Natal and breeding dispersal in the Baltic Greylag Goose *Anser anser*

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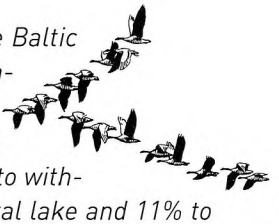

Dispersal from the centre of the breeding range of the Baltic Greylag Goose Anser anser *was studied using observations of individuals with neck collars. The median natal dispersal distance was 0 km in females and 25 km in males, respectively. All of the females recruited to within 7 km of where they had been reared, 87% to the natal lake and 11% to neighbouring water bodies. Of the males, only 11% recruited to the natal lake, while one individual was found more than 1,000 km from its place of birth. Even though the males dispersed to a greater distance within the population's breeding range, their distribution was still highly skewed towards their point of origin. Two thirds of all males recruited within 30 km of the site where they had been reared. Once recruited, both sexes exhibited an extremely strong philopatry to their breeding area. Only 1.5% of the males and 0.5% of the females changed breeding site between successive years. All breeding dispersal occurred within the local population, and in no case exceeded 6 km.*

Key Words: Breeding dispersal, natal dispersal, Greylag Goose, Sweden

"The question of the return of birds to their homes is one of perennial interest. How faithfully do adult birds, males and females, return to their territories? How far from their birth place do young birds settle? Over how much ground does one family scatter?" (Nice 1937). These questions remain highly relevant today, though now phrased in modern behavioural terminology. Movement from the site of birth to that of first reproduction or potential reproduction is termed natal dispersal, while subsequent movement between sites is termed breeding dispersal (Greenwood 1980).

Dispersal pattern is of fundamental importance to several aspects of popu-

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lation biology, being an essential component of meta-population and source-sink dynamics, gene flow, genetic structure and evolutionary change. However, large-scale studies addressing these issues are rare (for a summary, see Clarke *et al.* 1997). Detailed field studies are appropriate for investigating small-scale dispersal, but they are usually unable to follow individuals that leave the study area. Small-scale studies are valuable in evaluating the proximate causes of dispersal, but dispersal outside such local areas can only be studied with a marking scheme operating over a much larger scale.

Neck collaring of both breeding adult and gosling Greylag Geese *Anser anser*, has been undertaken annually in southwestern Scania, in southernmost Sweden since 1985 (Nilsson & Persson 1994, Nilsson *et al.* 1997). Besides detailed studies in the breeding area, these birds have also been followed outside the study area by a network of volunteers. Thus, we are now able to analyse natal and breeding dispersal throughout the Baltic populations breeding range.

Methods

A total of 1,014 goslings, 552 males and 462 females were neck collared in Lakes Klosterviken, Börringesjön, Fjällfotasjön and Yddingesjön during the years 1985-1994 (Persson 1994, 2000; Figure 1).The first generation of neck collars used in the project was of an inferior quality, resulting in an exceptionally high rate of collar loss among males. For that reason, all individuals marked with such collars were excluded from the analysis.

During the years 1985-1999, regular checks for the occurrence of neck collared geese were undertaken from the time of their arrival in spring until their departure in autumn. In spring, the study area was visited several times a week in order to establish the return of marked birds and their breeding performance. From the end of May until the last young fledged, the breeding area was visited almost daily to establish the fate of each neck collared gosling. Goslings were neck collared from the age of about six weeks until they were flying and impractical to catch. In summer and autumn, fieldwork was extended to cover neighbouring staging areas, especially the Foteviken area on the coast where a large proportion of the Greylag Geese from the study area gather at this time of year (cf. Nilsson & Persson 1992).

Knowledge of birds recruited to other parts of the species' breeding range is based mainly on reports from a network of more than 1,000 volunteers. Observers are located across much of the potential distribution area of the marked geese, although there is a marked bias towards the Netherlands. Fieldwork outside the study area was limited to irregular visits, mainly in late summer and autumn, to lakes situated within 30 km of our study area.

A bird defined as having eggs or

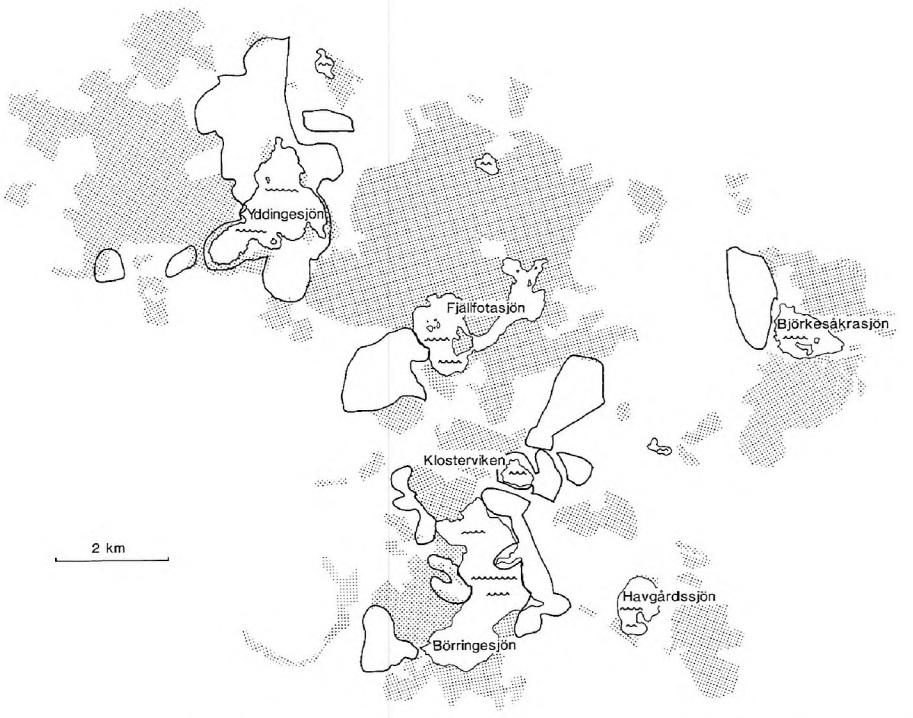

Figure 1. The study area. Lakes are indicated by shaded areas, and the feeding areas of the geese, regularly surveyed during the study, are bordered by solid lines. Woodland is stippled, farmland is open.

unfledged young was counted as breeding in that site. The same applied to a bird with newly fledged young, as families are were rarely seen more than four kilometres from the brood rearing area during the first two weeks after fledging, and most remained in the vicinity of the breeding site until the start of autumn migration (Nilsson & Persson unpubl.). In the light of this, a bird seen with a family in late summer or early autumn was counted as breeding in that site providing there were other sightings supporting such a conclusion. Most individuals had recruited to the breeding population when five years old, although new parents were often unsuccessful compared to experienced birds. Therefore, a paired bird in its fifth calendar year, or older, was counted as recruited if it remained faithful to a particular breeding site (cf. Nilsson & Persson 1994). In the latter case, fewer sightings were required outside the study area than within it.

The results obtained may be biased in three main ways: (1) an uneven sex ratio among the neck collared fledglings, (2) site-dependent variations in the likelihood of a recruited bird being

recorded and (3) loss of neck collar. A consequence of males having larger heads than females is that at a certain age male goslings can be neck collared but not females. In this way, a biased sex ratio can arise in the neck collared cohorts as in some families only the young males caught can be neck collared and often there will not be a second chance to catch the same family. Due to differences in the feeding habitats of families and pairs at the different breeding lakes, there will be differences in the chances of finding recruited birds. On account of the frequent visits within the study area there was confidence that all recruits were recorded, assuming the bird did not lose its neck collar before recruitment. Outside the study area, the likelihood that a recruit was recorded, was assumed to be the same everywhere. Visits to lakes in the vicinity of the study area compensated for an appreciably lower reporting rate among volunteers in this area. Based on re-captures, the annual neck collar loss in this population was estimated to be 5.5%±1.5 in males and 1.4%±0.6 in females (Persson 2000b).

The term breeding site needs to be defined, as breeding dispersal is a movement between sites. As breeding geese use one nesting site and one or more brood rearing areas for each breeding attempt, the breeding site must comprise all these sites. In the course of the present study, several birds changed nesting site, from one of the lakes to a pond close to the lake, but continued to use the same brood rearing area. Accordingly, a bird was counted as having dispersed, when it had changed its nesting site in such a way that it could no longer could use the same brood rearing area(s) as used the preceding season.

Lakes Klosterviken and Börringesjön are situated very close to each other and connected with a short canal, through which a number of broods change site after hatching each year. For this reason, in terms of breeding dispersal, these two lakes are counted as one breeding site.

Results

Natal dispersal

Among the neck collared goslings, 433 males and 354 females fledged during the years 1985-1994. Up to 1999, 82 of these males and 114 females were found breeding. All of the females were found within the study area, 99 on the natal lake and 15 on a neighbouring water body 2-7 km from where they were reared. Only 15 of the males were found on their natal lake, another 29 found within the study area (Table1). The other 38 had dispersed further afield with 50% at about 20-30 km, 8% at about 50 km, 24% at about 75-95 km and 10% at about 300 km, while single birds were found at distances of roughly 115, 230 and 1,050 km, the latter being in another flyway (**Figure 2**).

There was a strong correlation between food supplies during the brood

Table 1. Natal dispersal of males from the four lakes in the study area. Number of recruits assigned to distance classes based on distance between brood rearing area and breeding lake. Lakes are ranked based on food supplies during the brood rearing period, from the best to the worst (Nilsson *et al.* 1997).

Natal Lake	0-1 km	1-10 km	>10 km	Total	Percentage in natal lake
1. Yddingesjön	10	6	12	28	36
2. Börringesjön	4	6	7	17	24
3. Klosterviken	1	11	15	27	4
4. Fjällfotasjön	0	6	4	10	0
Total	15	29	38	82	18

rearing period and the proportion of males subsequently recruiting to their natal lake (**Table 1**, Spearman r=0.73, P<0.001). Two thirds of all males that recruited to their natal lake were found in Lake Yddingesjön, the lake offering the best feeding conditions. On the other hand there was no such tendency among the minority of females recruiting to another lake in the study

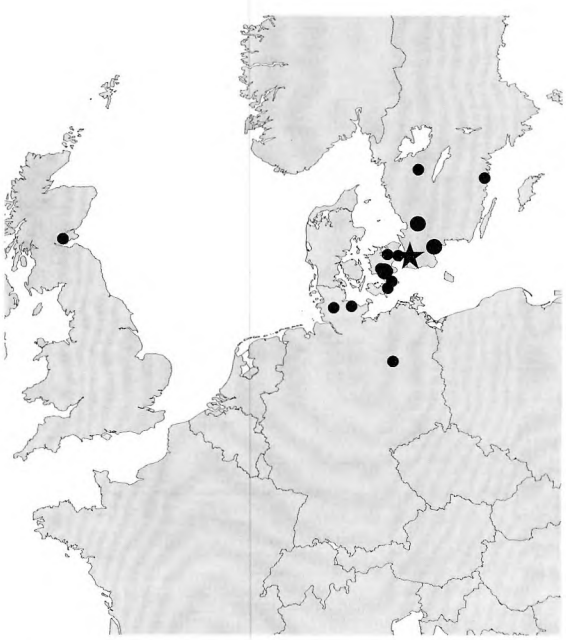

Figure 2. Positions of all male recruits recorded more than 50 km from the study area (star). Larger dots denote two recruits in the same area.

area than their natal lake. The proportion of local recruits to Lake Yddingesjön was significantly higher than for the other three lakes combined (χ^2=8.63, df=1, P<0.01).

Providing that no females recruited to outside of the study area, the number of recruited females that lost their neck collars up to the age of four is estimated to be six (cf. Persson 2000b). Two of these were recaptured, giving the total number of recruited females to be 118. Accordingly, 33.3% of the fledged females were subsequently recruited.

Assuming the same recruitment rate for both sexes, the total number of recruited males from the marked sample was estimated to be 144. Compensating for neck collar losses, the total number of locally recruited males was 51. Accordingly, 35% of all male recruits were local. Accepting this percentage, median distance of natal dispersal in females and males amounted to 0 and 25 km respectively (**Figure 3**).

The estimated number of male recruits outside the study area still wearing a neck collar after four years is 74, as a total of 19 is estimated to have lost theirs. Accordingly, roughly half of all males recruited outside the study area were found and reported.

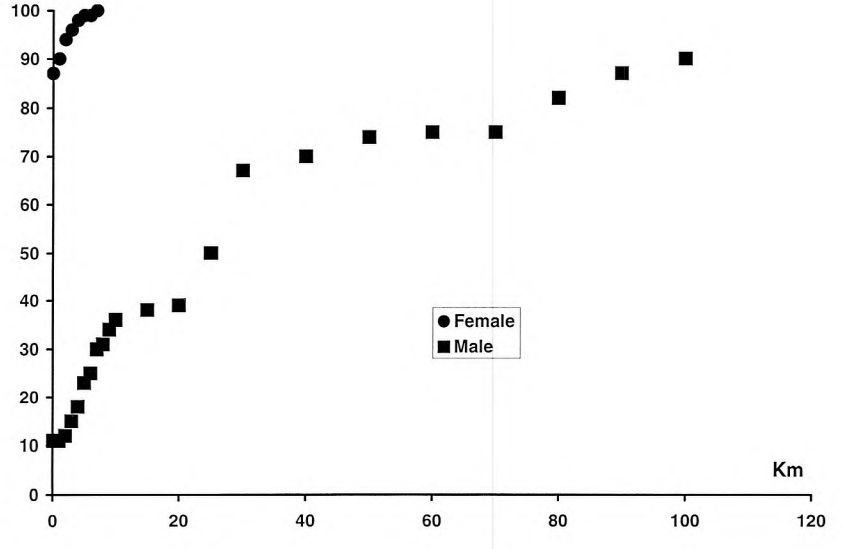

Figure 3. Distribution of natal dispersal distances among female and male Scanian Greylag Geese, up to 100 km from the point of origin. It is based on the assumption that all recruits (still wearing their neck collars) were recorded in the study area and that the likelihood that a recruit should be recorded outside the study area was the same everywhere.

Table 2. Rate of breeding dispersal of males and females from the four lakes in the study area, given as proportion of individuals that changed breeding site between successive years. Lakes are ranked based on food supplies during the brood rearing period, from the best to the worse (Nilsson *et al.* 1997).

Lake	Males		Females	
	Change (%)	n	Change (%)	n
1. Yddingen	0.3	293	0.0	263
2. Börringesjön	0.8	124	0.0	211
3. Klosterviken	2.7	149	1.3	219
4. Fjällfotasjön	5.3	76	0.9	109
Total	1.6	642	0.5	802

Breeding dispersal

Once recruited to a breeding area, the geese showed a very high degree of site tenacity. The rate of dispersal was three times higher among males than females, but extremely low in both sexes (**Table 2**). Among the dispersing individuals, eight males and four females changed to a neighbouring lake (2-3 km away), while two males changed to a lake situated 6 km away. No breeder dispersed further than 6 km.

Apparently the food supplies in the breeding lakes influenced the change of breeding site of established breeders (**Table 2**). Among the few breeders changing lakes, four males changed from Lake Fjällfotasjön to another lake, Lake Fjällfotasjön having inferior rearing areas compared to the other lakes. In the two lakes offering the best feeding conditions during that period, Yddingesjön and Börringesjön, no female and only one male in each lake changed site in the course of the study.

Discussion

In this study, there is no reason to assume that the true dispersal pattern of females differs from that presented here. A larger sample size could, however, reveal cases of dispersal distances exceeding seven kilometers (see below). For males, the result is associated with three potential biases. First of all, it might be questioned if the sexes really are recruited in identical proportions, but there is nothing indicating that it should not be the case. Second, if an annual neck collar loss rate calculated for males marked as goslings (8.4%) is used, the proportion of recruits recruiting locally increases from 35% to 40%. That loss rate was not used, however, as it was based on only 15 retraps (Persson 2000b). Instead, one based on all neck collared males was used, independent of age at marking. A third crucial question is whether reports from volunteers give a skewed picture. Based on the large number of resightings of the only

known male that recruited in Britain (Insley 1997) it can safely be stated that no other bird was recruited to that flyway. In the Atlantic flyway, however, there is currently no way of invalidating the assumption that the likelihood of a recruit being recorded outside the study area was the same everywhere. But, the distribution obtained seems to be fairly robust, as more than half of all potential recruits outside the study area were recorded. For instance, even in the extreme case that the outcome of the visits to the lakes within 30 km of the study area was that all recruits in that area were recorded, the median dispersal distance changes only from 25 to 26 km.

Most goose families congregate in brood rearing areas, sometimes situated up to 30 km from nesting areas (Cooke *et al.* 1995), adding a complicating factor when defining natal dispersal. In the present study, dispersal distance was measured from the brood rearing area, where the gosling was neck collared. In most cases, the place of hatching was unknown. For that reason a zero distance was applied when a bird recruited to the same lake in which it was reared. More correct, however, is to define a natal area. Greylag Goose families can walk a few kilometers over land, from a nesting water body to a rearing area (Nilsson & Persson 1994). Moreover, families regularly move from Lake Klosterviken to Lake Börringesjön during the latter part of the brood rearing period. Accordingly, it seems reasonable that a natal area includes both the natal lake and surrounding nesting waters lacking rearing areas, as well as that Lakes Klosterviken and Börringesjön are treated as one natal area. In such case, 98% of all females recruited in their natal area.

For males, on the other hand, it seems appropriate to extend the natal area to comprise the entire study area. Such an extension is supported by the fact that for three of the lakes, the proportion of known recruits found in the study area falls within an extremely narrow range, 57-60%. In the natal area, the recruitment is governed by where the male can find a mate, independent of which lake he was born or reared on.

A consequence of the faithfulness of females to their natal area is that the Greylag Goose spreads to new breeding areas very slowly, especially when the bird is forced to disperse more than a few kilometers. Local breeding populations can increase to sizeable numbers, while neighbouring potential sites, situated more than ten kilometers away, remain unoccupied (Persson 1990). However, the fact that these sites also finally become occupied demonstrates that a female can disperse a longer distance than shown in this study.

A strong pattern of natal female philopatry and male dispersal is the usual pattern in *Anatidae*, having been reported for Mute Swan *Cygnus olor* (Coleman & Minton 1979), Lesser Snow Goose *Anser caerulescens caerulescens* (Cooke *et al.* 1975) and Canada Goose

Branta canadensis (Lessels 1985) in addition to the present study. In the Lesser Snow Goose, some of the females also dispersed, while very few males were re-encountered in their natal colony. But as the fieldwork was more or less restricted to one colony, the well-studied La Pérouse Bay colony, hardly anything is known of how far the males dispersed (Cooke *et al.* 1975, 1995).

Even though the males in this study dispersed over large parts of the breeding range of the Baltic Greylag Goose, but none to the peripheral parts, their distribution was highly skewed towards the point of origin. Two thirds of all males were recruited within 30 km of the site where they had been reared. A factor facilitating this dispersal pattern might be that the point of origin was situated in the centre of the population's breeding range.

This study also gives an example of a bird establishing itself in another flyway. The main population in the British Isles is feral, being the result of a number of re-introduction projects, which made use of founding individuals of a mixed origin (Callaghan 1996).

In this study, both sexes exhibited an extremely strong philopatry to their breeding area once they were recruited. This was also the case for males after re-mating, which contrasts to earlier findings. In the Lesser Snow Goose, repairing after loss of mate takes place in winter or during spring migration, whereafter the male follows the female to her natal colony (Cooke *et al.* 1995). In the Baltic Greylag Goose, on the other hand, pair formation after divorce or death of a partner normally takes place in the breeding area, just after arrival in spring, or before the onset of autumn migration (Nilsson & Persson unpubl.). Apparently, the Greylag Goose re-pair with a familiar individual, while the Lesser Snow Goose does not.

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