INTRODUCTION

Dispersal is a process that influences population dynamics, mediates gene flow between populations, determines the rate of colonisation of new habitats and is a major component in the process of speciation. It therefore lies at the heart of modern evolutionary ecology. The phenomenon of individuals that are sighted outside their normal range has inspired research for at least a century and has supported a growing body of literature (see Clobert et al. 2001 for a review). However, much has still to be learned as the study of dispersal is beset with many practical problems. Natal
dispersal, the movement of individuals from their natal site to the site of first breeding, is especially difficult to study because dispersing individuals are not hindered by the boundaries of the study area and potentially can settle anywhere where suitable habitat exists (van Noordwijk 1995). This inevitably underestimates long-distance dispersal, although the introduction of genetic techniques has partly overcome these problems. However rare, long-distance dispersal potentially has far-reaching consequences as it can inhibit genetic divergence between seemingly isolated populations. Practical problems aside, long-distance dispersal probably remains rare in most species and the distribution of distances between natal and first breeding sites is typically skewed, with many individuals settling in or very close to the natal site, and few individuals dispersing long distances. For those staying ‘at home’, there are the potential benefits of interacting with kin, while long-distance dispersers might benefit from new and better opportunities or (re-)colonise new areas. There are also costs associated with both philopatry and dispersal. Individuals remaining ‘at home’ face the risk of inbreeding depression, whereas individuals dispersing far might not be well adapted to their new environments.

The relative costs and benefits of dispersal differ between individuals of differing quality, and this determines which individuals stay ‘at home’ and which disperse (e.g. Greenwood 1980, Verhulst et al. 1997, van der Jeugd 2001, Clobert et al. 2001). Long-distance dispersal might require special attributes or even morphological adaptations to be successful. Indeed, in Naked Mole-rats *Heterocephalus glaber* the probability of death during dispersal is extremely high, but recently a special dispersal morph has been discovered amongst captive-bred Mole-rats (O’Riain et al. 1996). This morph is behaviourally as well as morphologically adapted to long-distance dispersal between colonies. In insects, special life-history stages adapted to dispersal, usually recognised by the development of wings, are common (Zera 2003). There is evidence that exploratory behaviour in Common Lizards *Lacerta vivipara* (Clobert et al. 2001) and Great Tits *Parus major* (Dingemanse et al. 2003) is associated with dispersal.

Here we investigate the phenotypic correlates of long-distance dispersal in Barnacle Geese *Branta leucopsis* hatched and ringed in two colonies in the Baltic and resighted or recovered far outside their natal area. Colonial breeding birds like Barnacle Geese are highly suitable for the study of dispersal, since colonies are clearly separated, often conspicuous, and comparatively easily monitored, so that dispersers are identified unambiguously (Pradel 1996).

**METHODS**

Of the three East Atlantic flyway populations of the Barnacle Goose, the Russian-based population is by far the largest, with a nesting range traditionally centred on Novaya Zemlya and Vaigach, and wintering on the European mainland (mainly in Germany and The Netherlands). Within three decades, this population has undergone a dramatic change in breeding range and numbers through colonisation of new breeding areas to the southwest of their original breeding grounds (Ganter et al. 1999). In 1971, the first breeding pair was found in the Baltic (Larsson et al. 1988), and this population has since grown rapidly (Larsson & van der Jeugd 1998; Fig. 1). More recently, a breeding population was established in the southwest of The Netherlands, also growing rapidly (Ouweneel 2002, Pouw et al. 2005, van der Graaf et al. 2006; Fig. 1). New populations have adopted considerably shorter migration distances or become sedentary. Southern populations breed six to seven weeks earlier than populations in the north. Three populations, (Barents Sea, Baltic and North Sea) are now recognised, although information on the amount of exchange between these populations is currently lacking. There is evidence that, although winter ranges overlap, habitat choice on a smaller scale differs, i.e. even at the same staging site a subtle form of segregation prevails (van der Jeugd et al. 2001).
Smaller numbers of Barnacle Geese also breed in Greenland and Svalbard. Birds from these populations winter in Northern Ireland and on the island of Islay, and in South-western Scotland, respectively. Their wintering ranges do not overlap with those of the Barents Sea, Baltic and North Sea populations. Small numbers of individuals from the Svalbard population winter on the European mainland however, based on resightings of ringed birds (Black et al. 2007). Exchange of individuals between the wintering areas of the Greenland and Svalbard populations has also been observed (Black et al. 2007).

In this study, we only consider birds hatched and ringed in the Baltic population. Ringing commenced here in 1984 and continues to the present. Flocks of adult and juvenile Barnacle Geese were captured by round-ups at up to five different moulting localities on Gotland and Öland in the Swedish Baltic in mid-July each year. Captured birds were individually marked with metal rings, usually in combination with engraved coloured plastic leg rings, which allowed individual identification up to a distance of a few hundred meters. Among captured birds, adults, defined as birds one year old or older, were distinguished from juveniles. Each year until 2000 between 77 and 245 juveniles have been ringed with colour rings. In addition to these, up to 154 fledglings were ringed annually with metal rings only. From 2001 onwards, ringing was performed using metal rings only, and between 163 and 420 fledglings have been ringed annually until 2003. In total, 2662 fledglings were ringed with colour rings and another 1984 with metal rings only. Taken together, more than 4500 birds were available for detection at breeding localities away from their natal colony.

All birds were measured and weighed upon ringing when they were five to eight weeks of age, just prior to fledging. Sex was determined by cloacal examination (Owen 1980). Body mass, tarsus length and head length of captured birds were measured to the nearest 25 g, 0.1 mm and 1 mm, respectively (see Larsson et al. 1998 for details on measuring techniques). Tarsus length and head length have reached their final size when birds are one year old. Tarsus length, head length and body mass of juveniles are affected by genetic factors (Larsson & Forslund 1992, Larsson 1993, Cooke et al. 1995) but, to a considerable extent, also by the quantity and quality of the food eaten during

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Figure 1. Population trend of the East Atlantic Flyway population of Barnacle Geese (filled triangles) and number of breeding pairs in two recently established populations in the Baltic (SE) and The Netherlands (NL). The location of these populations, as well as the third study population mentioned in the text in northern Russia (RUS), is shown in the map.
growth (Cooch et al. 1991a,b, Larsson & Forslund 1991, Sedinger & Flint 1991, Lindholm et al. 1994). Body size measures therefore vary both within and among years and mean values of cohorts can be used as an index of the availability of high quality food and other environmental conditions to which the juveniles have been exposed after hatching (Loonen et al. 1997, Larsson et al. 1998). Here, tarsus length is used as an index of the overall size of individual juveniles. Because of sexual size dimorphism, tarsus length of juvenile males was standardised to female equivalents before further analyses by multiplying male tarsus length with a constant (0.938) reflecting the female/male ratio observed in the total sample of juveniles of known sex where tarsus length had been measured ($n = 4344$). After this procedure no difference in mean or variance between the sexes was detected. To correct for differences in the overall size and mass of juveniles between years and colonies, relative standardized tarsus length was calculated by subtracting colony and year specific means from individual values.

Observations from the public, birds shot by hunters, and resightings and recaptures by the authors and other workers in Barnacle Goose colonies were used to trace birds that had dispersed to places far from their natal area. Sampling was especially intensive in one of the recently established Barnacle Goose populations along the Barents Sea coast at the mouth of the Kolokolkova Bay (68°21'N, 52°12'E; Fig. 1). During July 2002, c. 4000 adult birds were captured during moult (van der Jeugd et al. 2003). In 2003 and 2004, some 2000 breeding pairs were monitored closely each year and 2950 and 3775 adult birds were captured during moult, respectively. All ringed birds that were observed outside the normal Baltic breeding range during the breeding season (May–August) when at least two years of age, i.e. when capable of breeding, were considered to have bred or at least to have attempted to breed in the area where they were observed. In addition, we added one bird that was observed among wintering Svalbard Barnacle Geese in Scotland during two consecutive winters, since it was likely that this bird had dispersed to Svalbard. Two more birds observed in Scotland had to be excluded because they could not be identified at individual level. In only a few cases is good evidence of proven breeding available.

Body size and body mass at fledging have previously been found to affect post-fledging survival in both males and females (van der Jeugd & Larsson 1998). The probability of natal dispersal increased with increasing mass and tarsus length in males, but not in females (van der Jeugd 2001). In the latter analysis, birds were classified as having dispersed when they were known to be alive at the age of five years – the maximum age of first breeding – but had not recruited into their natal colony. However, the resighting rate on the wintering grounds has decreased in later years because the number of observations received did not keep up with the increasing amount of ringed birds. Therefore it was not meaningful to select only birds that had survived up to a certain age for the analyses in this paper because too many birds would have been classified as being dead.

**RESULTS**

Out of 4646 birds that were ringed, 18 satisfied the criteria outlined in the methods (Table 1). Only three out of these 18 birds were observed breeding (nest with eggs or a brood), in 14 cases breeding was likely because birds were observed in suitable breeding habitat during the breeding season. In one case probable breeding was inferred because the bird wintered in Scotland during two years among birds belonging to the Svalbard population.

Of the 18 birds, 16 were males and two were females. Although ringing in the Baltic started in 1984, most birds were hatched recently, 14 after 1995, and only 4 before that year, probably due to increased search effort at potential breeding areas in recent years. For example, observations and catching of Barnacle Geese at Kolokolkova bay, Russia started in 2002 and has continued annually since. Six out of the 18 long-distance dispersers were detected here (Table 1).
Table 1. Characteristics of 18 long-distance dispersers among 4500 Barnacle Geese ringed as juvenile on the island of Gotland in the Swedish Baltic (57°17′N, 18°45′E) between 1988 and 2001. Tarsus rank refers to the rank of the bird according to its tarsus length at capture just prior to fledging compared to the other members of its cohort.

<table>
<thead>
<tr>
<th>Code</th>
<th>Sex</th>
<th>Hatched</th>
<th>Tarsus rank</th>
<th>Siblings</th>
<th>Evidence for long-distance dispersal</th>
<th>Coordinates</th>
<th>Distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>9164473</td>
<td>M</td>
<td>2000</td>
<td>1 (131)</td>
<td>?</td>
<td>Shot Kolokolkova Bay, Russia, May 2004</td>
<td>68°35′N, 52°18′E</td>
<td>2074</td>
</tr>
<tr>
<td>WDGE</td>
<td>M</td>
<td>2000</td>
<td>2 (150)</td>
<td>0</td>
<td>Probably breeding Hellegatsplaten, Netherlands, 2004</td>
<td>51°42′N, 04°22′E</td>
<td>1116</td>
</tr>
<tr>
<td>BHGE</td>
<td>M</td>
<td>1996</td>
<td>7 (218)</td>
<td>0</td>
<td>Found dead Mezen, Russia, July 2002</td>
<td>65°51′N, 44°14′E</td>
<td>1634</td>
</tr>
<tr>
<td>WFGP</td>
<td>F</td>
<td>2000</td>
<td>11 (150)</td>
<td>M</td>
<td>Caught Kolokolkova Bay, Russia, July 2002</td>
<td>68°36′N, 52°27′E</td>
<td>2080</td>
</tr>
<tr>
<td>R5B-</td>
<td>M</td>
<td>1993</td>
<td>19 (197)</td>
<td>F, F</td>
<td>Probably breeding Hellegatsplaten, Netherlands, 2004</td>
<td>51°42′N, 04°22′E</td>
<td>1116</td>
</tr>
<tr>
<td>YCW2</td>
<td>M</td>
<td>1997</td>
<td>23 (184)</td>
<td>0</td>
<td>Breeding Kolokolkova Bay, Russia, 2003–2004</td>
<td>68°34′N, 52°22′E</td>
<td>2075</td>
</tr>
<tr>
<td>9164432</td>
<td>M</td>
<td>2000</td>
<td>30 (131)</td>
<td>?</td>
<td>Observed Southern Finland, summer 2002</td>
<td>60°24′N, 22°12′E</td>
<td>401</td>
</tr>
<tr>
<td>BSG9</td>
<td>M</td>
<td>1995</td>
<td>31 (200)</td>
<td>0</td>
<td>Shot Kolguev, Russia, 2001</td>
<td>69°00′N, 49°00′E</td>
<td>1971</td>
</tr>
<tr>
<td>W=G-</td>
<td>M</td>
<td>1999</td>
<td>32 (157)</td>
<td>M, F</td>
<td>Shot Kanin, Russia, May 2002</td>
<td>68°00′N, 44°30′E</td>
<td>1756</td>
</tr>
<tr>
<td>BEG</td>
<td>F</td>
<td>1996</td>
<td>34 (110)</td>
<td>?</td>
<td>Shot Shoina, Russia, May 1999</td>
<td>67°55′N, 44°19′E</td>
<td>1741</td>
</tr>
<tr>
<td>9167052</td>
<td>M</td>
<td>2001</td>
<td>36 (267)</td>
<td>?</td>
<td>Observed southern Finland, summer 2003</td>
<td>60°24′N, 22°12′E</td>
<td>401</td>
</tr>
<tr>
<td>W=G1</td>
<td>M</td>
<td>1999</td>
<td>38 (157)</td>
<td>0</td>
<td>Breeding Kolokolkova Bay, Russia, 2004</td>
<td>68°34′N, 52°22′E</td>
<td>2075</td>
</tr>
<tr>
<td>BPWH</td>
<td>M</td>
<td>1991</td>
<td>48 (126)</td>
<td>0</td>
<td>Caught Kolokolkova Bay, Russia, August 2003</td>
<td>68°36′N, 52°27′E</td>
<td>2080</td>
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<tr>
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<td>?</td>
<td>Shot Kolokolkova Bay, Russia, May 2004</td>
<td>68°35′N, 52°18′E</td>
<td>2074</td>
</tr>
<tr>
<td>G6RK</td>
<td>M</td>
<td>1994</td>
<td>60 (181)</td>
<td>F</td>
<td>Breeding 't Zwin, Belgium, 1996–2002</td>
<td>51°22′N, 03°21′E</td>
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<tr>
<td>9166685</td>
<td>M</td>
<td>2001</td>
<td>77 (267)</td>
<td>?</td>
<td>Observed southern Finland, summer 2003</td>
<td>60°24′N, 22°12′E</td>
<td>401</td>
</tr>
</tbody>
</table>
The total number of Gotland immigrants in other populations is a function of the proportion of juveniles actually dispersing over long distances, and their annual survival. Van der Jeugd (2001) identified 231 dispersers among a sample of 1302 individuals that were hatched and ringed on Gotland between 1984 and 1993. Of these, 59 were found breeding at other localities in the Baltic. The rest (74%) was never observed during summer but they were inferred to have dispersed as they never returned to their natal colony yet were known to be alive from winter observations at an age of at least five years, when Barnacle Geese normally would breed. Assuming that few or no birds that dispersed to other areas within the Baltic were missed, this would mean that 172/1302 = 13.2% had dispersed to areas further away. Applying that figure to the 4500 birds that were the subject of this study, and taking an annual adult survival of 95% into account (Larsen et al. 1998), c. 330 Gotland dispersers should have been present in 2003 in populations outside the Baltic. Because the Russian population is by far the largest, most of these birds should be attempting to breed somewhere in northern Russia. Under less stringent assumptions, for example when half of the dispersers in the study by van der Jeugd (2001) that settled in the Baltic were actually missed, the proportion dispersing decreases to 6.6%, and the total number of dispersers to 170. Only 18 birds were actually found, a detection probability of 5.5 or at most 11%.

During three moult catches at Kolokolkova Bay in 2002, 2003, and 2004 a total of 10 725 adult Barnacle Geese were captured. Among these were three Gotland-hatched immigrants. Given that the Russian Barnacle Goose population numbered about 370 000 individuals in 2003 this means 103 ringed Gotland immigrants must have been present in the entire Russian population at that time. This is less than the 170–330 calculated above, but given that Arctic-breeding Barnacle Geese have lower survival (Ebbinge et al. 1991) that number reduces to c. 110–230. According to Pearson & Hartley (1962) the 95% confidence interval of our estimate from Kolokolkova Bay based on three captured immigrants is 58–182, which is of similar order of magnitude.

Although the sample size is too small to allow for rigorous analyses, one thing stands out: most of the 18 long-distance dispersers were large or very large compared to the other members of their cohorts (Fig. 2). Seven out of 18 birds were among the largest ten percent of their cohort, and the four largest birds (all males) ranked number 1, 2, 5 and 7 in their cohorts, which ranged in size from 131 to 218 birds (Table 1). Before calculating these ranks, male body size was standardized to female equivalents to control for sexual size dimorphism (see methods). In an analysis where differences in mean size between cohorts were controlled for by calculating relative values, tarsus length of long-distance dispersers was clearly larger than that of other birds ($t_{18,3693} = 4.16; P < 0.001$).

The 18 individual cases are briefly described below.

9164432
Hatched in 2000 at the island Skenholmen, male, unknown hatch date, with a tarsus length of 87.3 mm it ranked number 30 out of 131 fledglings ringed there that year. Because he lacked colour rings there were no observations until he
was seen (ring number read) at various locations near Turku in southern Finland in August 2002.

**9164473**
Like the previous bird, also hatched in 2000 at Skenholmen, male, unknown hatch date, with a tarsus of 93.0 mm one of the largest fledglings we ever caught, and the largest of the 131 members of his cohort. Because he had no colour rings we have no observations before he was shot at Kolokolkova Bay on 26 May 2004.

**WDGE**
Hatched 2000 at Laus holmar, male, unknown hatch date, the only surviving son of two ringed parents. A tarsus of 90.0, the second largest fledging of his cohort (n = 150). Seen on 10 March 2001 at the Frisian coast in The Netherlands with his parents, but never seen thereafter until May 2004 when observed in suitable breeding habitat at Hellegatsplaten, The Netherlands.

**BKGH**
Hatched 31 May 1996, at Laus holmar, male, one surviving sister, two ringed parents. Tarsus length of 86.7, fifth among 218 fledglings in his cohort. Seen 6 February 1997 in northwestern Germany without his parents, which were seen almost simultaneously 200 km to the southwest. Parents always wintered in Germany, but BKGH was seen a few times during winter in The Netherlands, and then turned up in northern Scotland in December 1999, to be seen again at Eastpark, Caerlaverock, Scotland in January 2001 among wintering birds from the Svalbard population with an unringed female. Presumably he had migrated to Svalbard during summer 1999 or 2000.

**BHGE**
Hatched also in 1996 at Laus holmar, male, unknown hatch date, ringed one day before the previous bird, the only surviving son of two ringed parents. A tarsus length of 86.5 mm was seventh largest among the 218 fledglings in his cohort. No observations of parents or son in the first winter, but the second winter there is one observation of BHGE in Friesland, The Netherlands. On 5 July 2002, in the middle of the breeding season, he was found dead near Mezen at the eastern coast of the White Sea in northern Russia.

**WFGP**
One of two females among the 18 long-distance dispersers. Hatched at Laus holmar as early as 17 May 2000. Fledged together with one brother. With a tarsus length of 80.1 mm number 11 among 150 fledged young. Parents both ringed. Although not observed together, parents and daughter spent the first three winters in the same area in the southwest of The Netherlands. Brother still with the parents in January 2001, but sister already on her own. During the first expedition to the Kolokolkova Bay she was caught on 21 July without signs of breeding (but few birds bred that year). She was never caught or seen again, and probably bred elsewhere in the area.

**WKR2**
Hatched at Laus holmar 22 May 1988, male. With a tarsus of 88.6 mm the largest of four siblings (three brothers and a sister) that made it to fledging. All four were seen during their first autumn without their parents, three of them, WKR2, a brother and the sister together, the other brother alone. None of the brothers ever returned to Gotland, although observations from the wintering grounds showed they were alive. The sister recruited into her natal colony at the age of three years and still breeds there to the present. WKR2 attempted breeding at Oostvaardersplassen where he was seen on 10 June 1991.

**R5B-**
Hatched on 24 may 1993 at Laus holmar. Male, ringed parents and two ringed sisters. Its tarsus length of 85.1 mm is well above average, rank 19 out of 197. Parents were very faithful to their wintering site in German Schleswig-Holstein, where they were observed more than one hundred times. They never travelled to The Netherlands. During the winter of 1993 they went to Germany again, accompanied by their two daughters. Son R5B- however did not accompany them and was alone right from the start of that autumn and went straight to the southwest of The Netherlands. He went back there during subsequent winters. On 10 April 2004 he was observed among the local breeders at Hellegatsplaten, The Netherlands, apparently preparing for breeding. His two sisters both returned to their natal colony on Gotland and breed at less than 100 m from their parents and each other.

**YCW2**
Hatched 24 May 1997 at Laus holmar, male. Tarsus length 85.0 mm (23/184). The only surviving fledgling of marked parents. After fledging it was never seen again, while the parents were seen regularly without young. It was caught six years later, on 6 August 2003 at Kolokolkova Bay, and seen shortly after with two fledged young and a marked female. One of the three birds out of the 18 that we know are breeding in their new surroundings, and as yet the only one that also produced fledged young.

Astonishingly, the whole family was seen again on 24 April 2004 on Gotland among Gotland breeding birds, and less than 1 km away from the place where the male was raised 7 years before. Russian birds are not seen in these parts of Gotland generally, and most birds from the colony at Kolokolkova Bay do not visit Gotland during their spring migration (Eichhorn et al. 2006). In fact, YCW2 and family were the only ones identified in the field on Gotland in the spring of 2004. The next day, they were gone, and two months later, on 30 June 2004, YCW2 and partner were
back at their breeding site at Kolokolkova Bay, where they produced a nest with six eggs that hatched on 12 July.

**B5G9**
Hatched on 27 May 1995 at Laus holmar, male. Tarsus length 85.7 mm (31/200). The only surviving son of two ringed parents. In winter, it was never seen with the parents, which usually stayed in the southwest of The Netherlands and were observed many times. After two years it was observed for the first time wintering along the Elbe river in Germany. On 23 August 1999 it was shot on Kolguev Island in northern Russia, where large colonies of Barnacle Geese exist.

**W=G=**
Hatched in 1999 at Laus holmar, male, unknown hatch date, tarsus length of 86.3 mm (rank 32 out of 157), ringed together with one brother, one sister and both their parents. There are no observations of this bird until it was shot at the Kanin Peninsula in Northern Russia in May 2002 at the age of three years. Parents, daughter, and the other son where regularly observed at various localities in The Netherlands during winter.

**BEGY**
The second of the two female dispersers. Hatched in 1996 at the island of Skenholmen with unknown hatch date, where it was retrapped one year later. With a tarsus length of 81.7 mm it ranked number 34 out of 110 fledglings ringed there that year. There are four observations at various sites in The Netherlands in winter before it was shot on 26 May 1999 at Shoina, northern Russia at the age of three.

**9164493**
Hatched on 28 May 1999 at Laus holmar, male. Tarsus length 85.7 mm (38/157). Only son of two ringed parents. Between its birth and 2004 the parents were observed 64 times during winter in The Netherlands, whereas their son was seen three times during the same period, and never with its parents, not even when it was still young. In 2004 it was found breeding at Kolokolkova Bay, northern Russia with an unringed female.

**9167052**
Hatched in 2001 at Laus holmar, male, unknown hatch date, tarsus length of 86.2 mm (rank 36 out of 267). Because it had no colour rings, there are no observations of this bird until it was seen in Southern Finland in August 2002, where it was killed by a golf ball.

**W=G1**
Hatched on 28 May 1999 at Laus holmar, male. Tarsus length 85.7 mm (38/157). Only son of two ringed parents. Between its birth and 2004 the parents were observed 64 times during winter in The Netherlands, whereas their son was seen three times during the same period, and never with its parents, not even when it was still young. In 2004 it was found breeding at Kolokolkova Bay, northern Russia with an unringed female.

**BPWH**
This male was hatched on 25 may 1991 at Laus holmar and had no surviving siblings. A tarsus length of 83.8 mm earned it rank 48 out of 126 birds. Its parents, also ringed, where observed many times during winter, but BPWH was already alone during its first autumn. It was then observed only a few times until it was trapped during moult at Kolokolkova Bay in August 2003.

**G6RK**
This male was hatched on 28 May 1994 at Laus holmar. Upon fledging its tarsus measured 82.7 mm, which made it an average bird (48/181). In contrast to other long-distance dispersers, it wintered in the same general area as its parents and sister in the southwest of The Netherlands. Already in 1996, at the age of two, it settled as a breeding bird in ‘t Zwin in nearby Belgium, together with an unmarked female. It was the first breeding Barnacle Goose in Belgium of proven wild origin. It was reported by many observers and is generally ‘well-known’ in Belgium. It was seen in the area again during subsequent breeding seasons until 1999. During at least two seasons it was seen with goslings but there is no proof that any of those ever fledged. Its sister settled close to her parents at Laus holmar, while its brother was never seen again and presumably died young.

**9166685**
Hatched at Laus holmar in 2001 with unknown hatch date with a tarsus of 83.0 mm (77/2670). No observations and never retrapped on Gotland until it was observed in southern Finland during the summer of 2003.

The common denominators of these case histories are that long-distance dispersers are predominantly males, that they are relatively large (Fig. 2), and that they seem to have become independent from their parents relatively early in life. Normally, offspring of geese stay with their parents during their first winter, and female offspring can even join their parents during subsequent winters (Ely 1993, van der Jeugd & Blaakmeer 2001, van der Jeugd unpubl.). In some cases, the stories of these dispersing male Barnacle Geese are strikingly different from those of their sisters hatched in the same year. Quite the opposite of males, female Barnacle Geese tend to return to their natal colony, and actively settle close to female kin (van der Jeugd 2001, van der Jeugd et al. 2002).
DISCUSSION

Natal dispersal is nearly always female-biased in birds, but the opposite is observed in waterfowl. Greenwood (1980) suggested that male dispersal is the rule in this group because the mating system in waterfowl is based on mate-defence rather than resource-defence, in contrast to most other bird species. In addition, Lessells (1985) and Rohwer & Anderson (1988) proposed that the benefits of knowledge of the breeding area may be greater in female than in male waterfowl because of their larger investment in reproduction. In an earlier study on the Baltic population, van der Jeugd (2001) found that 63% of dispersers that were found breeding in other colonies in the Baltic were males. Out of 172 that were not observed in the Baltic and, at least partly, must have bred at other localities further away, 70% were males. In the study reported here, 16 out of 18 (89%) true long-distance-dispersers were males. Taken together, these results suggest that especially long-distance dispersal in Barnacle Geese seems to involve mainly males. Moreover, many of these males were disproportionately large compared to other members of their cohorts, and were observed independently of parents and siblings early in life. Interestingly, in addition to three birds ringed as juveniles on Gotland, two males that were ringed as adults on Gotland were captured during moult in Kolokolkova Bay, Russia. Apart from their initial capture, these males were never seen again on Gotland. Both were over one standard deviation above the average size for adult males.

That dispersers are larger than philopatric individuals has been shown before in this species (van der Jeugd 2001, Black et al. 2007) as well as others (Verhulst et al. 1997). Van der Jeugd (2001) explained this by proposing that larger males are better at winning agonistic interactions at unfamiliar sites. The present study may suggest that there is something special about long-distance dispersers that make them actively search for new horizons. Their early independence may suggest that they are behaviourally programmed to do so, in a similar way that Great Tits with certain exploratory personalities are more prone to disperse (Dingemanse et al. 2003). The fact that long-distance dispersers were disproportionately large might suggest that the origin of their behaviour might lie in the conditions they experienced during early childhood.

Making calculations about the true number of long-distance dispersers based on the 18 birds that are the subject of this paper is hazardous and bound to be biased given all the factors that contribute to the probability of such birds actually being detected. Different calculations yielded somewhat different estimates of the total number of birds that disperse over long-distances. A proportion of at most 6.6% seems realistic and yields a detection probability of around 11%. Johnson (1995) reported similar results from a thirteen-year study on Lesser Snow Geese Chen caerulescens caerulescens in Northern Alaska. Only 17 out of 4000 birds ringed as juveniles were resighted in other colonies situated between 500 and 1200 kilometres away from their natal colony, pointing to a detection probability of at most 15%. These figures illustrate that finding long-distance dispersers is difficult, and that many years of intensive studies at various localities are needed to determine its full extent. The use of large numbers of cheap tracking devices that have a lifespan of more than one year and can transmit data would be a big step forward, but as yet such devices are not available. Geolocators (Eichhorn et al. 2006) and GPS loggers, although very useful for other types of studies, have the disadvantage that birds carrying them have to be retrieved to download data and thus are of little help in the study of dispersal.

Breeding was very likely in the 18 long-distance dispersers detected in this study, but was definitely proven in only three birds (all males), of which one was successful in at least one season. One other bird breeding in Belgium produced goslings in several years, but there are no observations of fledged young. This shows that long-distance dispersers are capable of breeding in environments that differ widely from their natal one, and that gene flow between different populations
along the east-Atlantic Flyway does occur. So far, only males have actually been observed breeding, and the majority of long-distance dispersers were males. Hence, gene flow probably only occurs along the male-line, and this could be detected using molecular techniques that can distinguish between male and female-biased gene flow (Helbig et al. 2001, Prugnolle & de Meeus 2002). One could indeed wonder whether female Barnacle Geese are at all capable of breeding at latitudes that are very different than their natal one, considering that the traits that are associated with timing of breeding, and hence differ between latitudes, are female traits, which could have a genetic origin or result from cultural transmission from mother to daughter.

The study of long-distance dispersal and the mechanisms behind it requires long-term field studies of large numbers of individuals, as this study showed. Only large numbers of detailed observations can reveal the different strategies that individuals follow to achieve their goals and how personality, previous experience, and learning act in concert to shape the dispersal patterns that we observe. Undoubtedly, more fascinating results and extraordinary tales of individuals’ travels will emerge during the coming years.

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REFERENCES


SAMENVATTING

Dispersie kan grote gevolgen hebben voor de mate van uitwisseling van genetisch materiaal tussen populaties, maar is vaak moeilijk te bestuderen omdat individuen zich ver buiten het studiegebied kunnen vestigen. In dit onderzoek werd het lot nagegaan van circa 4500 individueel herkenbare Brandganzen Branta leucopsis die tussen 1984 en 2002 uit het ei waren gekropen op het Zweedse eiland Gotland. Van deze vogels werden er slechts acht-


tien (zestien mannetjes, twee vrouwtjes) teruggevonden in andere populaties binnen het verspreidingsgebied van de Brandgans (Noordzee, Barentszsee, Spitsbergen). De meeste van deze ganzen waren erg groot vergeleken met andere vogels die in hetzelfde jaar waren geboren. Ze waren bovendien vaak al vroeg in hun leven zelfstandig. We schatten dat ongeveer 6,6% van alle jonge Brandganzen zich over zulke grote afstanden verspreidt, maar dat ten hoogste 11% van deze bewegingen ook daadwerkelijk kon worden vastgesteld. De meeste vogels vertrokken naar de grote Barentszzeepopulatie, waar verschillende vogels tijdens veldwerk in 2002–2004 broedend werden gezien of werden teruggevangen. Er werd één geval vastgesteld waarbij een mannetje geboren op Gotland naar Spitsbergen was getrokken. Ook in België werd een op Gotland geboren mannetje broedend vastgesteld. Broeden kon echter maar in drie van de achttien gevallen worden bewezen, en slechts één van deze broedgevallen was succesvol. Tijdens de voorjaarstrek op weg naar Rusland werd deze vogel, vergezeld van vrouw en drie geringde jongen, gedurende één dag waargenomen nabij zijn geboortekolonie op Gotland, waar normaal gesproken geen Brandganzen van de Barentszzeepopulatie verblijven. Ongetwijfeld gaan er meer intrigerende verhalen schuil achter het fenomeen van langeafstandsdispersie. Het is echter duidelijk dat onderzoek naar dit proces vele jaren in beslag neemt en dat daarbij verscheidene populaties intensief bestudeerd dienen te worden.

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