Turnover of individuals in a local population of Pink-footed Geese *Anser brachyrhynchus*

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Abstract

The turnover of individually neck-collared Pink-footed Geese *Anser brachyrhynchus* was measured at the Loch of Strathbeg, Grampian, Scotland, from September to mid-November, 1999–2002. The observations, carried out from hides near the birds' roosting sites, were shown to sample the local population reasonably randomly and to detect 62% of the marked birds in the area. The proportion of 'new' individuals, not seen previously in the same autumn, stabilised at around 40%, suggesting strongly that there was a turnover of individuals. Most individual geese stayed in the area for a minimum period of only a few weeks, and about one third were seen elsewhere in the UK during the autumn study period. The proportion of geese with collars decreased from September to November, more steeply in 2000 than in 2001 or 2002. The first sighting dates of individual birds were not correlated between years. The findings show that there was a high degree of turnover of individual geese at the site, suggesting that over one third of the whole population passes through Strathbeg, and that different components of the population might pass through the area at different times during the autumn. This has important implications for the measurement of productivity, particularly the timing of sampling.

Key words: Loch of Strathbeg, neck collars, productivity, duration of stay.

Swann *et al.* (2005) showed that Greylag Geese *Anser anser* in Scotland were highly mobile in the first three months after their arrival from Iceland, and that there was a considerable amount of turnover of individuals at both a regional and site level. Such turnover of individuals in a local population can be important for a number of reasons. For example, the volume of birds using a staging site (Routledge *et al.* 1999; Frederiksen *et al.* 2001) may be greatly underestimated by counts of the peak number present at any one time. Similarly, measures to control crop damage should take into account the number

of individuals that normally pass through an area (Summers *et al.* 1985). Assessments of productivity, using counts of age ratio and family size after arrival in the wintering area, may also have to take into account the possible turnover of individuals at any particular site, since counts at different times may sample different components of the population.

Measurements of age ratio and family size in Pink-footed Geese *Anser brachyrhynchus* at the Loch of Strathbeg, Grampian, Scotland, in 1998–2002 showed a consistent decline in both measures over the autumn, mid-September to mid-November (Patterson & Hearn 2006). This trend, which was also apparent in other parts of the birds' range in the UK, might be associated with a number of factors. One possibility is differential shooting mortality: juveniles are more vulnerable than adults, with their proportion in the shooting bag typically at least twice that in the local population at the same time (Hearn & Mitchell 1995; Patterson, unpubl. data). However, given the relatively small estimated total bag (Frederiksen 2003), it is unlikely that such mortality is sufficient to explain all of the seasonal change in age ratio and family size. Another possible explanation is that there is turnover of birds during the autumn, so that different components of the population, with different levels of productivity, may have passed through the area at different times. The best time to make productivity measurements, on first arrival or later in the autumn, will depend on which of these possible factors is most important in the decline in proportion of juveniles and in family size.

The aim of the present study is to determine whether there is turnover of individual birds at a particular site over the autumn, to estimate the minimum length of stay of individuals, and to find whether different components of the population are present at different times.

Study Area and Methods

The study was carried out at the Loch of Strathbeg, Grampian, northeast Scotland (57°37'N, 1°54'W), on a reserve owned by the Royal Society for the Protection of Birds (RSPB), from mid-September to mid-November 1999–2002. Pink-footed Geese arrive in the area during September, and numbers are usually in the range of 20,000–40,000 (and occasionally over 50,000) during October and November (RSPB, unpubl. data). Most of the birds roost overnight on the northwest part of the loch, with others at the southeast end, some on the estuary of the outlet stream and up to 5,000 on pools close to the loch (Fig. 1). During the morning departure, while many birds from the loch fly directly to outlying feeding areas, large numbers usually land again beside the birds at the pools. Here they spread out over the adjoining grassland to feed for some time before final departure. Geese returning to the reserve in the late afternoon tend to feed and loaf in the fields adjacent to the loch, before moving on to the water at dusk.

A small proportion of the adult geese (around 0.7% at the start of the study) had been individually marked with plastic neck collars, mainly on the breeding grounds in Iceland by personnel from the Icelandic

Figure 1. The study area at the northwest end of the Loch of Strathbeg (large shaded area), showing the main subsidiary roost pool (small shaded area), roosting areas (hatched), departure flight directions (arrows) and observation hides (spots).

Institute of Natural History (IINH) and the Wildfowl & Wetlands Trust (WWT). Most birds had been caught while moulting in the central and northern (including 'north central') highlands of Iceland, but a few were caught elsewhere, including some in the UK in winter. Other birds had been marked in earlier years with lettered plastic leg rings, but these were seen less frequently and were not used in the study.

Morning observations, starting at dawn, were made from hides on the edge of the main subsidiary roost pool (Fig. 1), and those in the afternoon from a hide in the middle of the fields of the reserve, where birds returning from feeding were likely to settle. From the hides, it was possible to identify individual marked geese at up to 400 m, using a 60x telescope. A record was discarded unless the combination of two or three letters on the collar was seen fully and clearly. Many collars were identified again on subsequent independent scans of the flock and were recorded as confirmed.

The proportion of geese with collars was determined by counting large samples, of just over 1,000 birds if possible, excluding any whose lower necks were not clearly visible, for example because they were asleep with their backs to the observer. When only smaller flocks were available, separate independent counts made on the same day were combined to achieve sample sizes of over 1,000 birds. Juvenile geese were rarely marked with collars, but were included in the counts because it would have been too time consuming to exclude them. However, the proportion of marked birds among the adults was estimated by correcting for the percentage of juveniles in the population in the same period, measured as part of a separate study.

The randomness of sampling was checked to guard against the possibility that only a consistent sub-set of the geese used the areas within range of the observation hides. An indirect method was used, based on simple capture–recapture estimates of local population size. Since such estimates assume random mixing of individuals and random recapture probabilities, these assumptions can be tested in a situation like that at Strathbeg, where the actual population size is determined independently (RSPB, unpubl. data). In 2000 and 2001, observations were made on pairs of consecutive days, so that the proportion of individuals seen on the first day that were also seen on the second day could be determined. This allowed estimation of the total number of marked geese in the area, using the bias-adjusted Lincoln-Petersen estimator (Seber 1982), and hence the total local population size (since the proportion of geese with collars was counted separately). This estimate could then be compared with the actual population, determined from direct counts. This method assumes no movement of geese over the 2-day period and would be rendered invalid by a large overnight arrival between the two days. This possibility was minimised by counting for each day the percentage of birds that were 'new', defined as not seen in earlier weeks in the same autumn. Pairs of days were excluded from the analysis if there was a significant difference in the proportion of 'new' birds between the two days (χ^2 tests).

Records of marked geese seen during the study and also seen independently by

	2000	2001	Total
Birds seen at or around Strathbeg by others	52	94	146
Of these, birds also seen in the present study	25	66	91
Percentage seen in the present study	48.1	70.2	62.3

Table 1. The percentage of individually marked geese, seen independently at Strathbeg by other observers, that were also seen in the present study.

other observers during the same autumn were obtained from the database of goose sightings maintained by WWT. These additional records were made either: a) at the Strathbeg reserve or within the normal local feeding range of the Strathbeg geese (mainly by RSPB staff, volunteer helpers and visitors), or b) elsewhere in the UK (by WWT staff and volunteer observers). Multiple sightings in the latter category in the same direction, for example to the south of the Strathbeg area, were counted as one occurrence. The database also gave the location where each goose was marked and the date of capture, so that birds of different origin could be identified.

Statistical comparisons of proportions were made by χ^2 tests and correlations by Pearson correlation.

Results

Sampling

The proportion of local marked geese seen in the study was estimated from the independent samples of birds seen at or around Strathbeg by other observers. The mean percentage seen in the study was 62%, with a higher percentage in 2001 than in 2000 (Table 1). All but one of the six population estimates derived from collar resightings were of the same order as those from direct counts (Table 2), although each of the latter fell outside the confidence interval of the associated estimate. Crucially, the estimates were much closer to the direct total counts than to the usual number (2,000 to 4,000) of geese present near the observation hides at any one time.

Percentage of 'new' collars

If there was no turnover of individuals, the proportion of collars seen for the first time in a given autumn ('new' collars) should decline asymptotically towards zero after a few weeks, given the 62% probability of sighting a particular collar during a bird's stay at Strathbeg (see above). However, the percentage of 'new' collars decreased only slowly and remained at over 40% even after nine weeks (Fig. 2). There were some increases in the percentage from one week to the next; some of these may have resulted from sampling error, but some undoubtedly represented new arrivals. For example, in week seven in 2000 (Fig. 2), the percentage 'new' was 27% on the first day and 73% on

Table 2. Estimates of the local Strathbeg population based on resightings of collars and on direct counts by the RSPB. The data are: the number of different collars identified on each day; the proportion of those seen on the second day that had also been seen on the first day; the resulting estimate of the total number of collars in the local population; the number of geese represented by each collar (from separate counts); the resulting estimate of the total number of geese in the local population; the direct counts by the RSPB during the same period. The data are from separate weeks in October and the first week of November in both years.

	Collars seen		Proportion resighted	Total collars	Geese /collar	Estimated total	RSPB counts
	Day 1	Day 2					
2000							
	15	19	0.105	100	247	24,700	42,600
	19	24	0.167	99	247	24,453	28,000
	23	13	0.154	111	296	32,856	25,000
Mean						**27,336**	**35,300**
2001							
	19	22	0.182	91	337	30,667	40,960
	20	26	0.154	112	629	70,448	
	22	12	0.500	43	571	24,553	39,700
Mean						**41,889**	**40,340**

Table 3. The percentage of individually marked geese, seen independently by other observers at or around Strathbeg, within one week (i.e. the same week, previous week or following week) of their sighting in the present study.

	2000	2001	Total
Number of sightings by others	25	82	107
Seen in the present study within one week	20	58	78
Percentage seen within one week	80.0	70.7	72.9

the second ($\chi^2_1 = 7.240$, $P = 0.007$). Large numbers of geese were seen arriving (from a much higher altitude than was usual for feeding flights) in the late evening of the first day (Scott Paterson (RSPB), pers. comm.).

Length of stay by individuals

In all three years of the study, most of the individually marked geese were seen in only one week, and none was seen in more than six weeks, out of the 9-week or 10-week study period (Fig. 3). For those collared geese seen in more than one week, the interval between the first and last sighting was most commonly one week in 1999 and 2001 and two weeks in 2000 (Fig. 4). Over 70% of collars seen both in the present study and independently by other observers in the Strathbeg area were seen by both sets of observers in the same week, or within one week before or after (Table 3).

Sightings elsewhere during the autumn

Over one third of the collars seen in the study were also seen outside the Strathbeg area within the study period, up to mid-November (1999, 31.3% of 67 collars; 2000, 25.6% of 191, 2001, 50.3% of 173; overall 36.1%). Some of these individuals were seen in Norfolk, at the southern limit of the winter range, within a month of having been seen at Strathbeg. Most were seen to the south after having been seen at Strathbeg (Table 4), presumably because of the latter's position at the north of the species' winter range, with most roost sites (and most observers) situated to the south. However, 35% of the birds seen elsewhere were seen either to the south before being seen at Strathbeg or to the west afterwards (Table 4). Some individuals were seen elsewhere in the UK in the period between sightings at Strathbeg. Over the three years of the study, birds seen at Strathbeg for only one week were significantly more likely to be seen elsewhere than were those seen in the study for two or more weeks (Fig. 5).

Proportion of geese with collars

In all three years when measurements were made, the number of collars per thousand adult geese declined through the autumn (Fig. 6). The steepest decrease was in the first of the three years considered (2000), when the number of collars per thousand geese more than halved between the first half of October and the first half of November. There was little change over winter, with the proportion of geese with collars in April 2002 only slightly lower than that in the preceding November (Fig. 6). The proportion of geese with collars declined from year to year, with fewer than one per thousand in November 2002, presumably because there had been no marking of geese in Iceland in the summers of 2001 and 2002 (WWT, pers. comm.).

Correlation between first sighting dates in consecutive years

The first sighting dates of individual birds seen at Strathbeg in consecutive years were not correlated between years ($r = 0.150$, $n = 25$, n.s. in 1999–2000; $r = 0.229$, $n = 55$, n.s. in 2000–2001; $r = 0.060$, $n = 15$, n.s. in 2001–

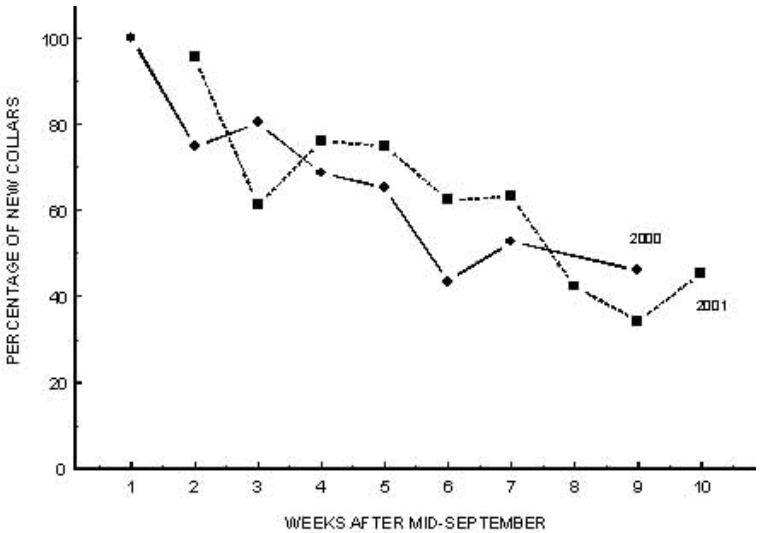

Figure 2. The percentage of collars that were 'new', i.e. not seen previously in the same autumn, each week from mid-September to mid-November, 2000 (circles) and 2001 (squares). Sample sizes: 2000, mean 39, range 16–49; 2001, mean 30, range 8–49.

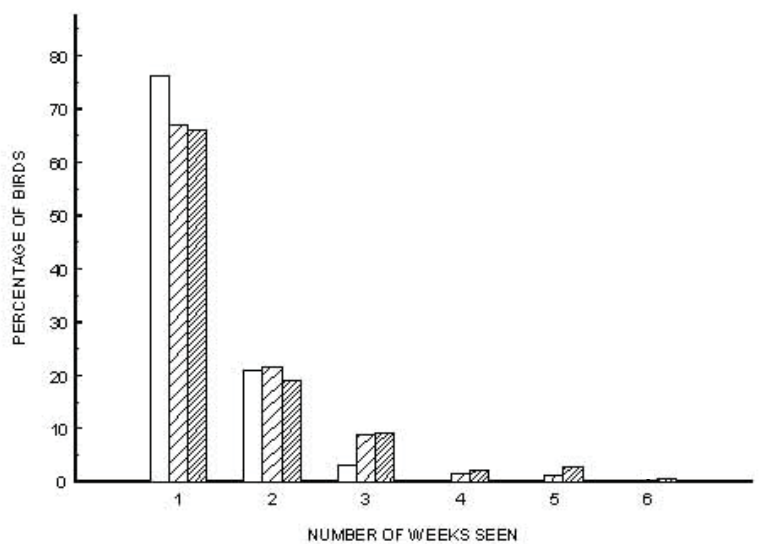

Figure 3. The percentage of individually marked geese that were seen for different periods, in 1999 (open bars), 2000 (widely hatched bars) and 2001 (closely hatched bars). Sample sizes: 1999, 67; 2000, 191; 2001, 173.

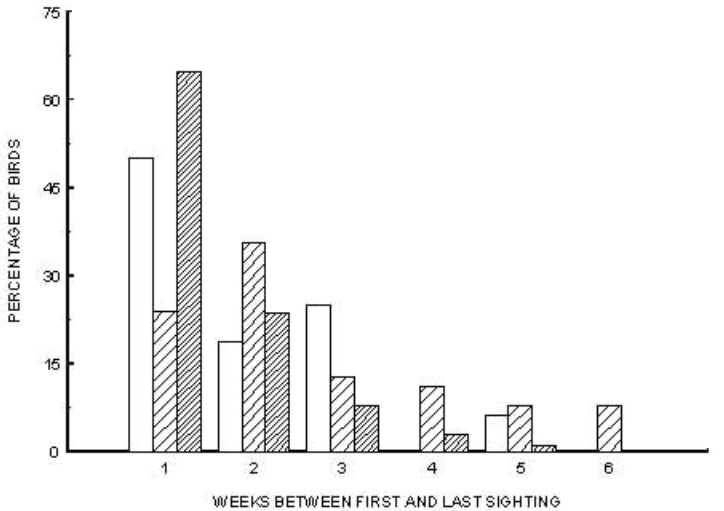

Figure 4. The percentage of individually marked geese with different intervals between their first and last sighting in 1999 (open bars), 2000 (widely hatched bars) and 2001 (closely hatched bars). Sample sizes: 1999, 16; 2000, 63; 2001, 102.

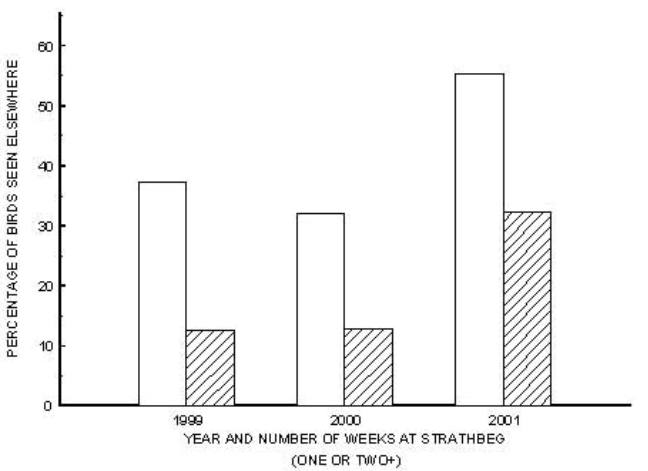

Figure 5. The percentage of individually marked geese that were seen elsewhere in the UK during the mid-September to mid-November study period in 1999 to 2001, in relation to the period over which they were seen at Strathbeg, one week (open bars) or two or more weeks (hatched bars). Sample sizes: one week; 1999, 51; 2000, 128; 2001, 114: two weeks; 1999, 16; 2000, 63; 2001, 59. Statistical tests: combined data; $\chi^2 = 18.062$, $P < 0.001$: 1999; $\chi^2 = 3.469$, $P = 0.063$: 2000; $\chi^2 = 8.274$, $P = 0.004$: 2001; $\chi^2 = 8.292$, $P = 0.004$).

2002). This finding was confirmed in a wider study of first sighting dates throughout the UK (Patterson & Hearn, unpubl. data).

Total number of geese passing through Strathbeg

The marked geese seen in the current study and independently by other observers at Strathbeg (Table 1) can be used in a two-sample capture-recapture analysis, using the adjusted Lincoln-Petersen estimator (Seber 1982) to calculate the total number of geese with collars that visited the area each autumn. Using the total number of different collars seen in the study in each of the two years (192 in 2000 and 173 in 2001), the estimated number of marked individuals that occurred in the area was 393 in 2000 and 246 in 2001. Using the mean number of geese represented by one collar (260 in 2000 and 459 in 2001; from separate counts), the estimated total number of individual geese that occurred at Strathbeg between mid-September and mid-November was 102,200 in 2000 and 112,900 in 2001. Although this calculation is necessarily crude, the two values are reasonably consistent and suggest that well over one third of the whole of the Pink-footed Goose population passes through Strathbeg in the autumn.

Table 4. The percentage of (165) individually marked geese, seen elsewhere in the UK as well as at Strathbeg in September to mid-November 1999–2001, that were seen in other areas before or afterwards and to the south or to the west of Strathbeg.

	Before Strathbeg	After Strathbeg	Total
Seen to the west	4.2	13.9	18.2
Seen to the south	21.2	60.6	81.8
Total	25.5	74.5	100.0

Discussion

Sampling

It is perhaps surprising that observations made in only a limited part of the roosting area appeared to sample the whole local population reasonably randomly. Estimates of population size based on the resighting of collars approximated to the independent counts by the RSPB (Table 2) and were much larger than the usual number of birds around the observation hides at any one time. Individual geese may have varied their time and direction of departure from day to day and may also have returned to the roost area at different times in the afternoon. This may have resulted in birds from much of the local population occurring in the observed areas over periods of a week or two.

Since over 60% of the marked birds in the area were seen in the present study (Table 1), any individual not seen for two weeks (four observation days) was very likely to have been absent from Strathbeg. This is supported by sightings of over a third of the marked individuals in other parts of the UK during the September to November study period.

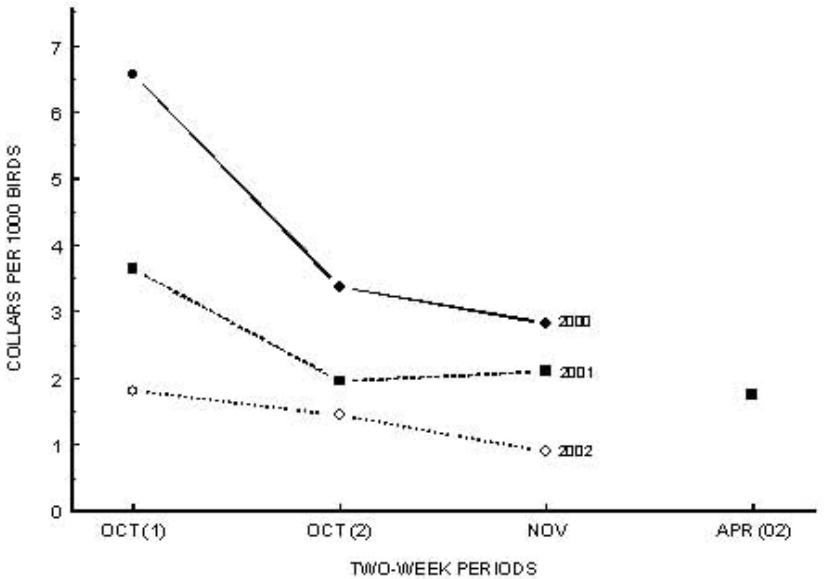

Figure 6. The mean number of geese with collars per 1,000 birds in 2-week periods in October and November 2000 (closed circles), 2001 (squares) and 2002 (open circles), corrected for the percentage of juveniles in the same period. The mean number in April 2002 is shown as a separate point and is not corrected. All mean values are based on at least 5,000 birds and most on more than 10,000.

Percentage of 'new' collars

The continued sighting of 'new' collars, i.e. those not seen previously in the same autumn (Fig. 2), suggests strongly that there were constant arrivals of new geese in the area. These arrivals continued well after the period when the birds normally migrate from the breeding areas, indicating that they remain mobile long after they first reach the UK. The movement of birds was not exclusively from north to south, since 21% of the birds had been seen to the south (some as far as Perthshire and Tayside) before being seen at Strathbeg, and 14% were seen to the west afterwards (Table 4).

Turnover and length of stay

The finding that most marked birds were seen in only one week, with most of those seen over a longer period being seen in only a 3-week period (Figs. 3 & 4), also suggests strongly that there was turnover of individuals at Strathbeg. The independent sample of sightings by other observers in the same area confirmed this, with most birds seen within one week of their sighting in the present study. Some apparently longer stays, with many weeks between the first and last sightings at Strathbeg (Fig. 4), were by birds that were seen elsewhere in the UK in the interval (Fig. 5).

The recorded interval between the first and last sighting of each individual goose was clearly a minimum estimate of its duration of stay, since the bird may well have arrived in the area some time before it was first seen and may have stayed on, without being detected, after its last sighting. However, it is likely that most birds may have stayed at Strathbeg for only a few weeks. A more detailed analysis of duration of stay, based on capture-recapture analysis and the calculation of resighting probabilities (Schaub *et al.* 2001), is beyond the scope of the present study, which aimed to detect whether there was turnover in the local population rather than to determine exact duration of stay.

Arrival of different components of the population

It is likely that different components of the Pink-footed Goose population would have different probabilities of individuals being marked with collars. Since most captures of Pink-footed Geese for attachment of collars have been made while the birds were flightless in or near a number of breeding areas in Iceland, it is likely that birds that spent the summer there, either as successful breeders, unsuccessful breeders or non-breeders, would be more likely to have collars than birds that summered elsewhere (including Greenland and other parts of Iceland). Only a few of the latter, caught in the UK in winter, would be expected to have collars. Strong site fidelity among nesting Pink-footed Geese (WWT, unpubl. data) will tend to perpetuate this pattern.

The striking and consistent decline from September to November in the proportion of geese with collars (Fig. 6) suggests that geese that had summered in the areas of Iceland where most were captured (those most likely to have collars) were among the earliest arrivals, and that birds that had summered elsewhere (those least likely to have collars) were commoner among the later arrivals. The tendency for the seasonal decline in the proportion of birds with collars to be somewhat less in 2001 and 2002 than in 2000 (Fig. 6) might be explained by progressive mixing of birds with collars through the whole population, so that there would be a more similar proportion of them among both early and late arrivals.

Implications for the measurement of productivity

The finding that an estimated one third or more of the whole Pink-footed Goose population may pass through the Loch of Strathbeg area during the autumn suggests that measurement of age ratio and family size at a single site may sample a much larger proportion of the whole population than the number of geese present at any one time would indicate. Counts at regular intervals through the autumn will tend to include a proportion of new arrivals and not be confined to a small sub-set of the population.

The suggestion that different components of the Pink-footed Goose population might arrive at different times suggests that measurements of productivity should be carried out late in the autumn, for instance after mid-October, when the

whole population would have arrived in the UK and would have mixed thoroughly. However, differential shooting mortality in September and October would meanwhile tend to decrease the percentage of juveniles and perhaps also the average brood size, so producing an underestimate of productivity. A solution to this problem might be to stratify the sampling of productivity over the whole autumn, with approximately the same sample size in each month. Alternatively, the data from October alone could be used, as a compromise between the opposing trends of different arrival dates of different components of the population on the one hand and shooting mortality on the other.

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