Field choice in spring and breeding performance of Greylag Geese *Anser anser* in southern Sweden.

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Selection and exploitation of feeding areas by pre-breeding and non-breeding Greylag Geese *Anser anser*, as well as by families, was studied in a breeding area consisting of four lakes in Scania, southernmost Sweden, in the years 1997-2000. Total production of young in each lake as well as the breeding performance of neck collared individuals was established annually, 1985-2000. This breeding population increased on average 15.3% per annum, from 93 pairs in 1985 to 910 pairs in 2001. The two main field types used by pre-breeding pairs, males of incubating females and non-breeders in flocks were winter wheat and grassland, often switching from the former to the latter in mid-season. Almost all feeding during brood-rearing took place on pastures grazed by livestock or on a golf-course. Generally in spring, the rates of exploitation were below 300-400 goose days ha^{-1}, but rates of >1,000 goose days ha^{-1} were noted for one cereal field and two grassland areas. The rates of exploitation by families varied markedly among brood-rearing areas as well as years, being highest all through the study period on a grazed pasture, where it ranged 800-1,350 goose days ha^{-1}. Including the utilisation by non-breeders, the annual exploitation of this pasture ranged from 1,400 to 2,500 goose days ha^{-1}. At the only lake without grazing by livestock (since the mid-1990s), significantly fewer goslings survived to fledging than at the other lakes (45% vs 70%). Indications of density-dependent effects on the productivity of small young were noted at one of the lakes (Klosterviken) but not at another (Yddingen). Most likely, the lack of any density dependent effect, in spite of the very marked increase in the breeding population during the study period at Yddingen, is the result of access to highly fertilized grass on a golf course.

Key Words: Greylag Goose, breeding result, field choice, Sweden

Fitness consequences of the utilisation of different habitats with different qualities have been studied for a number of goose species (Bédard & Gauthier 1989; Black *et al.* 1991; Gauthier *et al.* 1984; Prop *et al.* 1998). In most cases, these studies did not go beyond the population level, not looking into habitat selection of different individuals (but see Black *et al.* 1991). In the Greylag Goose *Anser anser*, Nilsson & Persson (1994) established marked differences in breeding performance of individuals from different lakes situated in a small area in southernmost Sweden. Young hatched in these lakes also showed differences in survival during the following winter and also in their future recruitment into the breeding population (Nilsson *et al.* 1997).

In this paper, use and exploitation of feeding areas by pre-breeding pairs and families of Greylag Geese with known breeding results was studied. In order to establish whether there is competition for food between breeding and non-breeding geese, the selection of feeding areas by non-breeding birds was also studied. Finally, density-dependent effects on the production of young in this rapidly increasing population were investigated.

Study Area

The study was conducted in a breeding area with four lakes (Klosterviken, Börringesjön, Fjällfotasjön and Yddingen) in southwest Scania, southernmost Sweden (**Figure 1**), where catching and neck collaring of Greylag Geese started in 1984, as a part of a Nordic project (Andersson *et al.* 2001). The lakes are situated in a rolling agricultural landscape with extensive areas of cereal crops (cf. Nilsson & Persson 1992, 1998), but also including grazed areas close to the lakes.

The lakes are all eutrophic, with plankton blooms and extensive reeds. Suitable reeds for nesting Greylag Geese are available in all lakes. Moreover, Lake Fjällfotasjön has several good nesting islands and there are also a few islands in Lake Yddingen. There are extensive areas of grazed pastures close to Lakes Yddingen and Börringesjön. Lake Klosterviken has only one good grazing area for goslings and Lake Fjällfotasjön has few suitable brood-rearing areas. Lake Yddingen is bordered by a golf course, giving easy access to large areas with highly fertilised grass.

All brood-rearing areas, with the exception of the golf-course and at Lake Fjällfotasjön, were grazed by either cattle or horses. At Lake Fjällfotasjön, grazing by livestock ceased in the mid-90s.

Lakes Klosterviken and Yddingen were chosen for more intensive studies as they offered possibilities to measure overall breeding success. These parameters could only be studied for individually marked geese in the other lakes, where more extensive studies of field choice were made.

Figure 1. Map of the study area showing the four lakes with the main feeding areas in black. Light-shaded = woodland areas. 1. Klosterviken; 2. Börringesjön; 3. Fjällfotasjön; 4. Yddingen. Map of south Sweden showing the general position of the study area inserted.

Methods

During 1984-2000, 551 adult and 1,632 young Greylag Geese were neck collared in the study area, in the last few years mainly at Lakes Klosterviken and Yddingen (Persson 2000). Regular checks for the occurrence of marked individuals were made from the arrival of the first geese in spring until their departure in autumn. In spring, the study area was visited several times a week, whereas observations were made once or twice a week during the autumn period. Observations with the aim to establish the breeding results of all neck collared birds were especially intensive during the period from hatching until the young were fledged. The autumn checks included important staging areas at the coast.

All Greylags present at the different lakes were counted two to three times a week from their arrival in spring until late May. The counts covered all feeding areas at the different lakes during the same day. Pairs, single birds and flocks of non-breeders were counted separately. For each lake, the number of breeding pairs each year was established as the maximum pair count before start of incubation.

During 1997-2000, the distribution of geese on different fields was established on all surveys in spring. On the basis of these observations the percentage frequency of geese on different fields and field types was established for pairs and unpaired geese, respectively. Exploitation rates (goose days ha^{-1}, abbreviated gd ha^{-1}) of different fields by geese of different categories were calculated by using before mentioned estimates and the number of pairs and non-breeders (estimates for ten-day periods).

Most broods at Lakes Klosterviken and Yddingen concentrated on a few feeding areas, which were searched several times a week during 1985-2000 to establish the total production of young. During 1997-2000, the rate of exploitation of the main brood-rearing areas was calculated as goose days ha^{-1} for adults and young in the broods based on the accumulated brood and young totals for the different rearing areas. Owing to large demands of protein, goslings need to consume at least as much food as their parents during the brood-rearing period (Massé *et al.* 2001). Therefore, the concept of goose days was used uniformly in this study.

Rainfall during early brood rearing can reduce survival among goslings ≤5 days of age (Nilsson & Persson 1994; Schmutz *et al.* 2001). For that reason, years with rainfall occurring on >50% of the days during the hatching period were excluded from the calculations of regressions (**Figure 2**). As the exact timing of the hatching period often varies slightly among sites, the effect of rainfall might vary among the breeding lakes. This is the case in the study area where breeding at Lake Yddingen generally is earlier than at Lake Klosterviken.

Results

Goose numbers

When the counts started in 1985, the total breeding population was 93 pairs, increasing to 710 pairs in 2000 and 910 pairs in 2001 (**Figure 3**). The increase, on average 15.3% per annum, was not the same throughout the study period. There was a more or less steady increase in the number of pairs during 1985 to 1992, followed by five years with relatively stable numbers of around 440 pairs. Then, the number of breeding pairs increased markedly again.

In addition to the breeding pairs, flocks of non-breeding Greylags were regularly found in the study area (**Figure 4**). Maximum total counts for this category ranged between 600 and 800 birds in 1997-1999, and increased

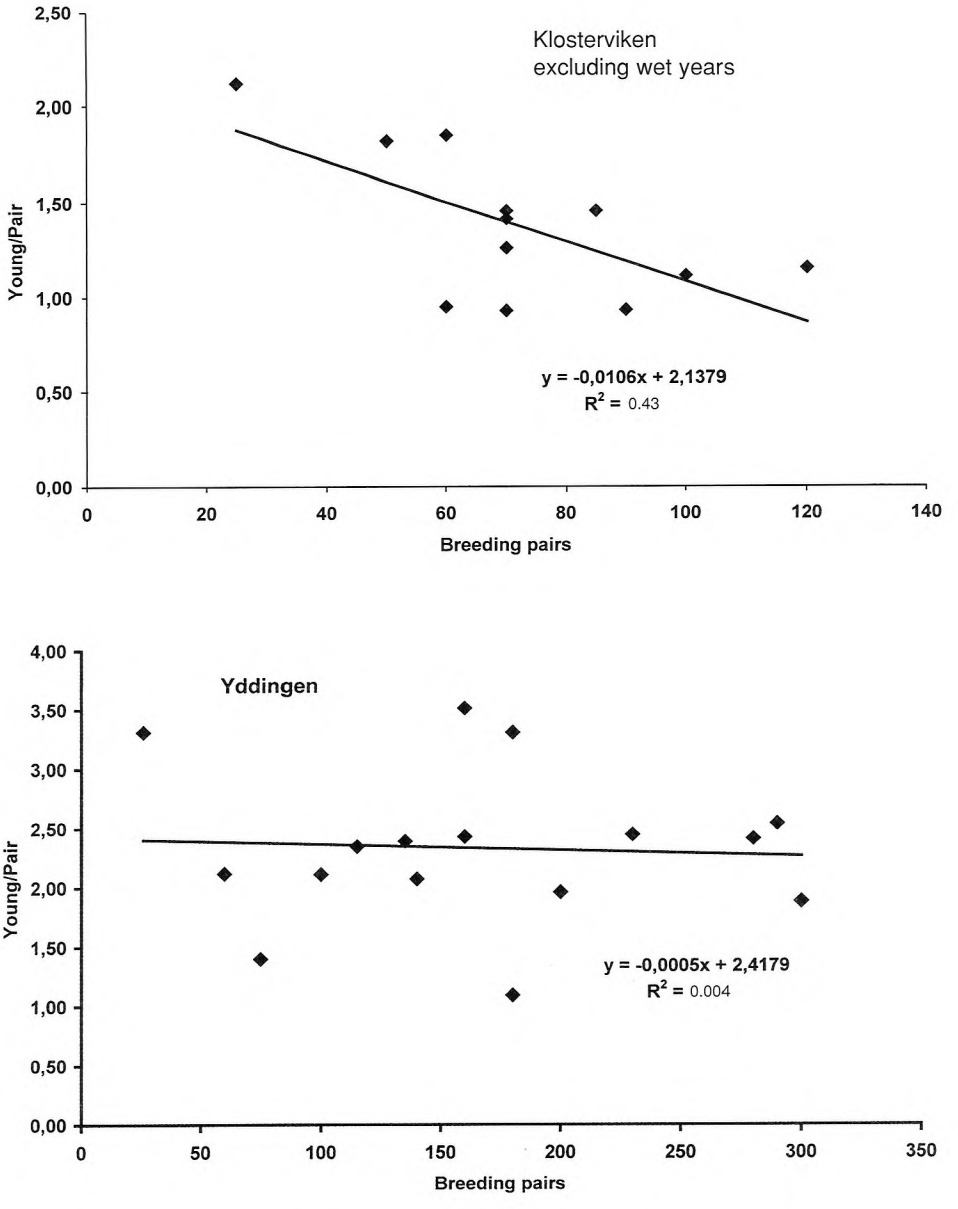

Figure 2. Number of young per pair initiating breeding in relation to the number of breeding pairs at Lakes Klosterviken and Yddingen, 1985-2000. Years with extreme weather conditions during brood rearing are not included (see Methods).

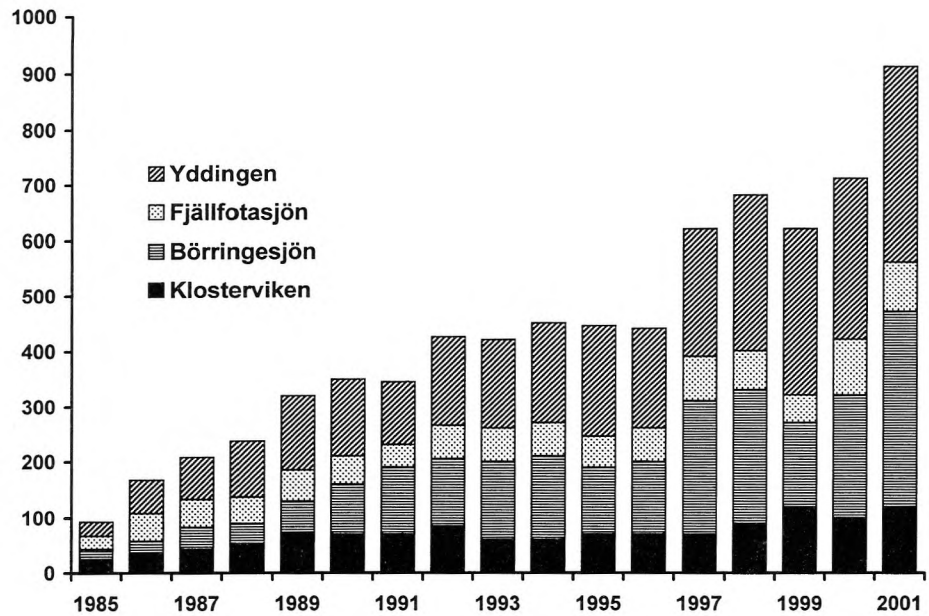

Figure 3. Numbers of breeding pairs of Greylag Geese in the study lakes, 1985-2001.

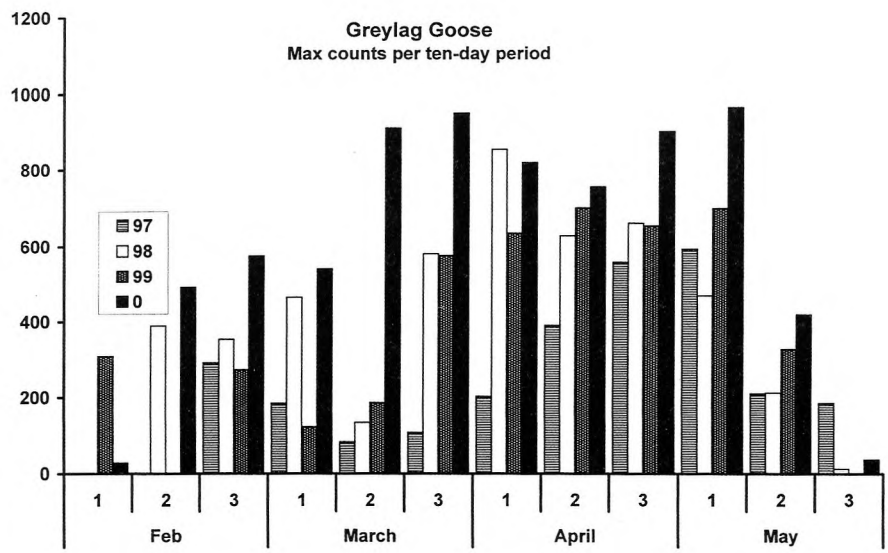

Figure 4. Total number of non-breeding Greylag Geese in the study area, in ten-day periods during the springs of 1997-2000.

to about 1,000 birds in 2000. There was a large turnover among the non-breeders, demonstrated by re-sightings of neck collared individuals (Leif Nilsson & Hakon Persson, unpublished data). The non-breeders arrived in the area during February and March, together with the breeders, but left in early to mid May to moult elsewhere (Nilsson *et al.* 2001).

Field choice

The two main field types used by both pre-breeding pairs, males of incubating females and non-breeders in flocks were winter wheat and grassland (in the latter case including the golf-course at Lake Yddingen) (**Figure 5**). Yddingen differed from the other lakes as the golf-course accounted for about 50%, of the geese. Cereal fields were much less used at Lake Yddingen than at the other lakes.

Early in the season, the geese at Lakes Klosterviken and Börringesjön used winter wheat for 50-60% of their feeding. In April, almost all pairs and most flocks, fed on grassland at these lakes, but some flocks used winter wheat. In May, some flocks at Lakes Börringesjön and Yddingen fed on winter wheat and some on newly sown cereal, whereas all geese at Lake Klosterviken were found on grassland.

Exploitation of feeding areas

Most geese at Lakes Klosterviken and Yddingen were feeding close to the lakes, the longest flights to regularly visited fields being about 2 km (**Figure 1**). Similarly, most Greylags at Lake Börringesjön were also flying only relatively short distances to their feeding areas. Somewhat longer feeding flights were made by Greylags from Lake Fjällfotasjön, where there were no good feeding areas close to the lake.

At Lake Klosterviken, the highest rate of exploitation (1,017 goose days ha^{-1}) was found for the shore meadow in 1999 (**Table 1**). This meadow was regularly frequented in all years, especially in the latter part of the spring season. In the early part of the season, the geese mainly used winter wheat either on fields C or D close to the lake, but at a somewhat longer distance in 1998, when both these fields were used for other crops.

At Lake Klosterviken, only one feeding area was available for the families (B, **Table 2**). The total number of goose days ha^{-1} in this meadow ranged 190-330 for young and 300-1,155 for adults (breeders and non-breeders).

At Lake Yddingen, the highest rates of exploitation by non-breeders were found for a field with winter wheat in 2000 and a grassland along the shore of the lake in 1998, which attained 1,260 and 1,170 goose days ha^{-1}, respectively (**Table 3**). Generally, the rates of exploitation were much lower and below 300-400 goose days ha^{-1}.

At Lake Yddingen, families used a number of different feeding grounds (**Figure 1**). The rate of exploitation could be established at three of these areas: A (a grazed pasture at the shore) + U (an open, grazed woodland), E (the golf-course) and V (a grazed pasture close to a pond). The golf course was only partly used by the families. During daytime, when there were golf players present, the families fed close to the shore and in a marshland. In the evening and early morning with few golf players, they used larger parts of the golf course. Exploitation rates for families were calculated for the part of the golf course close to the shore and marshland, whereas exploitation values for non-breeders refer to the entire golf course.

Table 1. Exploitation (goose days ha^{-1}) by all non-breeding Greylag Geese of different sub-areas at Lake Klosterviken in spring, 1997-2000. Field types in different years are given in brackets. GR=Grazing area, HS=Autumn sown cereals, SS=set aside, RA=winter rape, ST=stubble fields, TR=ley fields, VA=mown grass, GO=golf course, M=energy plantation (Salix), BS=grazed forest.

Sub-area	Area (ha)	1997	1998	1999	2000
B	15.2	220(GR)	665(GR)	1017(GR)	339(GR)
C (part)	19.5	124(HS)	0(SS)	0(RA)	0(HS)
D	28.3	170(ST)	8(RA)	303(HS)	595(HS)
E	12.6	5(GR)	68(GR)	41(GR)	143(GR)
G	27.1	3(GR)	34(GR)	28(GR)	56(GR)
L	8.7	5(GR)	96(GR)	158(GR)	259(GR)
N	63.9	0(SS)	45(VA)	0(SS)	0(HS)
P	76.5	0(TR)	50(HS)	0(HS)	0(SS)

Table 2. Exploitation (goose days ha^{-1}) by Greylag Geese of the main brood-rearing area (shore meadow B), at Lake Kosterviken, 1997-2000. Total area of the shore meadow is 15.2 ha. Total number of young and parents in the different years are given in brackets. for comparison, the rate of exploitation by non-breeding Greylags for the brood-rearing area is shown both for the whole spring and for the brood-rearing period.

	1997	1998	1999	2000
Young	191(88)	205(84)	332(138)	273(111)
Parents	83(38)	93(38)	138(58)	126(54)
Adults without family:				
Whole spring	220	665	1017	339
April and May	172	233	844	207

Table 3. Exploitation (goose days ha^{-1}) by all non-breeding Greylag Geese of different sub-areas at Lake Yddingen in spring, 1997-2000. Field types (see **Table 1**) in different years are given in brackets.

Sub-area	Area (ha)	1997	1998	1999	2000
A	4.5	995(GR)	1170(GR)	590(GR)	420(GR)
E	110.2	130(GO)	238(GO)	371(GO)	369(GO)
F	6.9	345(GR)	162(GR)	145(GR)	477(GR)
G	13.2	111(GR)	177(GR)	151(GR)	352(GR)
H	10.2	264(VA)	328(VA)	237(VA)	373(VA)
K	23.2	147(GR)	97(GR)	256(GR)	163(GR)
R	18.5	34(ST)	200(VA)	45(HS)	100(VA)
S	18.7	2(VA)	29(VA)	11(VA)	5(VA)
T	23.2	137(HS)	45(HS)	109(HS)	69(HS)
V	12.3	112(GR)	179(GR)	107(GR)	132(GR)
Y	5.5	12(VA)	37(HS)	0(RA)	1260(HS)

There were marked differences in the rate of exploitation by Greylags between the different areas at Lake Yddingen (**Table 4**). The shore (A+U) yielded the highest rates of exploitation, with more than 1,000 goose days ha^{-1} for young in two years out of four, and for adults in two years. The highest rate of exploitation was noted in 1998, with an overall rate of >2,500 goose days ha^{-1}. In the same year >1,100 goose days ha^{-1} was noted for non-breeders in this area. There was an increase in the rate of exploitation by Greylags both for area E and V but there was no such tendency over the four years for area A+U (**Table 4**).

Breeding performance

The longer series of data now available confirms the differences in breeding output among the study lakes found by Nilsson & Persson (1994). The proportion of successful pairs differed between the lakes (F=3.00, P=0.03, **Table 5**). Brood sizes also differed between the lakes (F=4.74, P=0.003 for small young, F=7.92, P=0.00004 for fledged young, **Table 5**). Average numbers of small young at Lakes Klosterviken and Börringesjön were significantly lower than at Lake Yddingen (t=-3.64, P=0.000 and t=-2.21, P=0.028, respectively, **Table 5**), while there was no significant difference between Lake Fjällfotasjön and Lake Yddingen (t=-1.25, P=0.21, **Table 5**) . The number of fledged young was significantly lower at Lakes Klosterviken and Fjällfotasjön than at Lake Yddingen (t=-3.21, P=0.01 and t=-4-45, P=0.00001, **Table 5**). There was only a numerical ten-

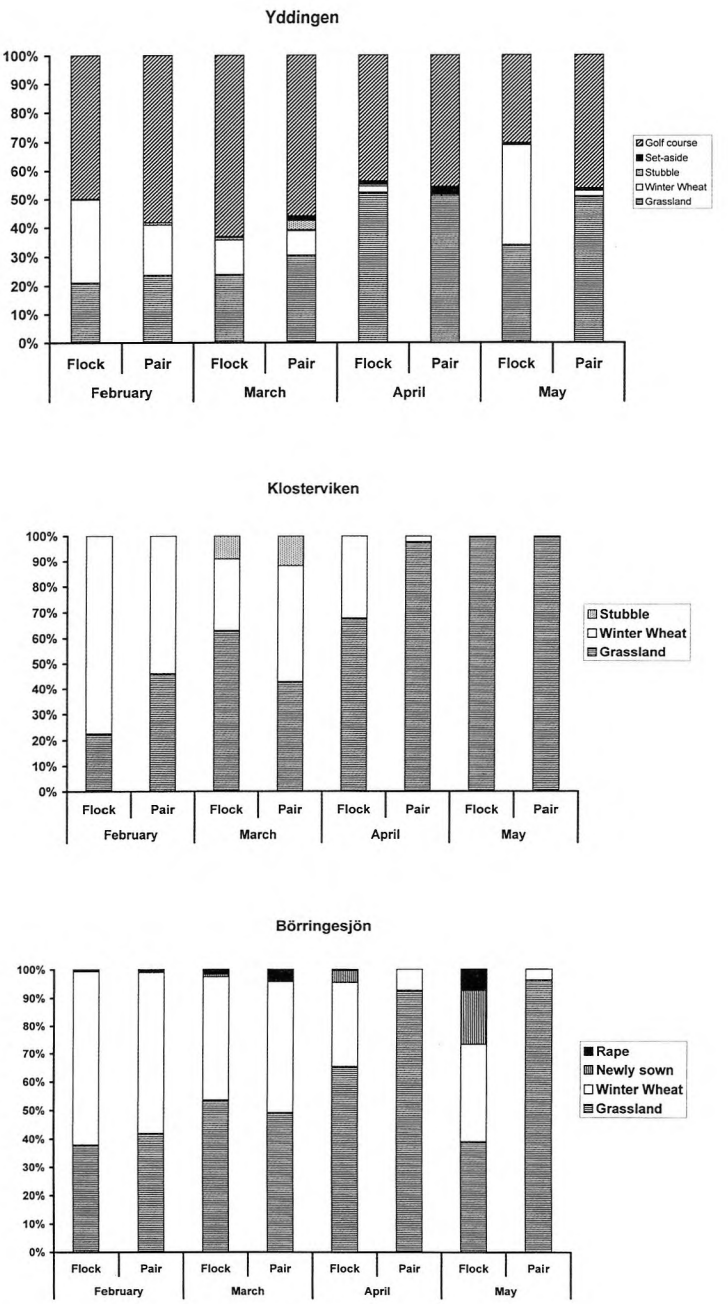

Figure 5. Field choice of Greylag Geese in flocks and pairs, respectively, in different months at Lakes Klosterviken, Börringesjön and Yddingen. Pooled data for the years 1997-2000.

dency for lower numbers of fledglings at Lake Börringesjön (t=-1.68, P=0.09, **Table 5**). Whereas 68-71% of the small young survived to fledging in the three lakes Klosterviken, Börringesjön and Yddingen, only 45% did so in Lake Fjällfotasjön (χ^2_1=84.8, P=0.001; **Table 5**).

Due to the low number of Greylag Geese neck collared in Lakes Börringesjön and Fjällfotasjön, annual variation in breeding result could only be studied for Lakes Klosterviken and Yddingen. Whereas there was no significant differences in proportion of successful pairs at Lake Yddingen over

Table 4. Exploitation (goose days ha^{-1}) by Greylag Geese of the three main brood rearing areas at Lake Yddingen (**Figure 2b**), 1997-2000. Total number of young and parents in the different areas and years are given in brackets. For comparison, the rate of exploitation by non-breeding Greylags of the brood-rearing areas is shown both for the whole spring and for the brood-rearing period.

	1997	1998	1999	2000
Young:				
A+U	891(151)	1128(188)	645(110)	1087(149)
E	123(191)	159(222)	179(274)	242(297)
V	226(193)	242(87)	435(144)	594(182)
Parents:				
A+U	169(58)	236(72)	142(50)	193(54)
E	26(78)	32(86)	37(112)	54(132)
V	48(40)	57(42)	77(56)	92(56)
Adults without family				
Whole spring:				
A+U	995	1172	589	424
E	130	238	371	369
V	112	179	107	132
April and May:				
A+U	550	316	342	254
E	55	35	156	77
V	88	54	65	86

Table 5. Comparison of breeding performance of Greylag Geese in the study lakes, 1987-2000.

	Klosterv	Börringe	Fjällfota	Yddingen
Per cent successful pairs (>=1 fledged young)	54(321)	63(237)	57(147)	69(481)
Brood sizes (seen with small young and checked fledged young)				
N	140	105	68	227
Small young	4.36±2.04	4.71±2.65	4.96±2.16	5.43±3.28
Fledged young	2.93±2.27	3.33±2.53	2.18±2.01	3.89±3.31
Small young surviving to fledging (%)	68	70	45	71

Table 6. Fledging success and mean brood sizes in relation to feeding areas of Greylag Goose pairs seen with small young at Lake Yddingen 1997-2000.

Feeding area	% with >= 1 fledged young	Small young	Fledged young	No. of Families
Golf course	91.0	4.61±2.12	3.67±2.60	66
North shore	95.0	4.80±2.13	3.90±2.05	20
South shore+pond	89.7	5.70±2.79	4.03±3.14	29

the study period (χ^2_{13}=17.4, *P*=0.18; **Figure 6**), there was a significant annual variation for Lake Klosterviken (χ^2_{13}=31.2, *P*=0.003; **Figure 6**).

For Lake Yddingen, no differences in breeding performance could be established among families using the three different brood-rearing areas studied (**Table 6**, χ^2_2=0.46, n.s.).

For Lake Klosterviken there was a significant negative correlation between the number of breeding pairs and the number of young per breeding attempt (numbers of pairs seen at the start of the breeding used as equivalent of the number of breeding attempts) (**Figure 2**, *r*=0. 0.65, *P*=0.02), indicating density-dependent effects on the production of young at this lake. There were no indications of any density-dependent effects on the productivity of small young at Lake Yddingen (**Figure 2**, *r*=0. 0.06, n.s).

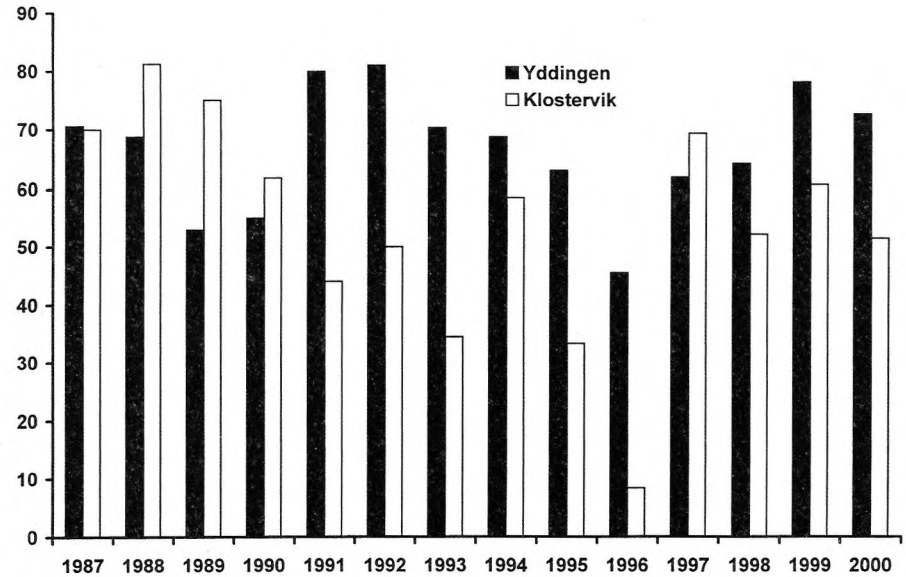

Figure 6. Reproductive success (percentage of breeding attempts results in at least one fledgling) at Lakes Klosterviken and Yddingen, 1987-2000.

Discussion

Geese generally switch from a simple carbohydrate-rich diet in autumn and early winter to more protein-rich vegetation in spring (Alisauskas & Ankney 1992; Bromley & Jarvis 1993; Budeau *et al.* 1991; Gauthier 1993; Mainguy & Thomas 1985; Owen 1980; Prevett *et al.* 1985). The two main field types exploited by feeding Greylag Geese in late winter and spring in this study, as well as in other parts of the breeding range (Persson 2002), were winter cereals and grassland, both offering leaves rich in protein (Therkildsen & Madsen 2000). The observed shift from winter wheat to grass was probably governed by a continual decline of protein content of young leaves of winter cereals (Groot 1989). Differences in soil characteristics and varieties of cereals grown give rise to large within-field differences in growth rate of seedlings in the study area. As a result, winter cereal fields reach the stage when they become unsuitable as feeding grounds for geese at different times. The timing of shifts from one field type to another is largely conditioned by air temperature (Prins & Ydenberg 1985, Therkildsen & Madsen 2000).

There is considerable literature on exploitation rates of different field types by geese, almost exclusively referring to non-breeding conditions. The number of goose days ha^{-1} reported from these studies were, in most cases, of the same magnitude as those obtained from the breeding areas in the present study. The variation in rates of utilisation was great among the published information from the non-breeding studies as well as from the study area in Scania.

In the study area the exploitation of pea fields and cereal stubbles by post-breeding Greylags was 100-350 goose days ha^{-1} in the mid-80s (Nilsson & Persson 1992). The estimated use of the Dutch portion of the Ems Dollard estuary by Greylag Geese as spring and autumn staging area ranged 329-803 goose days ha^{-1} for 1983-1994 (Esselink *et al.* 1997). Maximum recorded utilisation of different field types by Greylags and Pink-footed Geese *Anser brachyrhynchus* combined in Scotland over a winter was 1,350 goose days ha^{-1} for ley grass and 640 goose days ha^{-1} for permanent grass (Newton & Campbell 1973). Recorded peak grazing pressure of Pink-feet in Denmark was 950-1,200 goose days ha^{-1} (Lorenzen & Madsen 1985). Grazing pressure by mixed flocks of Greater White-fronted Geese *Anser albifrons* and Tundra Bean Geese *Anser fabalis rossicus* in the Lower Rhine area reached 3,000 goose days ha^{-1} on grasslands, 2,600 goose days ha^{-1} on winter barley and 3,500 goose days ha^{-1} on winter wheat (Mooij 1998). Van Impe (1980) reported 1,030 goose days ha^{-1} for Taiga Bean Geese *Anser fabalis* on grassland. Lower exploitation rates of grasslands and winter cereals by Taiga Bean Geese, Greater White-fronted Geese and Canada Geese *Branta canadensis* were reported from Scania, but one field of winter cereals experienced 5,100 goose days ha^{-1} (Nilsson & Persson 1991). Considerably higher grazing pressures have been reported for the smaller goose species, with up to 10,000 goose days ha^{-1} by Barnacle Geese *Branta leucopsis* during the period October-April (Lok 1978, 1982).

The nutritional carrying capacity of freshwater wetland habitats for breeding Greater Snow Geese *Anser caerulescens atlanticus* at the Bylot Island colony, Nunavut, Canada was assessed to be on average 2,800 goose days ha^{-1} (Massé *et al.* 2001). This value is marginally higher than the highest recorded grazing pressure in the Scania area (2,550 goose days ha^{-1}). In most broad-rearing areas, however, the geese have to share the primary production with livestock or it is removed by lawn mowers. The total consumption by livestock in the different areas was beyond the scope of this study. In either case, the grazing pressure on the most heavily used brood-rearing area exceeded the calculated carrying capacity of a well managed grassland in Britain: 1,900 goose days ha^{-1} (Owen 1977). In most cases, the calculated exploitation rates in the study area were considerably lower, the highest value at Lake Yddingen referring to a small highly fertilised shore meadow.

When fledged, the families as a rule immediately stop feeding on the brood-rearing areas, even though they usually continue to use the breeding lake for roosting. Instead, they switch to grasslands situated between one and four kilometers from the roosts (Nilsson & Persson 1992, 1998). There is one exception to this rule however. On the golf course most families (together with large numbers of non-breeders and failed breeders that have returned after moult elsewhere), continue to feed on the brood-rearing area for about one month after fledging, grazing golf-course grasses and stripping grass-seed. The most probable reason for this difference is that the food quality on the golf course continues to be higher, or at least as high as in alternative areas, while it has become inferior on the other brood-rearing areas. A seasonal decline in growth rate of grass is a commonly observed pattern for forage plants grazed by geese (Cargill & Jefferies 1984), but timing of the decline varies among areas as well as years (van der Veen *et al.* 1999).

In contrast to Arctic-breeding geese, the Greylag seems unable to maintain a profitably short grass sward. At Lake Fjällfotasjön, lacking grazing by livestock since the mid-1990s, the fledging rate was significantly lower than at the other lakes. Most of this additional mortality occurred around fledging time (Hakon Persson, pers. obs.). Breast muscles start to grow very late, which concentrates the resource requirements for the development of this large muscle mass in a short span of time near fledging (Lesage & Gauthier 1997; Sedinger 1986). As food quality deteriorates throughout the breeding season (Spedding 1971), the protein contents might reach such low levels that goslings are unable to obtain enough for the development of their breast muscles (cf. Lesage & Gauthier 1998).

Several studies have shown that gosling and juvenile survival decreases with increasing density of goose populations (Cooch *et al.* 2001, Loonen *et al.* 1997; Sedinger *et al.* 1998, 2001; Williams *et al.* 1993). Studies of the Barnacle Goose (Black *et al.* 1998) and Snow Goose (Cooch *et al.* 1991, Reed & Plante 1997) show that body size declines at higher densities. Moreover, clutch size and breeding probability may be influenced by adult size (Sedinger *et al.* 1995, 2001). This can explain a relationship between high density and lower reproductive output in the two species. However, Sedinger *et al.* (1998, 2001) did not find any similar effects in the Black Brant *Branta nigricans*, nor Reed & Plante (1997) in the Greater Snow Goose.

In the Greylag Goose, density-dependent effects were found on the number of small young produced at Klosterviken but not at Yddingen. Furthermore, the average number of fledged young per brood were lower at Klosterviken than at Yddingen. There were also differencens in weight of the young and survival rate of the fledged young between the two lakes (Nilsson

et al. 1997). Lake Yddingen had significantly heavier young that showed a higher first-winter survival than the young from Lake Klosterviken. The brood rearing areas at both lakes had high densities of both breeding and non-breeding geese, making competition between breeding and non-breeding birds likely. The easy access to highly fertilized grass on the golf-course at Yddingen does probably allow both a better pre-breeding condition of birds (larger clutches laid), and a higher survival of young (higher average fledgling brood size and higher first-winter survival).

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