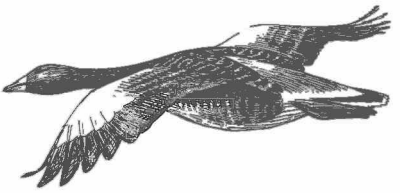
Factors affecting the breeding performance of a marked Greylag Goose *Anser anser* population in south Sweden



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The variation in breeding performance of Greylag Geese marked with individual neck-collars in an increasing population at four lakes in southwest Scania was studied during 1985-1992. During this period, the population increased from 93 to about 425 pairs. By neck-banding, the migration routes, staging areas and wintering areas can be established for a high proportion of the breeding birds. Overall, 65% of experienced breeders produced a brood of young. The mean clutch size was 5.36 eggs, the mean brood size of small young 4.60, and at fledging 3.72. Early arriving pairs were more successful than late pairs. Dutch wintering birds were more successful than Spanish wintering ones. Significant differences in brood size were found between lakes, and these differences were not related to arrival pattern or wintering area. Eighty-nine per cent of the broods produced at least one fledged young. Survival to fledging was significantly lower at lakes with poor feeding areas. Geese marked as young were recruited to the breeding population at ages from two to six years, pairs including inexperienced birds having a poor result.

Keywords: Freshwater Lake, Reedbed, Breeding Ecology, Population Dynamics, Ringing, Greylag Goose

The Greylag Goose *Anser anser* has a wide breeding distribution, from Iceland in the west to the eastern coast of Asia. As most of the breeding range is situated well south of the Arctic Circle, different factors might affect this goose in comparison with arctic breeding ones.

Local studies on the breeding ecology of the Greylag Goose have been undertaken on a number of localities, mainly in central Europe (cf. Hudec & Rooth 1970, Hudex & Kux 1970, Kux & Hudec 1970, Hauff 1982, Litzbarski 1982, Witkowski 1983, Knief 1991) but also in Scotland (Newton & Kerbes 1974, Paterson *et al.* 1990). These studies however, were not based on individually marked birds.

The breeding population of Greylag Geese in Sweden, as in a number of other countries, has increased markedly in recent years (Fog *et al.* 1984, Madsen 1991). As a result of this increase, large summer and autumn concentrations were established in different places leading to management discussions. In the Nordic countries, a Greylag Goose Project was therefore started in 1984 by the Nordic Council for Wildlife Research (NKV) with the main aim of establishing detailed migration and movement patterns. The project included marking Greylag Geese with individually coded neck-collars in different areas (Andersson *et al.* in prep.).

Neck-banding proved to be a very successful method of obtaining information about staging, wintering and moulting areas, and the movements between these areas of Greylag Geese from known breeding grounds. Eighty-seven per cent of all marked adults and 60% of all marked young were actually seen on staging and wintering areas in the Netherlands, France and Spain. Thus, we had an opportunity to follow the geese throughout the annual cycle. The original study in southwest Scania was extended to include various aspects of breeding ecology and population dynamics. In this paper, we present data on breeding performance on an individual basis for the population in southwest Scania. Specifically, we analyze the influence of key factors such as breeeding area, choice of wintering area, timing of breeding, weather, age and former breeding experience on the annual production of young and on the survival of those young until fledging.

Study Area

The study was undertaken in a lake area in soutwest Scania, southernmost Sweden

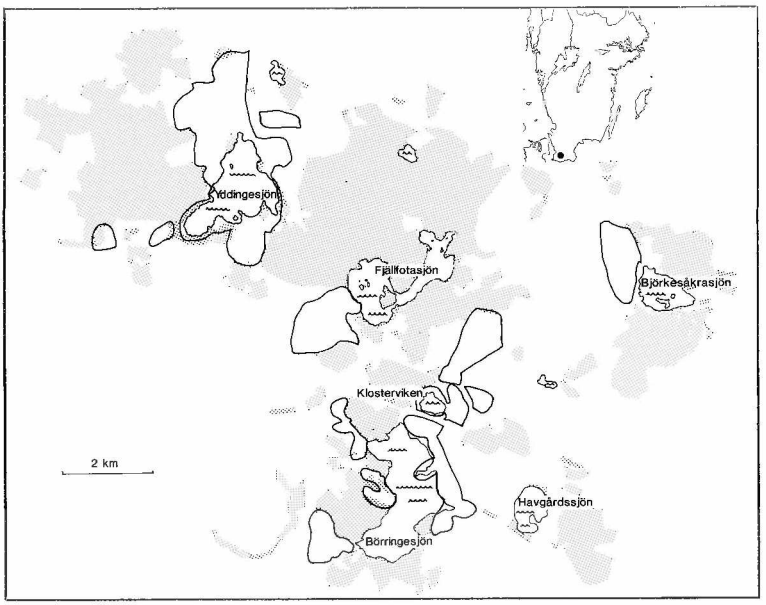

Figure 1. Map of the study area, showing the extent of feeding areas around the different lakes used by Greylag pairs in spring (heavy lines). Woodland areas hatched. The general position in south Sweden is shown on the inserted map.

(**Figure 1**). During wing-moult, families have been caught annually since 1984 in the four 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. For further details of crops grown etc. see Nilsson & Persson (1992).

All lakes are eutrophic with a rich bloom of phytoplankton and fairly extensive reed beds (**Table 1**). Lakes Yddingen and Börringesjön have extensive areas of grazed pastures close to the shore. At Lake Yddingen, a golf course with highly fertilized grass is also available for the feeding geese. In Lake Klosterviken, one fertilized and grazed shore meadow offers, good feeding conditions for the goslings during the early part of the growing period before the grass becomes too coarse. Good feeding areas for the young, with short grass, were limited at Lake Fjällfotasjön. Lakes Fjällfotasjön and Yddingen offer islands for nesting geese in addition to reedbeds.

Table 1. Habitat data for the four study lakes.

Lake	Area (ha)	Shore length (km)	Reed area (ha)	Shore meadows (ha)	Islands n
Klosterviken	16	1.6	11	5.5	0
Börringesjön	265	10.2	20	28.0	0
Fjällfotasjön	171	10.7	8	0.5	8
Yddingen	190	8.9	10	*7.0	7

* 12 ha of golf course close to the lake in addition to the natural shore meadows.

Methods

During 1984-1991, 235 adult and 698 young Greylag Geese were neck-banded in the study area. Moreover, 23 adults and 67 young were neck-banded at Lake Snogeholmssjön c. 30 km to the east, during 1985-1987.

Regular checks for the occurrence of neck-banded individuals were undertaken from the arrival in spring to the departure of the geese in late autumn, the area (including Lake Björkesåkrasjön, see **Figure 1**) being visited several times a week from the arrival of the geese in spring until the end of May; thereafter, almost daily visits were made in the area until all young were fledged and parents could fly again. In late summer and autumn, checks for neck-banded birds were extended to neighbouring lakes and, particularly, to the Foteviken area at the coast of soutwest Scania, an important staging area for the geese at this time of the year (Nilsson & Persson 1992). During the post-breeding period, checks were made approximately twice a week until the last geese migrated southwards in late October to mid November.

The number of pairs counted just prior to the onset of incubation was used as an estimate of the size of the breeding population. Repeated counts on the lakes and surrounding feeding grounds were undertaken. In Lakes Fjällfotasjön and Yddingen, where a large proportion of the geese breeds on islands, the islands and accessible reedbeds were searched for nests once or twice annually.

Most broods in Lakes Yddingen and Klosterviken occur concentrated in certain areas that were searched several times a week from the time the first broods were seen in order to establish the total production of young. In Lake Börringesjön in recent years, and in Lake Fjällfotasjön, the broods were dispersed on too many irregular sites to make this possible, but the accessible areas were covered with the same time schedule with an aim of establishing the breeding results of all marked pairs.

Outside Scania, observations of neck-banded Greylag Geese were obtained from a network of observers organized by the Nordic Greylag Goose Project (Andersson *et al.* in prep.). The main staging and wintering areas of the population, especially in The Netherlands and Spain (field work by HP), were searched intensively for marked Greylag Geese, thus providing information on staging and wintering areas for a large proportion of the population.

The majority of the neck-banded breeding birds were caught as adults with young. Thus, for the marking year, we have only data on the number of fledglings produced. Moreover, most individuals included in the dataset have at least one season of previous breeding experience. In the last years of the study, a number of geese marked as young were recruited into the breeding segment of the population. They are treated separately in the analyses.

During the first years of the study, relatively few neck-banded Greylag were available for observation. The number of marked pairs (i.e. at least one individual of the pair neck-banded) increased from 14 (8% of the population) in 1986 to 117 (27%) in 1992, excluding newly marked pairs. Thus many analyses were restricted to the latter part of the period when sample sizes were adequate. Young up to the age of about one week are classified as small in the analyses. Pairs in which the marked individual(s) bred for the first time were classified as new pairs. Due to the intensive observations it is not probable that any marked breeding geese were entirely overlooked. In a few cases, a marked pair with a brood was not seen until the young were about two weeks old. This and similar cases lead to different sample sizes between analyses in some cases. In analyzing the effect of breeding areas, we refer to the lake where the parents nested; this in almost all cases was the rearing lake.

Results

Population size

Breeding Greylag Geese were first noticed in the study area during the late 1960s, when broods were observed, but details on the size of the breeding population are lacking before 1979 when 29 breeding pairs were established. No introductions have been made in the area. Another survey in 1982 counted 25 breeding pairs (Karlsson *et al.* 1982), but these early estimates were probably a bit too low as observations were made relatively late in the spring and

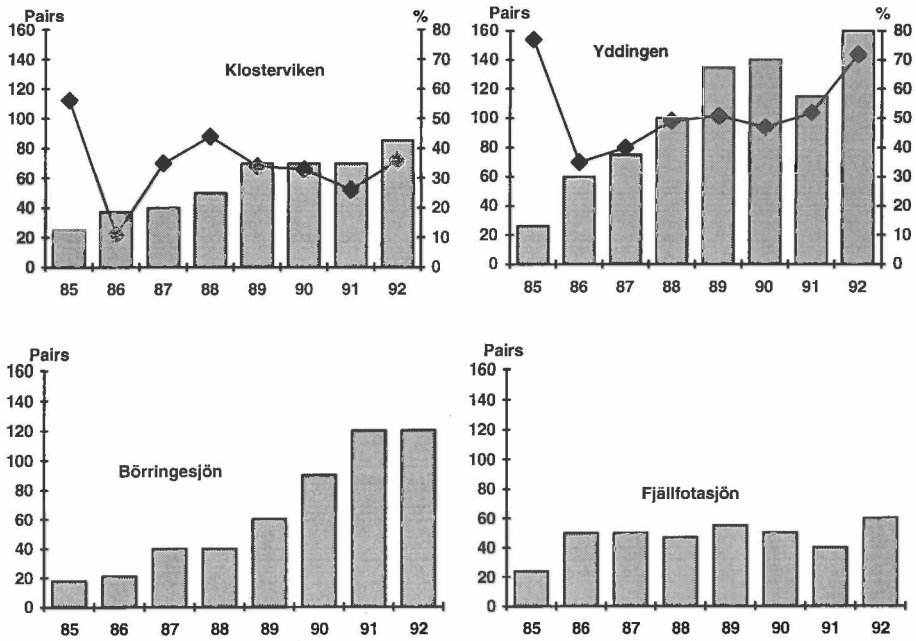

Figure 2. Number of Greylag Goose pairs (bars) at the different lakes in 1985-1992. For Klosterviken and Yddingen, the number of broods as a percentage of the number of pairs is also shown (line graphs).

some pairs had probably started to incubate. During 1985-1990, the population in the study area was monitored closely and increased explosively from 93 to 425 pairs (**Figure 2**). The increase has not been the same at all lakes (**Figure 2**). The number of pairs using Lake Fjällfotasjön increased between 1985 and 1986 but has been steady since then. Lake Klosterviken showed an increase to 1989 followed by a steady level, whereas the other lakes increased over the whole period with the exception of the drop at Yddingen in 1991.

Arrival and timing of breeding

First observations of marked pairs in the study area varied between 15 March for the extremely cold winter and late spring of 1987 to 6 February in the mild winter and spring of 1990 (**Table 2**). In 1991, some marked birds were seen at Foteviken, on the coast of southwest Scania, on 13 January, but they did not move into the breeding area until mid-February. These birds had been seen in The Netherlands during the previous winter.

Table 2. Arrival of marked breeding Greylag pairs to the nesting area, and first observations of families 1987 -1992.

	Earliest Arrival	First observation of broods			Days between arrival and observation of small young
		Mean±SE	Range	Mean±SE	Mean±SE
1987	15 Mar	31 Mar±1.4 (12)	6 May - 24 May	14 May ± 2.2 (8)	52 ± 3.5 (8)
1988	20 Feb	17 Mar±1.8 (39)	17 Apr - 20 May	6 May ± 1.5 (30)	53 ± 2.3 (30)
1989	13 Feb	6 Mar±1.7 (69)	13 Apr - 20 May	28 Apr ± 1.7 (42)	60 ± 1.9 (42)
1990	6 Feb	4 Mar±2.0 (76)	17 Apr - 15 May	26 Apr ± 1.0 (51)	58 ± 1.5 (51)
1991	1 Feb	14 Mar±2.1 (74)	22 Apr - 25 May	2 May ± 1.2 (45)	57 ± 2.3 (45)
1992	27 Jan	22 Feb±1.4 (78)	20 Apr - 24 May	29 Apr ± 0.8 (80)	65 ± 1.5 (78)

In 1989, the first observation of a brood was made as early as 30 March. The next brood that year was, however, not seen until 13 April. In 1990 and 1991, first broods were seen on 2 April and 15 April, respectively. All these observations were made at Lake Yddingen. First observations of broods of pairs with at least one marked parent were generally a few days later. Mean dates of arrival and first observations of broods of marked pairs differed significantly between years (**Table 2**, Ch^2=27.8, df=4, P<0.001 and Ch^2=9.9, df=4, P<0.05, respectively). No significant differences were noted in arrival (adjusted in relation to the annual mean) between lakes (Analysis of Variance, F=2.48, df=3, P=0.06).

The annual mean intervals between first observations in the breeding area and first observations of broods for marked pairs were 52 to 65 days (**Table 2**). The longest intervals were found in the mildest years with an earlier arrival of the geese. Differences between annual means were not significant. On the individual level, the number of days between first observation in the area and first observation of a brood was significantly negatively correlated to the time of first observation adjusted to the annual mean arrival (r=-0.67, P<0.001, n=227) and to the actual arrival date (r= -0.79, P<0.001). The latest pairs showed up with broods 40 days after their arrival. With an incubation period of 27-28 days (Owen 1980), and allowing five to seven days for egg-laying, breeding must have started about six (5-8) days after arrival in the breeding area.

Greylag Goose pairs wintering in The Netherlands (Delta area) returned to the breeding area earlier than those wintering in Spain. First observations for pairs win-

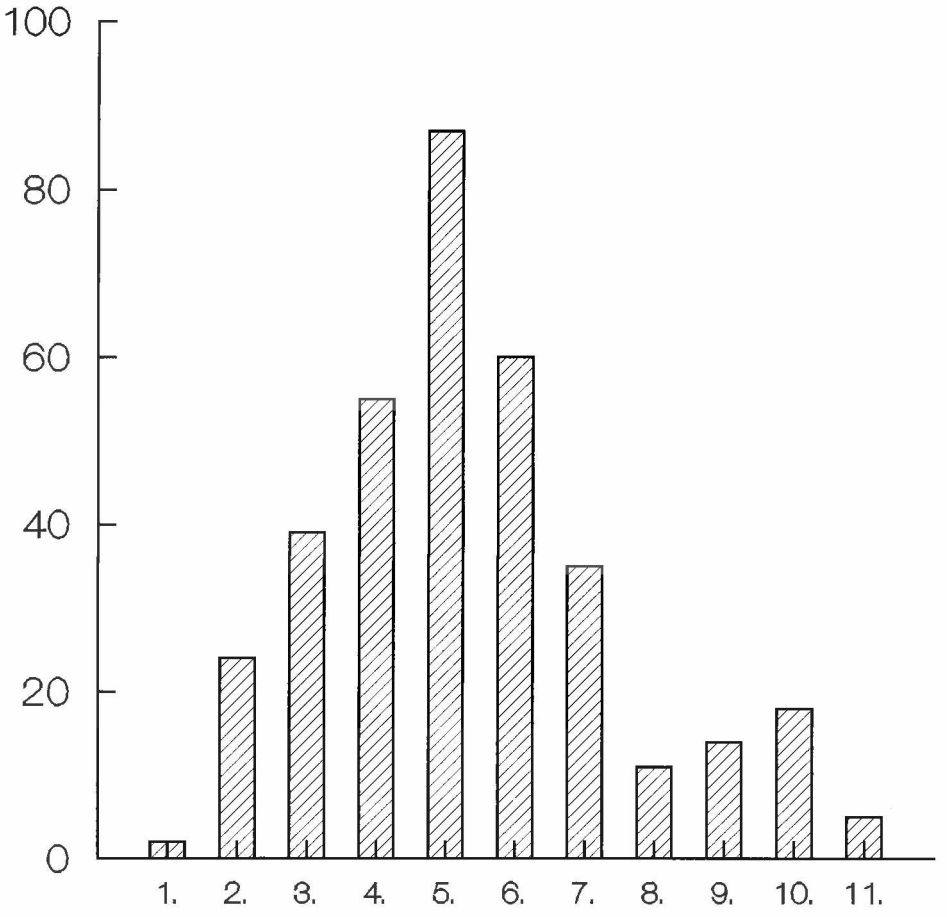

Figure 3. Frequency distribution for clutches of Greylag Geese in the study area, 1985-1992.

Table 3. Mean clutch sizes (with standard error, number of clutches in brackets) of Greylags at Lakes Fjällfotasjön and Yddingen 1985 - 1992. Nests with more than 11 eggs have been excluded.

	Fjällfotasjön	Yddingen	Total
1985	5.36±0.56 (11)	3.67±0.67 (6)	4.76±0.47 (17)
1986	5.73±0.57 (15)	6.09±0.79 (11)	5.88±0.46 (26)
1987	5.86±0.51 (29)	5.04±0.44 (27)	5.46±0.34 (56)
1988	5.16±0.48 (19)	5.05±0.44 (19)	5.10±0.32 (38)
1989	5.15±0.29 (45)	5.46±0.38 (24)	5.26±0.23 (69)
1990	5.41±0.32 (44)	5.15±0.34 (20)	5.33±0.24 (64)
1991	5.42±0.35 (38)	5.53±0.49 (17)	5.46±0.28 (55)
1992	5.52±0.45 (25)	5.52±0.45 (25)	
Total	5.43±0.14(226)	5.15±0.18(124)	5.36±0.11(350)

tering in the Dutch Delta were made 4.01±1.72 (n=80) days before the adjusted mean arrival for all pairs, whereas first observations of pairs wintering in Spain were made 1.72±0.89 (n=257) after, the difference being significant (t=3.08, P=0.002).

Frequency of breeding

As many of the Greylag Geese in our study area breed in inaccessible reedbeds, it was not possible to establish the proportion of the pairs present in the study area that actually started egg-laying. In Lake Fjällfotasjön, where the geese breed on islands, we recorded an almost complete match between the number of pairs counted just before the onset of incubation and the number of nests found.

At Lakes Klosterviken and Yddingen, where broods gather in places where they can easily be checked, 33 and 55% respectively of the pairs were later seen with broods (**Figure 2**). A relatively large variation was found between years, but generally more pairs produced a brood at Lake Yddingen than at Lake Klosterviken.

Clutch size

Normal clutch sizes were between two and 11 eggs, with the most frequent clutch size being five (**Figure 3**), but not all clutches were laid by one female, as birds laying eggs in other females' nests were noted. The frequency of this behaviour is unknown (cf. Witkowski 1983). Moreover, some unincubated dump nests, containing up to 17 eggs, were found as well as the extreme exception, an incubated clutch of 20 eggs.

The overall mean clutch size was 5.36 with some variation between years and lakes (**Table 3**), but the differences were not significant (Analysis of Variance, F=0.67, df=13, P=0.79).

Brood production

Seventy-eight per cent of 198 marked pairs arriving early (i.e. before the median arrival date in each year) were seen with a brood, compared to 58% of 133 arriving late, the difference being highly significant (Ch^2=15.77, df=1, P<0.001). Similarly, 63% of 210 pairs arriving early produced at least one fledged young compared to 43% of 152 late pairs, the difference being highly significant (Ch^2=13.4, df=1, P<0.001).

Of pairs seen in the Dutch Delta the preceeding winter, 81% of 48 were seen with a brood of small young compared to 64% of 112 wintering in Spain (difference significant, Ch^2=4.55, df=1, P=0.033). Of 52 Dutch wintering pairs, 67% produced at least one fledged young compared to 50% of 121 pairs wintering in Spain, the difference being significant (Ch^2=4.20, df=1, P=0.04).

Pairs breeding successfully in one year were more likely than unsuccessful pairs to be successful, in a following year. Of 143 pairs producing a brood in year t-1, 75% were seen with a brood in year t compared to 58% of 43 pairs seen without a brood in year t-1 (difference significant, Ch^2=4.47, df=1, P=0.03). The same relationship holds for fledged young; of the pairs producing fledged young in year t-1, 66% (of 203) produced fledged young also in year t compared to 53% (of 112) of those that did not produce any fledged young in year t-1 (difference significant, Ch^2=5.41, df=1, P=0.020).

About 35% of two-year-olds appeared in pairs in the study area but less than 10% of

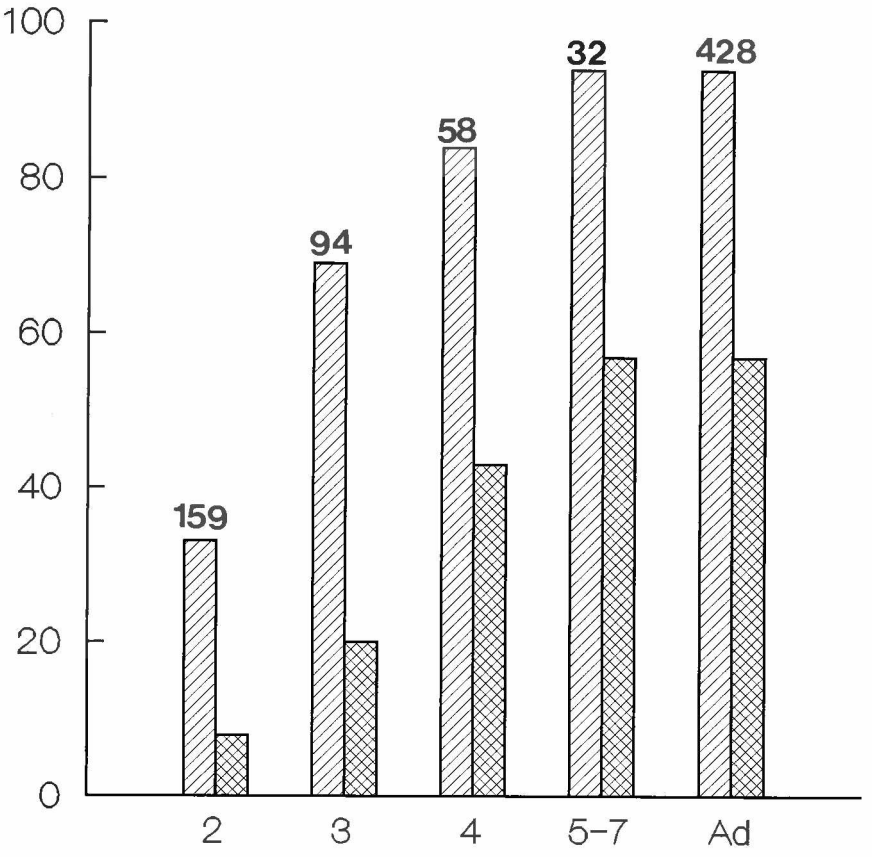

Figure 4. Percentage of marked Greylag Geese of different ages seen paired (hatched) or with a family (cross-hatched) in the study area during spring. Adults = birds marked as breeders in a previous year. Accumulated number of individuals shown for each age-group.

pairs including at least one two-year-old goose produced a brood. Pairs in which the marked individual(s) were three and four years old were also less successful than pairs where the marked individual was marked as an adult (**Figure 4**).

Brood size

The number of small young in broods with at least one marked parent varied between one and 11 (**Figure 5**), with a mean of 4.74 for pairs where the marked bird had previous breeding experience. During 1988-1992, the overall mean size for all broods of small young with one or both parents marked was 4.60±0.13 young (n=239) compared to 4.44±0.09 (n=420) for broods with unmarked parents (difference not significant, t=1.02, P=0.31).

The mean number of small young in the broods of marked pairs showed significant variation between lakes but not between years for 1989-1992, when a sufficient number of marked pairs were available in all lakes (Two-way Analysis of Variance, F=4.40,df=3, P=0.005, F=1.02, df=3, P=0.38, Interaction F=0.93, df=9, P=0.50; Table 4, Fig. 6,7). Lake Klosterviken showed significantly lower brood sizes than Lakes Yddingen (P=0.006) and Fjällfotasjön (P=0.04).

Pairs arriving early had generally larger broods than pairs arriving later (**Table 5**). The difference between early and late pairs in the number of small young produced was, however, not significant (t=1.69,

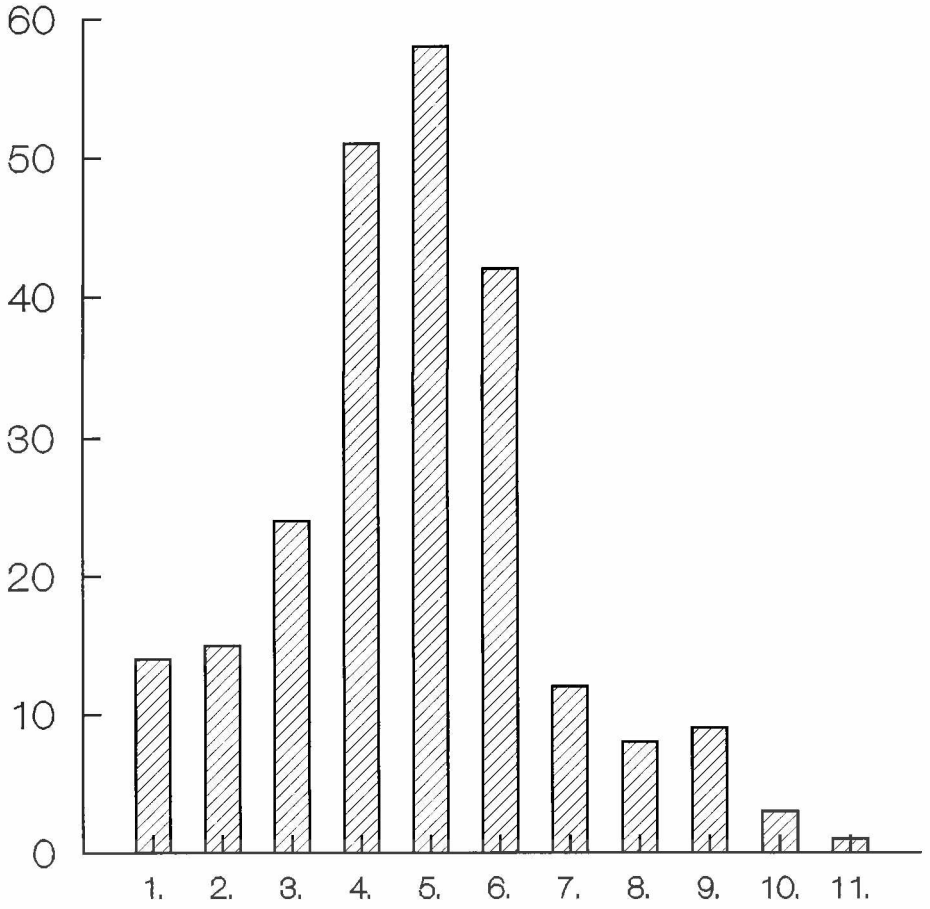

Figure 5A. Frequency distribution of brood sizes for marked Greylag families with small young, 1985-1992.

P=0.09). A significant negative correlation was found between the arrival date (adjusted in relation to the mean arrival of the season) and the number of small young (r= -0.26, n=318, P<0.001), but it explained only a small proportion of the total variation in breeding performance.

Comparing pairs wintering in The Netherlands and in Spain, there were no significant differences in brood size of small (3.68±0.35 and 3.17±0.27, respectively, t=0.27, n.s.) or fledged young (2.42±0.33 and 2.11±0.32, respectively, t=0.37,n.s.).

Age affected brood size, and pairs with at least one bird that was two or three years old had a significantly lower production of small young than older pairs, whereas the production of small young for pairs with the marked individual four or five years old was the same as for those marked as breeding birds (**Figure 8**). It may be noted, however, that we normally only knew the age of one of the birds in the pair but, even so, an age effect was found.

Production of fledged young

During 1986-1992, 235 breeding attempts could be followed from hatching until fledging. Of these, 89% led to one or more fledged young, the variation between years being small (**Table 6**). In these years, 69% of the small young seen in families with marked parents were actually fledged, annual variation being small here too, from 58 to 80% fledged, differences between years being nonsignificant.

Broods from Lake Fjällfotasjön had a sig-

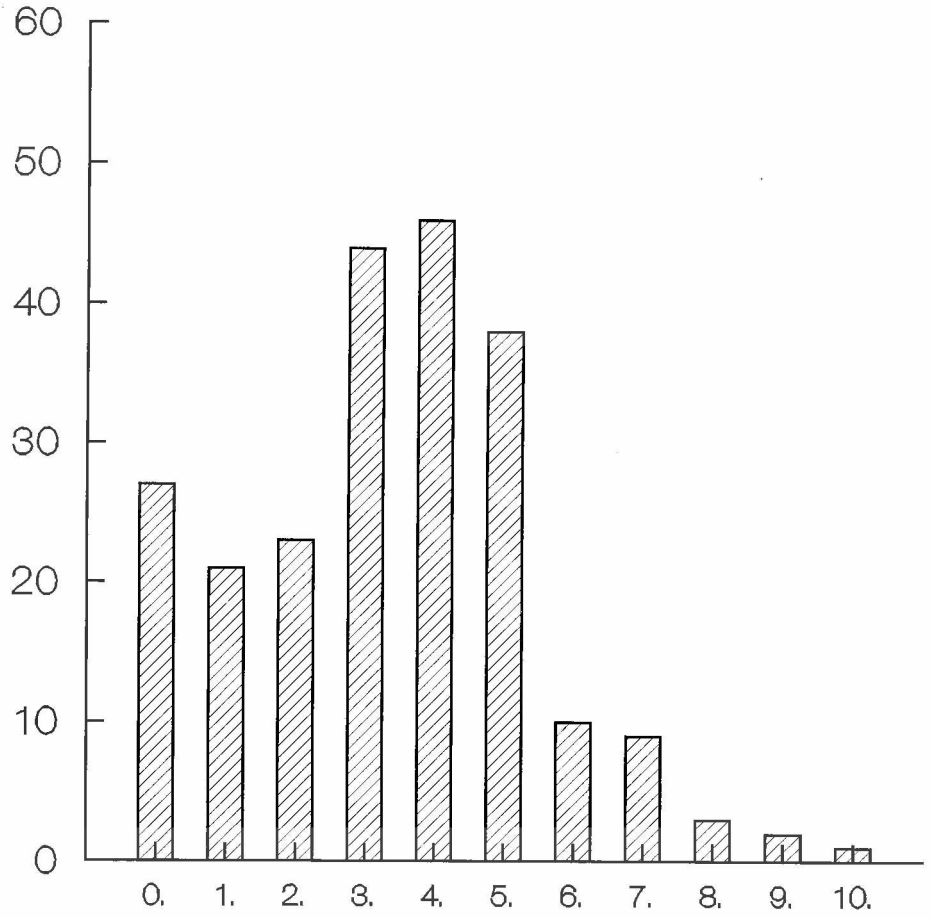

Figure 5B. Frequency distribution of brood sizes for marked Greylag families with newly fledged young, 1985-1992.

nificantly lower survival rate of young from hatching to fledging than broods from the other lakes (**Figure 7**, (Ch^2=29.14, df=3, P<0.001). Differences between the other lakes were only slight. Some pairs moved their brood to another lake for rearing, but this had only a negligible effect on the comparisions between lakes. Among marked broods that could be intensively monitored during the entire rearing period, none was moved from Lake Börringesjön (n=50) and Lake Yddingen (n=74) to another lake for rearing. Nine of 72 broods (12%) moved from Klosterviken to Börringesjön, the two lakes being connected by a short canal. Three of 24 (12%) broods from Fjällfotasjön moved to another rearing lake: two to Lake Yddingen and one to Lake Björkesåkrasjön, envolving an overland journey of 2 km and 5 km, respectively.

As found above, a higher percentage of early than of late arriving pairs produced a brood. Survival to fledging of young hatched by early and late arriving pairs was also significantly different, being 66% (of 693) for early pairs and 57% (of 296) for late pairs (Ch^2=8.98, df=1, P<0.005). At Lake Klosterviken, several newly recruited pairs produced a brood of small young in 1992. Only 20% of 20 young of these new pairs fledged compared to 73% of 77 young of experienced parents (Ch^2=18.7, df=1, P<0.001, **Table 6**). At the other lakes the survival to fledging for young of "new" parents was similar to that of experienced parents.

Young in small broods (1-2 small goslings) showed a significantly lower survival

Table 4. Mean number (with standard error) of small and fledged Greylag young in broods with marked parents (seen with small young) per lake and year, 1985 - 1992. Number of pairs checked is given in parentheses. Only pairs where the marked bird had earlier breeding experience are included.

	Small	Fledged
Yddingen		
1987	5.67±1.14 (6)	4.50±1.18 (6)
1988	5.08±0.55 (13)	3.31±0.71 (13)
1989	5.54±0.39 (11)	4.67±0.33 (9)
1990	4.93±0.22 (14)	3.50±0.45 (12)
1991	5.50±0.60 (10)	4.20±0.47 (10)
1992	5.04±0.36 (21)	3.95±0.48 (20)
TOTAL	5.21±0.19 (75)	3.93±0.24 (70)
Fjällfotasjön		
1987	4.00 (1)	3.00 (1)
1988	4.00 (3)	2.33±1.20 (3)
1989	4.17±0.70 (6)	2.00±0.68 (6)
1990	5.33±0.73 (9)	3.89±0.48 (9)
1991	5.60±0.98 (5)	2.75±1.70 (4)
1992	5.08±0.80 (12)	2.40±0.60 (10)
TOTAL	4.94±0.37 (36)	2.79±0.34 (33)
Klosterviken		
1987	5.50±0.50 (2)	4.50±0.50 (2)
1988	5.11±0.75 (9)	2.67±0.58 (9)
1989	4.38±0.68 (13)	3.15±0.55 (13)
1990	4.75±0.60 (12)	3.75±0.58 (12)
1991	4.00±0.42 (14)	2.71±0.41 (14)
1992	3.95±0.39 (19)	2.95±0.47 (19)
TOTAL	4.38±0.23 (69)	3.09±0.22 (69)
Börringesjön		
1988	7.00 (1)	5.00 (1)
1989	3.25±0.37 (8)	2.25±0.59 (8)
1990	5.17±0.65 (12)	4.27±0.70 (11)
1991	4.43±0.46 (14)	3.08±0.66 (13)
1992	4.20±0.54 (15)	2.58±0.70 (12)
TOTAL	4.40±0.28 (50)	3.13±0.34 (45)
OVERALL TOTAL	4.60±0.12 (230)	3.14±0.13 (217)

to fledging than young in larger broods (3-9 small goslings): 53% (n=64) and 73% (n=1158) of the young fledging (Ch^2=10.73, df=1, P<0.001). This is probably related to the age of the parents (see above).

In some years, the weather affected the survival of young to fledging. The spring of 1991 was the wettest during the immediately post-hatching period (from the appearence of the first brood until five days after the appearence of the last brood), with a total precipitation of 82 mm compared to between 20 and 35 in other years. In 1991, 79% of 53 small goslings

Table 5. Mean brood sizes (with standard error, number of broods in parentheses), for small and fledged young Greylag produced by early (i.e.arriving before the mean arrival date of breeding pairs) and late pairs in 1988 - 1992. Only pairs seen with small young are included.

	Small young		Fledged young	
	Early	Late	Early	Late
1988	5.23±0.57 (13)	4.25±0.43 (12)	3.15±0.58 (13)	2.08±0.57 (12)
1989	4.12±0.35 (32)	4.75±0.48 (4)	3.21±0.37 (29)	2.25±1.32 (4)
1990	5.10±0.37 (30)	4.46±0.18 (13)	3.89±0.41 (28)	3.08±0.43 (12)
1991	4.48±0.34 (25)	3.86±0.55 (14)	3.44±0.34 (23)	2.00±0.43 (14)
1992	4.38±0.30 (50)	4.07±0.29 (28)	2.91±0.33 (46)	2.54±0.42 (26)
TOTAL	4.62±0.16 (150)	4.17±0.18 (71)	3.28±0.18 (139)	2.43±0.23 (68)

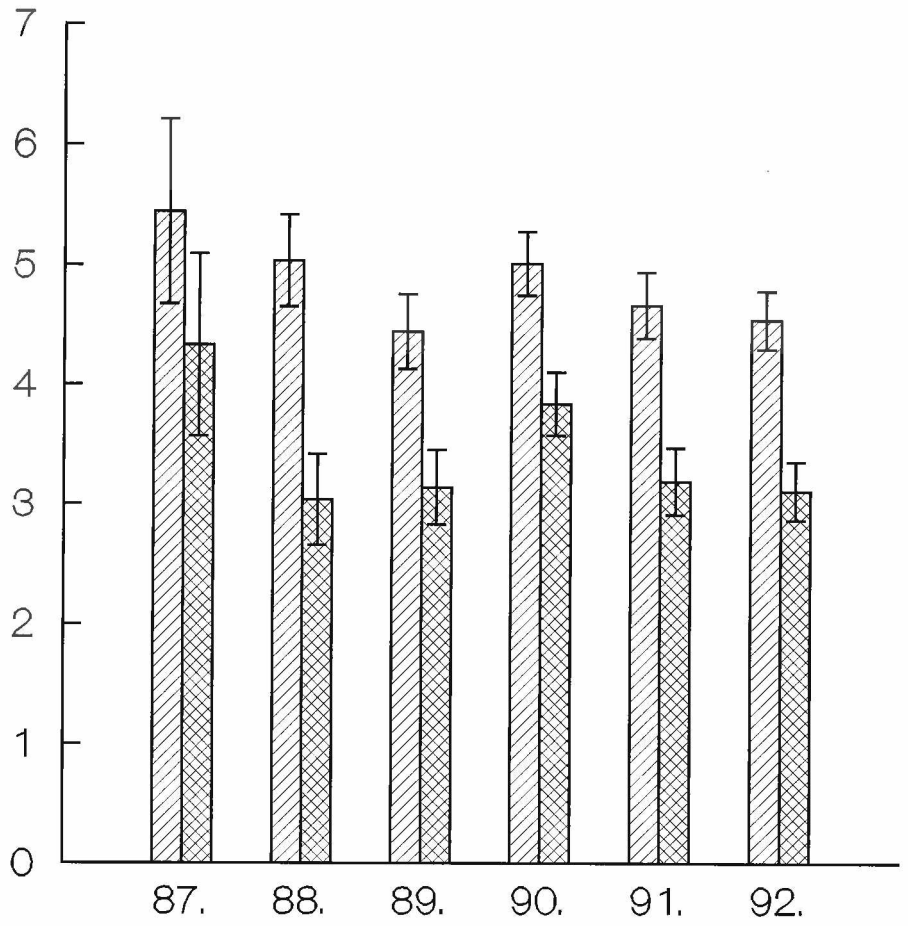

Figure 6. Mean production per year of small (hatched) and fledged (cross-hatched) young per Greylag pair seen with a brood of small young in the study area between 1987 and 1992. Data pooled over lakes. Bars show standard errors of the means.

Table 6. Percentage survival from first observation to fledging of young Greylag Geese in families with marked parents in different lakes, 1986 - 1992. Pairs where the marked individual (one or both) had bred before was denoted "old pairs" whereas pairs where the marked individual(s) had not bred before was denoted "new pairs". For the different lakes numbers in parentheses show number of small young and number of families, respectively, whereas these totals are shown separately for the overall results. + = too few families to calculate separate survival rates but included in totals.

	Yddingen	Fjällfotasjön	Klosterviken	Börringesjön	Overall survival of young	% families producing fledglings
Old pairs						
1986	84 (19,3)	27 (15,2)	+	+	58 (34)	83 (6)
1987	79 (34,6)	+	+	+	80 (44)	88 (8)
1988	65 (66,13)	58 (12,3)	55 (44,9)	+	61 (129)	85 (26)
1989	89 (53,10)	48 (25,6)	78 (54,12)	69 (26,8)	75 (158)	92 (36)
1990	61 (71,14)	74 (46,8)	78 (54,10)	82 (57,11)	73 (228)	93 (43)
1991	77 (56,11)	48 (23,4)	68 (56,14)	65 (48,12)	67 (183)	85 (41)
1992	75 (92,19)	40 (50,9)	74 (77,19)	70 (60,14)	67 (279)	89 (61)
Total	74 (391,76)	52 (175,33)	71 (293,66)	72 (198,46)	69 (1057)	89 (221)
New pairs						
1992	79 (28,8)	47 (15,3)	20 (20,7)	+	56 (75)	71 (21)

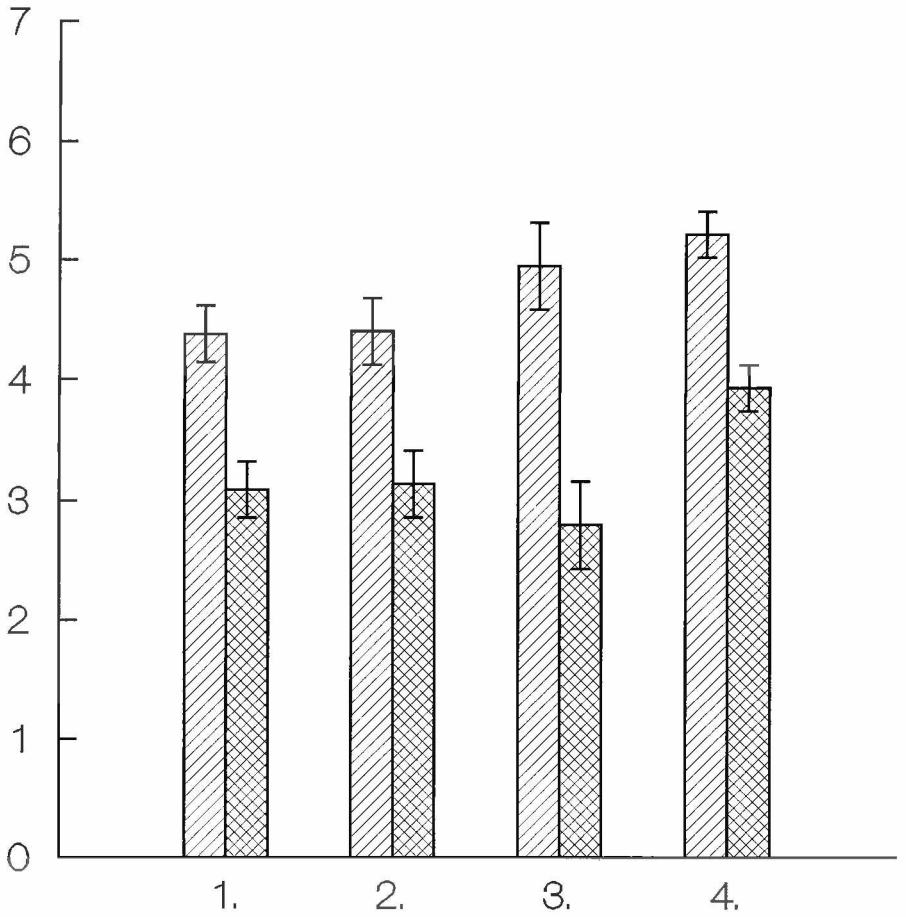

Figure 7. Mean production per lake of small (hatched) and fledged (cross-hatched) Greylag young per pair seen with a brood of small young in the study area between 1987 and 1992. Data pooled over years. Bars show standard errors of the means. 1 = Klostervikles, 2 = Börringesjön, 3 = Fjällfotasjön, 4 = Yddingen

experiencing a precipitation of less than 20 mm during their first five days, fledged compared to 63% of 116 experiencing a precipitation of more than 20 mm during their first five days, the difference being significant (Ch^2=4.02, df=1, P<0.05). During the other years there were no periods with more than 20 mm precipitation.

The mean number of fledged young of pairs seen with small young was 3.14 for experienced pairs (**Table 4**), the number ranging from one to ten for all families seen with fledged young (**Figure 5**). As with the number of small young in the brood, the mean number of fledged young varied between years and lakes. The differences were significant between lakes but not between years (Two-Way Analysis of Variance, F=2,79, df=3, P=0.04, and F=2.08, df=3, P=0.10, respectively, Interaction F=1.16, P=0.32). The families of fledged young were significantly larger at Lake Yddingen than at Lakes Klosterviken and Fjällfotasjön (P=0.009 and P=0.05, respectively, Tukey test).

As for small young, a significant correlation was found between the adjusted arrival date and the number of fledged young per brood (r=0.26, n=349, P<0.001), but the date of arrival only explained a small part of the total variation.

Parental age affected the number of fledged young in families (**Figure 8**). Whereas the number of small young in broods with one parent four years old was the same as for older adults, the number of

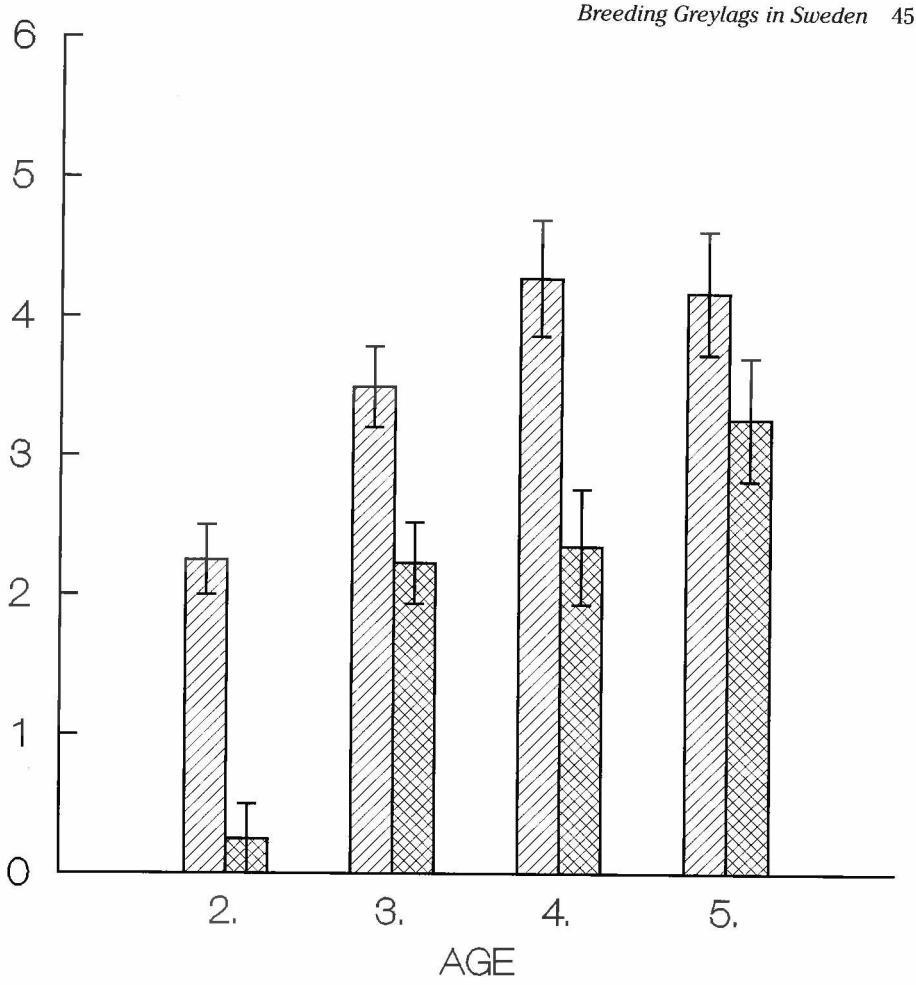

Figure 8. Mean production of small (hatched) and fledged (cross-hatched) young Greylag pairs producing a brood of small young in relation to the age of the parent(s) of known age, 1987-1992. Bars show standard errors of the means.

fledged young in these families was significantly lower, and similar to families in which the known-age parent was three years old. The survival from hatching to fledging was thus lower for goslings with young parents.

The number of fledglings produced per pair showed only a slight correlation with the production of small and fledged young in the preceeding year (r=0.19, n=197, P=0.008 and r=0.15, n=301, P=0.008).

Discussion

The mean clutch size in our study area is in line with the values presented in other studies. In Estonia (Paakspuu 1974), as well as in Schleswig-Holstein (Knief 1991), the clutch size was 5.0 and in Scotland (Newton & Kerbes 1974) 5.1 compared to 5.3 eggs in Poland (Witkowski 1983). From Czechoslovakia, Hudec & Kux (1970) reported a clutch size of 5.75 eggs, while Hauff (1982) and Young (1972) found clutch sizes of about 5.9 from an area of eastern Germany and south Scotland, respectively. It may be noted that clutch sizes can vary also between nearby sites (Paterson *et al.* 1990, Persson unpubl.).

From Schleswig-Holstein, Knief (1991) reported that about 50% of breeding pairs were found to produce a brood and, in general, the number of fledged young per brood was around 4, i.e. in fair agreement with our results. From Scotland, Newton &

Kerbes (1974) reported similar results but noted that the percentage of successful pairs varied markedly between years, with low success in years with a late spring. In east Germany, between 50 and 65% of the pairs bred successfully in different years, average brood size at fledging being 3.9 (Naacke 1993). Data from Poland are similar to data from our area (cf. Witkowski 1983).

Comparable data on the actual losses of young from hatching to fledging are scarce for the Greylag Goose as, without marked parents, total losses of broods that do occur to some extent (11% of broods in our study) cannot be accounted for. Witkowski (1983) found, however, a survival rate of 72.6%, similar to the 69% we found.

The lower survival to fledging at Lakes Klosterviken and Fjällfotasjön, compared to Lakes Yddingen and Börringesjön, can be related to marked differences in feeding conditions. While Lakes Yddingen and Börringesjön are partly surrounded by large pastures grazed by cattle and horses, such pastures are small at Lake Klosterviken and non-existent at Lake Fjällfotasjön. Moreover, a golf course with a high rate of fertilizer application is an important feeding area for many broods at Lake Yddingen. It seems possible that the number of breeding pairs at Lake Fjällfotasjön is limited by the availability of feeding areas for the broods, whereas the number of potential nest sites on the islands there is high. This view is supported by the movements of families from Lake Fjällfotasjön and Lake Klosterviken.

Differences in feeding conditions for the goslings can also be of importance for later stages in their lives (cf. Lieff 1973, Owen & Black 1989). Preliminary results from our study area show that goslings feeding at Lake Yddingen are significantly heavier than similar-aged goslings from the other lakes (Nilsson *et. al.* in prep.).

Individuals differ in their breeding performance, a small number of pairs accounting for a high proportion of the young (Nilsson & Persson unpubl.). The importance of individual quality was also clear from the significant correlation between the breeding performance in year t and the breeding performance in year t-1. Similarly, Raveling (1981) found that individual Giant Canada Geese *Branta canadensis maxima* that succeeded in rearing a brood were more than twice as likely to be successful in producing young in following years.

The breeding performance of individual pairs could be related to the start of breeding, early-arriving pairs being much more successful than late-arriving ones. Hauff (1982) reported a decrease in clutch size with the progression of the season, and Witkowski (1983) produced data showing much lower hatching success for later nests. Newton & Kerbes (1974) noted much higher nesting success in early seasons compared to late seasons. This time effect can probably, at least to a great extent, be related to the quality of the plant food, the nutritive value decreasing with the progress of the season (Iedema & Kik 1985).

The choice of winter area also affected breeding success. Even if no differences were found in brood sizes at hatching or fledging between geese wintering in The Netherlands and in Spain, a much higher proportion of geese wintering in The Netherlands produced a brood of young.

Density has been reported to affect production in many increasing goose populations (Ogilvie & Boyd 1976, Owen & Norderhaug 1977, Ebbinge 1985, Forslund 1992). In the present study, the same effect seems to be present; thus a smaller proportion of pairs produce young at the small Lake Klosterviken, with a very dense population, than at Lakes Yddingen and Börringesjön, where densities are lower.

Young Greylags are recruited successively into the breeding population from the age of two but, as reported for several other species, the breeding output is much lower among young birds than among older ones. Geese did not have the same breeding success as experienced breeders until they were five years old (cf. Forslund & Larsson 1992 for the Barnacle Goose *Branta leucopsis*).

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