Declining winter survival and fitness implications associated with latitudinal distribution in Norwegian Greylag Geese *Anser anser*

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The Norwegian Greylag Goose *Anser anser* population has been increasing steadily over the past few decades, causing increasing nuisance in terms of agricultural crop damage. This, in combination with the importance of Greylags as a hunting target, has called for demographic estimates for the population to assist in management decisions. To this end, we analysed long-term mark–recapture data using Cormack–Jolly–Seber models embedded in program MARK to obtain survival estimates for the population. No sex-specific difference, or age effect on survival after juveniles had completed their first migration (3 months of age), was evident. Mean first-year survival was reported as 0.485 and annual survival of older birds as 0.700. On a monthly basis, survival in Greylags during summer and winter was very similar over the study period. A significant linear decline in winter survival from 0.909 to 0.807 was, however, apparent during the study period. Over the second half of the study (1994–2002), summer survival was about 3% lower than in the first half (1986–94) but no linear relationship was evident. We found a significant inverse relationship between Greylag survival during summer and latitudinal distribution in Norway. A similar relationship was evident between survival and annual bag numbers. The changes in adult survival observed in this study are likely to have had a substantial impact on the growth rate of the Norwegian Greylag population.

The breeding populations of Greylag Geese *Anser anser* in the Nordic countries have recovered markedly over recent decades after previous over-exploitation (Fog *et al.* 1984, Madsen 1991, Follestad 1994a, Kampe-Persson 2002). The growing Greylag numbers, together with an expansion of their breeding ranges, have been reported to result in increased damage of agricultural crops (Follestad 1994b). Despite this nuisance aspect, Greylags are held in high regard among hunters in Norway, where they are among the most important coastal small game target species. It has therefore become a growing challenge to establish sound management guidelines in order to balance acceptable levels of agricultural crop damage, hunting constraints and population integrity. Demographic estimates, including inter-annual variability, and the factors that influence them, are particularly important for the management of exploited bird populations.

In long-lived species such as geese, changes in population numbers are predominantly a response to changes in survival rates, with fecundity playing a minor role (Lebreton & Clobert 1991, Sæther *et al.* 1996, Rockwell *et al.* 1997, Schmutz *et al.* 1997, Menu *et al.* 2002, Pistorius *et al.* 2004). Long-term changes in several goose populations have been attributed to shifts in survival, particularly in adults (Ebbinge 1991, Francis *et al.* 1992, Madsen *et al.* 2002). Obtaining these survival estimates requires large-scale marking and recapturing of birds over an extended period (Lebreton *et al.* 1992).

Norwegian Greylags have been marked with neck-bands for individual recognition since 1986 at several localities along the Norwegian coast as part of the Greylag Goose Project managed by the Nordic Council for Wildlife Research. The initial aim of this neck-banding was to allow investigation into migration and local patterns of movement. This has provided insight into the important staging, wintering and moulting areas of Norwegian Greylags and movement between these areas and the breeding sites

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(Andersson *et al.* 2001). A large database of annual resightings of these neck-banded individuals has developed since 1986, which now provides an opportunity to assess survival rates within the population.

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 with some differences between populations (northern breeding populations depart from their breeding grounds later than southern populations). A recent temporal shift in the breeding season has been reported and attributed to climate change (Pistorius *et al.* in press). All individuals migrate in autumn along the Atlantic flyway to the Netherlands (main areas being Dollard, Lauwersmeer, Flevoland and the Dutch Delta), where staging occurs. Although some individuals remain here to over-winter, the vast majority migrate further south in November to their Spanish winter quarters, situated in the Duero basin, province of Toledo, Extremadura and the Guadalquivir Marismas (Kampe-Persson 2002). The geese leave Spain in February to stage for about a month in the Netherlands between February and April, before returning to their breeding sites.

In this study we use mark–recapture techniques to study survival patterns in Norwegian Greylag Geese over the period 1986–2002. In particular we estimate the effect of age, sex and year on survival. In addition, we compare estimates derived from five different subpopulations to assess the effect of latitudinal distribution on survival of Greylags. Marked Greylags were resighted during two discrete periods in their annual cycle in the Netherlands (in autumn before migrating further south to Spain and in spring before migrating north to Norway for the breeding season). This allowed us to independently investigate temporal patterns in winter and summer survival in Norwegian Greylags. No previous attempts have been made to estimate survival probabilities within this population, despite its importance for management.

METHODS

Study areas

Greylags were neck-banded at several localities along the coast of western and northern Norway, following a latitudinal gradient from Haram in the south (62°42'N, 6°22'E) to Store Tamsøy in the north (70°42'N, 25°49'E; Fig. 1). The majority of individuals were marked on the island of Vega (65°42'N,

Figure 1. Greylag neckbanding locations in Norway grouped by area. Sample sizes give number of Greylags neckbanded in each area between 1986–2002.

11°51'E) and the surrounding archipelago on the Helgeland coast. High numbers were also marked at Smøla and Frøya in mid-Norway.

The main breeding areas and the majority of moulting sites for non-breeding Greylags in Norway were covered by this study (Follestad *et al.* 1988, Follestad 1994a, 1994b). The Greylags mainly breed on islands covered with grass and heather along the outermost coast (Follestad 1994a, 1994b). In the northern parts of Troms and in Finnmark, the main part of the population breeds on islands or on bogs in the fjord areas, often considerable distances from the seashore (Follestad & Golovkin 2000). The main agricultural activity in these areas is grass production; there is little cereal cultivation.

Data collection

Between 1986 and 2002, 2899 Greylag Geese were caught and marked throughout Norway (Fig. 1).

Adult Greylags were caught when they were unable to fly due to remex moult (and goslings were not yet full-winged). Most individuals (breeding and moulting) were caught when they were in the water and they were captured in a sweep-net after short pursuits by boat. Some family groups were often caught by rounding them up where they were grazing on pastures and forcing them into nets that were mounted in advance. Individuals were sexed by means of cloacal eversion. Each Greylag captured received a Darvik neck-band. These were uniquely engraved for subsequent individual recognition, and were readable from up to 600 m with a telescope under good light conditions. The marking of geese took place from mid-June to early August each year, coinciding with the Greylag breeding season.

In the Netherlands (staging area for most Norwegian Greylags during the spring and autumn migration to and from Spain and wintering site for some, Andersson *et al.* 2001) observations of neck-banded Greylag Geese were made by a network of observers (mostly volunteers) during the monthly national censuses during spring and autumn. More frequent observations were made on an ad-hoc basis. Over the study period, 2231 out of the 2899 individuals that were marked in Norway were identified here (Table 1).

Data analyses

Although geese were marked in Norway during the breeding season, we made use of resighting data collected in the Netherlands for our analyses. The resighting rate in the Netherlands (a mean of approximately 80% annual resighting probability; see Results) is much higher than in Norway due to the relatively small and easily accessible areas occupied by the geese and the even landscape allowing for good coverage. We received about ten times more resightings here than from Norway and about five times more than from Spain (Andersson *et al.* 2001).

When a bird was not seen for 2 years followed by a single resighting we considered the record to be a resighting error (in light of the high resighting probabilities recorded in this study and the fact that most birds were resighted on several occasions within a season), and discarded it.

In order to examine a potential age and sex effect on annual survival we used resightings of birds marked as goslings. Resighting data were collected from these birds while they were staging in the Netherlands during autumn en route to Spain (September–November; Andersson *et al.* 2001), and our annual estimates stretch from one autumn to the next. When constructing an encounter-history

Table 1. Numbers of Norwegian Greylag Geese resighted for the first time in the Netherlands during autumn (September–December) from 1986–2002.

Year	Subpopulations						Sexes			Total	Goslings ringed
	Møre-Romsdal Sør-Trøndelag	Nord-Trøndelag	Vega/ Herøy	Bodø	Troms/ Finnmark	Other	Male	Female	Unsexed		
1986	14	17					13	12	6	31	9
1987	82	32					57	50	7	114	5
1988	117	129	51				117	122	58	297	107
1989	16	56	65				74	59	4	137	45
1990	7	9	121	9	18	9	67	57	49	173	44
1991	3	16	103	1	5	11	25	27	87	139	72
1992	39	5	143	22	2	5	68	72	76	216	62
1993	26	5	137	19	3	7	84	71	42	197	43
1994	6	3	142	19	3	3	89	50	37	176	51
1995	38		79	2	42	1	73	61	28	162	90
1996	19		57	3	4	1	44	25	15	84	31
1997	32		53	1	27		59	51	3	113	45
1998	65		12	1	9		32	41	14	87	13
1999	68		5		3		32	41	3	76	26
2000	38		19		8		34	31		65	32
2001	16	20	45		9	1	42	30	19	91	39
2002	41	9	21		2		34	22	17	73	9
Total	627	301	1053	77	135	38	944	822	465	2231	723

matrix (required for capture–mark–recapture analyses) from these data we distinguished three groups: males, females and individuals that were not sexed during the initial capture and marking. To allow estimation of survival over the first period of life extending from the breeding season to autumn (approximately 3 months, and subsequently referred to as juvenile survival), our first release of goslings was during marking (Norway) with all subsequent resightings from the Netherlands over annual intervals after the first autumn. Goslings are fitted with neck-bands at about 7 weeks of age (when younger, the head is too small and the neck-band slips off) and our survival estimates do not incorporate mortality prior to this.

Norwegian Greylags also stage in the Netherlands on the return journey to Norway during spring (February–April). To estimate over-wintering survival in Spain and summer survival in Norway we used both these staging periods to produce seasonal intervals when constructing the second encounter-history matrix, and all marked individuals were included (Table 1). We divided the Greylag population into five subpopulations according to marking location in Norway (Fig. 1) in order to investigate the effect of latitudinal distribution on survival. The above-mentioned encounter-history matrix consequently had five groups. No sex effect on survival or resighting probability was apparent from the age-specific dataset (see Results) and we consequently pooled our resighting data from the two sexes for the seasonal analysis.

Over the study period, peak numbers of marked Greylags in the Netherlands were observed on 14 October in autumn and 1 April in spring. Our annual survival estimates therefore span from 14 October in one year to 14 October in the next, our winter estimates from 14 October to 1 April (5.5 months) and our summer estimates from 1 April to 14 October (6.5 months). We refer to summer and winter survival (coinciding with the periods the Greylags spend in Norway and Spain, respectively) for convenience, and realize that the time periods for which we estimate survival stretch beyond these two seasons.

Resighting data from 1986 to 2002 were used for the purpose of this study, which yielded 16 years of resighting data. The software program MARK (G. White & Burnham 1999), which is an application for the analysis of encounter-history matrices of marked individuals, was used to obtain likelihood estimates of survival and resighting probabilities of the Greylags. The software program provides parameter estimates under the essential Cormack–Jolly–Seber (CJS) model, but also under several models that appear as

special cases of this model (Lebreton *et al.* 1992). When analysing resighting data from known-age birds (i.e. marked as goslings), we used age-dependent CJS models to assess the effect of age on survival (starting with a model with four separate age classes), after which we used models allowing for time-dependent juvenile survival to investigate a time effect on this parameter. We used the full time-dependent model as a starting point when analysing the seasonal resighting data.

Goodness-of-fit (GOF) tests of the CJS model were performed using the program RELEASE (Burnham *et al.* 1987) to check whether the assumptions pertaining to the model were met (see Lebreton *et al.* 1992). When the tests were significant, we corrected for extra-binomial variation in the data by using a variance inflation factor, $\hat{C}$, which is the ratio of the χ^2 goodness-of-fit test divided by the degrees of freedom (Lebreton *et al.* 1992).

Akaike's Information Criterion (AIC) was used to select between models with various constraints on survival and resighting probability (Lebreton *et al.* 1993, Anderson *et al.* 1994). Likelihood-ratio tests (LRT) were also used to test hypotheses related to our estimates. AIC and LRT also had to be corrected for $\hat{C}$. With the inflation factor, the AIC becomes the quasi-likelihood AIC (QAIC) (Lebreton *et al.* 1992, Anderson *et al.* 1994).

We tested for a number of parametric relationships between survival and explanatory variables. We tested for a logistic-linear relationship between the migration distance to the Netherlands (from Norway) of the five respective subpopulations of Greylags and summer survival. Bag numbers have been recorded on an annual basis in Norway. We also fitted a model constraining summer survival to be a logistic-linear function of bag size. This was done in an attempt to reveal the relationship between hunting and summer survival and to reach the most parsimonious model. We also tested for a linear trend in juvenile, winter and summer survival.

The loss of neck-bands is a potential source of error in mark–recapture studies on birds and results in survival estimates being negatively biased. We had no data to allow for the estimation of neck-band retention rates in our study and assume this to have had a minor effect on our estimates (see Discussion). Our primary focus here was to investigate temporal and group effects on survival of the same population, and neck-band loss is not expected to have influenced these comparisons (owing to similar expected bias over time and groups).

Table 2. Goodness-of-fit tests of the Cormack–Jolly–Seber model for Norwegian Greylag resighting data.

		χ^2	df	P
Greylags marked as goslings (initial release Norway)				
	Test 2	37.42	40	0.587
	Test 3	60.01	67	0.715
	Test 2 & 3	97.43	107	0.735
Marked Greylags separated by subpopulation (initial release Netherlands)				
Group 1	Test 2	11.80	16	0.758
	Test 3	38.96	29	0.103
	Test 2 & 3	50.79	45	0.257
Group 2	Test 2	1.20	10	0.899
	Test 3	9.01	13	0.772
	Test 2 & 3	10.21	23	0.889
Group 3	Test 2	41.36	36	0.248
	Test 3	63.11	46	0.048
	Test 2 & 3	104.46	82	0.048
Group 4	Test 2	24.95	25	0.466
	Test 3	28.79	26	0.321
	Test 2 & 3	53.74	51	0.370
Group 5	Test 2	37.60	31	0.193
	Test 3	58.35	50	0.195
	Test 2 & 3	95.95	81	0.128
Total	Test 2	116.91	118	0.511
	Test 3	198.21	164	0.035
	Test 2 & 3	315.12	282	0.085

RESULTS

Goodness-of-fit tests of the CJS model

The CJS model adequately fitted the resighting data from Greylags marked as goslings (Table 2). When considering seasonal resightings separated by subpopulation, Test 3 from the third subpopulation was significant, resulting in a significant test for the dataset. Failure to comply with Test 3 could be due to heterogeneity in survival or resighting rates among individuals. In order to correct for this limited extra-binomial variation in our data, we used an inflation factor to adjust our estimates.

Age- and sex-dependent survival

When modelling the effect of age on survival from resightings of the marked goslings, we found no significant difference in resighting probability between the sexes ($\chi^2 = 18.648$, $df = 17$, $P = 0.349$). Although there was some support for time-dependence in recapture probability ($\chi^2 = 25.916$, $df = 16$, $P = 0.055$), the most parsimonious model was one in which resighting probability was maintained constant across

Figure 2. Survival estimates (with standard errors) of juvenile Norwegian Greylag Geese (for the three month interval between neckbanding in Norway as goslings and resight in the Netherlands the first autumn).

sexes and over time (Table 3). There was no significant difference in survival between males and females ($\chi^2 = 0.978$, $df = 4$, $P = 0.913$) and survival was subsequently constrained across sexes. There was, furthermore, no significant difference between survival in the first and second year ($\chi^2 = 0.934$, $df = 1$, $P = 0.334$) or any subsequent age effect ($\chi^2 = 1.439$, $df = 2$, $P = 0.487$; Table 3) on survival after 3 months of age. The mean annual survival of geese older than 3 months of age was estimated at 0.700 (95% CI 0.672–0.727). Juvenile survival was estimated at 0.601 (95% CI 0.557–0.643) over the study period, but this varied significantly over time ($\chi^2 = 57.726$, $df = 17$, $P < 0.001$), with no linear trend ($\chi^2 = 36.224$, $df = 15$, $P = 0.002$; Table 3, Fig. 2). The most parsimonious model had two age classes: up to 3 months and older. During the second half of the study (1994–2002) juvenile survival was 5.2% lower than during the first half (1986–2004), although this was not significant ($\chi^2 = 1.477$, $df = 1$, $P = 0.224$). The

Table 3. Elimination of non-significant effects from the full CJS model in modelling survival in Norwegian Greylag Geese: for each model the number of estimable parameters (np), the deviance (DEV), and the Akaike information criterion (AIC) are given. In models 1–6, under seasonal survival, we considered a time-dependent group effect, after which the group effect was removed (models 7–13), and re-introduced without a time effect in models 13 and 14.

Model	np	(Q)DEV	(Q)AIC
Age-specific survival			
(1) ($\phi_{mfu(a4)}$, $p_{mfu(t)}$)	62	910.25	3336.95
(2) ($\phi_{mfu(a4)}$, $p_{m=f=u(t)}$)	29	964.38	3321.12
(3) ($\phi_{mfu(a4)}$, $p_{m=f=u(c)}$)	13	990.29	3314.17
(4) ($\phi_{m=f=u(a4)}$, p_c)	5	996.77	3304.45
(5) (ϕ_{a3} , p_c)	4	998.20	3303.87
(6) (ϕ_{a2} , p_c)	3	998.21	3301.87
(7) (ϕ_{a1} , p_c)	2	1010.73	3312.39
(8) (ϕ_{a2t} , p_c)	19	953.01	3289.13
(9) ($\phi_{a2linear}$, p_c)	4	989.23	3294.90
(10) ($\phi_{a2t(2year\ intervals-c)}$, p_c)	10	969.22	3287.00
(11) ($\phi_{a2t(3year\ intervals-c)}$, p_c)	8	972.68	3286.41
(12) ($\phi_{a2t(4year\ intervals-c)}$, p_c)	6	980.95	3290.65
Seasonal survival			
(1) ($\phi_{G \cdot S \cdot T}$, $p_{G \cdot S \cdot T}$)	271	5646.90	17149.48
(2) ($\phi_{G \cdot S \cdot T}$, $p_{S \cdot T}$)	170	5795.86	17084.03
(3) ($\phi_{G \cdot S \cdot T}$, $p_{S \cdot Tautumn}$)	156	5894.96	17153.86
(4) ($\phi_{G \cdot S \cdot T}$, $p_{S \cdot Tspring}$)	155	6161.29	17418.11
(5) ($\phi_{Gsummer \cdot S \cdot T}$, $p_{S \cdot T}$)	117	5843.43	17021.42
(6) ($\phi_{Gsummer-linear \cdot S \cdot T}$, $p_{S \cdot T}$)	63	5921.28	16988.62
(7) ($\phi_{S \cdot T}$, $p_{S \cdot T}$)	64	5910.91	16980.28
(8) ($\phi_{Swinter-linear \cdot T}$, $p_{S \cdot T}$)	49	5934.16	16973.07
(9) ($\phi_{Swinter \& summer-linear \cdot T}$, $p_{S \cdot T}$)	36	5972.86	16985.47
(10) ($\phi_{Ssummer-logBag \cdot T}$, $p_{S \cdot T}$)	49	5919.79	16958.71
(12) ($\phi_{S \cdot Tsummer (winter\ constant)}$, $p_{S \cdot T}$)	48	5942.41	16979.29
(12) ($\phi_{S \cdot Twinter (summer\ constant)}$, $p_{S \cdot T}$)	48	5936.63	16976.52
(13) ($\phi_{Gsummer \cdot S}$, $p_{S \cdot T}$)	38	6022.29	17047.03
(14) ($\phi_{GsummerLogDistance \cdot S}$, $p_{S \cdot T}$)	35	6034.63	17045.23
(15) (ϕ_{S} , $p_{S \cdot T}$)	34	6042.18	17050.75

ϕ_t , time-dependent survival; ϕ_c , survival constant over time; m, male; f, female; u, unknown; a, age classes; g, group; p_t , time-dependent resighting probability; p_c , constant resighting probability.
G, group; S, season; T, time.

most parsimonious model had juvenile survival constrained over 3-year intervals (Table 3; Fig. 2). From the above it is clear that juvenile Greylags are particularly prone to mortality factors during the first 3 months of life, after which they follow the survival schedule of adults. When assuming equal monthly survival in our annual estimates, mean survival between autumn and the breeding season (about 9 months) would be 0.775 (using 0.700 for annual mean survival, see above). Including survival over the first 3 months would imply a first year survival rate of 0.485.

Time-dependent seasonal survival and latitudinal effects

Strong support for time-dependence in resighting probability in both autumn ($\chi^2 = 99.097$, $df = 14$,

$P < 0.001$) and spring ($\chi^2 = 70.399$, $df = 14$, $P < 0.001$) was evident (Table 3, Fig. 3). Although resighting probability varied between the subpopulations according to LRT ($\chi^2 = 148.967$, $df = 101$, $P = 0.001$), the most parsimonious model had this parameter time-dependent and constrained over the groups (AIC 17084.03 vs. 17149.48; Table 3). Mean resighting probabilities during the autumn and spring staging period were 0.845 (95% CI 0.832–0.857) and 0.353 (95% CI 0.339–0.367), respectively.

An effect of latitudinal distribution in Norway is only likely to operate on summer survival, and constraining winter survival over the subpopulations did indeed provide a better model (Table 3, model 5). Although we found an inverse linear relationship between latitudinal distribution and summer survival ($\chi^2 = 10.367$, $df = 1$, $P = 0.001$; Table 3, model 6),

Figure 3. Resight probabilities (with standard errors) of Norwegian Greylag Geese during the Spring (Feb–Apr) and Autumn (Sep–Nov) staging periods in the Netherlands.

removing the latitudinal effect and constraining survival over the subpopulations provided a more parsimonious model (Table 3, model 7) to explore a time effect on survival.

A decline in winter survival was evident from the estimates that the time-dependent model yielded and we consequently constrained winter survival to vary linearly with time (Table 3, model 8). We found a significant linear decline in winter survival ($\chi^2 = 10.938$, $df = 1$, $P = 0.009$) and the model yielded a slope of -0.058 (95% CI -0.102 to -0.014). During the study period, winter survival declined by 10% from 0.909 (95% CI 0.879–0.932) to 0.807 (95% CI 0.733–0.864). On average, during the second half of the study, summer survival was about 3% lower than during the first half of the study, and over the study period showed substantial variation over time ($\chi^2 = 29.125$, $df = 15$, $P = 0.020$).

We found a significant relationship between bag size and summer survival ($\chi^2 = 22.612$, $df = 1$, $P < 0.001$; Table 3, model 10). Although a linear effect on winter survival was evident (see above), the most parsimonious model had winter survival as time-dependent and summer survival as a function of bag size (Table 3, model 10). Survival estimates from this model are presented in Figure 4 and the relationship between bag size and survival in Figure 5. The inverse relationship between survival and bag size suggests that hunting is the primary mortality agent in this population during summer.

We estimated a mean summer survival of 0.823 (95% CI 0.802–0.842) and winter survival of 0.859 (95% CI 0.839–0.878) over the study period. This

Figure 4. Winter (14 Oct–1 Apr) and Summer (1 Apr–14 Oct) survival estimates (with standard errors) for adult Greylag Geese neckbanded in Norway.

Figure 5. Summer (1 Apr–14 Oct) survival of Greylag Geese neckbanded in Norway from 1986 to 2002 against annual bag size of Greylag Geese hunted in Norway over the same period.

Table 4. Mean summer survival (1986–2002) of Greylags from five different subpopulations following a north–south gradient in Norway.

Year	ϕ	SE (ϕ)	95% CI
Subpopulation			
1	0.765	0.025	0.713–0.810
2	0.796	0.014	0.767–0.822
3	0.818	0.010	0.797–0.837
4	0.824	0.011	0.804–0.843
5	0.843	0.012	0.818–0.866

translates into the same mean monthly survival of 0.973 and 0.974 for the two seasons, respectively.

We found a significant latitudinal gradient in mean survival of the different subpopulations ($\chi^2 = 7.954$, $df = 1$, $P = 0.005$; Table 3, model 14) and estimates for the respective subpopulations are given in Table 4.

DISCUSSION

Potential sources of error

A fundamental assumption under the CJS-based models stipulates that the study population must be closed, so that permanent emigration does not negatively bias the survival estimates. A few Greylags from Norway have been observed outside the Atlantic flyway, mainly from England (Andersson *et al.* 2001). As with most geese breeding in the arctic or temperate zones, Norwegian Greylags have distinct migration routes with traditional staging and wintering sites being used from year to year (Owen 1980, Andersson *et al.* 2001). In spring and autumn, all Norwegian Greylags pass through the same staging areas in the Netherlands, where extensive observations were conducted (Andersson *et al.* 2001). Birds that emigrated from the marking areas could therefore be resighted on the staging areas. We consequently expect bias associated with permanent emigration from our study areas to be minimal and that our apparent survival estimates closely approximate true survival estimates for the population.

A further assumption of mark–recapture models is that the study animals do not lose their marks (Lebreton *et al.* 1992). However, neck-band loss is a reality, as has been documented in several demographic studies on goose populations (e.g. Johnson *et al.* 1995, Persson 2000, Gauthier *et al.* 2001, Sheaffer *et al.* 2004). We did not have sufficient data in this study to estimate neck-band loss in Norwegian

Greylags, and we did not compensate for neck-band loss in our survival estimates. Owing to similar negative bias in our estimates, neck-band loss would not have influenced our temporal comparisons. For the purpose of age- and sex-specific comparisons we had to assume that there was no age or sex effect on neck-band retention. Neck-band retention rates in the Baltic population of Greylags have been estimated as 97.1% (Persson 2000). Assuming similar loss rates in the Norwegian population would imply that our estimates would be negatively biased by between 2 and 2.5%.

Age and sex effects on annual survival

We found no age effect on survival once the Greylag goslings had fledged and successfully completed their first migration to the Netherlands. Prior to this, however, survival was significantly lower than subsequent survival (as would be expected) with a mean survival probability of 0.601 over this first stage in life (to about 3 months) and 0.480 over the first year (excluding premarking mortality). Our first-year estimate is very close to that of 0.472 recently reported for first-year survival in Icelandic Greylags (Frederiksen *et al.* 2004). Nilsson and Persson (1993) reported a relatively high estimate of 0.760 for first-year survival in Greylags from southern Sweden, with significant variation between years, from 0.650 to 0.920. Although that estimate spanned from when the goslings fledged, ours commenced from marking and incorporated about 10–14 days of prefledging mortality. During their study period there was also no hunting for Greylags in Sweden. Both these factors could have contributed to their relatively high mean estimate. Our mean estimate for first-year survival is similar to, but higher than, those reported for other species of geese (0.471, Schmutz & Ely 1999; 0.360, Menu *et al.* 2002; 0.380, Francis *et al.* 1992).

We draw attention to our finding that the distinction between juvenile and subsequent survival in Norwegian Greylags only continues up until the first migration to their staging grounds has been completed. No significant age effect on survival was apparent after this (unlike observations for Swedish Greylags, Nilsson & Persson 1993) and for purposes of future monitoring of this population, survival of two age-classes (juvenile (3 months) and subsequent survival) need to be distinguished. This also implies that including different-aged birds within a cohort would not result in heterogeneity in survival among individuals within that cohort, a violation of the CJS model (Lebreton *et al.* 1992).

Large variation in point estimates of juvenile survival is characteristic in demographic studies on geese (Francis *et al.* 1992, Schmutz & Ely 1999, Menu *et al.* 2002). Similarly, we found significant and substantially more temporal variability (with no apparent trend) in juvenile survival relative to survival in older birds. Juvenile survival was not correlated with survival of older birds over the same time, suggesting that different regulating factors govern survival in these two population groups. Goslings and adults are likely to suffer similar hunting mortality, but mortality incurred during the autumn migration could be much more variable in goslings. Both body condition prior to the migration and unfavourable weather conditions during the migration are likely to have a greater influence on goslings than on older birds. On the breeding grounds, goslings are flightless for an extended period when they are susceptible to predators, mainly the White-tailed Eagle *Haliaeetus albicilla* and Great Black-backed Gull *Larus marinus*. Predation is, however, likely to be most substantial prior to goslings being marked, at which time they are much smaller than the adults. It is worth noting that hunting activity before goslings are fully fledged has been observed to result in the southward migration being initiated prior to full development of wing feathers (A.F. pers. obs.). This is likely to diminish the chances of successfully completing the migration.

Adult survival in geese has formed the focus of numerous studies, with the emphasis often being on the relationship between survival and different hunting regimes, allowing for management recommendations. Survival estimates of Greylags from southern Sweden prior to 1993 have been reported as 0.740 for subadults and 0.830 for adults (Nilsson & Persson 1993). We found no significant difference in survival between subadults and adults and our estimated survival of Norwegian Greylags is lower than the combined estimate (adults and subadults) for the Swedish population. As with juvenile survival, our estimate for adult survival closely resembles that reported by Frederiksen *et al.* (2004) for the Icelandic Greylag population (0.700 vs. 0.727) during a period when the population was thought to be stable after a recent decline.

Estimates for adult survival in geese vary greatly, but 0.870 and 0.910 have been reported for protected populations (Pettifor *et al.* 1998, Clausen *et al.* 2001), 0.830 for an increasing population (Gauthier *et al.* 2001, Menu *et al.* 2002), and 0.749 and 0.631 for stable populations (Schmutz *et al.* 1994, Schmutz

& Ely 1999). Our mean adult survival estimate is relatively low in relation to most of these estimates. It is important to note that unlike several of the above studies, our estimates were not corrected for neck-band loss. As stated above, we expect our estimates to be negatively biased by about 2–2.5% (Persson 2000).

Most studies on goose populations have found no sex-specific differences in survival (Samuel *et al.* 1990, Francis & Cooke 1992, Schmutz *et al.* 1994, Ward *et al.* 1997, Schmutz & Ely 1999, Menu *et al.* 2002), as would be expected for monogamous species with long-term pair bonds (Stearns 1992). Both seasonal and annual intersexual variation in survival of geese has, however, been documented (Raveling *et al.* 1992, Schmutz *et al.* 1994, Schmutz & Ely 1999, Madsen *et al.* 2002), and this has been inferred to result from behavioural differences between the sexes (Schmutz & Ely 1999). For example, it has been reported that adult female Greater Snow Geese are more likely to cross the firing line (apparently due to behavioural differences in defence of young), and therefore have a higher hunting mortality, than males (Giroux & Bédard 1986). Differences in vigilance behaviour and energetic demands associated with breeding are also plausible explanations for these differences. The absence of sex-specific differences in survival observed in this study suggests that behavioural differences between Greylag sexes, and the additional energetic expenditure of females relative to males during the breeding season, do not have fitness implications in terms of survival.

Seasonal survival

When dealing with seasonal survival we found that Greylags experienced the same mean monthly survival during winter and summer. Assuming that hunting is the primary mortality factor in the population, this would suggest that over the study period hunting in Norway had the same impact on the demographics of the population per time interval as hunting in their winter distribution. It is important to note, however, that summer survival was relatively stable (although a slight decline was apparent) whereas a significant decline in winter survival was evident. If hunting is the primary mortality factor in Norwegian Greylags, hunting activities need to be considered in the Netherlands where they stage, in France which they pass through en route to Spain, and in Spain where the majority (about 11% remain in the Netherlands) overwinter. Summer survival did not change significantly

over the study period, and hunting activity in Norway would therefore appear to have been similar during the study period. Overall hunting pressure in the Netherlands has been considered to be low, whereas heavy, but variable hunting pressure has been noted in southern Spain (Nilsson & Persson 1993). We have no indication of the hunting mortality that Greylags experience while passing through France, but this could be substantial.

Long-term changes in survival have been demonstrated for a number of bird populations. Increases in survival in a population of Lesser Snow Geese were apparently due to alleviated hunting pressure (Francis *et al.* 1992). A similar increase in survival of Barnacle Geese wintering in northern Britain has been noted following the introduction of new reserves that reduced illegal hunting pressure (Owen 1984). Annual survival in Pink-footed Geese *Anser brachyrhynchus* declined significantly from 0.900 to 0.790 between 1990 and 1999 due to natural mortality factors operating on the breeding grounds (Madsen *et al.* 2002). At least in some studies on exploited populations, changes in survival have been attributed to changes in hunting pressure.

The Imperial Eagle *Aquila heliaca* is the main predator of Greylags in Spain; it could also have contributed to the observed changes in Greylag survival. It does, however, seem improbable that the relatively small number of Imperial Eagles would have had an impact on the large numbers of wintering Greylags. The decline in survival could also be a density-dependent response to food availability. An increase in population density has been correlated with lower survival rates in Barnacle Geese (Owen & Black 1991). The increasing number of Greylags observed over the past few decades could have given rise to increased competition for food at the wintering grounds in Spain as well as at their staging sites in the Netherlands. Similarly, changes in food availability (agricultural foods, primarily rice) for Greater White-fronted Geese *Anser albifrons* in California are thought to have caused changes in survival (Schmutz & Ely 1999). The absence of reliable counts of Norwegian Greylags over-wintering in Spain prevented us from testing for a density-dependent relationship in survival.

A recent study screened for coronavirus in Norwegian Greylags. Of a sample of 163 Geese, 40 were found to be coronavirus-positive (Jonassen *et al.* in press). The clinical significance of this newly identified infection was suggested by the observation that infected Greylags had significantly lower body weights

than virus-negative birds. It is unclear whether the virus could cause Greylag mortality directly, but by affecting body condition it might make the birds more vulnerable to other mortality agents. Further research is necessary to determine whether this virus could have played a role in the declining Greylag survival observed in this study.

The question of whether hunting mortality is additive (animals would have survived if not hunted) or compensatory (most animals hunted would otherwise have died from natural causes) underlies much of the demographic literature on goose populations. Most researchers believe that hunting mortality in geese is additive to natural mortality and that most goose populations are not subjected to density-dependent regulation (Francis *et al.* 1992, Rexstad 1992, Schmutz *et al.* 1994, Gauthier *et al.* 2001). In this study we demonstrated that survival in Norwegian Greylags was a function of bag size: a fact that suggests that hunting mortality is additive to natural mortality in our study population (at least over their summer range).

Latitudinal effects on survival

We found a significant inverse linear relationship between the distance that the respective subpopulations need to migrate to reach the Netherlands and their survival. This could be a consequence of several factors. The relative increase in energetic demands as the migration distance increases could have fitness implications in terms of reduced survival. Furthermore, climatic variables and food availability may affect the Greylags as they deteriorate along a latitudinal gradient. The strong relationship between bag size and survival (see above), however, suggests that hunting is the primary regulating factor controlling Greylag numbers in their summer distribution. We expect that the longer migration distance, over which the northern subpopulations are subjected to hunting, is largely responsible for the observed relationship in survival. These birds also stop over in central or southern Norway for an extended period on the southward migration. Here they are often the last remaining Greylags and are likely to suffer high hunting mortality.

CONCLUSION

Monitoring the Norwegian Greylag population is hindered by the birds' patchy distribution throughout a large number of small islands (often with

limited access) along the Norwegian coast. When present in the rest of their distribution (e.g. the Netherlands and Spain) they occur with other Baltic Greylag populations, and this makes counts impracticable. Increases in numbers of Norwegian Greylags within certain areas of Norway have been documented, and it is thought that the population has been increasing steadily over the past few decades (Follestad 1994b). At one of the main breeding areas (Vega, Fig. 1) in recent years the population has been described as stable or even declining (A.F. unpubl. data). This may, however, be due to a local management plan aimed at reducing agricultural crop damage.

In the present study we observed more than a 10% decline in survival of Norwegian Greylags. This significant recent decline would have had a substantial effect on the population growth. A similar decline in Emperor Goose *Anser canagicus* survival has been demonstrated to result in a 10% reduction in population growth rate λ (Schmutz *et al.* 1997), and several other studies on goose populations have attributed long-term changes in population numbers to concurrent changes in adult survival (Owen 1984, Ebbsinge 1991, Francis *et al.* 1992). Although we do not have sufficient data to determine how the decline in adult survival has affected the population growth rate, we would expect that with the reduced survival observed over the latter half of this study, the population would not have been on the increase during this period and could well have been in decline. However, a population trajectory, using both reproductive and survival parameters, will be required to verify this.

A future research priority should be a comparative study of survival between the Norwegian and Baltic Greylag population using similar analytical procedures. Considering that the Baltic population, to a large extent, use the same wintering grounds as the Norwegian population, it is of prime interest to establish whether this population has experienced a similar decline in survival relative to the Norwegian population.

Norwegian Greylags make use of two areas in Spain, Guadalquivir Marismas in southern Spain and Villafáfila in central Spain. At Villafáfila there is virtually no hunting and comparing survival of individuals over-wintering in the two areas may clarify the role of hunting in the changes observed in Greylag survival.

As noted by Madsen *et al.* (2002), mark-recapture studies provide a reliable means of monitoring goose populations that are of management concern and a

time-lag of only 1 year between resightings and estimation of survival is required. This is particularly relevant for the Norwegian Greylag population, in which population counts provide a poor means of monitoring. We therefore encourage the continued use of mark-recapture methods as a management tool when dealing with this population.

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