

**Wintering site interchange amongst Greenland White-fronted Geese *Anser albifrons flavirostris* captured at Wexford Slobs, Ireland**

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## Wintering site interchange amongst Greenland White-fronted Geese *Anser albifrons flavirostris* captured at Wexford Slobs, Ireland

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*The maximum count of Greenland White-fronted Geese wintering at Wexford, south-east Ireland (where over a third of the population winters) increased from 7910 in 1984/85 to 9530 in 1989/90. Although the population tends to be highly site-loyal on the wintering grounds, 14% of 700 marked geese seen in two consecutive winters changed site. Counts elsewhere in the wintering range and the recorded movements of marked birds indicate that a large influx of geese from Scotland to Wexford occurred in 1988/89. In the previous and subsequent winters large numbers of geese from Wexford remained in Scotland. No sex-related difference in birds changing site could be detected, but 68% of known-age birds which moved did so in their second and third winters when pairing is most frequent. Only 39 marked geese were recorded moving within winters (an average of 2.8% of the population each year), virtually all of these involved geese staging on route to or from wintering sites within Britain and Ireland. The maximum numbers are reached at Wexford in January/February when marked birds arrive from more northerly staging areas within Britain and Ireland.*

Several goose species show site loyalty to their wintering sites, for example Giant Canada Geese *Branta canadensis maxima*<sup>1</sup> staging Barnacle Geese *Branta leucopsis*,<sup>2</sup> and Dark-bellied Brent *Branta bernicla bernicla*.<sup>3</sup> To acquire nutrient reserves, migrate and breed successfully, geese must locate habitats providing adequate food resources on the wintering grounds. The major advantage of returning to familiar wintering sites is that the locations of reliable, undisturbed food resources in proximity to safe roosts are known. The evolutionary advantages of monogamous pair bonds and extended family cohesion are well demonstrated in arctic-nesting geese.<sup>4,5</sup> Separated mates and family members can re-unite at traditional roost sites if separated during the

course of a winter or on migration.<sup>1,6</sup>

Greenland White-fronted Geese *Anser albifrons flavirostris* are extremely site faithful, often returning to the same few fields each year.<sup>7,8</sup> At peatland sites on the breeding, staging and wintering grounds they traditionally feed on energy rich bog-plants such as *Eriophorum angustifolium*.<sup>9</sup> These feeding sites are frequently small patches within extensive remote lowland peatlands or wet grasslands. Returning to traditional sites with a knowledge of a patchy food resource is advantageous. If habitat conditions change unfavourably, through disturbance<sup>10</sup> or land drainage,<sup>11</sup> flocks of geese seem reluctant to move to alternative sites. During a period of rapid land-use change, extreme site loyalty amongst Greenland White-

fronted Geese may have resulted in several flock extinctions in recent years.<sup>8</sup>

An understanding of inter-site movements and their causes is therefore fundamental to the conservation of the population. Analysis of movements within the wintering range is important when interpreting within-winter trends in abundance at Wexford and elsewhere. It has been suggested, for instance, that past increases at Wexford have been due to immigration of birds from sites where flocks have declined, although no evidence has been available to support this idea. Although it is not possible to look at dispersal from the breeding grounds, it is possible to look at the age and sex of geese making moves within and between winters with particular reference to geese which may move as a result of pairing or family break-up. In this way, the causes of goose movements can be identified, to assess, for example, whether geese move site primarily for social or site-related reasons (e.g. reduced food availability, land-use change or disturbance).

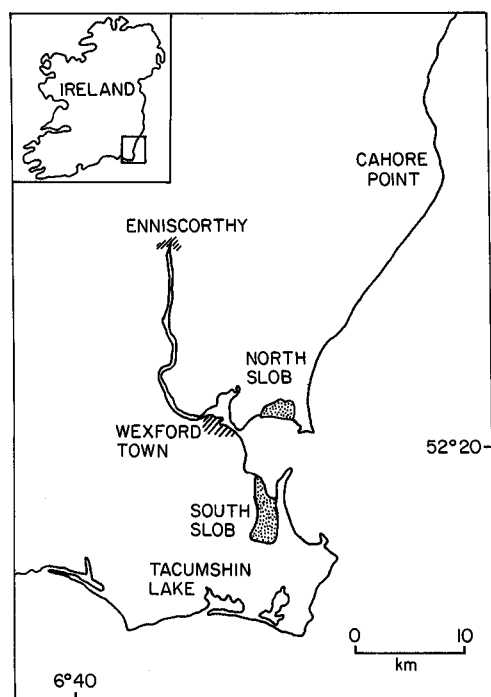
## STUDY AREA AND METHODS

The main wintering area comprises the North and South Slobs which were claimed from Wexford Harbour over 90 years ago (Fig. 1). The Slobs are intensively managed as grassland for stock, with some root crop cultivation and winter- and spring-sown cereal. Since the 1970s, between one-third and one-quarter of the entire world population of Greenland White-fronted Geese has wintered there.<sup>11</sup> The North Slob Reserve was established in 1969 and extended to its present size of 190 ha in 1990. Geese roost on offshore sandbanks at The Raven Nature Reserve, on the east flank of the reserve. In recent years, grassland at Cahore, 30 km north of Wexford (Fig. 1), has become increasingly important as an alternative feeding area for geese wintering at Wexford. Birds feeding there by day return to roost at the point of The Raven NR at night. Geese are also regularly seen at Tacumshin Lake, south of Wexford Harbour. Throughout this paper, the 'Wexford' wintering site comprises all these 4 separate but linked wintering resorts. The term 'stage' describes those birds which stop off at one wintering site (usually in Scotland) before moving on to their main wintering resort.

Monthly counts of geese were carried out at Wexford each winter by driving along the roads throughout the Slobs and recording numbers of geese in each field. Both Slobs were counted simultaneously (2 teams in all) and twice in quick succession: if counts differed by more than 3.5% a third count was made. Cahore and Tacumshin Lake were counted once at the same time.

Geese were cannon-netted at Wexford between October and December (1983/84 to 1989/90) and marked with BTO metal leg rings and individually coded plastic leg-rings and neck-collars (which could be read with a telescope from up to 800 m). Geese were sexed by cloacal examination and aged on plumage characteristics.<sup>12</sup> A total of 706 geese had been caught at Wexford by March 1990, plus a further 53 elsewhere in Ireland. Of these, 355 (47%) were juveniles (birds in their first winter) and hence of known age.

On 3 or 4 days each week from late September to April, 1 or 2 observers searched for marked geese on the Wexford Slobs. Other Irish sites used by Greenland White-fronted



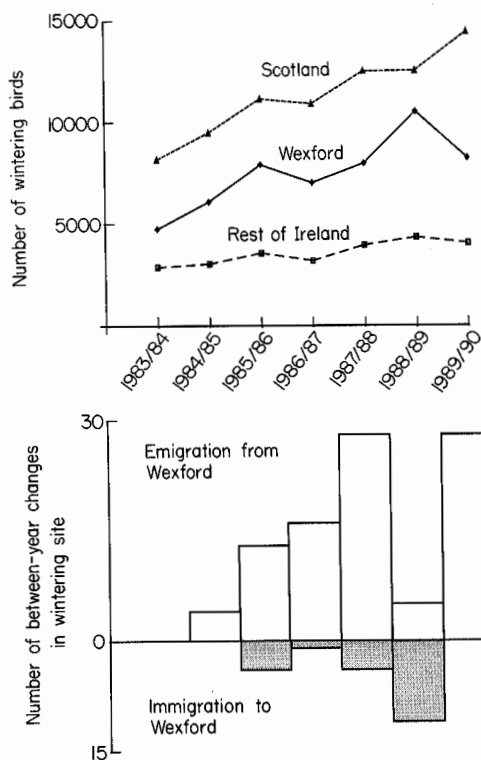
**Figure 1.** Location of Wexford Greenland White-fronted Goose wintering resorts mentioned in the text.

Geese were also covered on a regular basis, whilst volunteers counting at British resorts also recorded the presence of collars on a largely opportunistic basis. Up until the end of March 1990, there had been 15 945 resightings of marked birds. One Wexford-caught goose was known to have lost its leg-ring and 35 (4.6%) have lost collars out of 759 marked.

## RESULTS

### Overall trends in numbers at Wexford

The total Greenland White-fronted Goose population rose from *c.* 15 800 in November 1983 to *c.* 27 700 in November 1989, at an average rate of 8.0% per year.<sup>13</sup> The Wexford population increased at an average of 8.7% per annum (calculated from November counts).



**Figure 2.** Maximum counts of Greenland White-fronted Geese wintering Scotland, at Wexford and in the rest of Ireland, 1984/5–1989/90. Also shown are the frequencies of individually marked geese making between-year changes in wintering site to and from Wexford.

The maximum count rose from 7906 in 1984/85 to 9533 in 1989/90 (Fig. 2).

The number of geese wintering at Wexford was exceptionally high in 1988/89 (maximum count 11 026) but relatively low in 1989/90 (maximum count 9533). The most likely explanation is that in 1988/89, a large influx of geese from Scotland occurred, followed by large numbers of Wexford geese remaining in Scotland in 1989/90. Two lines of evidence support this explanation.

### Count information

The number of geese at Wexford in 1988/89 increased by 31.6% over the preceding November. At the same time, the number in the rest of Ireland increased by 9.5%, and in Britain by only 0.3%, whilst the population as a whole increased by 12%. In 1989/90, Wexford numbers decreased by 21.6% from the November count in 1988/89, those in the rest of Ireland decreased by 6.6%, those in Britain increased by 15%, but the population as a whole increased by only 1.2%. These data suggest that in 1988/89, although the population as a whole increased in line with the long-term trends (i.e. at an average rate of 8.0% per annum), there was an influx to Wexford of geese which normally wintered in Scotland. In 1989/90, geese were lost from Wexford (and the rest of Ireland to some extent) to Scotland as Wexford numbers fell by 21.6% over the preceding winter, whereas British numbers increased by 15%.

### Movements of marked birds

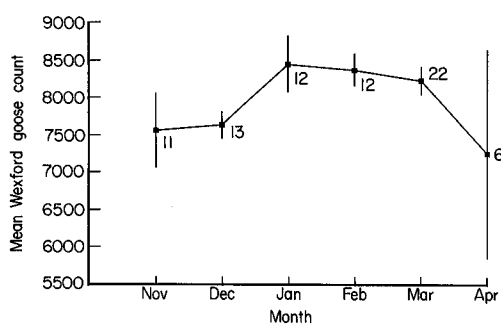
In 1988/89, the highest immigration rate (5%, 11 birds) and lowest emigration rate (2.3%, 5 birds) amongst marked birds occurred at Wexford (Table 1). This was in marked contrast to the winter immediately before and after; indeed, no marked geese moved to Wexford during 1989/90, although 11.5% of birds seen there in previous years wintered elsewhere. This suggests that the high totals recorded at Wexford in 1988/89 resulted from an unusual influx of geese from elsewhere that particular winter. The decrease in Wexford numbers in the following winter is explained by a large proportion of these immigrant geese reverting to wintering at other sites.

**Table 1.** Between-winter movements of Greenland White-fronted Geese ringed in Wexford, Ireland. Data expressed as the number (*n*) of marked geese seen in two separate sites in two consecutive winters. Figures in brackets indicate the percentage of marked geese making between-winter movements expressed as a proportion of the total number of marked geese seen in each two consecutive winters

	Winter					
	83/84-84/85 (n)	84/85-85/86 (n)	85/86-86/87 (n)	86/87-87/88 (n)	87/88-88/89 (n)	88/89-89/90 (n)
<b>Movement</b>						
Islay to Wexford	0	2	1	4	4	0
Argyll to Wexford	0	2	0	0	1	0
Galloway to Wexford	0	0	0	0	1	0
Rest of Ireland to Wexford	0	0	0	0	5	0
Wexford to Islay	2	7	14	10	5	21
Wexford to Argyll	2	3	0	7	0	5
Wexford to Galloway	0	0	2	4	0	0
Wexford to Rest of Ireland	0	3	0	7	0	2
Other	0	0	1	2	7	1
To Wexford	0	4 (3.0)	1 (0.5)	4 (2.1)	11 (5.1)	0
From Wexford	4 (14.2)	13 (9.6)	16 (8.1)	28 (14.0)	5 (2.3)	28 (11.5)
Total no. moves	4 (14.2)	17 (12.6)	18 (9.1)	34 (17.0)	23 (10.6)	29 (11.9)
No. non-movers	24	118	180	168	196	215

**Within-winter trends in Wexford numbers**

Each winter there is a gradual build up in numbers through October to December leading to maximum counts in January or February (depending on the year), followed by a slight drop in March (Fig. 3). In some years, there is another increase prior to the final departure in April, although full counts at this time are very variable according to time of departure. For



**Figure 3.** Mean monthly count data for Greenland White-fronted Geese at Wexford, Ireland, 1984/5-1989/90. Bars represent  $\pm$ SE about the means, digits indicate sample sizes (number of counts for each month).

example, in 1989/90 there was a gradual increase in the total count until January (9507), then a small drop in the middle of February of around 900 geese, then an increase to mid-March (9353), followed by a final decline as the geese departed.<sup>12</sup> The timing of within-winter movements of marked geese are consistent with this pattern (see below).

**Within-winter movements of marked birds**

Forty marked geese were recorded at more than one site within a winter: 36 made one move, while 4 have shown multiple within-winter changes in different seasons (3 made 2 moves and 1 made 3). The mean time interval between the resighting dates of birds making within winter movements was 48.2 days ( $n = 45$ ,  $SD = 34.9$ ). Estimates of annual emigration and immigration rates represent minimum values because of the lower resighting intensity in wintering sites away from Wexford. Sixteen (36%) geese moved elsewhere in Ireland, 37% were staging moves from Scotland to Ireland: 22% ( $n = 10$ ) from Islay, 13% ( $n = 6$ ) from Argyll, and 2% (1) from the Uists (Table 2). Another bird moved

**Table 2.** Within-winter movements of Greenland White-fronted Geese ringed in Wexford, Ireland. Data expressed as the number (*n*) of marked geese seen in two separate sites in each winter. Figures in brackets indicate the percentage of marked geese making within-winter movements expressed as a proportion of the total number of marked geese seen in each winter. No marked geese were recorded moving within winters 1983/84 and 1984/85

	Winter				
	85/86 (n)	86/87 (n)	87/88 (n)	88/89 (n)	89/90 (n)
<b>Movement</b>					
To Wexford from Islay	2	3	1	2	2
To Wexford from Argyll	0	0	4	1	1
To Wexford from Uists	0	0	0	1	0
Wexford to Islay	0	0	0	0	1
Wexford to Rest of Ireland	4	2	4	0	6
Within Ireland	2	0	0	0	0
Within Scotland	0	2	6	0	0
Scotland to rest of Ireland	0	0	0	0	1
To Wexford	2 (0.8)	3 (1.0)	5 (1.5)	4 (1.2)	3 (0.8)
From Wexford	4 (1.5)	2 (0.7)	4 (1.2)	0	7 (1.9)
Total no. moves	8 (3.0)	7 (2.4)	15 (4.6)	4 (1.2)	11 (3.0)
No. non-movers	255	288	313	336	356

from Wexford to Islay. The remaining 25% ( $n = 11$ ) included movements within Ireland and Scotland and movements between Scotland and Ireland (excluding Wexford).

An average of 2.8% of geese moved site within each winter but this varied slightly from year to year (see Table 2). Variation is likely to be a consequence of the number of marked geese in the population, and the low resighting intensity at areas away from Wexford in some years, as well as genuine between-year changes.

#### Timing of within-winter moves

The timing of within-winter movements of marked geese into and out of Wexford (Table 3) are consistent with the within-winter trends in numbers there. Eighteen (95%) of 19 geese seen 'elsewhere' were seen in Scotland, and only one (5%) occurred elsewhere in Ireland before wintering at Wexford. Table 3 illustrates the timing of geese moving into Wexford with a peak in November or December (13 geese seen in Wexford after being seen elsewhere). This movement corresponds with the mid-winter

**Table 3.** The timing of within-winter movements into and out of Wexford, Ireland of Greenland White-fronted Geese ringed in Ireland

Geese moving into Wexford		Moving out of Wexford	
Month first seen at Wexford	No. first seen at Wexford after seen elsewhere	Month last seen at Wexford	No. first seen elsewhere after seen at Wexford
Oct	1	Oct	0
Nov	7	Nov	0
Dec	6	Dec	1
Jan	3	Jan	0
Feb	0	Feb	4
Mar	2	Mar	9
Apr	0	Apr	2
May	0	May	1

peak in numbers at Wexford (recorded in January or February, depending on the year). After this mid-winter peak, geese moved out of Wexford and marked geese appeared elsewhere (Table 3). Three (18%) of 17 geese seen elsewhere after being in Wexford, were seen in Scotland, but the remaining 14 birds (82%) were seen in Ireland.

**Age and sex of marked geese making within-winter moves**

Table 4 summarizes the age and sex of marked geese making within-winter movements. Eighteen out of 35 marked geese which moved within-winter were male. According to Binomial Probability this is not significantly different from the number expected ( $P = 0.13$ ). Although 70% of the geese of known age which moved did so within the first and second years (aged 0–2 years), this was not significantly different from the number expected to move by chance (number moving tested against the number of marked geese in the population of that age,  $\chi^2 = 7.69$ ,  $df = 3$ ,  $P = 0.053$ ). Similarly, of geese ringed as adults, 80% were younger (1, 2 or 3 years after capture) rather than older (> 3 years after capture), although this result was non-significant (number moving tested against the number of marked geese in the population of that age,  $\chi^2 = 7.26$ ,  $df = 3$ ,  $P = 0.064$ ).

**Between-winter movements of marked geese**

A total of 103 marked geese were recorded at different sites in consecutive winters: 70 of these made 1 move only, 26 made 2 moves, 7

made 3 moves and 1 bird made 4 moves (Table 5). Information on the number and nature of moves made between two consecutive winters is presented in Table 5. On average, 22 (14.3%) of geese seen in 2 consecutive winters (1026 resightings) changed site. The majority of moves (75%,  $n = 94$ ) involved geese moving out of Wexford, whereas 16% ( $n = 20$ ) involved geese moving into Wexford: the average emigration rate out of Wexford was 9.2% per year compared to a 2% immigration rate. Since most neck-collared birds originate from Wexford, it is difficult to measure immigration rates accurately. In order to assess accurately how many geese move into Wexford permanently from elsewhere, more geese must be ringed at other sites in Ireland and Scotland.

The number of marked geese moving site between winters varied from year to year (Table 1). The highest immigration rate into Wexford (5%) and lowest emigration rate (2%) were found in the winter of 1988/89 when record numbers of geese were recorded at Wexford.

**Age and sex of marked geese making between-winter moves**

Thirty-two out of 66 geese moving once were male which, according to Binomial Probability, is not significantly different from the proportion of males in the captured population ( $P = 0.095$ ). Similarly, 24 out of 48 birds moving twice and 6 out of 18 birds moving three times were male and likewise, according to Binomial Probability, these findings are non-significant (geese making 2 moves,  $P = 0.115$ , geese making 3 moves,  $P = 0.071$ ) (Table 5). Sixty-eight per cent of known aged geese

**Table 4.** (a) Age (years) and sex of Greenland White-fronted Geese ringed in Ireland making within-winter moves (geese making one move only)

Age		Males		Females		Unknown sex	
Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
> 1	0–1	4	1	1	3	0	0
> 2	1–2	4	6	4	4	2	0
> 3	2–3	0	1	1	2	0	1
> 4	3–4	0	0	1	0	0	1
> 5	4–5	1	1	1	0	0	0
Total		9	9	8	9	2	2



**Table 5.** (a) Age (years) and sex of Greenland White-fronted Geese ringed in Ireland making between-winter moves (geese making one move only);  
 (b) age (years) and sex of Greenland White-fronted Geese ringed in Ireland making between-winter moves (geese making 2 moves);  
 (c) age (years) and sex of Greenland White-fronted Geese ringed in Ireland making between-winter moves (geese making 3 moves)

	Age		Males		Females		Unknown sex	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
<b>(a)</b>								
> 1	0-1		0	0	0	0	0	0
> 2	1-2		4	8	4	15	2	0
> 3	2-3		1	11	2	8	1	1
> 4	3-4		2	2	0	1	0	0
> 5	4-5		1	2	1	1	0	0
> 6	5-6		0	1	2	0	0	0
Total			8	24	9	25	3	1
<b>(b)</b>								
> 1	0-1		0	0	0	0	0	0
> 2	1-2		3	7	0	1	0	1
> 3	2-3		1	5	3	6	0	1
> 4	3-4		2	5	3	5	1	0
> 5	4-5		0	0	0	4	0	1
> 6	5-6		0	1	0	2	0	0
Total			6	18	6	18	1	3
<b>(c)</b>								
> 1	0-1		0	0	0	0	0	0
> 2	1-2		0	1	2	1	0	0
> 3	2-3		0	1	1	1	0	1
> 4	3-4		0	1	2	1	0	0
> 5	4-5		0	2	3	0	0	1
> 6	5-6		0	1	1	0	0	1
Total			0	6	9	3	0	3

which moved, did so in their second and third winters (i.e. aged between 1-3 years of age) which was significantly different from the number expected to move by chance alone (number moving tested against the number of marked geese in the population of that age,  $\chi^2 = 20.29$ ,  $df = 6$ ,  $P < 0.01$ ). Although 81% of geese of unknown age which moved, did so when they were younger (1, 2 or 3 years after capture) rather than older (> 3 years after capture), this difference was non-significant (number moving tested against the number of marked geese in the population of that age,  $\chi^2 = 8.19$ ,  $df = 6$ ,  $P = 0.22$ ). Exceptionally, 1

goose moved each consecutive year for 4 years after its first winter.

## DISCUSSION

### Overall trends in numbers at Wexford

Between 1983/84 and 1989/90 the numbers of Greenland White-fronted Geese wintering at Wexford have increased annually by 8.7%, slightly more than the overall 8.0% per annum in the population as a whole. Geese wintering at Wexford show consistently higher productivity than elsewhere in Britain and Ireland,<sup>13</sup>

although little is known about the differential mortality rates of differing wintering elements of the population. Relatively little is known about levels of emigration and immigration away from the Wexford wintering population.

In 1989/90, unusually low numbers of geese were present at Wexford (and in Ireland generally), suggesting that geese may have remained in Britain. Although the shooting moratorium was lifted at Wexford Slobs in 1989/90, there was no dramatic increase in within-winter movements of marked birds dispersing from Wexford and no obvious decline in the Wexford totals after the opening of the hunting season. The reason for the influx to Wexford in 1988/89 is unclear. Emigration from Wexford was high in the winters immediately preceding and following that winter, when immigration was greater than in any other winter. Since some Wexford birds do stage in Scotland on autumn migration, conditions were presumably very good in Britain during autumn 1987 and 1989 and hence some geese remained rather than moving on to Ireland. In contrast, the increased immigration to Wexford may reflect poor conditions in Scotland, with fewer birds remaining to winter.

#### Within-winter movements of geese

The within-winter trends in the total number of geese on the Wexford Slobs showed peak counts in January or February, followed by a slight drop, followed by a second peak in some winters prior to the final departure. The build up of numbers in the first half of winter is consistent with the arrival from Scotland (particularly Argyll and Islay) where some Wexford-wintering birds briefly stage in autumn (as shown by resighting data in this study and Wilson *et al.*<sup>8</sup>). The slight subsequent drop seems to be due to dispersal to other sites in Ireland, with some wintering geese moving on after January. The later peak in March/April may result from an influx of geese back to Wexford from elsewhere in Ireland, prior to departure on spring migration, although there are no resighting data to support this. Peak counts are recorded in different months in different years.<sup>12</sup> This suggests that movements and hence within-winter trends in numbers are dependent on food availability, disturbance

and climatic conditions on the Slobs and elsewhere.

The proportion of geese making within-winter moves each winter was 2.8%, higher than the 0.4% calculated by Wilson *et al.*,<sup>8</sup> possibly due to the additional 2 years' data as well as the fact that their data includes Greenland ringed geese (only 1 of which has been recorded moving within a winter). The results show no age or sex bias amongst geese making within-winter moves. It is assumed that extended parent-offspring relationships<sup>12</sup> will decrease the likelihood of young geese becoming separated from their parents, and hence lost on migration.

#### Between-winter movements of geese

Wilson *et al.*<sup>8</sup> calculated that 14.9% of Wexford ringed geese move between winters. The slightly lower value from this study (14.3%) is based on an additional 2 years' data. They also calculated that 7.5% of Greenland ringed geese move site between winters but suggest that this value is probably underestimated because of the lower resighting rate of Greenland ringed geese.

It is still difficult to say how many geese from elsewhere (particularly Ireland) move into Wexford. Of the 40 geese ringed between 1987/88 and 1989/90 at Sheskinmore, Donegal, 6 have subsequently been seen at Wexford (15%), 3 of which spent a whole winter there. This suggests that geese from elsewhere in Ireland do sometimes move into Wexford permanently (i.e. for 1 or more winters). The fact that the remaining three geese were seen only once at Wexford (in early winter) adds evidence to the suggestion that Wexford is used for staging by geese which move on to other sites in Ireland. However, it is far from clear whether geese from flocks which are diminishing in size are moving into Wexford, or whether differential productivity and mortality is the major factor in flock extinctions. In order to answer these questions, more geese must be ringed at sites away from Wexford.

Several studies of dispersal from the breeding grounds have been made on species which are known to be extremely faithful to their traditional breeding sites. The review of Greenwood<sup>14</sup> illustrated how, in most bird

species, female dispersal from natal breeding sites is more common than male dispersal, i.e. first and subsequent breeding attempts are in sites away from the female's natal site. In goose populations, it appears that male dispersal and female philopatry is more common, i.e. when two geese pair up, they return to the female's natal site to breed.<sup>15,16</sup> No sex bias was found amongst geese making between-winter moves, nor amongst those moving in association with new mates. The lack of difference between the sexes may be a feature of the low sample size present in this study. The higher incidence of younger geese moving between winters is undoubtedly due to family break-up and pairing for the first time. Also, exploratory migration may be an important factor resulting in young geese moving site more than older geese.<sup>17</sup> A continued and more extensive programme of individual marking is required to fully address this and other questions, particularly to ensure the most effective management of this threatened population.

#### ACKNOWLEDGMENTS

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#### REFERENCES

1. Raveling, D.G. (1979) Traditional use of migration and winter roost sites by Canada Geese. *J. Wildl. Manag.* **43**, 229–235.
2. Gullestad, N., Owen, M. and Nugent, M.J. (1984) Numbers and distribution of Barnacle Geese *Branta leucopsis* on Norwegian staging islands and the importance of the staging area to the Svalbard population. *Nor. Polarinst. Skr.* **181**, 57–65.
3. St. Joseph, A.K.M. (1979) The seasonal distribution and movements of *Branta bernicla* in western Europe, pp. 45–59. In: Smart, M. (ed.) *Proc. 1st Tech. Mtng. on Migratory Bird Management, Paris 1977*. Slimbridge, IWRB.
4. Black, J.M. & Owen, M. (1987) Determinants of social rank in goose flocks: acquisition of social rank in young geese. *Behaviour*, **102**, 129–146.
5. Black, J.M. & Owen, M. (1989) Parent-offspring relationships in wintering Barnacle Geese. *Anim. Behav.* **36**, 187–198.
6. Prevett, J.P. and MacInnes, C.D. (1980) Family and other social groups in Snow Geese *Wildlife Monographs*, **71**, 1–46.
7. Fox, A.D., Madsen, J. and Stroud, D.A. (1983) The summer ecology of the Greenland White-fronted Goose (*Anser albifrons flavirostris*). *Dansk Orn. Forens. Tidsskr.* **77**, 43–55.
8. Wilson, H.J., Norriss, D.W., Walsh, A., Fox, A.D. & Stroud, D.A. (1991) Winter site fidelity in Greenland White-fronted Geese *Anser albifrons flavirostris*: implications for conservation and management. *Ardea*, **79**, 287–294.
9. Fox, A.D., Stroud, D.A. & Francis, I.S. (1990) Up-rooted Common Cotton-grass *Eriophorum angustifolium* as evidence of goose feeding in Britain and Ireland. *Bird Study*, **37**, 210–212.
10. Norriss, D.W. & Wilson, H.J. (1988) Disturbance and flock size changes in Greenland White-fronted Geese wintering in Ireland. *Wildfowl*, **39**, 63–70.
11. Ruttledge, R.F. & Ogilvie, M.A. (1979) The past and current status of the Greenland White-fronted Goose in Ireland and Britain. *Irish Birds*, **1**, 293–363.
12. Warren, S.M. (1990) An analysis of the Irish Wildlife Service Greenland White-fronted Goose Project 1983/4–1989/90. *Report to NP&WS, Ireland* by The Wildfowl and Wetlands Trust, Slimbridge.
13. Stroud, D.A., Fox, A.D., Wilson, H.J. & Norriss, D. (1991) Greenland White-fronted Geese in Ireland and Britain: population monitoring and conservation. *Biological Conservation*.
14. Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162.
15. Cooke, F., MacInnes, C.D. & Prevett, J.P. (1975) Gene flow between breeding populations of Lesser Snow Geese. *Auk*, **92**, 493–510.
16. Lessells, C.M. (1985) Natal and breeding dispersal of Canada Geese *Branta canadensis*. *Ibis*, **127**, 31–41.
17. Baker, R.R. (1978) *The Evolutionary Ecology of Animal Migrations*. Hodder & Stoughton, London.

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