FACTORS AFFECTING SURVIVAL OF YOUNG GREYLAG GEESE *ANSER ANSER* AND THEIR RECRUITMENT INTO THE BREEDING POPULATION

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Adult and young Greylag Geese have been neck-banded in a breeding area in southernmost Sweden since 1984 and have been followed intensively through the annual cycle. Fledging rate was correlated positively with the experience of parents and with early hatching; it was influenced also by choice of breeding area, wintering quarters and spring migration strategy of the parents. First year survival of fledglings was related to the same factors, but the heaviest goslings at the time of marking had a higher survival rate. Effects of wintering area and time of hatching were also apparent in the proportion of fledglings surviving to the age of three years. Greylag Geese started to recruit to the breeding population from the age of two, and recruitment age was lowest for those reared in the best breeding area. Weight at the time of marking had a marked influence on recruitment, almost all recruits being above median size at marking. Moreover, the recruitment rate was influenced by the choice of winter quarters of their parents, recruitment rate was also correlated positively with family size.

Keywords: Greylag Goose, Sweden, Young, Survival, Recruitment, Condition, Winter and Migration Strategies.

Environmental factors are important for the growth of geese as for as other vertebrates (Sedinger & Raveling 1986, Cooch *et al.* 1991, Larsson & Forslund 1991, Sedinger & Flint 1991, Sedinger *et al.* 1995). The consequences of early growth conditions, although important for the study of various life-history traits, have been studied relatively little due to the difficulties of estimating survival and future fecundity on an individual basis. Arctic geese have been considered suitable for the study of these and other aspects of life-history (*eg* Rohwer & Anderson 1988) because females return to their natal areas for breeding, making it possible to monitor survival and success in relation to rearing conditions. Arctic geese have also been studied intensively (*cf.* Cooke *et al.* 1995 for further references). Thus, mechanisms for the influence of early growth on adult size were studied by Ankney & MacInnes (1978), being a link through which early growth conditions can influence fitness, as arctic geese for breeding rely to a great extent on stored reserves obtained at staging areas further south, and as larger females can store larger reserves (Ankney & MacInnes 1978, Raveling 1979a, 1979b).

Studies of arctic geese have, however, been limited, as individuals have been followed mainly on the breeding grounds, and staging and wintering habits have not been studied as intensively (*cf.* Ebbinge 1992). For the Greylag Goose *Anser anser* of southern Sweden, a large database has been established, making it possible to follow the breeding performance and survival of individual geese for which we have a detailed knowledge of breeding, staging, wintering and, in many cases, moulting areas over a number of years. For an increasing

number of individuals, we now have data for some of their offspring, from hatching to their recruitment into the breeding population.

Greylag Goose studies in south Sweden started as a neck-banding project in the Nordic countries in 1984 which at first aimed to elucidate movements of different populations and to establish from where different concentrations were recruited. The study was initiated as a response to the increasing Greylag Goose populations in different parts of the Nordic countries as well as Europe as a whole (Nilsson 1995). The migration study was extended early to include a study of breeding ecology and population dynamics, especially in south-west Scania, southernmost Sweden.

The breeding population in south-west Scania was followed intensively during every season, beginning in 1985. The breeding performance of marked Greylag Geese has been established each year and the survival of the different individuals has been monitored intensively in relation to staging and wintering habits (Nilsson & Persson 1993, 1994, 1996, Persson 1996b).

Variation in the survival of young was found in relation to the choice of winter quarters of their parents (Nilsson & Persson 1993). Moreover, studies in Scania showed marked differences in the production of fledged young between breeding lakes (Nilsson & Persson 1994). Differences in breeding performance of geese wintering in different areas have also been established (Nilsson & Persson 1996). In this paper, we will analyse further the survival of young geese in relation to different factors and, moreover, we will follow the geese to their recruitment into the breeding population in Scania in order to examine factors influencing these life-history traits.

Study Areas

The study was undertaken in a lake area in south-west Scania, southernmost Sweden, where, since 1984, goose catching has been undertaken at Lakes Yddingen, Fjällfotasjön, Klosterviken and Börringesjön. The lakes are situated in a rolling landscape and all have extensive areas of grassland and cereal fields within short flying distances (see Nilsson & Persson 1992, 1996).

All lakes are eutrophic with a rich bloom of phytoplankton and fairly rich reedbeds. Lakes Yddingen and Börringesjön have extensive areas of grazed pasture close to the shore, while a highly-fertilized golf course borders Lake Yddingen on one side. Lake Klosterviken has one small grazed and fertilized grass area offering good grazing for goslings in the early season, before the grass gets too coarse. Feeding areas are very limited at Lake Fjällfotasjön. Lakes can be ranked based on food supplies during the brood-rearing period from the best to the worst: Yddingen - Börringesjön - Klosterviken - Fjällfotasjön (*cf.* Nilsson 1995, Nilsson & Persson 1994).

An indication of the quality of the feeding grounds can be obtained by comparing weight changes of geese between repeated weighings (see **Methods**). For goslings in June, the mean daily weight increase was 8.59±4.21 g/day (n=62). Splitting the data according to site, 41 young at Lake Yddingen gained on average 13.04±5.41 g/day compared to 12 young geese at Lake Klosterviken who lost 1.17±5.43 g/day. The difference between the two lakes was not significant (t-test), but it might be taken as an indication of differences in rearing conditions.

Methods

Catching operations for neck-banding were carried out when the goslings were approximately six weeks old, about three weeks before they fledged. The geese were caught by driving the adults with their offspring into nets on the feeding grounds (Persson 1994). The method used in Scania for catching and handling of the birds during marking has ensured rapid and complete regroupings of the families (Persson 1994). During 1984-1994, a total of 364 adult and 1,024 young Greylag Geese were neck-banded in the study area.

During marking from 1989 onwards, a large proportion of the geese was also weighed and measured. Marking was undertaken, on average, 22±0 days (n=294) before fledging. For goslings weighed twice, the weight was recorded, on average, 29±1 days and 19±1 days (n=62)

before fledging. These intervals did not differ significantly between lakes (ANOVA).

Regular checks for the occurrence of neck-banded geese were undertaken from their arrival in spring until their departure in autumn. In spring, the lake area was visited several times a week in order to establish the return of marked birds, breeding performance and the survival of young of marked parents. From the end of May until the last young fledged, the breeding area was visited almost daily to establish the exact number of fledged young in each family as well as the fate of each neck-banded gosling. In summer and autumn, field work was extended to cover neighbouring staging areas, especially the Foteviken area at the coast, where a large proportion of the Greylags from the study area gather at this time of year (*cf.* Nilsson & Persson 1992).

Weight at catching is used as an index of the general condition of the young. Even if the young were caught late in the rearing period, there was still variation in the size of young related to their age. To get a better index of their condition, we used relative weight, *ie* weight/skull length. Other measurements taken, body length, bill length, bill height, wing length and tarsus length, were all significantly correlated with skull length ($P<0.001$, Spearman Correlation Analysis). A PCI was not calculated, as it had not been possible to record all relevant measurements on more than a proportion of the geese due to lack of personnel. In some analyses, the young were classified as heavy or light according to the median of the relative weight (20.8 and 19.2 for males and females respectively).

Young were allocated to wintering area, the Dutch Delta in south-western Netherlands or the Guadalquivir Marismas in south-western Spain, based on observations of their neck-banded parents (*cf.* Nilsson & Persson 1996). Of all breeding attempts by marked experienced breeders in the study area during 1986-1995, 92.6% (n=792) were by birds with a known wintering area. Overall, no significant differences in the choice of winter quarters have been found among breeding birds from the different lakes (Ch^2 =6.24, df=3, $P>0.10$).

Calculation of pre-fledging survival was based on young in families having at least one neck-banded parent. All such families recorded in a rearing area within ten days after hatch were included. Full account was taken of pairs that lost all their young and left the study area to moult somewhere else, as well as of pairs that left the main rearing area before fledging. Permanent brood mixing, a rare event on the rearing grounds, was accounted for by assuming that it occurred between families having at least one neck-banded parent and that both broods were of the same age. In that way, survival estimates were not influenced as we used the individual as a sampling unit when following changes in brood size. During the latter half of the rearing period, goslings commonly left their parents without joining another family for shorter or longer periods (up to two weeks), but all recorded separations ended with a complete regrouping of the family.

First-year and three-year survival were expressed as the number of geese re-sighted

Table 1. Mean weight (g) of Greylag Goose goslings from different lakes at marking. Pooled data for the years 1989-1994.

Lake	Males	*n*	Females	*n*
Klosterviken	1979±41	56	1788±44	56
Börringesjön	2320±60	29	2063±83	15
Fjällfotasjön	2141±65	37	1997±64	29
Yddingen	2043±32	147	1944±27	120

after 1 July in year t+1 and t+3, respectively, as a percentage of the number that fledged in year t. Such a simple method was possible owing to an extremely high re-sighting frequency of all groups of geese (Nilsson & Persson 1993), supporting the assumption that the detection probability of a surviving neck-banded individual after the cut-off date (1 July) equals one. Neck-band loss negatively biases survival estimates, but the effect was considered too small for the calculation of correction factors (Nilsson & Persson 1993).

Our survival estimates are based on the assumption that survival of young within broods is independent (*cf.* Flint *et al.* 1995 for alternative methods). This assumption was possible due to the fact that we restricted our analysis of pre-fledging survival to the time that families spent in a brood-rearing area (one area per lake), excluding the sensitive period just after hatch when dependent factors might occur. The use of contingency tables might be inappropriate for calculation of first-year survival if families containing several neck-banded young are shot by groups of experienced hunters in the Guadalquivir Marismas (Persson 1996b). We regarded, however, the likelihood for this occurring as too low to let it influence our choice of method.

Results

Weight of young at marking

Mean weights of Greylag goslings at marking varied significantly between lakes, being lowest at Lake Klosterviken and highest at Lake Börringesjön (**Table 1**) (ANOVA, $F=10.78$, $df=3$, $P<0.001$). Within the lake samples males were significantly heavier in all cases (ANOVA, $F=19.89$, $df=1$, $P<0.001$). Using relative weights, no significant differences in the proportion of heavy or light young between the different lakes were found ($Ch^2=2.07$, $df=3$, $P=0.56$), nor in relation to the wintering area of their parents ($Ch^2=2.69$, $df=1$, $P= 0.10$). For goslings hatched during 11-20 April , 21-30 April and 1-10 May, 100% ($n=17$), 64 % ($n=100$) and 41% ($n=29$), respectively, were heavier than the median. The differences between the three periods were

Table 2. Losses of neck-banded Greylag Goose goslings between marking and fledging in the Scanian study area, 1987-1994. Days = number of days between marking and fledging (sample size is given in brackets). Data about the length of this period in 1989 and 1991 are missing, but those years did not differ from the following ones.

Marking year	marked *n*	fledged *n*	Loss (%)	Days (mean± s.e.)	Loss/day (%)
1987	112	97	13.4	27±1 (60)	0.50
1988	107	93	13.1	15±1 (42)	0.89
1989	128	115	10.2	-	-
1990	153	143	6.5	23±1 (69)	0.29
1991	44	40	9.1	-	-
1992	137	128	6.6	21±1 (93)	0.32
1993	71	61	14.1	23±1 (57)	0.62
1994	119	95	20.2	23±1 (81)	0.88
Total	871	772	11.4	22±0 (402)	0.52

highly significant (Ch^2=15.9, df=2, P<0.001).

Pre-fledging survival

Overall, 64±1% (n=2,048) of young seen as newly-hatched fledged in families where at least one parent was marked. Fledging rate could be related to breeding experience of the parents, thus 51±3% (n=243) fledged in families where at least the marked bird was inexperienced, compared to 65±1% (n=1,805) for experienced parents, the overall difference being highly significant (Ch^2=20.5, df=1, P<0.001). Among-year variation in fledging rate of young of experienced parents was highly significant for the study period as a whole (**Figure 1**, Ch^2=23.6, df=8, P<0.01), but not between late and early seasons pooled (1986-1987 v 1988-1994; Ch^2 =0.22, df=1, P>0.5). The survival to fledging of young of inexperienced parents was much lower in 1994 than in 1992 and 1993 (Ch^2=11.9, df=2, P<0.01).

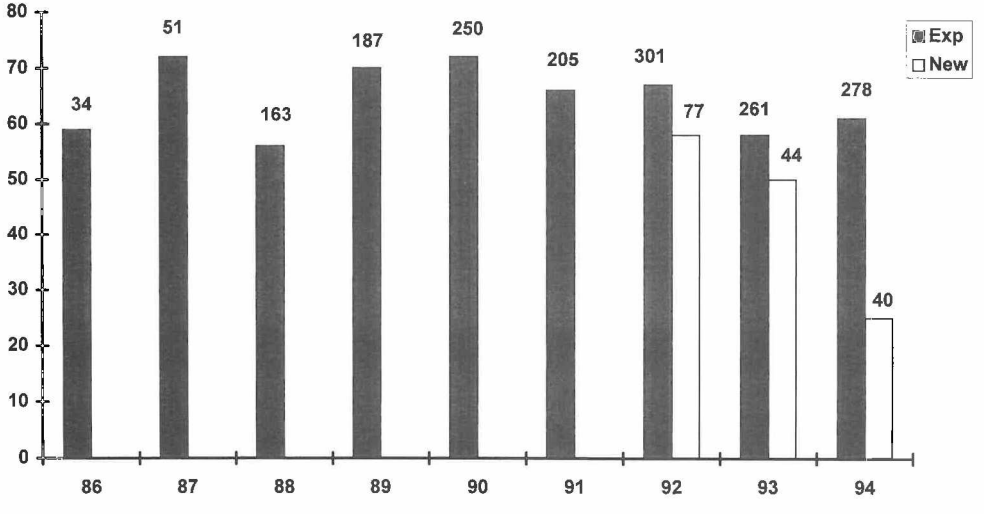
The time between marking and fledging was almost identical from year to year, averaging 22 days but, despite this fact, there were marked among-year variations in survival during this period (**Table 2**), the overall difference being highly significant (Ch^2=17.5, df=7, P<0.05).

The fledging rate varied noticeably between lakes over the years (**Figure 2**). For experienced breeders Lake Fjällfotasjön showed a significantly lower fledging rate than the other lakes (Ch^2=64.2, df=3, P<0.001). The situation was different for new breeders, where pairs at Lake Klosterviken had a significantly lower fledging success than the parents at other lakes (Ch^2=7.3, df=3, P<0.05).

A marked variation in survival to fledging was found in relation to hatching time (**Figure 3**). Fledging rate for experienced breeders decreased during consecutive ten-day periods, from 87% for those first seen during the period 11-20 April to 43% for those found 11-20 May, the differences being highly significant (Ch^2=84.1, df=3, P<<0.001). Too few data were available to analyse this aspect for new breeders. This analysis did not include years with a late season, *ie* was restricted to the period 1988-1994, with similar, early seasons (data from the wet periods in 1991, see below, were also excluded).

A slight, but insignificant, effect of the winter

Figure 1. Percentage of newly-hatched Greylag goslings in families with marked parents surviving until fledging in different years, pooled over lakes. Experienced breeders grey bars, new breeders white bars. Too few new breeders were available during the first years to produce annual figures. Sample sizes are shown over the bars.



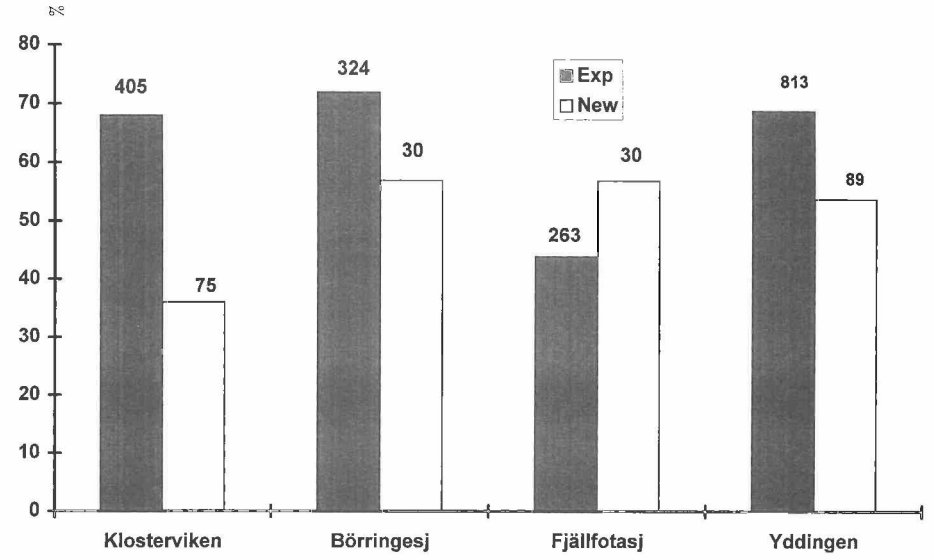


Figure 2. Percentage of newly-hatched Greylag goslings in families with marked parents surviving until fledging in different lakes, pooled over the years 1988-1994. Experienced breeders grey bars, new breeders white bars. Sample sizes are shown over the bars.

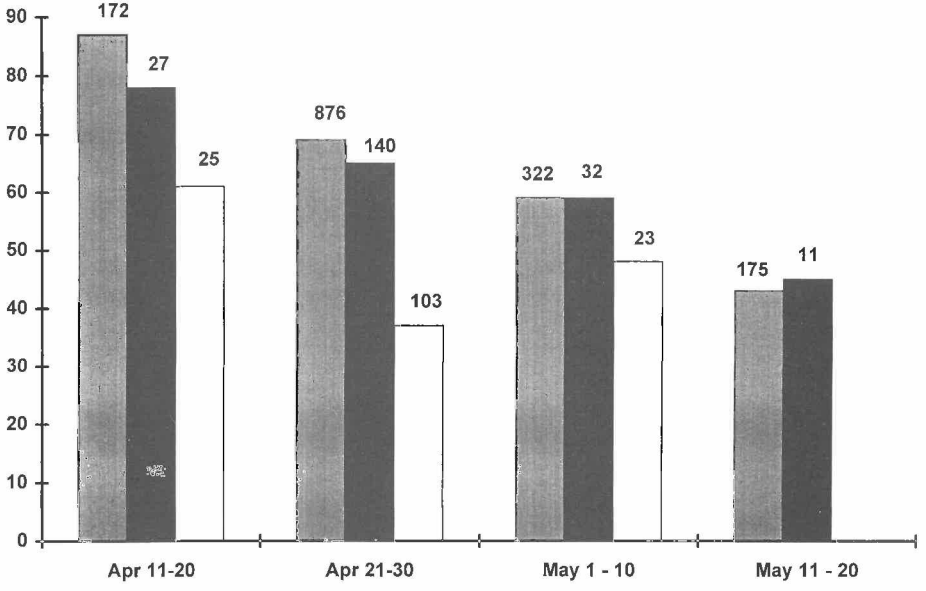


Figure 3.Survival (percentage) during different periods of life in relation to hatching date of Greylags. For each hatching period, the three columns show fledging rate (left), first- year survival (center) and three-year survival (right). Data were pooled for the hatching years 1988-1994, 1989-1993 and 1989-1992, respectively. Newly hatched young in families with marked parents were used for the calculation of fledging rate, neck-banded fledgings for the other two estimates. Sample sizes are shown over the bars.

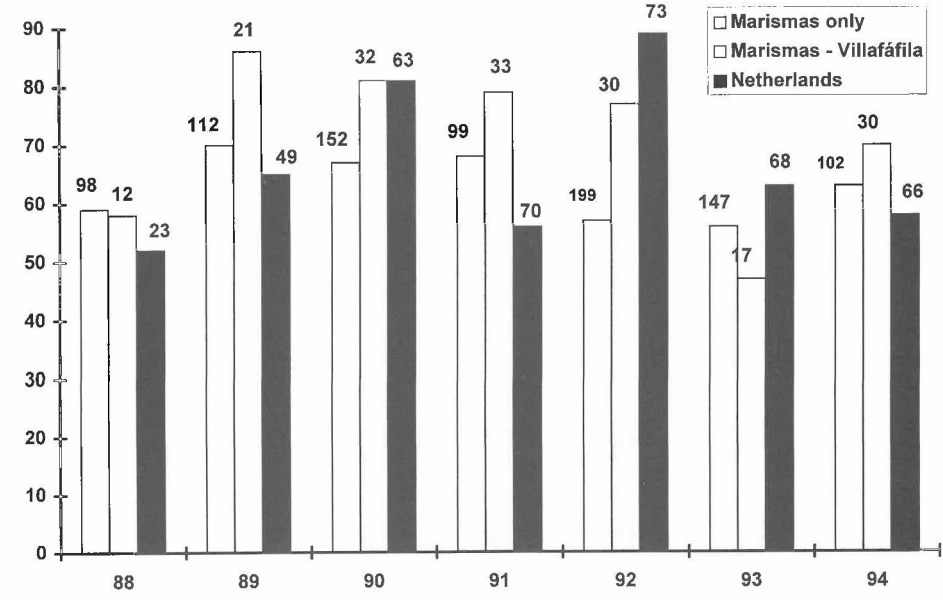


Figure 4. Annual variation in the survival (percentage) to fledging for Greylag goslings in 1988-1994 in relation to the choice of winter quarters of their parents. The geese wintering in the Marismas have been split into two groups, those never seen at Villafáfila in northern Spain, and those that have been seen there (see text). Sample sizes are shown over the bars.

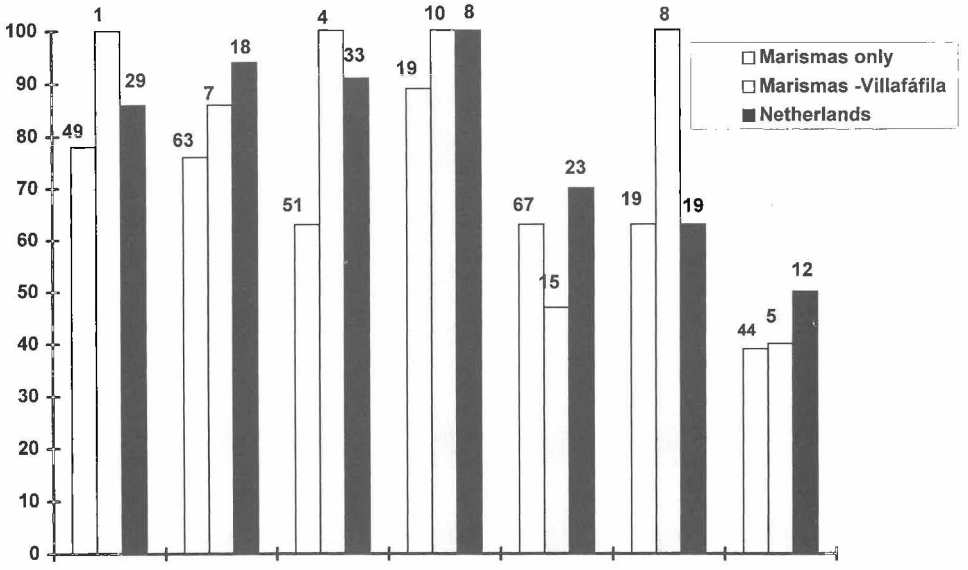


Figure 5. Annual variation in first-year survival (percentage) of young Greylag Geese in relation to the choice of winter quarters of their parents. The geese wintering in the Marismas have been split into two groups, those never seen at Villafáfila in northern Spain, and those that have been seen there (see text). Sample sizes are shown over the bars.

quarters of the parents on the fledging rate of their young was found; 64±1% (n=1,084) fledged of young from parents wintering in the Guadalquivir Marismas compared to 67±2% (n=401) of young from parents wintering in the Dutch Delta (**Figure 4**, Ch^2=1.49, df=1, P>0.10). Precipitation of more than 20 mm during the first days after hatching has a marked effect on survival (Nilsson & Persson 1994). As Spanish-wintering geese arrive back to the breeding area later than Dutch-wintering ones, on average, they might be affected differently by wet periods in spring. By excluding the 1991 season, the only year with such rainy periods, a significant difference in fledging success was found between goslings from parents wintering in the Guadalquivir Marismas and the Dutch Delta respectively (63±1% v 70±2%; Ch^2 =5.53, df=1, P<0.05).

A marked effect of spring migration strategy was found among those wintering in the Guadalquivir Marismas (**Figure 4**). Young of parents seen at Villafáfila, the only spring staging area of any importance between south-western Spain and south-western Holland (Persson 1995), had a significantly higher fledging rate than young of parents never reported from this site (74±3% and 62±2%, respectively; Ch^2=8.66, df=1, P<0.01).

First-year survival

First-year survival varied substantially among years and wintering areas (**Figure 5**). During 1988-89 to 1991-92, average first-year survival was 75% or higher every year, a marked difference being found between those birds wintering in the Guadalquivir Marismas and those wintering in the Dutch Delta, except in 1991-92 when survival was high also for the Spanish-wintering birds. The overall survival (Dutch + Spanish) of the young geese in 1991-92 was significantly higher than in 1990-91 and 1992-93 (Ch^2 =16.0, df =2, P<<0.001).

The survival of young geese over the winters 1992-93 and 1993-94 was lower than in the preceding years, but the difference was not very marked for the Spanish-wintering ones, whereas the difference was marked for those wintering in The Netherlands. For the latter group, the mean survival rate was significantly higher during the first four winters compared to the following three (91±3 % and 63±7 %, respectively; Ch^2=16.5, df=1, P<0.001). The

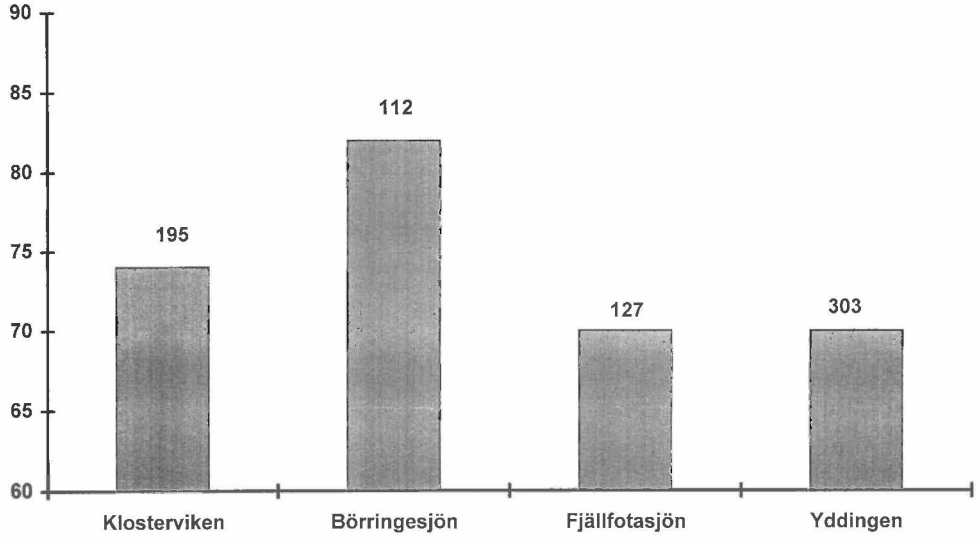


Figure 6. First-year survival (percentage) of young Greylag Geese from different breeding lakes pooled over the years 1984-1994. Sample sizes are shown over the bars.

1994-95 season deviated markedly, first-year survival of geese wintering in Spain being as low as 39%.

Young from parents seen at Villafáfila had an extremely high first-year survival during the whole study period, except during 1992-93 and 1994-95, the two driest winters in Spain during the last decade, the difference being highly significant between wet and dry winters (97±3 % and 45±11 %, respectively; Ch^2=17.6, df=1, P<<0.001).

Geese from Lake Börringesjön showed a significantly higher first-year survival than those from the other three lakes (**Figure 6**, Ch^2=5.75, df=1, P<0.05). In this context, however, it must be noted that in the cohorts 1992-1994, with a low first-year survival, no gosling from Börringesjön was included due to three consecutive years without neck-banding at that lake.

Goslings with a high (both relative and actual) weight at marking have a better chance of survival than lighter young. A clear relation between hatching date and first-year survival was found (**Figure 3**), which can be related to a higher proportion of heavy young among early-hatched goslings than among their later-hatched counterparts (see above). The difference in first-year survival between those above and those below the median relative weight was marked (**Figure 7**), being highly significant for males (70±5% v 41±5%, n=197; Ch^2= 17.4, df=1, P<<0.001) but not for females (65±5% v 53±6 %, N =163; Ch^2=2.56, df=1, P>0.10).

Three-year survival

For the 1989-1992 cohorts, three-year survival was 42±4 % (n=430). There was a pronounced effect of wintering-area on the three-year survival; 57±5% (n=82) of young from parents wintering in The Netherlands survived to the age of three years, compared to only 30±3% (n=200) of those from parents spending the winter in south-western Spain, the difference being highly significant (Ch^2 =18.4, df=1, P<<0.001). These estimates correspond to annual survival rates of 83% and 67% respectively, comparable to the average first-year survival rates found for Greylag Geese using these winter quarters during the last decade, 82±3 %(n=157) and 68±2% (n=416), respectively.

The effect of hatching was apparent even after three years, a higher proportion of early-hatched

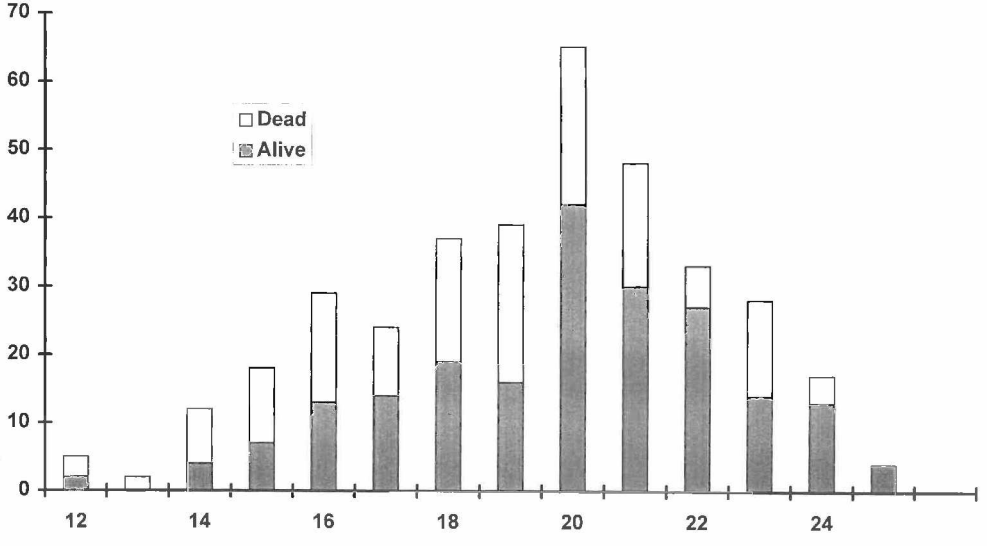


Figure 7. Number of young Greylag Geese surviving or dying during their first year in relation to their relative weight at marking (weight/skull length). Pooled data for the hatching years 1989-1993.

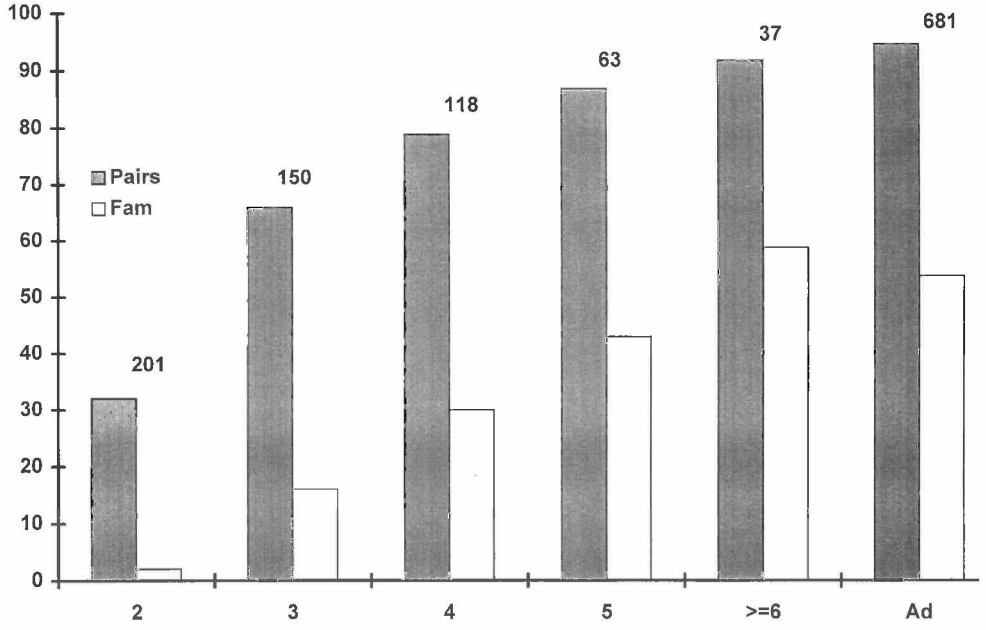


Figure 8. Percentage marked Greylag Geese of different ages seen in pairs and with families. Pooled data for 1989-1994. Sample sizes are shown over the bars.

young survived, the difference between geese hatched during the two periods in April being significant (**Figure 3**, Ch^2=4.46, df=1, P<0.05).

Recruitment to breeding

Few Greylag Geese breed at the age of two years, some more at the age of three, but normally they are older at recruitment (Nilsson & Persson 1994, **Figure 8**). Whereas 54% of all marked adult individuals present in the study area during 1989-1994 were seen with a family, a similar proportion of breeding individuals of those marked as goslings was found only among those aged six years or more.

Age at first breeding differed between lakes. For geese reared at Lake Yddingen, the majority of known-age breeders (sexes combined) recruited at an age of two or three years, whereas the majority of the recruits from the other lakes were four years or older (Ch^2=3.89, df=1, P<0.05). Mean age of recruits was 3.19±0.19 (n=27) for Lake Yddingen v 3.81±0.15 (n=52) for the other lakes taken together (t=2.51, df=77, P<0.05). The mean age at recruitment for Lake Klosterviken (3.84±0.21 (n=31) was also significantly different from that for Lake Yddingen (t=2.25, df=56, P<0.05). Means are probably slightly biased as some older individuals might not yet have been recruited into the breeding population but, given the marking intensity, this applies to all lakes and does not alter the comparisions between lakes, or between wintering areas (see below). The chances of detection did not vary between lakes.

Recruitment was related to the size of the goslings at the time of marking (**Figure 9**). Only two of 35 weighed goslings that later recruited into the local breeding population were lighter than the median relative weight; one of each sex, both just below the respective median. Even among those just over the median, surviving to at least three years of age, only a few were found breeding, whereas the majority of the heaviest goslings were found breeding. Of geese more than three years old, 33% (n=48) of those larger than the median

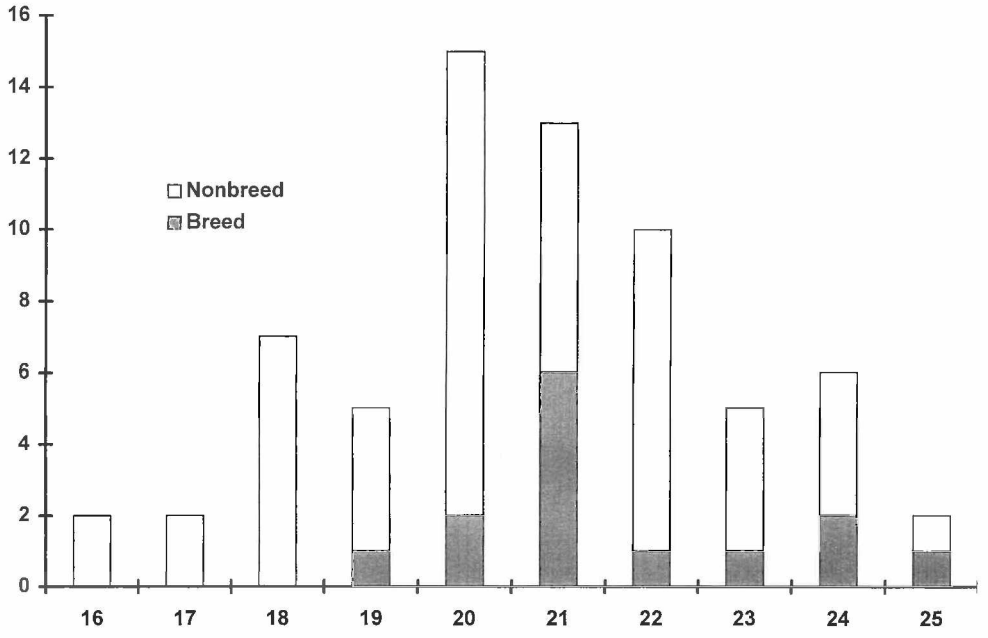


Figure 9. Number of breeding and non-breeding Greylag Geese aged three years in the population in southwest Scania in relation to relative weight at marking (weight/skull length). Data for young marked during 1989-1992.

were found breeding, compared to two of 20 with a relative weight below the median, the difference being significant (Ch^2= 3.95, df=1, P<0.05).

No effect of hatching period on the recruitment to breeding was found for birds that reached the age of three years. Four of 14 birds hatched during the period 11- 20 April were seen with a family compared to seven of 38 for the period 21-30 April (P=0.33, Fisher's exact test).

The majority of goslings that were recruited later into the breeding population came from families larger than the median, due to higher per capita recruitment of young from larger families (**Figure 10**). For newly-hatched young, 61% (n=36) of the future recruits were found in families larger than the median, whereas 71% (n=69) of the recruits with known family size at fledging were from families larger than the median, both differences being highly significant (Ch^2=7.89, df=1, P<0.01 and Ch^2=16.11, df=1, P<0.001, respectively).

Discussion

Pre-fledging survival

Of factors causing losses during the brood-rearing period, two show large variations between seasons, predation and rainfall during the first days after hatch. During the study period we only experienced one period with marked precipitation, resulting in significantly lower survival (Nilsson & Persson 1994). The importance of predation is difficult to measure, but some relevant observations were obtained. In June 1993, a Hooded Crow *Corvus corone* on average killed one gosling per day for a period at Lake Yddingen. Assuming constant predation rate during the period when goslings are vulnerable to predation by Crows, predation could account for about 17% of all young hatched here. However, for a Crow to be able to capture a gosling, it must be separated from its parents. Inexperienced parents have much

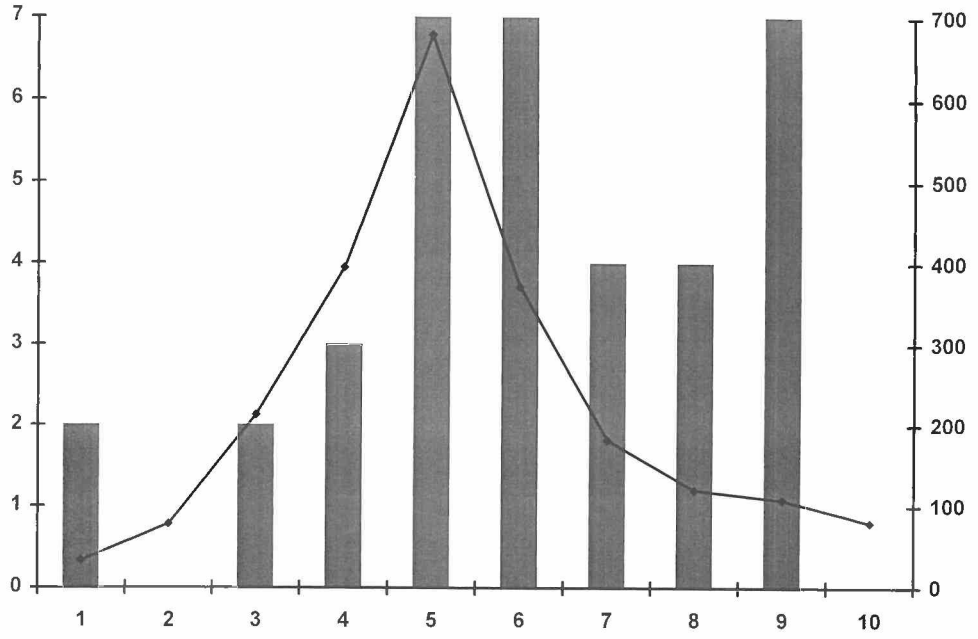
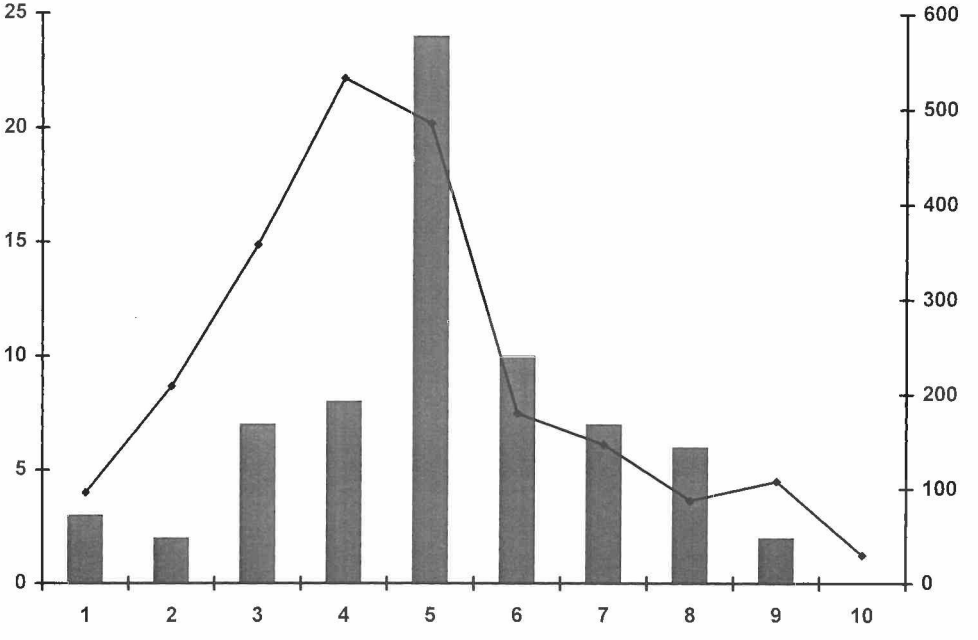


Figure 10. Family sizes of Greylags after hatching and at fledging from which recruits to the breeding population came (bars) compared to the total number of goslings for all families in the different sizes pooled over the years 1987-1994.
A. (above) Family sizes at hatching, B.(below) at fledging.



greater difficulties in defending their young from Crows than older geese (LN *pers obs*), which could account for the low productivity of young parents. During the first years of the study the Red Fox *Vulpes vulpes* was virtually absent from the area due to mange, but foxes were present during the last two years of the study, their presence being a possible explanation for the lower fledging rate of goslings in the those two years.

Even if there were no pronounced between-year differences in fledging rate, the timing of mortality varied markedly between years, as seen by the proportion of neck-banded young disappearing before fledging. One reason for this is that young in bad physical condition survive for longer periods during warm and dry seasons than during cold and wet ones, resulting in an accumulation of deaths at fledging (HP, *pers obs*). In most goose studies, survival until marking, or until an equivalent point one to two weeks before fledging, is used as a measure of fledging rate (Cooke & Rockwell 1988, Larsson & Forslund 1994). This might be a useful measure provided that survival between marking and fledging does not differ among years or groups, eg between young of experienced and inexperienced parents. However, bearing the marked variations in our study in mind, fledging rates based on data obtained before fledging should be treated with great caution.

In arctic-nesting geese, early-hatched goslings grow faster and are heavier at fledging than late-hatched ones (Sedinger & Flint 1991, Lindholm *et al.* 1994). Moreover, goslings that are lighter than the mean are more likely to die than heavier ones at any given age (Lindholm *et al.* 1994, Sedinger *et al.* 1995). The same applies to Scanian-breeding Greylag Geese. Access to high- quality food during brood-rearing is apparently the main factor explaining within-year differences in fledging rate. This factor expresses itself in two ways. First early-hatched goslings have a higher fledging rate than their later-hatched counterparts, which can be related to the length of time the young have access to high-quality food before the vegetation gets too coarse. Secondly, the fledging rate is related to the amount of grazed pasture or similar areas (a regularly cut and fertilized golf course) that the families have access to during the brood-rearing period. The lowest survival rate was found at the lake lacking such pastures (Lake Fjällfotasjön), whereas the highest rates were found at lakes with a rich supply of grazed pastures.

Nilsson & Persson (1996) demonstrated a substantial difference in breeding output between Scanian Greylag Geese wintering in the Dutch Delta and the Guadalquivir Marismas in Spain. Consequently, as there were only slight differences in fledging rate related to selection of winter quarters by parents, this factor must act on stages of the breeding cycle before hatching. Mechanisms could include (1) females in poor condition failing to breed or (2) females abandoning their nests. For arctic-breeding geese it is well-known that females are dependent on body reserves acquired in the winter and spring areas for breeding (Ankney & MacInnes 1978, Raveling 1979a, Alisauskas & Ankney 1992). Our data are consistent with the hypothesis that Scanian-breeding Greylag Geese also rely on reserves for successful reproduction.

Post-fledging survival

The observed differences in post-fledging mortality between Greylag Geese using different winter quarters can be related to unequal levels of hunting exploitation, those spending the winter in south-western Spain being exposed to a much higher shooting pressure, on average, than geese wintering in The Netherlands (Nilsson & Persson 1996). Moreover, the conditions in the south-west Spanish winter quarter differ markedly between years due to variations in the precipitation affecting the feeding areas (Nilsson & Persson 1996), which in turn will affect the local distribution of the geese in the area and their vulnerability to hunters (Persson 1996b). By moving to a refuge area, geese wintering in south-western Spain increase their likelihood of survival considerably. Currently, with the exception of Villafáfila in north-central Spain, such areas are hardly available.

The cause of the low survival of Dutch

wintering young during the last three winters must be sought in the wintering area; young wintering in Spain have maintained an average first-year survival rate of about 6% below the annual survival rate of adults wintering in the same area (Persson 1996b), whereas there is an increasing gap in survival rate between young and adults spending the winter in The Netherlands (Nilsson & Persson, *unpubl.*). The numbers wintering in the Dutch Delta have increased dramatically in recent years and the drop in survival of the young Scanian geese wintering here might be a density effect. Local studies in The Netherlands are lacking but urgently needed.

Greylag Geese learn staging and wintering areas from their parents during their first year of life as do other species of geese. After break-up of the families most geese live a mobile life (Nilsson & Persson *unpubl.*), exploring alternative areas, and so enhance their chances of selecting the most appropriate moulting, staging and wintering areas. At the same time, however, they run an increased risk of being shot, which gives a satisfactory explanation for the lower survival rates of subadults compared with adults (Nilsson & Persson 1993).

Recruitment into the breeding population

Recruitment into the breeding population takes place successively from the age of two years in the Greylag Goose (this study), as in other goose species (Raveling 1981, Cooke & Rockwell 1988, Warren *et al.* 1992). Most surviving Greylag Geese have started to breed at four years of age, but some are recruited at a much more advanced age, if ever.

In the Lesser Snow Goose *Anser caerulescens caerulescens*, early-hatched goslings showed higher recruitment rates than later-hatched counterparts, indicating a directional selection for early breeding (Cooke *et al.* 1984). A similar pattern was found among the Scanian Greylags. As early-hatching females had the highest fledging success among Greylag Geese, it seems logical that early-hatched goslings have a higher recruitment rate that later-hatched ones. In the Lesser Snow Goose, on the other hand, females whose clutches hatched in the middle (peak) period had the highest effective brood size (Findley & Cooke 1982). Early-hatching Lesser Snow Goose females are recruited at a higher rate despite slightly lower pre-fledging survival, which results from differences in survival rates during the post-fledging (post-banding) period. Arctic-nesting geese are generally very time-restricted, frequently resulting in goslings not having sufficient time for fattening before autumn migration. As early-hatched goslings are heavier, on average, than later-hatched ones at any time during the brood-rearing period they are better prepared to survive the autumn migration (*cf.* Owen & Black 1989, Sedinger *et al.* 1995).

The factor having the greatest influence on recruitment age is the brood-rearing conditions at the lakes where the recruits are hatched. Lake Yddingen was rated highest (available grassland area per family) in a comparision of the brood-rearing areas at the study lakes and, accordingly, Lake Yddingen had the lowest recruitment age of the lakes studied. This result was not unexpected, but in other aspects Lake Yddingen did not deviate markedly from other lakes. Neither the proportion of large young nor the fledging rate was higher at Lake Yddingen compared with the other lakes, except that the fledging rate for Lake Fjällfotasjön was significantly lower. Moreover, Lake Yddingen had the lowest proportion of Dutch-wintering breeders; in fact, this proportion was significantly lower than at Lake Klosterviken ($Ch^2=5.51$, $df=1$, $P<0.05$). However, when the food quality deteriorates at the other lakes during the summer, it is maintained at a high level at Lake Yddingen due to the golf course. The effect of this deterioration is seen in the earlier mentioned weight changes in June; an increase at Yddingen but a decrease at Klosterviken. Weighing the goslings at fledging, instead of three weeks earlier, should give us a completely different picture.

Apparently, Greylag Geese suffering from early food set-backs have difficulties in recovering even when they have at least three months before the initiation of autumn migration. This effect of the food conditions at

an early age still remains at recruitment two or three years later. This is further underlined by the fact that almost no individuals below the median relative weight at marking was later found to be breeding. The heaviest individuals also had the highest first-year survival. Similar relations between weight, survival and recruitment were reported for the Black Brant Goose *Branta bernicla nigricans* by Sedinger *et al.* (1995).

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