{AR,\ yr,\ NAO,\ Temp\ (D)}$	170.575
$FAD_{AR,\ yr}$	174.279
$FAD_{AR,\ Temp\ (D)}$	179.614
First hatching date (FHD)	
$FHD_{AR,\ yr,\ Temp\ (D),\ Temp\ (N)}$	172.528
$FHD_{AR,\ yr,\ Temp\ (D)}$	173.362
$FHD_{AR,\ yr,\ NAO,\ Temp\ (D),\ Temp\ (N)}$	173.622
$FHD_{AR,\ Temp\ (D)}$	175.768
$FHD_{AR,\ yr}$	177.355
Median arrival date (MAD)	
$MAD_{AR,\ yr}$	61.123
$MAD_{AR,\ Temp\ (D)}$	61.600
$MAD_{AR,\ yr,\ Temp\ (D)}$	63.041
$MAD_{AR,\ yr,\ NAO,\ Temp\ (D)}$	65.773

half of the study period compared to the first half was found for first hatching date, which on average shifted seven days earlier per decade. Median arrival date over the last seven years (1998–2004) was on average five days earlier than during the preceding seven years (1991–1997).

The time interval between first arrival and first hatching was on average 56.4 days, with a range of 48–65 days. The interval between first arrival and median arrival was on average 22 days, with a range of 15–34 days. No trend was apparent in either of these two intervals over time ($R^2_{27} = 0.105$, $P = 0.086$ and $R^2_{12} = 0.267$, $P = 0.061$ respectively).

Spring temperatures in the Netherlands showed an inverse relationship with first arrival and hatch dates, and with median arrival date (Tables 3 & 4, Fig. 1). First arrival and hatch dates were to a lesser extent also influenced by NAO (Table 3). Spring temperatures in the Netherlands increased significantly over the study period (Fig. 1; y

Table 4. Summary statistics for autoregression models assessing the association between independent variables (year, spring temperature in the Netherlands (D) and spring temperature in Norway (N)) and migration and breeding patterns in Norwegian Greylag Geese. Autoregression coefficient is abbreviated to AR.

Variable	B	s.e. (B)	*t*	*P*
First arrival date				
AR	-0.095	0.196	-0.486	0.631
Spring Temperature (D)	-2.090	0.776	-2.695	0.012
Year	-0.344	0.083	-4.143	<.001
Constant	785.558	161.418	4.867	<.001
First hatching date				
AR	0.276	0.182	1.518	0.142
Spring Temperature (D)	-2.273	0.895	-2.541	0.018
Spring Temperature (N)	-1.165	0.544	-2.142	0.042
Year	-0.421	0.122	-3.463	0.002
Constant	994.912	238.903	4.165	<.001
Median arrival date				
AR	0.202	0.319	0.631	0.542
Year	-0.605	0.224	-2.701	0.021
Spring Temperature (D)	-1.978	1.349	-1.556	0.021
Constant	1312.577	447.242	2.935	0.014

= 1947.89 + 5.67x, R^2 = 0.40, P < 0.001), and this may have played a major role in generating the negative trend in arrival and hatching dates observed in this study. No trend in spring temperatures was apparent from the limited data (1991–2004) for which median arrival dates (y = 7.51 + 0.03x, R^2 = 0.02, P = 0.639) were available.

First hatching date showed a significant inverse relationship with spring temperatures in Norway (Tables 3 & 4). There was also a positive relationship between the interval between first and median arrival and the preceding average spring temperature in the Netherlands (R^2_{11} = 0.395, β = 4.249, s.e., P= 0.025 = 1.61; Fig. 2).

Discussion

Trends in migration phenology

This study found a clear temporal trend in the onset of the Greylag Goose breeding season. Birds now arrive and nest in Norway more than two weeks earlier than they did in the 1970s. This may have repercussions on the vitality of the population, as laying dates in bird populations have been correlated with breeding success (Daan *et al.* 1990; Nilsson & Persson 1994; Bêty *et al.* 2003). Furthermore, these findings have management implications in terms of scheduling the hunting regimes.

The number of Greylag Geese breeding in Norway has being increasing since the monitoring at Vega commenced (Follestad 1994a). It is therefore possible that the increasing numbers of Greylag Geese, coupled with a normal distribution of migration dates, could account for the trend in first arrival dates observed in this study. Since the median arrival dates follow a similar trend to that of the first arrival dates, there does, however, seem to be a real change in the timing of migration. Nevertheless, it is reasonable to expect that the trend reported for first arrival dates is overestimated, due to a greater spread in migration dates attributable to increased population size.

Although goose populations generally do not appear to be limited by food availability (Owen 1980; Francis & Cooke 1992; Gauthier *et al.* 2001; Frederiksen *et al.* 2004), the depletion of food at the staging sites by a larger population may also have affected the documented movement patterns. The size of the Norwegian Greylag Goose population is incredibly difficult to monitor because the birds occupy numerous small islands along the Norwegian coast (Andersson *et al.* 2001). As a result, no annual estimates of population size or indication of population density are available that could have been used as a useful covariate in the analyses to elucidate the influence of population size on migratory movements.

Individual differences in migration phenology of birds within a season and the state variables (e.g. body condition) associated with migration have formed the focus of much recent research (Kokko 1999; Bêty *et al.* 2003; Drent *et al.* 2003; Prop *et al.* 2003). Between-year variation in migration and breeding phenology has received far less attention. Beintema *et al.* (1985) detailed an advance of up to four weeks in laying date in several wader species in the Netherlands over the period 1910–1975. More recently, similar shifts were recorded from waders breeding in the British Isles (Crick *et al.* 1997). At Greylag Goose breeding sites in southern Sweden, mean dates of arrival and first observations of broods of marked pairs differed significantly between years, and by 2002 birds were reported to be arriving 20 days earlier than in 1986 (Nilsson & Persson 1994; Nilsson in press). During the 1990s, first arrivals of Pink-footed Goose *Anser brachyrhynchus* migrating from Denmark *en route* to Svalbard demonstrated changing arrival dates despite median arrivals being stable (Madsen 2001). These temporal shifts in the spring migration of geese are likely to be attributed to an array of factors operating at different levels, including climate change, quality and quantity of food resources,

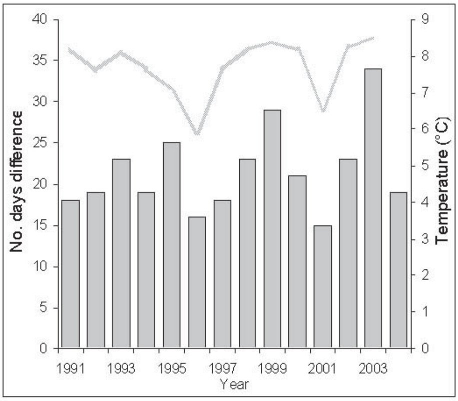

Figure 2. Difference in the number of days between the date on which the first geese arrived and the date on which 50% of the neck-banded Greylag Geese recorded at Vega had arrived, in relation to the average March and April temperatures in the Netherlands in that year.

hunting pressure or changing land-use patterns (Fox & Madsen 1997; Drent *et al.* 2003).

In this study an association was found between spring temperatures in the Netherlands, where the Greylag Geese stage, and the migratory dynamics of the population. Differences in spring temperatures explained, to a large extent, the variability in first and median arrival and first hatching dates observed in this study. It is accordingly suggested that an increase in spring temperatures has had a substantial effect on both the migratory patterns and the onset of the breeding season of Norwegian Greylag Geese.

Proximate factors influencing the timing of migration

In geese breeding at northern latitudes, the feeding conditions at both the spring staging areas and the breeding grounds are likely to influence reproductive success and how readily a female can achieve the body condition necessary for breeding (Ebbinge & Spaans 1995; Bêty *et al.* 2003). Thus, in the Greater Snow Goose *Chen caerulescens atlanticus* poor pre-breeding condition at the staging area accompanies a delay in breeding (Bêty *et al.* 2003). The temporal shifts in arrival and hatching dates described in the present study could therefore be a consequence of suitable fattening conditions on the staging sites in the Netherlands having been advanced through climate change. This is supported by the conclusion that the growing season for plants at northern latitudes has advanced by about eight days over the past eleven years (Menzel & Fabian 1999). Greylag Geese have a relatively short and undemanding migration compared to other migratory goose populations and, in the absence of empirical evidence, it is hard to say how important pre-migration body condition is for initiating migration. However, the migration phenology of Greylag Geese is similar to that of several arctic-breeding species (Drent *et al.* 2003; Prop *et al.* 2003), so factors influencing the migration may also be similar, even if the time scales differ.

A recent study on Pink-footed Geese demonstrated how adaptable the migration strategies in geese are, and suggested that they explore environmental conditions in order to adopt an optimal strategy (Madsen 2001). Relative to the rest of the population, individuals migrating early one year were shown to switch strategy and migrate late the following year. This dynamic behaviour in geese means that it is plausible that Greylag Geese are adjusting their spring migration phenology in accordance with changes in their food resources at their respective seasonal feeding areas.

The interval between first and median arrival dates in this study was positively related to the mean temperature in the Netherlands in spring (Fig. 2). Thus the migration period appeared to be longer, at least in terms of arrival patterns, in milder years. In years when conditions are not as favourable at the staging sites, geese may be held up by bad weather conditions, and then all migrate over a relatively short time period. It is also worth noting that wind conditions can affect the timing of goose migrations, as has been reported in several other studies (Wege & Raveling 1984; Green *et al.* 2002; Fox *et al.* 2003).

Management considerations

In many migratory birds, including Greylag Geese breeding in Sweden, reproductive success is inversely related to the date of egg laying (Daan *et al.* 1990; Nilsson & Persson 1994), and these parameters in turn tend to be a function of pre-migratory body condition (Bêty *et al.* 2003; Drent *et al.* 2003). Similar reproductive advantages associated with early breeding are well documented for northern breeding geese (Witkowski 1983; Prop & De Vries 1993; Sedinger *et al.* 1995; Kokko 1999; Bêty *et al.* 2003), but see Prop *et al.* (2003). By improving conditions at the staging sites, and allowing for an earlier onset of the breeding season, climate change could accordingly be having a profound impact on the dynamics of Norwegian Greylag Geese through their reproductive schedules.

Greylag Geese in Norway fed extensively on eelgrass *Zostera* sp. beds until around 1980, after which this food resource collapsed (Follestad, unpubl. data). Whereas Greylag Geese used to spend several weeks feeding on eelgrass after breeding, and migrating south in September and early October, they now leave the breeding grounds as soon as they have attained full flying ability during August (Andersson *et al.* 2001). When arriving in Denmark and the Netherlands they feed on stubble fields, which seem to form an abundant food resource (Nilsson *et al.* 1999). The Greylag Goose hunting season in Norway opens towards the end of their breeding season (21 August during the first part and 10 August during the latter part of this study; Follestad 1994a). This allows some early breeders to escape the hunting pressure but forces many others to migrate prematurely before the primary feathers have completed regrowth after moulting. In addition to escaping the hunting pressure, geese that breed early and can migrate relatively early from the breeding grounds will be rewarded with high quality food resources at their staging sites. It is therefore reasonable to expect that early breeding and migratory behaviour would entail fitness benefits, particularly in the light of increased hunting pressure in recent years (Follestad 1994a). Although the influence of hunting disturbance on the regional movement of migratory geese has been demonstrated (Fox & Madsen 1997; Béchet *et al.* 2003), no empirical studies were found that investigated the influence of hunting disturbance on the timing of migration between different seasonal sites. Further analyses investigating the timing of Greylag Goose migration in autumn, and the consequences of an earlier breeding season on the ability of goslings to fledge and on the families to migrate prior to the onset of the hunting season, are therefore warranted. This would provide insight into the future dynamics and viability of the population.

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