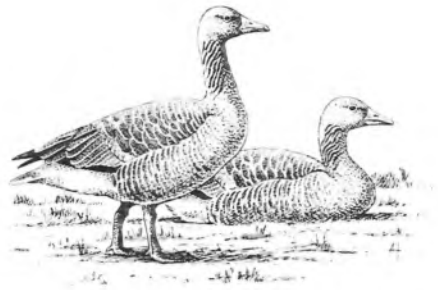


Variations in clutch size and breeding success of Greylag Geese *Anser anser* in the Uists, Scotland



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The native Greylag Goose population on the Uists, Scotland, has doubled since the 1960s and the principal breeding areas moved from South to North Uist. Comparisons of clutch and brood sizes found that both were significantly smaller on North Uist. Clutch sizes were not significantly smaller on South Uist than at Loch Druidibeg, South Uist, in 1968-72. The smaller clutch sizes and broods on North Uist were not due to differences in nesting habitat, predation rates, food quality, or differences in laying dates between North and South Uist. The differences may be attributable to young birds laying smaller clutches on North Uist due to changes in the age structure of the Uist population as it expanded.

Greylag Geese *Anser anser* on the Scottish islands of North Uist, Benbecula, and South Uist form a large part of the remaining wild, non-migratory British population (Paterson 1987a). Since the 1960s the Uist population has doubled to a post-breeding population of 1630 in 1986 (Paterson 1987a) and the distribution changed from centring on South Uist (Sharrock 1976, Thom 1986) to North Uist. Loch Druidibeg National Nature Reserve on South Uist was the principle breeding site until the 1970s (Newton & Kerbes 1974) but the principle breeding sites are now on North Uist (Paterson in press).

Since the 1960s the area of high quality grazing has increased throughout the Uists (Paterson 1987b). Between 1982 and 1987, 1500 ha, divided equally between North and South Uist, were sown for new grazing. Greylags fed on the new pastures (Paterson 1987b), which could contribute to the expansion of the population through improving female condition affecting clutch sizes (Klomp 1970, Ryder 1970). To determine whether breeding performance had improved, clutch and brood sizes were collected from North and South Uist in 1986 for comparison with comparable data from Loch Druidibeg obtained in 1968 to 1972 (Newton & Kerbes 1974). Initial results suggested that clutch and brood sizes were significantly smaller on North Uist than South Uist. The observations were repeated in 1987 and the results, together with some potential explanations, are examined in this paper.

Methods

In March 1986, preliminary surveys were conducted of moorland lochs and coastal areas on North Uist to identify breeding areas. By April most geese had left the arable land used in winter (Paterson 1987b), and since most clutches should be complete by the last week of April (Newton & Kerbes 1974), nesting areas were searched systematically and clutch sizes recorded from the last week of April onwards. Due to poor weather and the low density of nests in difficult terrain, it was rarely possible to revisit nests. The effort of locating nests on North Uist meant that little time was available to locate nests on South Uist outside Loch Druidibeg. Nests at Loch Druidibeg were checked regularly from April onwards by D.M. Clutch sizes elsewhere on South Uist were recorded from accessible nests from the last week of April. In 1987, poor weather restricted the time available for locating nests so clutch sizes were recorded only from known sites on North Uist and Loch Druidibeg.

Brood sizes were recorded on North and South Uist from mid-June, when most juveniles were nearly fledged, until September. In 1986, brood sizes were recorded during the whole period but, in 1987, only during August, and in 1988 the brood sizes were recorded during a 17-day period from 21 June.

While searching for goose nests, records were made of Hooded Crow *Corvus corone cornix* nests, as Hooded Crows were thought to

be the main predators of Greylag eggs (Newton & Kerbes 1974).

Where possible comparisons between clutch sizes were made by Student's T tests but when small sample sizes were involved Mann-Whitney U tests (Siegel 1956) were used.

Results

Breeding distribution, habitat and densities of 86 nests were examined in 1986, of which 74 were on North Uist and 12 on South Uist, including nine on Loch Druidibeg.

Table 1. Vegetation types and nest sites chosen by Uist Greylags.

| Nest site | n | Vegetation type | % |
|----------------|----|---------------------|----|
| Loch islands | 54 | Low heather <0.3 m | 15 |
| Loch shore | 7 | Deep heather >0.3 m | 62 |
| Coastal island | 80 | Grass/Juncus | 15 |
| Coastal shore | 5 | Low scrub | 7 |
| | | Other | 1 |

The habitat and vegetation types used by nesting geese are shown in Table 1. Most geese bred on islands, with over 90% using coastal island sites. Geese mainly nested in heather *Calluna vulgaris* which was the dominant vegetation of the breeding areas. Nesting densities were lower (mean 3 km⁻²), compared with 9-13 km⁻² at Loch Druidibeg 1968-72 (Newton & Kerbes 1974).

Clutch and brood sizes on North and South Uist

The likelihood that clutches were complete when recorded was checked in 1986 when 22 nests were visited twice, 10-19 days after the first visit. On the second visit 16 had hatched, five contained the same number of eggs, and one nest had lost two eggs. In addition five nests had hatched prior to a first visit. As incubation lasts 28 days (Newton & Kerbes 1974), these results suggest that clutches were complete when clutch size was recorded. Further analysis of estimated laying dates confirmed this (see below).

Table 2. A comparison of mean clutch sizes of Greylag Geese on North and South Uist.

| Year | North Uist | n | South Uist | n | z | P< |
|------|------------|----|------------|----|------|------|
| 1986 | 4.4 ± 0.15 | 65 | 5.8 ± 0.41 | 12 | 2.99 | 0.01 |
| 1987 | 3.7 ± 0.22 | 37 | 5.2 ± 0.40 | 9 | 2.67 | 0.01 |

Comparisons were made by Mann-Whitney U tests (Siegel 1956).

Mean clutch sizes for North and South Uist are shown in Table 2. In both years clutch sizes were significantly smaller on North Uist. Clutch sizes were smaller on both islands in 1987 than in 1986 (Table 2).

On North Uist, geese bred on coastal islands and freshwater lochs. Clutch sizes from these habitats were compared with clutch sizes on South Uist to determine if clutch sizes were related to nesting habitat (Table 3). Clutch sizes at coastal and freshwater sites on North Uist were not significantly different, but clutches from both North Uist habitats were smaller than those from South Uist.

Geese on North Uist nested mainly in heather whilst those on South Uist nested mainly in low scrub or reeds *Juncus spp.* A comparison of predation rates in different vegetation types is shown in Table 4. Observed predation rates were not significantly different from that expected if predation rates were equal across vegetation types.

Table 3. A comparison of mean clutch sizes from different nesting habitats selected by Greylag Geese on Uist.

| | Mean | n | Comparison | P< |
|--|------------|----|------------|------|
| 1. North Uist Coast Low Food Quality | 4.4 ± 0.17 | 51 | 1 v 2 | n/s |
| 2. North Uist Lochs High Food Quality | 4.6 ± 0.32 | 14 | 2 v 3 | 0.05 |
| 3. South Uist Lochs High Food Quality | 5.8 ± 0.41 | 12 | 1 v 3 | 0.05 |

Comparisons by Student-Newman-Keuls test (Sokal & Rohlf 1969).

Table 4. A comparison of predation rates on Greylag nests in different vegetation types.

| | Heather | Juncus/grass | scrub/other |
|---------------------|---------|--------------|-------------|
| Nests n | 109 | 23 | 12 |
| Predated n | 22 | 7 | 1 |
| Expected predations | 23 | 5 | 1 |

X² = 0.17, P = n/s

Predation rates at nests on North Uist were 16% in 1986 and 25% of nests in 1987. These rates may be a slight underestimate as observations stopped before all known nests hatched. Hooded Crow nests were found at a density of 13 nests in 12 km² of the coastal breeding areas in 1986. On Loch Druidibeg, six pairs nested in both 1986 and 1987 in 11 km² of the Reserve.

Brood sizes on North and South Uist were recorded from June until September when goose shooting started. Brood sizes are known to decline after hatching (Newton & Kerbes 1974).

As brood sizes from North Uist were collected over the whole period in 1986, brood sizes were compared between mid-June and August, but were not significantly different (mean June = 3.3 ± 0.4 , $n = 7$, mean August = 3.1 ± 0.2 , $n = 32$). Data from both months were combined for North Uist in 1986 for comparison with South Uist brood sizes, but in other years comparison of North and South Uist broods were made within the same month. Broods on North Uist were significantly smaller in all three years (Table 5).

Table 5. A comparison of Greylag brood sizes on North and South Uist.

| | <i>n</i> | North Uist Mean | <i>n</i> | South Uist Mean | <i>P</i> < |
|------|----------|--------------------|----------|--------------------|------------|
| 1986 | 32 | 3.1 ± 0.21 | 17 | 4.3 ± 0.30 | 0.01 |
| 1987 | 13 | 2.3 ± 0.46 | 14 | 4.5 ± 0.37 | 0.01 |
| 1988 | 33 | 3.7 ± 0.33 | 41 | 4.2 ± 0.28 | 0.01 |

Comparison by Mann-Whitney U tests (Siegel 1956).

Comparison with Loch Druidibeg

Clutch sizes from North and South Uist were compared with similar data from Loch Druidibeg in 1968-72 (Newton & Kerbes 1974). Mean clutch size at Loch Druidibeg in 1968-72 was 5.0 ± 0.08 ($n = 231$) for single female clutches and varied from 4.8 to 5.4 between years. North Uist clutches were significantly smaller in both years than the Loch Druidibeg mean (Student's T test, 1986, $t = 2.77$, $P < 0.01$, 1987, $t = 5.38$, $P < 0.001$) but South Uist clutches were not significantly different. A comparison of clutch size frequency distribution from North Uist and Loch Druidibeg in 1968-72 shows an increased

proportion of smaller clutches on North Uist (Fig. 1).

Laying dates could be estimated from nests where eggs were hatching or hatched when recorded, based on laying and hatching intervals and the known 28-day incubation period. The estimated first laying dates were compared with the known distribution of first laying dates from Loch Druidibeg in 1968-72. Of 67 viable nests examined on North Uist in 1986, 28 would have had a first egg laid on or before 14 April. This was not significantly different from the expected number of clutches started by this date (expected 29, $X^2 = 0.14$ $P = ns$), if laying dates on North Uist and Loch Druidibeg were the same. Mean sizes at Loch Druidibeg in 1968-72 varied from 3.6 to 4.0 between years, with years of larger clutch sizes producing larger broods near fledging. Detailed comparisons of brood sizes are difficult as goslings are known to switch broods, and only the mean brood size is provided by Newton & Kerbes (1974). However, brood sizes on North Uist appear to be lower than at Loch Druidibeg in 1968-72.

Discussion

Until the early 1970s the Uist Greylag population was centred on South Uist, and Loch Druidibeg was the principal breeding area (Newton & Kerbes 1974). Since then the population has doubled, the importance of Loch Druidibeg as a breeding site has declined, and the principal breeding area is now the coastal moorland of North Uist (Paterson in press). Although the breeding areas are now coastal, the nest sites are still mainly heather-dominated islands, which were also used on Loch Druidibeg,

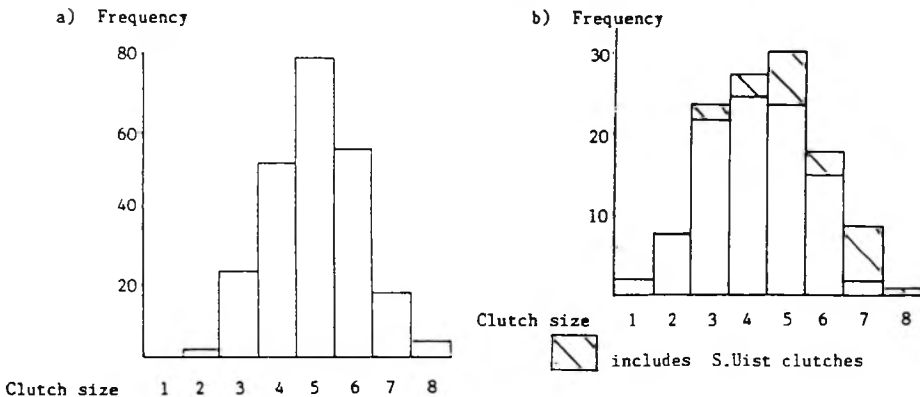


Figure 1. Frequency distribution of Greylag clutch sizes as a) L. Druidibeg 1968-72 ($n = 231$) (Newton & Kerbes 1974) and b) North and South Uist 1986 and 1987 ($n = 125$).

a moorland loch. The shift to North Uist was not to a different nesting habitat, and the reasons for the shift are not clear. Young Canada Geese *Branta canadensis maxima* are known to disperse to breed away from high densities of older breeding birds (Raveling 1981). Geese at Loch Druidibeg were at high densities between 1968-72 (Newton & Kerbes 1974), but not compared to those reached by Greylags in Galloway (Young 1972). The shift to North Uist may have been related to increased levels of human disturbance around Loch Druidibeg since the 1970s (Paterson in press), and coincided with the expansion of the population. The expansion may be partly due to increased breeding success in the main breeding areas of North Uist, which had higher success rates than at Loch Druidibeg in 1968-72. However, individual breeding performance, measured by clutch size was lower than on South Uist or Loch Druidibeg in 1968-72.

Clutch sizes on North Uist were significantly smaller than on South Uist in two years and brood sizes were higher on South Uist in three years. South Uist clutches were not significantly different from those at Loch Druidibeg in 1968-72.

Clutch sizes can be affected by a variety of factors: differences in laying dates (Newton & Kerbes 1974), maternal condition (Klomp 1970, Ryder 1970), age (Raveling 1981) and egg predation (Newton & Kerbes 1974). Clutch sizes were recorded over the same period on North and South Uist and the analysis of laying dates suggested that laying was completed when clutches were recorded. As first laying dates on North Uist were not different from Loch Druidibeg in 1968-72, later laying dates cannot explain smaller clutches on North Uist compared with South Uist or Loch Druidibeg in 1968-72. The size of maternal energy reserves influences clutch size (Klomp 1970, Ryder 1970), so South Uist geese with better quality or less disturbed feeding may lay larger clutches. In late summer geese on North and South Uist feed on large areas of ripening cereals when available, or stubble (Paterson 1987b). Feeding on energy rich cereals is more common on North than South Uist, where intensive scaring is conducted, particularly in the Loch Druidibeg area. In winter geese on the Uists mostly feed on high quality pastures which show little variation in fibre or nitrogen content (Paterson 1987b), but had different quality feeding at nesting areas. At two freshwater lochs on North Uist and at all sites on South Uist, geese fed on high quality reseeded and pastures, while coastal nesting geese fed on saltmarshes and maritime heaths. Clutch sizes at coastal sites and freshwater lochs on North Uist were not significantly different, but

both were smaller than on South Uist. Differences in food quality cannot explain the differences in clutch sizes between North and South Uist.

Competition for food also seems unlikely. Geese fed in small flocks (median 41, Paterson 1987b), flock sizes were not significantly different on North and South Uist, and flocks grazed on large grazings of 2 to 25 ha (Paterson 1987b). Systematic disturbance of feeding flocks was only practiced in a small area of North Uist in 1985 (Paterson 1987b), so cannot account for small clutches on North Uist.

Higher predation rates could have lowered clutch sizes on North Uist. Direct comparisons of predation rates on North and South Uist could not be made, as too few nests were visited regularly on South Uist for meaningful comparisons. Newton & Kerbes (1974) found that predation affected 37-57% of nests, removing at least one egg or destroying the clutch. This level of predation lowered clutch sizes by 0.5-0.8 eggs per clutch between laying and hatching. Hooded Crows were thought to be the principal egg predators at Loch Druidibeg in 1968-72 (Newton & Kerbes 1974). The nesting density of Hooded Crows on North Uist was similar to that at Loch Druidibeg in 1968-72. The predation rate of 16% in 1986 and 25% in 1987 suggests that predation was lower than at Loch Druidibeg in 1968-72. The loss of only two eggs from one nest out of 22 revisited on North Uist does not suggest a high rate of egg loss from North Uist nests. As the differences in clutch size between North and South Uist were greater than the effect of predation at Loch Druidibeg in 1968-72, predation seems unlikely to explain the differences in clutch size between North and South Uist.

A comparison of clutch size distributions found more smaller clutches on North Uist than at Loch Druidibeg in 1968-72. Smaller clutches tend to be laid later than larger clutches (Newton & Kerbes 1974), but there was no evidence of later laying on North Uist.

Young geese lay smaller clutches (Owen 1980). A lower average breeding age in the North Uist population could produce more smaller clutches than on South Uist or at Loch Druidibeg in 1968-72. No information is available currently on the age structure of the Uist population; change to increasing numbers of young birds laying smaller clutches does seem likely given the recent expansion of the population (Paterson in press), but it is not clear why younger birds should breed on North Uist.

Variations in clutch size within breeding ar-

eas have now been recorded among Canada Geese (Raveling 1981). Young Canada Geese laid smaller clutches than older geese which nested at high densities and forced younger birds to disperse. Although Greylags are semi-colonial breeders (Young 1972, Owen 1980), the Uist Greylags are now relatively dispersed (Paterson in press). The differences in clutch size between parts of the Uist Greylag population demonstrate that significant variation can occur in species which breed at low densities as well as in more colonial species.

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