Changes in the British-wintering population of the Pink-footed Goose from 1950 to 1975

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The Wildfowl Trust began a study of the biology of the Pink-footed Goose *Anser brachyrhynchus* in 1950. The early investigations followed two main paths. Expeditions to central Iceland in 1951 and 1953 added much to knowledge of the breeding biology and distribution of the species (Scott, Fisher and Gudmundsson 1953; Scott, Boyd and Sladen 1955) and ringed some 9,000 geese. In Britain the development of rocket-propelled nets for catching geese allowed another 11,800 Pinkfeet to be ringed from 1950 to 1959. Recaptures and recoveries of the ringed geese were used to obtain estimates of population size and mortality rates and to study distribution (Boyd 1955, 1956, Boyd and Scott 1955). For a long time it did not seem practicable to make a complete census of the geese, because they were widely scattered, not all their haunts were known and it seemed to be too difficult to count the birds even when they were found. The indirect approach through ringing was expensive and gradually became less satisfactory because of sampling problems, particularly the inability to catch geese in proportion to their regional abundance, while growing acquaintance with their distribution and habits made direct counting seem feasible. After several years of trials, including extensive aerial surveys and the formation of a network of observers, a census, covering all the haunts likely to be in use at that time of year, was made in early November 1960 and has since been repeated anually.

This paper reports and discusses the November censuses for 1960-68, using less complete information from earlier years to estimate numbers in the decade 1950-59. It includes information on the proportions of young geese seen and on the mean brood size each year from 1950 to 1968. In conjunction with the total counts these data make it possible to estimate the size of the successful breeding population and the crude mortality rate from one year to another. Some account is also given of changes in regional distribution over the years, though that and other topics will be discussed in greater detail in other papers. Finally it develops forecasts for the period 1969 to 1975.

Annual census

The Pink-footed Geese wintering in Britain breed in central Iceland and east Greenland and make up a closed population rarely occurring outside those areas. Some arrive in Scotland in late September but most migration occurs in the first half of October and geese may still be arriving until nearly the end of that month. So far as is known, none overwinter in Iceland. During the winter there are extensive, though often gradual, shifts from one part of the country to another, but no emigration. In the spring the geese move back to Iceland in April and early May, some perhaps as early as March. Geese may legally be shot from 1st September to 31st January, or 20th February on the coast. In practice most mortality from this cause occurs in December and January, and very little in October.

Presumably the highest numbers of full-grown geese must occur in Iceland in August, before the migration to Britain, which in some years may cause substantial losses. Aerial surveys in Iceland in 1963 and 1964 (Boyd 1964) have demonstrated that complete counting there would be difficult, and the additional cost and logistic problems of searching in east Greenland as well ruled out the possibility of censusing at the annual peak. Thus early November is in practice the best time for a census, soon after the completion of the autumn migration. The original intention was to carry out most of the survey from a light aircraft, using a single pilot-and-observer team, but this proved unsatisfactory. Short days and frequent spells of bad weather imposed serious restrictions on flying. It was also impossible to be sure that all the Pink-

feet in an area had been detected and frequently the actual counting was found to be difficult. Aerial photographs suitable for careful checking of the observer's estimates were rarely obtainable in the gloom of a Scottish November (Eltringham 1959). Thus the alternative method was tried of deploying a large team of volunteer observers counting the geese within comparatively short distances of their homes and supplemented by a small, roving crew, to fill in gaps in the network and to deal with some of the largest and most complicated groupings of geese. Counts had to be concentrated on a week-end so that enough people could take part. The week-end chosen was normally the first or second in November, the actual dates having varied from 6th to 13th. The counters were selected from persons with prior knowledge of the whereabouts and habits of geese in their vicinity and with a keen interest in counting. Many of them had already been taking part in the monthly National Wildfowl Counts organised by the Wildfowl Trust. Counters were asked to obtain as accurate a total as possible of the geese using a particular roost, preferably by counting the birds leaving the roost in the morning or returning to it in late afternoon. In some places that was not possible and then the geese had to be found while feeding in the fields, often many miles from a roost.

For a census undertaken in such a way to be of value it is necessary to ensure that all, or nearly all, the geese are found and identified, that each group of birds is included only once in the final sum, however often they may have been seen, and that the enumeration itself was reasonably precise. Identification did not often cause difficulty. Observers were also asked to record the numbers of all other species of geese seen, the network being set up to inspect all the November roosts of Greylag Geese *Anser anser* as well as those of the Pinkfoot. The winter ranges of the Greylag and Pinkfoot overlap extensively. But it is unusual for the two species to intermingle at a roost, even if both are using the same loch or estuary, and uncommon for them to occur in mixed flocks while feeding or in flight, apart from the occurrence of isolated stragglers in a flock of the 'wrong' sort. Measures to ensure complete searching and to avoid duplication of recording varied. In some areas local organisers made detailed arrangements for the siting of observers at agreed times to achieve a single thorough check. In others, replication of counts was arranged on the same day or on successive days, either by the same or by independent observers. In Perthshire, Angus and Kinross, where the greatest numbers of geese and most complicated juxtapositions of roosts were found, the geese were counted when flighting out from each roost and also pursued to their feeding places and counted there. Whenever confusion arose the counts were repeated on different days. Thus, it was unusual for any roost tally to be the unsupported observation of a single person and many checks on the thoroughness of the searching and counting were available. The distribution of the Pinkfoot roosts in the period 1965-68 are shown in Figure 1.

Counting flocks of several thousand geese is hardly ever easy. Sometimes conflicting records could not be reconciled and sometimes fog or other mischance prevented the observations from being conducted as intended, so that the final record is still not quite complete for some years and is to some extent dependent on the personal judgement of the compilers as well as that of the counters. While it is possible to assess the general ability of observers to count geese in a test situation, for example by showing them a set of photographs (Matthews 1960), every census total is the consequence of a set of special circumstances. As such, it cannot be provided with confidence limits by any of the recognised methods.

Obviously, a single annual count on an arbitrary date, however precise, is not a suitable basis for detailed analysis of a population. But, given that a single count is all that can be afforded, it will be argued below that the index provided by the censuses carried out in 1960-68, and certainly by those in the period 1963-68, is a useful means of detecting changes in abundance and of suggesting explanations for the changes. It may be noted that most of the results can also be demonstrated by ranking the counts, first by locality year by year then nationally, and evaluating them by rank correlation methods.

Because geese are large and gregarious birds, given to roosting habitually only in sites they know well and exploring new feeding places comparatively slowly, their distribution has been plotted in considerable detail. Recent studies of local distribution which deal with occurrences throughout the winter and with comparisons between years include those of Thom and Murray (1966) on geese in Perthshire, Brotherston (1964) on those

in the Lothians, and the comprehensive national and regional accounts by Atkinson-Willes (1963). Pinkfeet occur in larger flocks, at fewer roosts, in October and November than they do later in the winter, so that complete inspection of all likely sites is feasible. In the results tabled below sites that never held Pinkfeet on the occasion of the November census are omitted, and some used only occasionally and as alternatives are grouped together under a single name (e.g. 'Firth of Inverness', 'other Midlothian'). The grouping under 36 heads has other arbitrary features too. For most inland waters there is no difficulty in naming the site, although in some cases it is undesirable to do so in the interests of privacy. On the coast (e.g. the Firth of Tay, or the Solway Firth, or the Ribble Estuary) where the geese sit on sandbanks or on the water and may be moved by the tides for several miles, the focal points are harder to specify and different recorders would doubtless classify the data in other ways.

There is similar imprecision in the four regional groupings used: 'North Scotland', 'East Central Scotland', 'South Scotland' and 'England'. These correspond to some discontinuities in distribution and in mixing between groups of geese, as revealed by ringing (Boyd 1955)

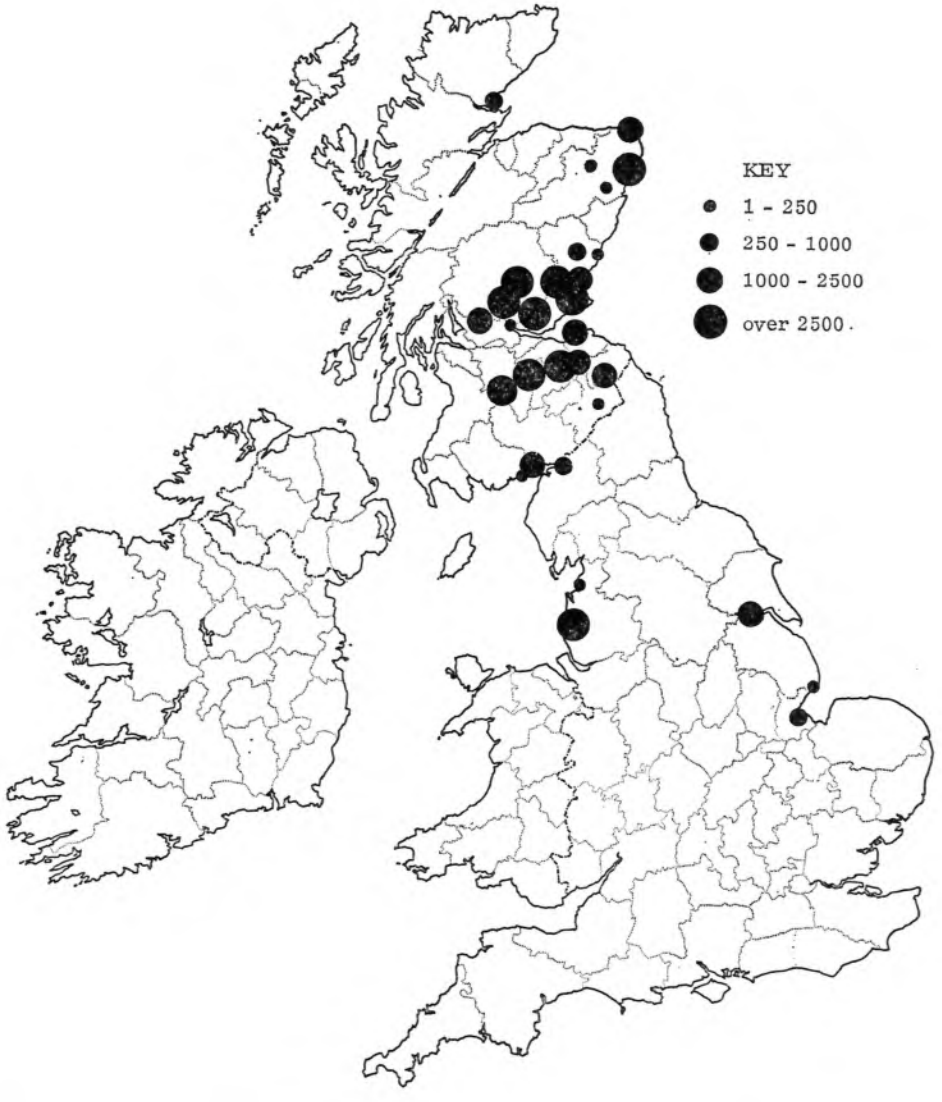

Figure 1. The distribution of roosts of the Pink-footed Goose in Britain in 1965-68.

Table I. Numbers of Pink-footed Geese counted at roosts in Scotland and England in early November, 1950-1968.

Roost	*1950*	*1951*	*1952*	*1953*	*1954*	*1955*	*1956*	*1957*	*1958*	*1959*	*1960*	*1961*	*1962*	*1963*	*1964*	*1965*	*1966*	*1967*	*1968*
Nigg							43	150			190	—	40	20	—	—	1650	—	250
Firth of Inverness					800	200		200			30	142	6	26	1	925	—	—	—
L. Strathbeg					90	200		600	1350	1110	*770*	1500	370	1650	2239	4600	2730	50	3500
Ythan				1500	1200	30	70	2000	—	—	485	218	900	1000	3300	6753	11468	15000	8340
mid-Don														—	—	—	89	130	120
L. Skene		—	19		107	—	—	—	128	—	—	—	140	—	180	290	—	—	240
Montrose				700	130			400			500	600	1050	*0*	1030	230	235	350	950
Forfar								1000			—	2050	—	600	250	750	650	—	1700
Outer Tay				5000	1200	1300		360			3140	4300	*7000*	3430	6800	4000	4635	2200	—
Inner Tay			1500	2000				4000			—	—	—	810	2000	*2500*	—	2750	11000
Strathearn				2000				2400			*4380*	11050	8240	8400	8375	15560	19320	13230	9000
Carsebreck		60	—								2090	2500	2960	1070	880	2700	1815	3000	3550
Flanders Moss		27	100	2000		1000		380			*12*	1380	660	1700	1775	*0*	650	2300	1300
Cameron Res.		350	1600	30	150	4095	4500	1150	1800	2000	4500	3200	6500	8000	6500	760	2000	3750	3500
other Fife											5	180	22	—	325	300	48	100	15
L. Leven							—	380	200		1350	50	2500	1350	3100	1000	5590	1540	1028
Alloa		75	176							183	700	179	565	320	—	42	—	—	310
Aberlady Bay				235	200	380	100	850	700	2360	1400	250	680	1380	950	255	2750	800	2200
Hule Moss	150		500	4000	2000	1410	3200	4660	4370	1100	3700	3800	3500	200	3400	3000	4200	850	13
Fala	250	1750	100	1500	—	750	—	900	10	270	600	50	2430	450	5	710	—	25	4000
Gladhouse Res.	2000	1300	4220	4000	2500	2700	3750	2550	3450	2000	680	4670	2200	4850	5500	3765	1400	7100	800
other Midlothian											480	270	133	10	11	40	80	—	—
Baddinsgill Res.				1200		2630	1980	1950	1500	530	300	5000	1450	1600	5500	330	1800	—	500
Westwater Res.											—	—	—	—	—	—	500	3800	1400
Lanark											*1700*	650	4460	3150	1040	3410	2575	*3180*	748
Roxburgh																290	450	—	—
Cree	—	—	50	20	100	10	10	12	16		—	11	—	—	80	46	—	—	—
Mersehead											*35*		270		150		290	250	—
Solway — Dumfries	2000	2000	3000		2310	4000	930	2000	2000		7000	1023	2000	6500	4300	7807	3700	1000	440
Solway — Cumberland											50	750	860	*350*	900	300	—	*2*	840
Cockerham				250	345			21		50	300	700	50	—	250	—	—	—	150
Southport			3000	350		3000	2750	3500	2800	4000	3000	4000	*3500*	1530	*3230*	2500	*3500*	1500	7910
Humber		7100	5300	850	5500	3400		6000	12000	15000	5335	5160	2140	*3000*	2000	2055	1750	3000	1500
Croft	4000	4200	3000	2000	4000	3750	6000	460	5000	3000	3400	2270	4500	4000	—	3400	60	—	—
Holbeach				600	4500	4000	4000	2000		3000	2500	3250	1420	1500	1350	1	2500	258	—
Slimbridge	60	—	70	100	120	70	70	140	40	10	110	40	54	—	—	—	—	—	—
Scattered records											55	6	—	2	19	76	5	—	—
Total	8460	16882	22635	28335	25252	32925	27403	36063	35364	34613	48737	59238	60600	56898	65440	68395	76440	66165	65304

Notes: no entry = not searched; — = no geese seen. Figures in italics are subject to question; the counts being suspected of being incomplete, or over-estimated, or selected from conflicting estimates. Rounding-off is as used by observers.

but are also influenced by the need to have classes containing several thousand birds from a variety of roosts to damp down the wild fluctuations from year to year characteristic of some groups.

Numbers in 1950-68

The only co-ordinated effort at a census in early November prior to 1960 was an unsatisfactory aerial survey in 1957, and the information for a population index for the years 1950-59 is therefore gathered from a variety of sources, including observations by the rocket-netting teams as well as by local observers. These counts have been assembled in Table I together with the census results for 1960-68. In calculating an index from the earlier counts it has seemed the best to use the census data for 1960-63 to provide a link between the estimates for the two decades. In this way too much weight is not given to the more complete censuses of later years. This first index could be based simply on the data as tabulated, with interpolations made by using the method devised by Gustav Elfving to obtain an annual population index for Tufted Ducks *Aythya fuligula* in the Finnish Archipelago from the numbers of pairs found in incomplete searches. It is described in an appendix to a paper by von Haartman (1958). Because that paper may not be widely available, an account of the method is given in Appendix I.

Table I shows that records from north and east Scotland are particularly sparse in earlier years. As numbers in the north have been rising while those further south have been steady or declining, it has seemed desirable to calculate a second and better national index for 1950-63. This has been obtained by calculating four separate regional indices and then weighting those by the regional totals observed in 1963 to arrive at a regionally weighted index. The results are presented in Table II, which demonstrates that, apart from 1957, an increase was nearly continuous from 1950. The 1957 results are quite likely to be erroneous, in a way defying correction: as noted earlier, the Scottish results that year were obtained by an aerial survey, in which the inspection of sites was probably not thorough, and the numbers of geese within large flocks were probably underestimated.

Table I also summarises the November census data since 1960. The roosts not visited at appropriate times were few and minor. More serious in their possible effects on the annual total are those figures (shown in italic type) for major haunts which, although the best available, are believed to be of low reliability, because of a high risk of duplications or omissions or because of a conflict of evidence. In order to discover whether these doubtful entries have an important effect upon the national total and, if so, whether an adjustment can be made, it is necessary to replace them by interpolations based on the row and column totals. Several procedures are available. For the sake of consistency, the method adopted here is the one that was also used with the data for 1950-59, which were far more incomplete.

The adjusted national estimates are shown in Table III which includes both the calculated indices and revised values for the totals obtained by standardising the index on 1963 (= 100), this being the first of a series of years for which the corrections produce trivial effects on the final total. Thus, when nearly all the geese were adequately searched for and counted, even substantial errors in counting at one or two major roosts have evidently not led to serious errors in the

Table II. National and regional indices for numbers of Pink-footed Geese in Britain in early November, 1950-63, adjusted to I (1963) = 100.

	1950	*1951*	*1952*	*1953*	*1954*	*1955*	*1956*	*1957*	*1958*	*1959*	*1960*	*1961*	*1962*	*1963*
N. Scotland				152	84	16	10	108	63	48	48	68	53	100
E.C. Scotland		5	30	53	14	57	71	42	31	38	72	96	100	100
S. Scotland	36	58	65	97	55	79	65	85	79	55	90	98	81	100
England	150	153	120	35	150	122	185	102	210	214	125	132	84	100
National	52	60	62	57	65	74	87	63	95	95	84	97	85	100

Table III. Annual counts and indices of the total numbers of Pink-footed Geese in Britain in early November, 1960-68.

	1960	*1961*	*1962*	*1963*	*1964*	*1965*	*1966*	*1967*	*1968*
total count	48737	59238	60600	56898	65440	68395	76440	66165	65304
omitting doubtful entries	41840	58649	50100	53548	62210	65895	72940	62983	65304
normalised index	90.4	93.2	88.2	89.8	103.1	109.1	120.2	103.7	102.3
index standardised to 1963	100.6	103.8	98.3	100.0	114.8	121.4	133.9	115.4	114.0
adjusted total	57292	59114	55982	56950	65379	69137	76256	65720	64923

national total. In 1960-62 there were enough rejected entries to lead to appreciable changes. However, those do not affect the general picture, summarized in Figure 2, of a sustained rise in total numbers from 1950 to a peak of about 76,000 in 1966. In 1967 and 1968 there is evidence of a decline.

Population estimates for 1950-53 from captures and recaptures of ringed geese were published by Boyd (1956) using Bailey's modification of the Lincoln Index method. These were 18,200 in 1950, 52,000 in 1951, 37,200 in 1952 and 49,000 in 1953, and do not accord at all closely with the estimates from observations. Unpublished Lincoln Index estimates for 1954-58 fit even less well: 71,800 in 1954, 85,000 in 1955, 86,600 in 1956, 109,700 in 1957 and 55,100 in 1958. These and other estimates derived from more sophisticated capture-recapture methods seem to have been vitiated by incomplete mixing of the geese from different places and, as mentioned earlier, by inability to catch the geese in suitable proportions regionally.

The regional totals do not change with the simplicity of the national totals, though a rapid increase in eastern Scotland coincided with the greatest national gains. A boom in north Scotland, confined in fact to Aberdeenshire, followed some five years later. That area still holds less than a quarter of the national total while Perth, Angus, Fife and Kinross now account for nearly half. ' South Scotland ', which combines the Lothians, Lanark and Berwick with the Solway, may be an improper grouping, for the Solway has been losing in relative importance while the Lothians have first gained and then held their strength. Regional differences within England have been marked too, with great reductions in autumn numbers on the Humber and Wash in recent years. Decreases and eventual disappearances from former strongholds in Norfolk and at Slimbridge began well before 1950. Only in Lancashire have the autumn numbers remained high.

Thorough assessment of regional changes requires consideration of numbers throughout the winter, outside the scope of this paper, but it may be remarked that the November counts generally reflect the picture for the entire season.

Recruitment and fertility

The analysis of goose populations by field observations on the proportions of first-winter birds and family groups has been used for many years (Lebret 1948, Lynch

Figure 2. The numbers of Pink-footed Geese estimated to have been present in early November in 1950-68 in Britain and in different parts of the country.

and Singleton 1964). It is not easy to distinguish first-winter Pinkfeet from older birds in the field except under infrequently favourable conditions of distance and light, nor are family groups readily identifiable in November, so that samples collected annually (Table IV, Figure 3) are small compared to population size. For the years 1950-59 the bulk of the annual sample for the ratio of first-winter to older birds was made up of geese caught in rocket-nets for ringing. Unlike most trapping methods, rocket-netting does not usually collect samples biased by age or sex because the nets are concealed and bait is not used to attract geese into the catching area. It was not possible to identify family groups in the

Table IV. First-winter ratios and observed brood-sizes of Pink-footed Geese in Britain in autumn, 1950-68.

	proportion of 1st w. birds		*1st w.*	*brood-size*						*total*	*total*	*mean*
Year	*1st w.*	*total*	*total*	*1*	*2*	*3*	*4*	*5*	*6*	*1st w.*	*broods*	*brood*
1950	285	583	.488	2	7	4	5	1	1	59	20	2.95
1951	205	821	.249	2	2	2	2			20	8	2.50
1952	300	1280	.234	4	2	3	4	1	2	50	16	3.13
1953	550	1651	.333	2	1	3	1	1		22	8	2.75
1954	610	1744	.349		1		2	1		15	4	3.75
1955	424	2483	.170	1	6	4	3	1		42	15	2.80
1956	238	1258	.184	1	3	1	3			22	8	2.75
1957	1157	3437	.336	3	9	2	6	2	1	67	23	2.91
1958	613	2363	.259	2	3	2	1			18	8	2.25
1959	318	1588	.200	1	1	6	2	2		39	12	3.25
1960	165	596	.276	6	16	18	7	1	2	137	50	2.74
1961	162	433	.374	12	12	11	4	7	2	132	48	2.75
1962	153	730	.209	1	7	4	1	1		31	14	2.21
1963	220	1088	.202		1			2		12	3	4.00
1964	362	1358	.266	2	4	3	5			39	14	2.79
1965	105	500	.210	2	1	2	2			18	7	2.57
1966	303	1400	.216	24	22	18	9	4	1	184	78	2.36
1967	63	585	.108	20	10	3				43	33	1.30
1968	94	804	.117	27	12	2				57	41	1.39
sum	6327	24732	.256	112	120	88	57	24	9	1007	410	2.46

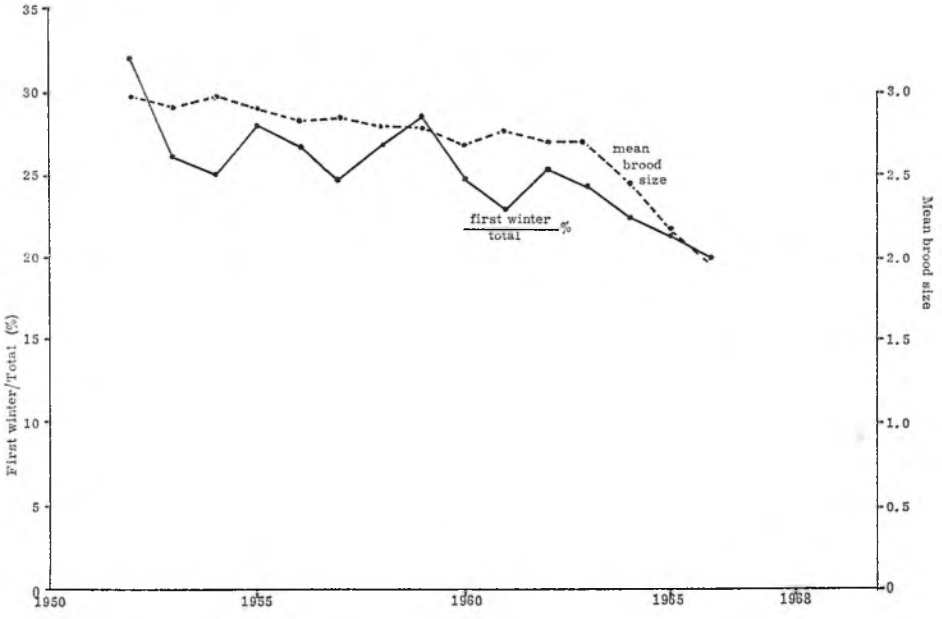

Figure 3. Changes in the mean brood size and in the proportion of first winter birds among Pink-footed Geese seen in Britain, 1950-68, shown by five-year moving averages.

Table V. A population model for the Pink-footed Goose, 1950–68

Year t	*Total Number* N_t	*1st w.* $\mathcal{J}_t$	*Parents* $(\mathcal{J}_t \times 2/b)$ P_t	*Non-breeders* $N_t - \mathcal{J}_t + P_t$	*Losses* L_t $N-(N-\mathcal{J})_{t+1}$	*Death-rate* (%) L_t/N_t
1950	29.85	14.57	9.84	5.44	4.14	13.8
1951	34.24	8.53	5.76	19.95	7.00	20.4
1952	35.56	8.32	5.62	21.62	13.89	39.0
1953	32.49	10.82	7.30	14.37	8.48	26.1
1954	36.88	12.87	8.69	15.32	1.90	5.1
1955	42.14	7.16	5.02	29.96	1.66	3.9
1956	49.61	9.13	6.40	34.08	25.41	51.2
1957	36.44	12.24	8.58	15.62	(−3.70)	(−10.1)
1598	54.17	14.03	9.84	30.30	10.80	19.9
1959	54.21	10.84	7.60	35.77	12.73	23.4
1960	57.29	15.81	11.62	29.86	20.29	35.4
1961	59.11	22.11	16.25	20.75	14.83	25.0
1962	55.98	11.70	8.60	35.68	10.53	18.8
1963	56.95	11.50	8.45	37.00	8.96	15.7
1964	65.38	17.39	12.78	35.21	10.76	16.4
1965	69.14	14.52	12.20	42.42	9.35	13.5
1966	76.26	16.47	13.83	45.96	17.64	23.1
1967	65.72	7.10	10.52	48.10	8.40	12.7
1968	64.92	7.60	11.26	46.06	—	—

All totals are in thousands of geese. The annual totals are derived from the national indices, standardized I (1963) = 100. Mean brood-sizes (b) used are: 1950-54 2.96; 1955-59 2.85; 1960-64 2.72; 1965-66 2.38; and 1967-68 1.35.

Figure 4. Changes in the numbers of first winter birds, of successful parents and of non-breeders within the Pink-footed Goose population in Britain, 1950-68, shown by five-year moving averages.

catches, so that the brood-size samples in most years are too small for effective comparisons between years.

The high proportion of young birds in 1950 was found in two different samples (from rocket-netting in south Scotland and observations at Slimbridge) and was confirmed by the presence of 48% first-winter birds in 173 geese caught in Lincolnshire in December 1950, though the latter are not entered in the table. Such a high proportion has not been approached subsequently, even though in several years the mean brood-size was apparently higher than in 1950.

Figure 3 shows the five-year moving averages for the proportion of first-winter birds and for the numbers of young geese in the country and also for the brood-size. (The averages were calculated from the cumulative sums of the data, not from the annual rates in columns four and thirteen of Table IV.) Both the age-ratio and brood-size show a significant decline over the years, though the trends are not immediately apparent from the tabulated annual values, apart from the exceptionally low production in 1967 and 1968.

In early November nearly all broods are still accompanied by both parents so that the number of successful parents can be found by multiplying the number of first-winter birds by 2/(mean brood-size). Because most samples of broods have been small, it seems better to use for that purpose mean brood-sizes based on pooled records for several consecutive years, rather than the tabulated annual values. The pooled values chosen are recorded in the caption of Table V, which summarises the calculated values for a number of the population statistics.

Figure 4 depicts the moving average values for the numbers of parents and 'adults without families' or 'non-breeders'. Both have increased. The average rate of increase of the latter (about 6.0% annually) has been only a little higher than that of parents (about 5.8%) but, starting from a high number and sustained over a long period, has led to a massive accumulation of 'non-breeders'. Most unfortunately, it is not possible to examine what processes have led to this result. To do so it would be necessary to know something of the age structure among the geese more than a year old and to see whether there are important differences between successful parents and other geese in that and other ways. No detailed investigation of the reproductive history of a group of Pink-footed Geese has ever been attempted, because the cost of doing so would be formidable by the standards of British field ecology. Scott, Boyd and Sladen (1955) did not know whether Pinkfeet might begin to breed at two years old. An examination of the ovaries of eight females marked as goslings in Iceland in 1953 and collected in Britain in the autumn of 1955 confirmed that none had yet bred, but many more known-age birds would have to be examined to answer the question satisfactorily. Work on the Canada Goose *Branta canadensis* shows that although reproductive maturity normally occurs in the third year, a small percentage of geese mature in the second year (Wood 1964).

In principle, recoveries of ringed geese could be used to model the age-structure of the population at different times but it now seems unlikely that this can be done with sufficient precision to be helpful, particularly as the Wildfowl Trust ringing programme did not overlap with the census.

Also, and perhaps more seriously, the estimates of mortality obtainable from recoveries are too high to be compatible with those derived from the observed population changes. Boyd (1956) estimated from recoveries up to 1954 of Pinkfeet marked in 1950-52 that the death-rate of geese between 4 and 16 months old was 42 $\pm$ 2.8% and that the annual death-rate of older geese was 26 $\pm$ 1.6%. Later unpublished work indicates rather lower rates.

Estimates of the crude death-rate can be obtained from the counts by subtracting the number of young from the total November population to give a figure for survivors from the previous year. Subtracting this figure from the previous year's total gives the number of deaths during the year, which can be converted to a rate by dividing by the total in the preceding year (Table V). Such an estimate is unlikely to be reliable, since it is susceptible to the effects of errors in the estimates of total numbers and of young birds, so that it is preferable, once again, to use moving averages rather than annual values to see how mortality may have varied. Figure 5 depicts the average losses and the average death-rate over the period. The smoothed values since 1960, which are derived from relatively good censuses, show very clear declines in absolute losses and in the death-rate. The most recent losses are still greater absolutely than they were ten years or so earlier, which is not at all surprising in

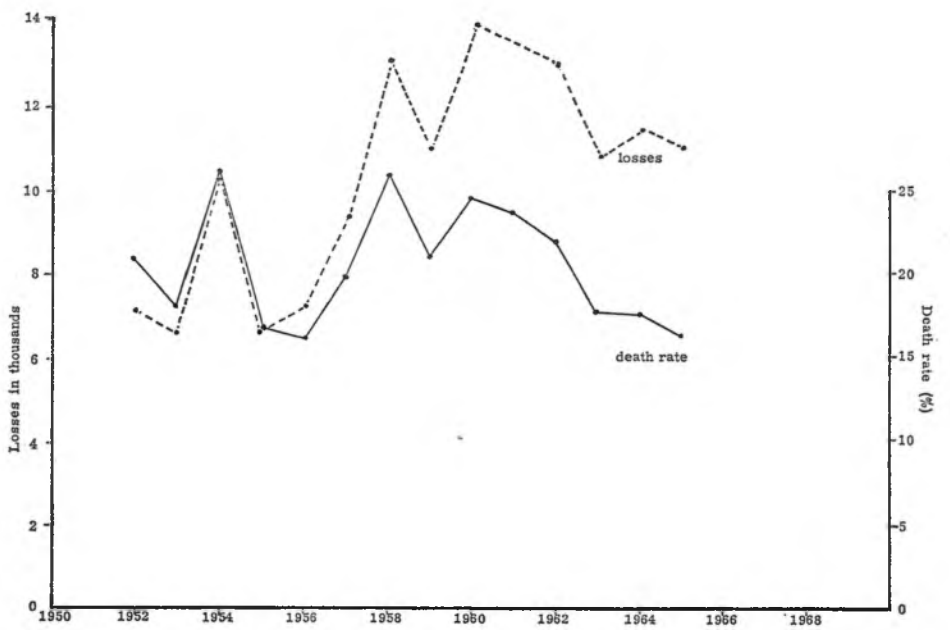

Figure 5. Changes in the annual losses of full-grown Pink-footed Geese, from November to November, and in the crude death-rate, 1950-68, shown by five-year moving averages.

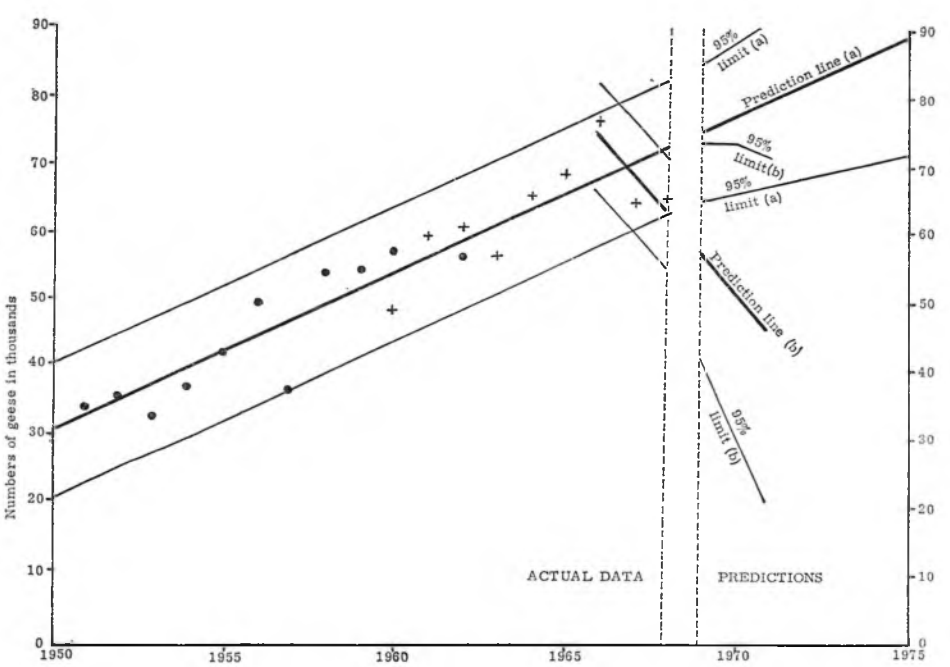

Figure 6. Forecasts of the numbers of Pink-footed Geese in Britain in 1969-75, based on the changes in the population between 1950 and 1968. Solid circles equal adjusted totals (see Tables II and III); crosses equal total counts.

view of the large increase in the number of geese at risk.

Numbers in 1969-75

The decline in 1967 and 1968 after the sustained increase in 1966 raises interesting questions about the size of the British wintering population of Pinkfeet in the future. Will its growth be resumed, will it now fluctuate about a November level of, say, 70,000 birds, or will it decline substantially? The safest answer is just to wait and see, and the most admirable one would be a convincing causal analysis. Neither is immediately attainable. But some guidance may be derived from mathematical extrapolation from the recent trends. Curve-fitting is a somewhat discredited art in those fields, such as econometrics and demography, where it has been most used but the method may still be useful in such an unsophisticated task as gross population projection.

There are two main difficulties in making informative projections. First, it is necessary to adopt a deterministic approch, making the assumption that the intrinsic and contingent factors affecting population size will continue to act and interact much as before. In most cases of real interest that is unlikely to be true. Second, it is a commonplace that when the usual mathematical trend curves are fitted to a set of data the closeness of fit is much the same within the range of the observations while the extrapolated values diverge, often widely. Thus it is necessary to find some objective method of choosing between predictors.

The trend curves usually fitted fall into two classes: polynomials, represented by the straight line or the parabola, and exponential curves where the increase at any moment is directly proportional to the size already attained. A helpful technique for selecting predictors has been introduced by Gregg, Hossell and Richardson (1964).

The data for the whole period 1950-68 are well fitted by the straight line $Yt = 27.85 + 2.35t$, where Yt is the number of geese in thousands in year t, and t_1 was 1950 (Figure 6). The 95% confidence limits, corresponding to $\pm$ 2 standard deviations, are also shown in Figure 6.

The close fit to the linear regression is to some extent spurious, particularly for the years 1950-59, because the estimating procedure for the incomplete data has the effect of smoothing out departures from the norm. But it is rather remarkable that a straight line fits the data for 1960-68 at least as well as any of the polynomials or exponentials tried, since population growth does not often appear simply additive.

The projection of the straight regression line suggests that the population would increase to about 90,000 in 1975 if conditions do not change importantly. The confidence limits for the projection diverge gradually, though not much, since the regression is based on a long run of years.

Alternatively, and pessimistically, it may be argued that the period of growth ended in 1966, the justification for doing so being that the decrease from 1966 to 1967 was not reversed in 1968, the first occasion in the whole period studied that no immediate resumption of growth had followed a check. On that view, the prospects for the future are better shown by the line of negative slope $Yt = 69.59 - 6.93t$, where t_1 was in 1966. Based on only three years data, that regression cannot properly be extrapolated beyond 1971 and even within that short period the 95% confidence limits diverge markedly. These limits, and those for the previous line, were obtained by extrapolation from the 90% confidence limits for linear trend forecasting given in Table F of Gregg, Hossell and Richardson (*loc. cit.*).

Depending on one's point of view, 1969 is either a crucial or merely an inconvenient year for which to make a forecast. From Figure 6 it can be inferred that if the population in November 1969 equals or exceeds 75,000 the long-term growth rate will have been restored. Should the 1969 total fall appreciably below 65,000 the predictor of growth must be abandoned and a new estimate of the rate of decline be calculated.

It is of some practical consequence that, even should the currently estimated rate of decline, of about 10% annually, be sustained, it may be difficult to be sure of this from one year to the next, since the annual decrement will only be of the same order of magnitude as the probable sampling error. To put it another way: because the year to year changes are likely to continue to be relatively small, it will be necessary to continue annual censuses at the highest practicable level of completeness and precision in order to have a chance of predicting how the population will change.

A consideration of some causal factors

This paper has described a population that was increasing substantially and steadily until 1966. Much of the increase,

at least since 1960, is apparently attributable to a decline in deaths amongst full-grown geese. The annual output of young tended to rise in absolute terms until 1964 but, when measured by the mean family size or by the proportion of young birds in the population in early November, it has been falling slowly since 1950. In 1967 and 1968 the number of young geese reaching Britain fell to 7-8,000, the fewest recruits since 1955, partly because of a decrease in the number of successful parents but more because of a marked reduction in brood-size. This led to a reduction in total numbers.

Unless the effective fertility returns quickly to the levels prevailing before 1960, or the adult death-rate diminishes even more rapidly than it has been doing, the total numbers must decline substantially in the next few years.

The reduction in adult mortality may have been affected by improved conditions in Britain: an enlarged food supply (Kear 1965, Kear and Rodger 1963, Atkinson-Willes 1963), or the increased number of statutory refuges provided for Pinkfeet (Atkinson-Willes *loc. cit.*). A prohibition on the sale of dead wild geese only came into effect in January 1968. These factors need further examination.

There is no evidence that conditions in Britain have contributed to the reduction in effective fertility, although it is at least possible that such agents as agricultural chemicals may have played some part. Very little is yet known of the factors controlling fertility in migratory geese. In North America there is growing evidence that the breeding success of geese nesting in the Arctic is affected not only by the state of the nesting grounds on their arrival but also by the experiences of the geese elsewhere earlier in the spring (C. D. MacInnes, J. P. Prevett, unpublished reports). The study of Pinkfeet in Britain in March, April and May might profitably be intensified.

It is certainly also true that more should be learned about the breeding biology of Pinkfeet in Iceland and Greenland, which has scarcely been looked at before late June, well after the completion of egg laying.

One possibility that might account for reduced breeding success is the deterioration in climate which started to become apparent in Iceland around 1960 and is returning the country to the conditions of the last cold spell, which ended about 1918 (Kristjansson 1969). It is unlikely that a close association between weather and success can be established on the basis of existing data, for there are few meteorological stations close to the nesting areas and standard records rarely include enough information on persistence of snow cover and other factors important to geese.

The need for fuller and up-to-date knowledge of the breeding distribution of the Pinkfoot and of the factors affecting it has been given real urgency by a proposal for a major hydro-electric scheme involving the inundation of most of Thjorsarver, the principal home of the Pinkfoot (Gudmundsson, *in litt.*). In mid-July 1953 Thjorsarver held about 8,200 adults and 10,200 goslings (Scott, Boyd and Sladen 1955). Using the mean brood-size of 4.3 observed at that time, this implies a successful breeding population of 4,700 there then. Some of those parents doubtless lost all their offspring by November, when it is now estimated that there were only 7,300 parents in the entire British-wintering population. Even so, it is likely that in 1953 more than half the effective breeders came from Thjorsarver. An aerial check of Iceland in May 1964 (Boyd 1964) confirmed that Pjorsarver had not lost its importance. Though the number of Pinkfeet breeding in Greenland has still to be determined, it is unlikely to exceed 1,000 pairs (Christensen 1967). Thus Thjorsarver is of enormous importance to Pinkfeet. The plans for the hydro-electric scheme show that the first stage would flood permanently nearly all the areas now favoured by the geese, while the second stage would immerse most of the oasis.

The evidence that, compared with the total stock, successful breeders have only increased slightly since 1955-1960 suggests that there cannot be large tracts of suitable nesting habitat waiting to be occupied. Thus the impending loss of Thjorsarver is a major threat to the future well-being of the Pink-footed Goose. But, even if the dams are never built, it looks as if in the next few years the Pinkfoot may present goose conservationists with an unusual and potentially serious problem. If the production of young Pinkfeet should continue to fall, is there anything that anyone could do about it?

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Counting geese is sometimes a miserably cold and tedious business if at other times a most exciting one. We are heavily indebted to the large group of collaborators who have, at their own considerable expense, provided much of the raw material for this paper. Miss V. M. Thom and W.

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Summary

The Pink-footed Geese breeding in Iceland and Greenland form a closed population which winters in Britain. Nearly complete censuses have been made annually since 1960 and earlier records permit less reliable estimates of total numbers to be made for 1950-59. The population increased rather steadily from about 30,000 in 1950 to over 76,000 in 1966, decreasing to 65,000 in 1968. Earlier Lincoln Index estimates of population size based on capture/recapture are shown to have been inaccurate. There have been substantial changes in different parts of the wintering range, with large increases in north-east and central Scotland and decreases on the Solway Firth and in England, except in Lancashire. Proportionate fertility has fallen slowly throughout the period, with a marked deterioration in 1967 and 1968. Mean brood-size fell from 2.96 in 1950-54 to 2.38 in 1965-66 and only 1.35 in 1967-68. The proportion of young birds to older ones has fallen similarly, though less steadily, while the numbers of geese old enough to have bred but not having done so have increased more than the numbers of successful parents. The crude death-rate of adults has been falling rapidly. Forecasts are made of future trends in numbers by mathematical extrapolation of the data. A continuing increase could lead to a population of 90,000 by 1975, but at present it seems more likely that the decline of the last two years could be continued, leading to a total of only 46,000 in 1971. In Britain conditions appear to have become more favourable, due to increases in food supplies and further legal restrictions on shooting. In the breeding range the climate is becoming more severe and a large hydro-electric project in central Iceland threatens to destroy the home of about half of the breeding population.

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Appendix I. A method for obtaining annual population indices from incomplete census records.

(Adapted, with minor textual changes, from G. Elfving: Statistical analysis of incomplete material, at pp. 9–11 in L. von Haartman (1957).)

Denote by x_{it} the number of geese at the ith roost in the year t. We make the following fundamental assumptions:

1. The number x_{it} is a random variable, with an expected value X_{it} depending on i and t. The fictitious quantity X_{it} may be interpreted as the average number of geese that would be observed, in the year t, at a large number of roosts all similar to roost number i and with a similar prehistory. The difference $y_{it} = x_{it} - X_{it}$ expresses the random component, analogous to the error in physical measurements.

2. The expected value is of the form $X_{it} = a_i b_t$, where a_i may be interpreted as the average X_{it} over a long sequence of years, while b_t is a yearly factor, exhibiting the effect of the particular conditions during the year t, including possible after effects from previous years. It seems reasonable to assume the year effect to be multiplicative, since a good year is likely to increase the population by a certain proportion, not by a certain absolute amount.

The hypotheses may be condensed into the formula:

(1) $x_{it} = a_i b_t + y_{it}$.

With this starting point, the purpose of the numerical analysis is to estimate the time series $\{b_t\}$. The series obtained from different data may then be compared among themselves as well as to other series such as, for example, those reflecting straightforward climatic fluctuations.

The estimation of the b_t is most readily achieved by an iterative procedure. Let Σ_i indicate summation over all years represented on the row of the roost number i and Σ^t summation over all roosts represented in the column of the year t. (The rows and columns used were various sections of Table I.) Applying those operations to equation (1) we have:

(2) $\Sigma_i x_{it} = a_i \Sigma_i b_t + \Sigma_i y_{it}$,

(3) $\Sigma^t x_{it} = b_t \Sigma^t a_i + \Sigma^t y_{it}$,

For a reasonably large number of terms, the last sums may be expected to be small, since the random components will largely cancel. If those sums are neglected, and if we know some approximate value for $\Sigma_i b_t$, then (2) will give us an approximation for a. Similarly, if we know $\Sigma^t a_i$ approximately, (3) will give us b_t.

Since the average of b_t is assumed to be 1 in the long run, we may start with the approximation that $\Sigma_i b_t$ be equal to the number n_i of years represented on row number i. We then have the first approximation $a_i^{(1)} = \frac{\Sigma_i x_{it}}{n_i}$. Inserting that approximation in (3) we get $b_t^{(1)} = \frac{\Sigma^t x_{it}}{\Sigma^t a_i^{(1)}}$.

The next step yields $a_i^{(2)} = \frac{\Sigma_i x_{it}}{\Sigma_i b_t^{(1)}}$, $b_t^{(2)} = \frac{\Sigma^t x_{it}}{\Sigma^t a_i^{(2)}}$ and so on.

After a few steps the b_t becomes stable, yielding the desired estimate of the yearly factor The series obtained may, if desired, be normalized to average 1.

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