Site fidelity and range size of wintering Barnacle Geese *Brantaleucopsis*

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Geese, amongst other migratory species, show considerable philopatry not only to their breeding sites but also to traditional wintering and staging areas (Owen 1980, Robertson & Cooke 1999). This may reflect the selective advantage of having local knowledge of resource availability, habitat heterogeneity, vulnerability to predation and levels of disturbance, or be a mechanism for individuals to maintain social bonds with conspecifics (for a recent review see Robertson & Cooke 1999).

Although wintering geese may return to the same general region, on a smaller scale individuals frequently move between separate feeding areas within and between seasons. Some of these movements are predictable; many geese show a pronounced habitat switch in midwinter, or in the spring prior to migration to staging or breeding grounds (Ydenberg & Prins 1981, McKay et al. 1994). Spring shifts from intensively managed areas to saltmarsh are often attributed to changes in nutritional requirements from energy-dense, highly digestible sown grasses, to protein-rich saltmarsh grasses and herbs (Prins & Ydenberg 1985, McKay et al. 1994).

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Midwinter movements are more probably due to depletion of local food resources because of slow vegetation growth rates during cold weather (Owen et al. 1992, Vickery et al. 1995). Some birds may then either choose to disperse to a more suitable feeding site, or are forced to do so because of increased competition (Hupp et al. 1996).

Because of protective legislation and the provision of refuge areas, the Svalbard breeding population of Barnacle Geese Branta leucopsis has shown a remarkable recovery from around 300 birds in 1948 to c. 24 000 birds in 1999–2000 (Owen et al. 1987, Phillips et al. 2000). The birds winter on the Solway Firth, where they have amongst the smallest wintering range of any goose population (Owen 1980). Although the population shows almost complete philopatry to the Solway as a whole, very little is known about fidelity to particular feeding areas and variation in ranging behaviour of individuals within the region.

Previous research has examined local site fidelity of wintering Barnacle Geese from both the Greenland and Russian/Baltic breeding populations using resight- ings of ringed individuals (Percival 1991, Ganter 1994). This approach, although clearly very useful, can only be applied within study areas where ring reading is

possible, and is not practical on the Solway where the great majority of past resighting effort has been concentrated around a single site. In addition, ring resightings are rarely frequent enough to provide detailed information on timing of movements. As an alternative, we used radiotelemetry to locate individual Barnacle Geese every 2–3 days over several months. We investigated individual variation in site fidelity, the timing and duration of visits to different feeding areas, range sizes and overlap, seasonal changes in habitat use and whether certain foraging strategies were common among different individuals. In addition, we wanted to compare groups of birds caught in two different parts of the wintering range.

METHODS

Study site

The Svalbard breeding population of Barnacle Geese winters on the Solway Firth, southwest Scotland (54°57′N 3°28′W) arriving in late September/early October and remaining until late April/early May, when they depart to staging areas in the Helgeland archipelagos, off the central Norwegian coast (65°45′N 12°E). During the winter, the geese are protected from shooting and human disturbance when feeding on reserves or in a network of core fields within a local goose management and compensation scheme (administered by Scottish Natural Heritage, Dumfries). Their diet is predominantly grasses and herbs (Puccinellia maritima, Festuca rubra and Triglochin maritima) and White Clover Trifolium repens stolons on the saltmarsh, and cultivated grasses (mainly Lolium perenne with some Agrostis and Poa spp.) on inland pasture (Owen et al. 1992).

The overall wintering area is small, extending no more than 50 km west to east, with birds rarely ranging further than 5 km from the Solway coast. However, the geese only feed in a small fraction of the available habitat and the range can be split into four discrete areas, Southerness, Caerlaverock (including Kirkconnell merse), northwest Cumbria (including Moricambe Bay) and Rockcliffe Marsh (including Burgh; Fig. 1). Caerlaverock is the traditional arrival site, and Rockcliffe Marsh the main departure point for most, if not all the geese (see Discussion). There are three reserves on the Solway actively managed to attract geese; Eastpark Farm (Caerlaverock) managed by The Wildfowl and Wetlands Trust (WWT) since 1970 and totalling 340 ha, Mersehead Farm (Southerness), a 250-ha reserve managed by the Royal Society for the Protection of Birds (RSPB) since 1993, and North Plain Farm (northwest Cumbria), a 72-ha reserve man- aged by the RSPB since 1990.

Overall distribution

A coordinated census of all barnacle geese on the Solway was carried out each month from mid-October

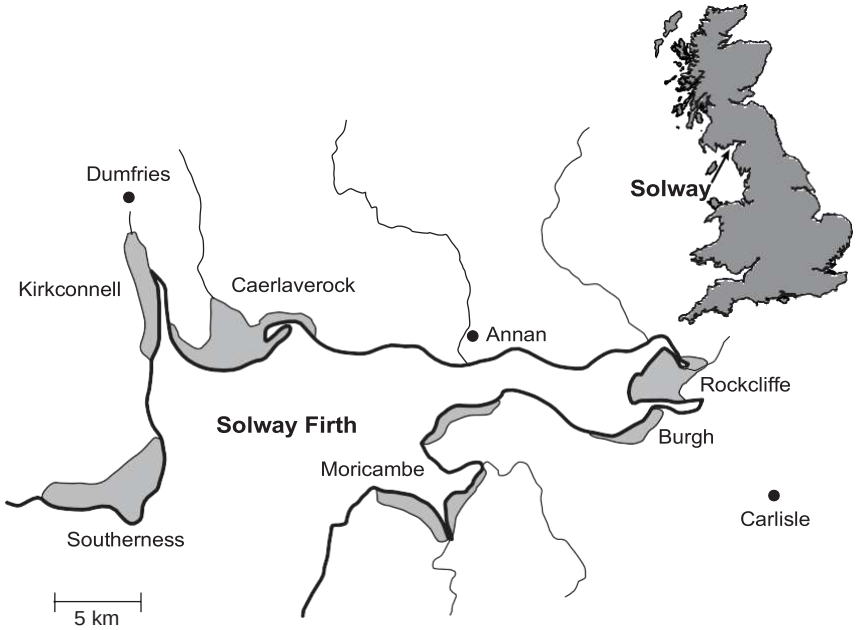

Figure 1. Location of study site and areas (shaded) used by Barnacle Geese on the Solway.

1999 to March 2000. All known feeding sites were surveyed during low tide (when all saltmarsh areas were potentially accessible) and before noon, within a period of one hour by a total of 10–12 observers, and flock locations and numbers of geese recorded.

Radiotracking

Geese were caught using cannon nets on improved pasture at two sites; Newfield Farm (54°57′N 3°29′W), adjacent to the WWT Caerlaverock Reserve, on 2 November 1999, and RSPB Mersehead Reserve, Southerness (54°53′N 3°41′W) on 14 December 1999 and 27 January 2000. Birds were sexed by cloacal examination, aged as juvenile (< 1 year old) or adult according to plumage characteristics, and if not already ringed, fitted with unique metal and plastic leg rings. Eight adult and two juvenile males from the first catch at Newfield Farm (hereafter referred to as Caerlaverock birds) and five adult males from each of the two following catches (hereafter referred to as Southerness birds) were fitted with tail-mounted TW-3 radiotransmitters (Biotrack, Dorset, UK). Transmitters weighed 17 g, corresponding to < 1% of mean body mass of tagged birds (2000 g, n = 20). Birds were of unknown pair and breeding status, and only males were radio- tagged to maximize sample sizes by ensuring we did not follow both members of a pair (which remain together during the winter).

Movements of radiotagged birds were followed from capture to departure from the Solway in late April/early May 2000, or until transmitters were lost. Visits were made three to four times a week to all known feeding sites and the presence of tagged geese detected using three-element Yagi antennae and M-57 receivers (Mariner Radar). Each individual was generally located a minimum of once every three days throughout the period of transmitter attachment. Any movement between each of the four main areas (Southerness, Caerlaverock, Rockcliffe Marsh or northwest Cumbria) was considered to have occurred mid-way between the dates of the fixes at either site.

The season was split into four stages according to the dates when transmitters were attached, and to an obvious predeparture shift to Rockcliffe Marsh. These were 2 November to 13 December 1999, 14 December 1999 to 26 January 2000, 27 January to 31 March 2000 and 1 April until departure. The last cut-off date of 1 April was selected as several geese previously feeding at Caerlaverock and Southerness moved to Rockcliffe Marsh in early or mid-April (see Results).

From 14 December until the end of the season, birds were located as far as possible to particular fields by visual observations of flocks from elevated vantage points or by triangulation. The exception was at Rockcliffe Marsh, where although it was straightforward to detect the presence of tagged birds, logistical difficulties, including access restrictions, problems with disturbance and the absence of good vantage points precluded obtaining more accurate fixes.

Several measures of home range size and structure for birds within the Caerlaverock and Southerness areas were calculated using Ranges V software (Kenward & Hodder 1996). In order to avoid any bias resulting from unevenness in recording effort, fixes were only included when all potential feeding sites within these areas were checked by observers within a two-day period. If a tagged goose was located more than once within this time, a single fix per bird was selected at random. The purpose of this analysis was to examine range characteristics (size, overlap etc.) within these two areas rather than maximum range extent during the winter, which would be heavily dependent on whether indi- viduals visited Rockcliffe or northwest Cumbria.

Range statistics calculated were: (i) a minimum convex polygon (MCP) enclosing 100% of fixes, which provides an indication of the maximum extent of the foraging area, (ii) a core range in which each goose concentrated its activity (based on apparent discontinuities in utilization plots) and corresponding to the area of 85% cluster polygons (Cx_{85}) and (iii) the partial area (C_{part}) of 85% cluster polygons, which is the area of the separate clusters divided by the area of a single polygon that would include all clusters (Hodder et al. 1998, Walls et al. 1999). If C_{part} tends to 0, this indicates that the range is more fragmented, if C_{part} tends to 1, this indicates that the nuclei are close to one another, and if $C_{part} = 1$, there is only one nucleus (Kenward & Hodder 1996). Ranges V software was also used to calculate the percentage overlap of MCPs and core ranges among birds to determine the extent to which individuals used the same foraging areas during the winter.

RESULTS

Changes in overall distribution

Numbers in the Caerlaverock area (the traditional arrival site) were high in mid-October, but subsequently declined as geese dispersed to other areas (Fig. 2). The total number in mid-February was much lower than

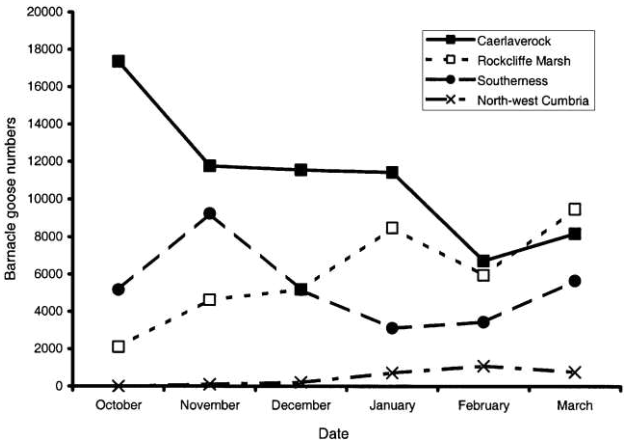

Figure 2. Numbers of Barnacle Geese in different areas on the Solway from October 1999 to March 2000.

expected, suggesting that several thousand geese may have moved out of the census areas entirely. These birds could either have been feeding at sites much further inland or have travelled further afield to join other Barnacle goose populations wintering on Islay or in The Netherlands/Denmark.

Duration of transmitter attachment

Both juveniles caught at Caerlaverock lost their transmitters within a week and were excluded from further analysis. Four adult Caerlaverock birds and one Southerness bird caught in December also lost transmitters before the end of March. Fixes from these birds were included in the results. Geese were easily detected up to 5–10 km from appropriate vantage points in each area. All tagged geese departed between 29 April and 8 May.

Use of different feeding areas: seasonal pattern

Seasonal changes in the proportion of time spent by tagged geese in each of the four main areas is summarized in Table 1. Caerlaverock birds initially spent the majority of their time feeding in the Caerlaverock area and the remainder at Rockcliffe Marsh, but with the relative importance of Rockcliffe gradually increasing as the season progressed. By comparison, Southerness birds spent the majority of their time at Southerness in mid-season. Time spent at Southerness then declined and that at the other areas rose, with a substantial increase in use of Rockcliffe at the end of the winter.

Use of different feeding areas: individual pattern

All Caerlaverock birds made substantial use of both Caerlaverock and Rockcliffe, with just two birds (B and F) visiting other areas in February and March (Fig. 3). With the exception of Bird G that lost its transmitter in mid-February, all made one or more trips to Rockcliffe Marsh before the end of March. Southerness birds exhibited more variable strategies. From tagging until mid-April, two birds (J and O) never left the Southerness area, two others (I and Q) only made single visits, of 2 and 16 days respectively, to Caerlaverock, and another (R) moved immediately to Caerlaverock and then to Rockcliffe where it remained for most of the season. By contrast, the remaining Southerness birds ranged much more widely before mid-April, although the number of areas used varied considerably. All Caerlaverock birds and all but one Southerness bird stopped at Rockcliffe for at least a few days immediately prior to departure from the Solway.

Range size and structure

At Caerlaverock and Southerness, MCP and core range (CX_{85}) sizes were stable once there were 15 or more locations per individual. All individuals with fewer data were therefore excluded from home range analyses.

Table 1. Seasonal changes in the percentage of time spent in different areas by radiotagged Barnacle Geese in 1999–2000.

Original capture site	Sample size		Period	Proportion of time (%) spent at			
	Birds	Goose days		Caerlaverock	Rockcliffe Marsh	Southerness	Northwest Cumbria
Caerlaverock	8	336	2 Nov–13 Dec	78	22	0	0
	8	352	14 Dec–26 Jan	81	19	0	0
	7	372	27 Jan–31 Mar	56	38	3	3
	4	152	1 Apr–departure	9	91	0	0
Southerness	5	220	14 Dec–26 Jan	10	4	87	0
	10	640	27 Jan–31 Mar	18	14	62	6
	9	307	1 Apr–departure	11	44	45	0

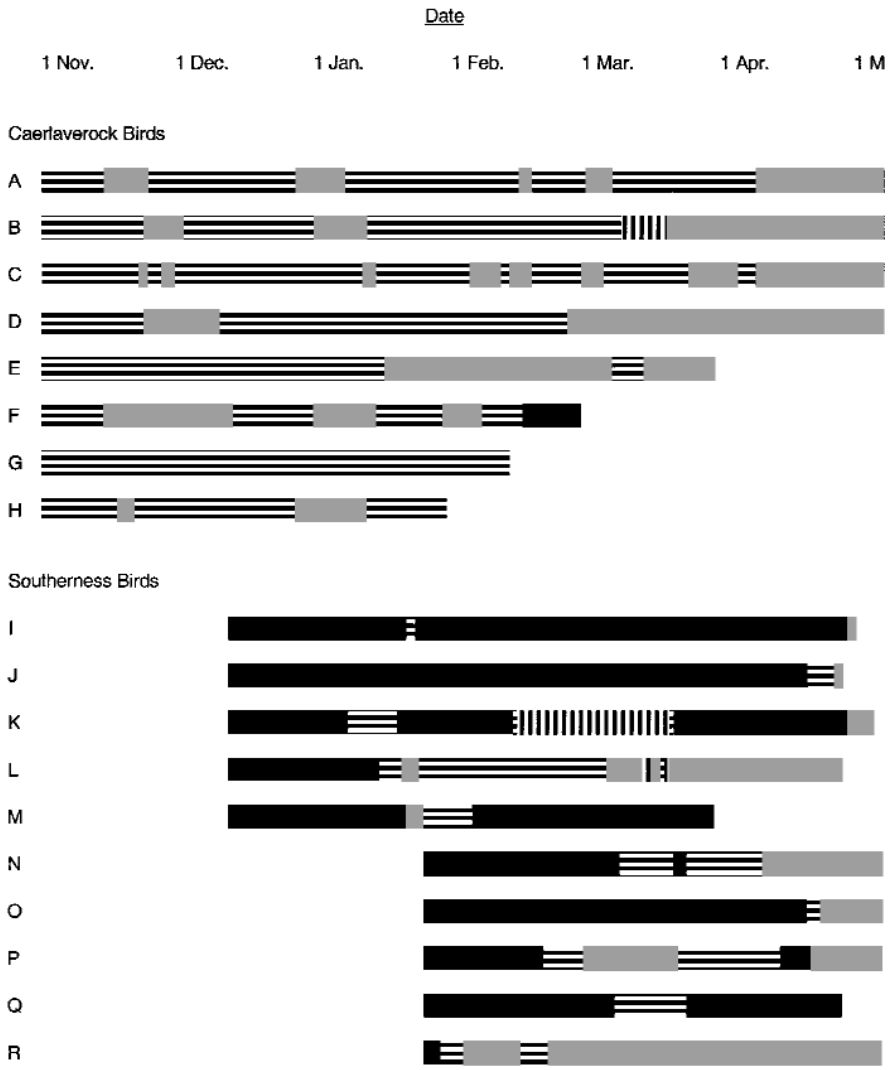

Figure 3. Time spent in different areas by individual radiotagged Barnacle Geese in 1999–2000. Note that several birds (E, F, G, H and M) lost their transmitters before the end of March. Horizontal shading = Caerlaverock, Grey fill = Rockcliffe Marsh, Black fill = Southerness, vertical shading = northwest Cumbria.

Range statistics for Caerlaverock and Southerness birds while at Caerlaverock, and for Southerness birds at Southerness are summarized in Table 2. There were no significant correlations between the number of fixes or the total time spent by each individual at either Caerlaverock or Southerness, and range size (MCP or Cx_{85}) ($r = 0.11–0.55$, $n = 7–10$, all ns).

Maximum foraging ranges (MCPS) were approximately five times larger (Mann–Whitney U test, $Z_{adj} = 3.42$, $P < 0.001$), and core ranges (Cx_{85}) two times greater (Mann–Whitney U test, $Z_{adj} = 2.24$, $P < 0.05$) at Caerlaverock when compared to Southerness (Table 2). The difference in C_{part} values was almost significant (Mann–Whitney U test, $Z_{adj} = 1.86$, $P = 0.06$). Excluding the two birds at Caerlaverock with C_{part} values of 1 (i.e. with mono-nuclear core ranges), the difference became highly significant (Mann–Whitney U test, $Z_{adj} = 3.01$, $P < 0.005$).

Overlaps between foraging ranges of individuals were high at Southerness. The mean percentage overlaps in MCP and Cx_{85} areas were 86% and 64%, with 37 MCP pairs and 21 Cx_{85} pairs out of 42 paired ranges from the seven tagged geese overlapping by > 70%, and only one Cx_{85} pair overlapping by less than 40%. At Caerlaverock, the corresponding mean values for overlaps in MCP and Cx_{85} areas were 58% and 42% (i.e. each > 20% lower than at Southerness), with only 32 MCP pairs and 11 Cx_{85} pairs out of 90 paired ranges from the 10 tagged birds overlapping by > 70%, and 25 and 47, respectively, overlapping by less than 40%.

Table 2. Comparison of ranges of radiotagged Barnacle Geese in the Caerlaverock and Southerness areas from 14 December 1999 to departure or tag loss. Note that only for three Southerness birds were sufficient fixes obtained to determine their range characteristics during visits to the Caerlaverock area.

	Caerlaverock area				Southerness area	
	Caerlaverock birds (n = 7)		Southerness birds (n = 3)		Southerness birds (n = 7)	
	Median	Range	Median	Range	Median	Range
Days in area	75	41–97	32	29–48	91	46–136
Number of fixes	35	17–56	21	18–26	37	18–59
MCP area (ha)	3400	1284–5022	4328	3129–6948	618	399–723
Cx_{85} area (ha)	558	231–1032	360	334–442	254	176–338
C_{part}	0.28	0.13–1.00	0.14	0.09–0.15	0.53	0.48–0.62

Compared with those at Caerlaverock, geese at Southerness were therefore considerably more likely to use the same foraging sites during the winter.

DISCUSSION

General pattern

Few studies have tracked movements of individual wintering geese for long periods prior to departure on migration (but see Summers & Critchley 1990, Hill & Frederick 1997). Here we provide data on intraspecific variation in ranging behaviour on a much finer scale than could be achieved using ring resightings or frequent censuses. However, as birds were sometimes located in our study only every c. 3 days, brief (1–2 day) visits to some feeding areas may have been undetected. There may therefore be some small errors in estimates of number of visits or time spent in particular areas, but these are unlikely to have any effect on our general conclusions. There is also the possibility in radiotracking studies that study birds were in some way unusual. Although we restricted our study to adult males, these were selected at random, their relative use of different areas mirrored that of many others in the population, and there is therefore no reason to consider their behaviour atypical.

Individuals adopted one of a number of strategies usually common to several geese trapped in the same area (Fig. 3). Those caught at Caerlaverock were almost all wide-ranging, making the c. 24 km trip to Rockcliffe Marsh on several occasions. Excluding the predeparture period (from 1 April), they spent 20–45% of the season at Rockcliffe Marsh, compared with 46–80% at Caerlaverock. Only one Caerlaverock bird visited Southerness and another went to northwest Cumbria. In contrast, notwithstanding their shorter tracking period, four of the geese trapped at Southerness were more sedentary, rarely or never moving from that area in several months, and staying within a core area of only 180–340 ha (median 250 ha; Table 2). These birds only dispersed to Rockcliffe Marsh at the end of the winter just prior to the spring migration, in two cases with a brief stop at Caerlaverock. Other Southerness birds travelled much further afield, particularly during February and March, although to different areas. Somewhat surprisingly, it was exceptional for more than one tagged bird to change area on the same date (Fig. 3), with this lack of synchrony suggesting that movements were little influenced by short-term environmental variability such as changes in tidal state or a sudden increase in levels of disturbance.

It is difficult to determine what general characteristics attracted individuals to forage in the four main areas (see Fig. 1), especially as many apparently suitable fields and saltmarsh areas are never visited. However, core areas may be less prone to disturbance or more productive. In The Netherlands, Barnacle Geese grazed most frequently at sites where grass growth rates were high, and as a consequence there was sustained regeneration of young plants with a high protein content (Ydenberg & Prins 1981). Some, but not all saltmarsh areas are grazed cyclically by Brent Geese Branta bernicla (Rowcliffe et al. 1995). So presumably the concentration of foraging within relatively limited areas on the Solway may actually improve grass quality.

Individual variation

Although some foraging strategies were clearly common to several birds from a particular area, considerable individual variability in ranging behav- iour was apparent. Part of the explanation may be

historical tradition, with some birds simply unaware of the potential range of alternative feeding sites. The bulk of the population always arrives initially at Caerlaverock at the end of the autumn migration and, as this study has shown, depart from Rockcliffe. By contrast, Southerness was rarely or never visited by Barnacle Geese until the mid-1980s, after which time flocks began to move there increasingly earlier in the season (Owen et al. 1987). Use of northwest Cumbrian sites is even more recent, with numbers increasing to several hundred or more only in the last 3–4 years (Phillips et al. 2000). The great majority of birds may therefore be aware of the extent of feeding opportunities at Caerlaverock and Rockcliffe, but not necessarily elsewhere, which may explain why some never visited Southerness or northwest Cumbria.

Range characteristics

Although tagged birds differed a great deal from each other in terms of the number, timing and duration of visits to the four main feeding areas, there was much less variation in field selection within each area, with much of the foraging concentrated at comparatively few key sites. The overlaps between individuals in the maximum extent of foraging ranges (MCP) and core areas (Cx_{85} polygons) were high (means of 42–86%) at both Caerlaverock and Southerness, indicating that birds were using many of the same fields. However, ranges were in general much more patchy at Caerlaverock than Southerness, perhaps because more geese are usually present there, forcing individuals to move more frequently to alternative feeding sites because of rapid resource depletion.

Seasonal changes in distribution

There was a tendency for several birds to range further from their capture area from mid- to late winter onwards (Table 1). Increased use of alternative feeding sites in February and March corresponds to the period when temperatures are low, day length short and consequently grass growth slow. Barnacle Geese are in negative energy balance during some midwinter months, and tend to lose mass accumulated since arrival in the autumn despite an increase in foraging effort (Owen et al. 1992). By this point, grazing will have depleted the food supply at preferred sites which are less susceptible to disturbance or predation, result- ing in increased intraspecific competition and consequent range expansion. Similarly, Brent Geese deplete intertidal algal beds within a few months after arrival in the UK, and are then forced to disperse to agricultural fields (Summers & Critchley 1990, Vickery et al. 1995, Percival & Evans 1997).

Predeparture habitat shift

With one exception, all radiotagged geese moved to Rockcliffe Marsh prior to departure on the spring migration. That so many birds should show this highly consistent pattern was unexpected despite regular monitoring of goose numbers and distribution in previous years, emphasising an inability to estimate turnover rates from counting birds alone without identifying known individuals.

The choice of Rockcliffe Marsh, the largest area (c. 1000 ha) of saltmarsh on the Solway, as the primary departure point is probably for a number of reasons. Firstly, Rockcliffe is much less disturbed than other sites from agricultural activity in the early spring. In addition, there is a strong selective advantage to geese to maximize their intake of high quality forage prior to migration, and deposition of large nutrient reserves in wintering or staging areas is probably a prerequisite for successful breeding (Black et al. 1991, Prop & Deerenberg 1991, Ebbinge & Spaans 1995). Barnacle Geese wintering in The Netherlands shift from dairy pasture to saltmarsh in the spring, at a time when dietary protein availability in saltmarsh vegetation is at least as great as in the agricultural fields (Prins & Ydenberg 1985). Geese at Rockcliffe Marsh often graze within the mixed colony of several thousand pairs of Lesser Black-backed Gulls Larus fuscus and Herring Gulls L. argentatus. Barnacle Geese in the Netherlands preferentially select feeding sites around gull nests, and Bazely et al. (1991) found that the nitrogen content of Festuca rubra was 25% greater in these than adjacent areas. Although we have no data on seasonal changes in grass quality, it seems likely that geese moving to Rockcliffe will benefit from the high productivity and protein content of saltmarsh plants in the spring.

However, although accumulation of nutrient reserves for migration is probably the primary explanation for a predeparture shift by most geese, it seems unlikely to account for the relatively brief visits to Rockcliffe by several of the Southerness birds. Instead, Rockcliffe Marsh may function as a traditional departure point for migration. The journey to the staging areas in Norway is long (1500 km), and it is possible that Barnacle Geese require the stimulus of large numbers of con- specifics and appropriate weather conditions, before

departing. It is also conceivable that geese separated during the winter might use this time to re-establish pair bonds or associations with others from the same breeding areas, assuming there could be a selective advantage to synchronize arrival at staging or breeding sites.

Population structure

Our data suggest that a degree of segregation exists within the wintering population, although distinctions between subgroups were far from clear-cut. Several Southerness birds spent little or no time at Caerlaverock during most of the winter, and only one Caerlaverock bird visited Southerness. However, other Southerness birds did spend longer at Caerlaverock, where their ranges overlapped with Caerlaverock birds (Table 2), and individuals from both samples mixed at Rockcliffe Marsh and northwest Cumbria. Therefore, while some individuals from Southerness could be regarded as fairly site-faithful, other birds from both areas were highly mobile. This shows close parallels with the population structure of Barnacle Geese wintering in northern Germany, but contrasts some- what with the situation on Islay, where birds appear to have a stronger tendency to be site-faithful (Percival 1991, Ganter 1994). It is unclear whether this apparent variation is an artefact of methodological differences between the three studies, or results from extrinsic factors such as climate (see Percival 1991).

Management implications

The partial population segregation has consequences for effective management of the Barnacle Goose population on the Solway, insofar as it is clearly desirable to at least maintain, if not expand, the existing network of reserves and dispersed range of feeding opportunities. Furthermore, a characteristic common to many of the tagged birds was to spend several weeks in the area of their capture site interspersed with shorter periods spent elsewhere (often at Rockcliffe), which could indicate that large-scale movements are somehow costly. This need not be related to the energy expend- ed in long-distance flight, but could reflect the disadvantage of moving to an area with only restricted experience of alternative local feeding sites.

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