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Breeding success of White-fronted Geese from the Nenets National Area

HUGH BOYD

Summary

The breeding success of White-fronted Geese has been inferred from the age composition of flocks wintering at Slimbridge, Gloucestershire, since 1947. These Whitefronts breed in the north east of European Russia. Annual variations in brood-size (average 3·24) have been comparatively slight, though there were unusual numbers of small broods in 1950 and 1958 and of large broods in 1951 and 1956. The proportion of first-winter geese has varied widely about a mean of 33·3%. The fluctuations seem to have reflected changes in output rather than in adult mortality. Attempts to relate production to the limited weather data from the breeding areas by means of correlation methods suggest that wet weather in July has markedly reduced production. Snow in late May and early June has been less important, while low temperatures without snow have had no perceptible effect. Marked geese breeding for the first time, at nearly three years old, have had smaller families than parents four to six years old. So have those more than seven years old.

Introduction

The best way of studying the fertility of geese and the factors affecting it is by direct observations on breeding groups continued over many years. For species nesting in the Arctic such investigations are very rarely practicable but much of the pertinent statistical information can be obtained by studying flocks in winter (Lynch and Singleton, 1964). The White fronted Geese *Anser albifrons albifrons* that visit Slimbridge, Gloucestershire, have been studied in this way since 1947 (Lebret 1948, Boyd 1954, 1957). The present paper adds data collected since 1956 and examines three factors likely to affect the output of young. First, attempts are made to use published weather records to investigate the effects of weather conditions on the breeding grounds upon reproductive success. Second, records of the family-sizes of marked geese are used to illustrate variation in output with age. Third, the proportion of young geese is compared with annual variations in the losses of full-grown birds. The results of all three lines of inquiry are tentative. Their thorough exploration would require a great increase in efforts to catch and mark geese, as well as access to detailed weather records not available outside the U.S.S.R.

Recoveries of ringed birds have shown that nearly all the Whitefronts visiting Slimbridge breed at the western end of the range of *A.a.albifrons*, on the south island of Novaya Zemlya and on Vaygach and Kolguev Islands and on the tundra of the Nenets mainland from the Kanin peninsula east to about 55°E (Shevareva 1959, Boyd 1961). The Slimbridge-visiting Whitefronts do not form a simple closed group. They are part of a much larger stock wintering chiefly in east Germany and the Netherlands with a breeding range extending as far as 70°E. (Philippona and Mulder, 1960). The consistent reappearance of ringed geese suggests that a high proportion of the geese that have once visited Slimbridge continue to do so, but the extent of the gains and losses due to infidelity to tradition, rather than to births and deaths, has yet to be measured. For the purpose of the ensuing analyses it is assumed that the reproductive performance of immigrants is much the same as that of persistent members of the group, although recent work in the Netherlands has shown marked differences between flocks wintering in different parts of that country (W. J. Doude van Troostwijk, personal communication).

Fertility

Two measures of annual production can be got by looking at Whitefront flocks in autumn: the proportion of birds in first-winter plumage and the sizes of family parties. Both measures tend to diminish through the winter, because young geese are more vulnerable than older ones (Boyd 1957), so that records collected in the autumn best reflect the success of the previous breeding season. Whitefronts have been scarce at Slimbridge before December, particularly in recent years, and the earliest arrivals tend to be unrepresentative, so that for adequate samples it is necessary to lump together data from October, November and December. Since most early arrivals remain for long periods, and so may be looked at repeatedly, the subsamples within any year are not independent. Because of differences in the accessibility of the geese and in the amount of time spent in searching, the annual samples summarised in Table I do not reflect the changes in the numbers of geese arriving at Slimbridge in autumn (compare columns (1) and (4) with column (6)).

The means and the frequency distributions of brood-size show considerable superficial differences between years. The standard errors of the means are relatively large, often because the samples have been small but also because the distributions are platykurtic and positively skewed. The coefficient of variation is always very high (from 36·2 to 53·8 even in the largest samples). Thus significant departures from the average are only demonstrable in four of the seventeen years. In 1950 and 1958 there were few large broods: in 1958 there were very few broods at all and an unusually high proportion of ones and twos, while in 1950 there was a marked excess of twos and threes. In 1951 and 1956 there were exceptionally many broods of more than four young.

Column (5) of Table I records the proportion of first-winter birds observed each autumn. Marked departures from the average value for the total sample appear to have occurred in thirteen of the seventeen years, only the values for 1949, 1954, 1956 and 1959 lying close to the mean. This great variability is paralleled in the sub-

Table I. Annual measures of breeding success of White-fronted Geese seen at Slimbridge in October-December, 1947–63. Values in italics show departures from the long-term means significant at the 5% level.

	no. of broods (1)	*mean brood size* (2)	*s.e. of means* (3)	*proportion 1st winter birds* — *sample size* (4)	*proportion 1st winter birds* — *1st w. per 1000* (5)	*max. number seen before 31 Dec.* (6)
1947	11	3·55	0·47	606	*206*	3000
1948	49	3·22	0·21	184	*196*	1500
1949	45	3·29	0·18	466	290	650
1950	252	*3·04*	0·08	3511	*391*	3000
1951	176	*3·66*	0·14	3166	*402*	1900
1952	282	3·22	0·09	3647	*372*	3900
1953	105	3·19	0·16	1900	*242*	1500
1954	4	4·75	0·55	900	311	1000
1955	114	3·24	0·16	900	*470*	1270
1956	102	*3·67*	0·19	683	326	1700
1957	133	3·54	0·15	1500	*462*	2200
1958	48	*2·54*	0·15	807	*124*	700
1959	239	3·05	0·10	2893	346	1400
1960	106	3·30	0·16	994	*371*	780
1961	22	3·86	0·36	381	*454*	450
1962	43	2·79	0·20	2039	108	1450
1963	37	2·84	0·23	615	228	1000
total	1756	3·24	0·038	25192	mean 333	mean 1610

samples within a year and is undoubtedly affected by incomplete mixing of young and old birds within flocks due to the persistence of family parties. Boyd (1956) has discussed a similar situation in *Anser brachyrhynchus* from a statistical point of view.

Although by ingenuous statistical criteria the mean brood-sizes show few 'significant' differences while the proportions of young birds show many, the correlation between the annual values for the two measures is much greater than might be expected ($r = +0{\cdot}62$). Taken in conjunction with the fact that even in 1958 and 1962 the proportion of young geese did not fall below 10% this leads to a general inference of major importance: the variations in production of young seem more likely to be due to differences in rearing success than to alterations in the number of geese laying eggs. Clearly, taking the entire range of this Nenets stock as a whole, no year since 1947 has been a "non-breeding" year in the sense of a year in which breeding was wholly prevented or abandoned (Marshall, 1952). Variations in brood-size in autumn might reflect either differences in the numbers of eggs laid or in hatching or fledging success. Only direct observations in nesting areas could distinguish between these alternatives with certainty but it is possible to make some progress by studying the phenology of nesting and the effects of weather.

Breeding phenology and weather data

Irregular observations scattered over many years, summarised by Dementiev and Gladkov (1952) and Shevareva (1959) led to the general phenological picture given in Table II. In addition to the evident differences between one place and another, there are important differences from year to year, though the data are too fragmentary to show this well. Both types of variation are due to climatic differences.

The weather around the shores of the Barents Sea is usually extremely unpleasant. Snow cover persists on Kolguev for over 230 days a year and on Vaygach for 250 days, while the rivers of the Kanin peninsula are frozen over for more than seven months (Zaborski, 1955). In the summer "Kolguev is exceedingly subject to fogs and gales of great duration" (Trevor-Battye, 1895) and Novaya Zemlya is even worse. Though there is a long-established chain of weather stations in the area, full records are not published outside the U.S.S.R. and the only data immediately available are those provided by The Daily Weather Report of the British Meteorological Office. The synoptic map for 1200 h. GMT published in the Report includes data from three mainland stations in or near the breeding range of Slimbridge-visiting Whitefronts (at Cape Kanin, Tabseda and Amderma), from Vaygach Island and from Malye Karmakuly on the west coast of the south island of Novaya Zemlya. There is no report from Kolguev. The data comprise wind direction and speed, present weather, temperature and cloud cover. Such a set of instantaneous observations is far from ideal for assessing the impact of the weather upon nesting geese, especially as until very recently there were many gaps in the plotted records. For 1947–50 it has been possible to supplement the D.W.R. records with the monthly mean temperature and total precipitation at Malye Karmakuly and Voygach published in *World Weather Records 1941–50* (Weather Bureau, U.S. Dept. of Commerce, Washington, 1959). There is an encouraging measure of agreement between the published monthly mean temperatures and those calculated from the D.W.R. data. More surprisingly, there is a satisfactory consistency of trend between the records of total precipitation and an index of "days-with-precipitation recorded at 1200 h. GMT" derived from the D.W.R.

From studies of other geese nesting in various parts of the Arctic (see especially Barry 1962, Cooch 1961, Goodhart and

Table II. Phenology of White-fronted Geese in the Nenets National Okrug, around the south-east shores of the Barents Sea.

	Kanin peninsula	*Kolgnev Island*	*Novaya Zemlya*
first arrivals	May 9–23	May 25–June 5	May 15–25
laying begins	May 29–June 8	June 4–20	
incubation begins	June 5–15	June 11–28	
hatching begins	July 1–12	July 7–25	July 13–28
first young fledged	August 4–26	Zug. 10–Sep. 10	
final departures	after Sep. 19	from Aug. 31	Sep. 4–Oct. 7
length of stay	105–140 days		

Table III. Yearly variations in temperature and rainfall in Whitefront breeding areas, May–July.

	May 16–June 15 mean temperature & rainfall index						July		
	mainland		N. Zemlya		weighted means		rainfall index		
	°C	rain	°C	rain	°C	rain	mainland	N. Zemlya	mean
1947	−0·7	0?	−0·6	0?	−0·6	0?	31	250	140
1948	+2·6	80	−1·1	95	+0·5	88	56	0	28
1949	+3·3	61	+0·5	62	+1·8	62	48	133	93
1950	+6·9	139	−0·9	148	+2·6	144	132	107	120
1951	+4·3	0	−1·3	130	+1·2	65	0	160	80
1952	+4·1	67	+1·6	111	+2·7	89	26	71	49
1953	+7·1	20	+1·0	36	+3·7	29	78	69	74
1954	+6·2	92	+2·4	65	+4·1	79	20	32	26
1955	+5·6	89	−0.3	43	+2·4	66	41	0	20
1956	+4·7	87	+0·4	148	+2·3	118	0	0	0
1957	+3·4	240	−0.2	276	+1·4	258	43	129	86
1958	−0·6	182	+2·7	321	−1·7	252	104	345	225
1959	+2·5	244	−0·2	281	+1·0	263	0	348	174
1960	+1·8	305	+0·1	111	+0·9	208	83	200	142
1961	+0·4	138	−1·1	250	−0·5	194	14	77	46
1962	+3·7	207	−1·0	200	+1·1	204	133	172	203
1963	+2·2	235	−0·1	100	+0·9	168	127	103	115

Wright 1958, MacInnes 1962) it seems likely that weather conditions are especially liable to affect breeding success at two periods in the nesting cycle. First, cold weather at the time of arrival of the geese in the spring may make it difficult or impossible for them to lay eggs, by delaying the disappearance of snow cover from nest sites or by fresh falls of snow. Second, cold, and especially wet-and-cold, weather around the time when most clutches are hatching or goslings are less than two weeks old may also lead to relatively high losses. Table II shows that in the Nenets region the first of these critical periods falls somewhere between 16th May and 15th June, while the second may occur during most of July. Table III summarises the relevant weather data for each year from 1947 to 1963. Means for late May and for early June were also calculated separately. Their use affords no additional insight. The two means are positively correlated, especially on the Nenets mainland. Craddock and Ward (1962) have demonstrated an association between temperature anomalies in May and June in this region.

In testing hypotheses about association between weather characteristics and breeding success it is proper to use non-parametric techniques, since the available weather measurements are unlikely to be metrical with respect to the factors that directly influence egg-laying or the survival of goslings. On the assumption that the relationship between the variables is linear, rank correlation coefficients have been calculated to test association between the scales of breeding success provided by mean brood-size, proportion of first-winter birds and their joint rank order and the indices of May-June temperature and precipitation, July precipitation and their combined rank orders (Table IV). From

Table IV. Rank correlation coefficients between measures of breeding success and of weather in the breeding season

	measures of breeding success		
	mean brood-size	proportion of young	combined ranking
weather 16 May–15 June			
temperature	+0·27	+0·41	+0·10
precipitation	−0·45*	−0·01	−0·05
combined ranking	+0·25	+0·09	+0·23
July rainfall index	−0·61**	−0·57*	−0·62**
good summer weather			+0·43*

* significant at 5% level; ** significant at 1% level

these coefficients, successful breeding appears to be positively correlated with generally fair spring and summer weather. The only correlation between measures of success and the weather in late May and early June that is significant at the 5% level suggests that broods were larger after dry springs.

Since the assumption of linearity in the relationships between weather and breeding success may be unreasonable, contingency tables have also been used to compare the observed frequencies of good, average and bad output with various groupings of weather conditions. No convincing association between spring temperatures and breeding success could be demonstrated in this way either.

Analogy with the reported behaviour of other geese nesting in other parts of the Arctic led to the expectation that the condition of the environment at the times of arrival of the geese would be of primary importance. In particular the extent and persistence of snow cover has been shown to determine how soon *Branta bernicla* and *A. caerulescens* may begin to nest (Barry, 1962, Cooch, 1961). The weather at the time of return is important in such cases because of its effect on the snow cover, rather than on the geese themselves, which arrive ready to lay eggs. Dementiev and Gladkov (1952) state not only that a delay of 10–16 days occurs between the arrival of Whitefronts and the beginning of laying but also that the geese arrive with the gonads in a relatively undeveloped state. If there is indeed little urgency about the beginning of nesting in this Whitefront population the weakness of correlations between early spring weather and breeding success becomes less surprising, especially since no measure of the extent of snow cover in the middle of May has been available. There seems to be a marked difference between the relation of Nenets Whitefronts to the spring weather and that of the Barnacle Geese *Branta leucopsis* and Brent Geese *B.b.bernicla* which nest in the same region. For those species, both in Siberia and elsewhere, a delay in the start of nesting leads to the abandonment of laying for that year. Perhaps the apparent relative invulnerability of the Whitefront population is due to ability to remain on its breeding grounds well into September, which the other species seem not to do. However, too little is known about the timing of departures for this point to be explored thoroughly at present.

All three indices of breeding success are strongly correlated with the rainfall in July, production being high in years of low rainfall and poor in wet years. Perhaps this correlation is well marked because the annual differences in rainfall in July tend to be great.

Effects of age upon fertility

Continued observations upon the small number of ringed geese in the flocks at Slimbridge have confirmed the earlier evidence that one- and two-year-old geese are not accompanied by offspring and that a smaller proportion of three-year-olds have families than do geese four years or more old (Boyd, 1954, 1957). More remarkably, it now appears possible that production of young may fall off with increasing age after no more than four years of maturity. The evidence is meagre, because very few geese of precisely-known age can be found, so that the performance of older birds can only be inferred by comparing the output in successive years after marking of all ringed geese seen, including those whose age at marking was not known. Perhaps Table V shows no more than a

Table V. Variations in production of young with increasing age, from observations of families accompanying ringed White-fronted Geese at Slimbridge

(*a*) *Proportion with broods*

	years after marking 1	2	3	4	5	6+	*total*
with broods	36	39	36	24	7	4	146
without broods	25	18	12	7	10	4	76
	61	57	48	31	17	8	222
proportion with broods	0·59	0·68	0·75	0·77	0·41	0·50	

$\chi^2 = 10{\cdot}55,\ 0{\cdot}10 > P > 0{\cdot}05$

(*b*) *Size of broods*

		broods of 1,2	3,4	5+	*total*	*proportion of broods* *small*	*large*
years	1,2	38	28	9	75	0·50	0·12
later	3,4	28	16	16	60	0·47	0·27
	5+	3	7	1	11	0·27	0·09
total		69	51	26	146		

$\chi^1 = 9{\cdot}60,\ 0{\cdot}05 > P > 0{\cdot}02$

tendency to stability of breeding performance with increasing age. The point needs further exploration, though this cannot be done without a great increase in the number of geese ringed and successfully detected many years later. It seems unlikely that a reduction in the number of young reared after the age of eight or nine years could be related to senescence, for captive White-fronted Geese have often lived for fifteen years or more and wild-caught birds have sometimes not begun to breed in captivity until over ten years old.

The suggestion in Table V that a high proportion of young parents rear only one or two goslings is consistent with observations on geese of several species nesting in captivity, in which there is a general tendency for geese nesting for the first time to do less well than more experienced individuals. This inefficiency of first breeders may account for the existence of a negative serial correlation ($r_s = -0{\cdot}516$) between the proportions of young birds observed in year N and in year N + 3, a year of large output being followed three years later by an increase in the breeding stock but a reduction in breeding success. In contrast, no statistically significant correlation is apparent between the proportion of young birds seen in year N and those found one, two, four or five years later.

Annual mortality and production

It has so far been assumed that variations in the observed proportion of young geese in the autumn are chiefly due to differences in the number of young reared. This assumption needs justification because it is theoretically possible that the changes could be brought about in another way, if the number of young reared were relatively constant but the survival of adults altered appreciably from year to year. A detailed study of adult losses is in preparation. For the immediate purpose attention will be confined to a set of estimates of annual losses in the years 1950–51 to 1963–64. These are derived from recoveries of geese ringed at Slimbridge in February or early March in eight years between 1948 and 1962. Applying the maximum-likelihood modification of Lack's method devised by Haldane (1955) to the entire recovery series, the average annual mortality rate is found to be 27·0 ± 3·6%, assuming that the rate does not vary with the ages of the birds. (This assumption appears to be well justified, especially since no Whitefront has been ringed before it was at least 7½ months old.) Using this constant value of 27% and the number of recoveries from each year of ringing it is possible to construct a table of the number of recoveries expected in each year. The losses in any one year can then be estimated by multiplying the average rate (27%) by the ratio (recoveries reported)/(recoveries expected). The results are summarised in Table VI.

Table VI. Estimates of annual losses of White-fronted Geese (from one 1st October to the next) obtained from recoveries of ringed birds, 1950–64

year	*recoveries reported*	*recoveries expected*	*annual losses (%)*
1950–51	2	5·39	10·0
1951–52	8	7·04	30·7
1952–53	11	10·50	28·3
1953–54	19	13·59	37·7
1954–55	6	9·93	16·3
1955–56	10	7·24	37·3
1956–57	6	5·29	30·6
1957–58	1	3·81	7·1
1958–59	16	15·15	28·5
1959–60	14	20·26	18·7
1960–61	12	14·59	22·2
1961–62	15	10·52	38·5
1962–63	19	12·07	42·5
1963–64	5	8·56	15·8
total	144	143·93	27·0

The hypothesis to be tested is that a relationship exists between the proportion of young geese found in the autumn and the losses of adults in the preceding year. The correlation coefficient between the proportion of young geese in the autumn of year N and the adult losses in the preceding twelve months is − 0·21, a value far too low to provide good evidence for such a relationship ($0{\cdot}5 > P > 0{\cdot}4$). The use of multiple regression coefficients, partialling out the effects of brood-size and of summer weather upon the proportion of young geese in autumn, serves to reduce the value of the coefficient. Thus, on the available data, it appears that annual variations in adult mortality do not lead to important differences in the autumn age ratio.

Discussion

The publication of results as tentative as these can best be justified by considering the feasibility of alternative, more rigorous, methods of studying the factors affecting gosling production. In the case of the Nenets Whitefronts political difficulties preclude direct observations by foreigners. Even in politically-accessible areas it will always be comparatively expensive to put observers into breeding areas in the spring before the return of the geese and to maintain a watch throughout the breeding cycle.

It can be done, as the outstanding efforts of the Canadian Wildlife Service have shown (Barry, 1962, Cooch, 1961, Lemieux, 1959). The present study should also have shown the desirability of looking at the behaviour of geese nesting in the low-arctic to see how it differs from that of the high-arctic species studied in Canada. But, supposing that observations in breeding areas must always be few and short-lived, any methods of maintaining continuous records of fertility and of analysing the effects of possibly relevant factors over many years deserve investigation. In the writer's opinion the work reported here suggests that in carefully-selected cases the combination of observations in winter and of weather data from established meteorological stations may be of value. Some Arctic weather stations keep records of the extent of snow cover. It would be instructive to repeat analyses of the type attempted here for a population nesting around a station providing such full weather data.

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Brent Geese in western Europe during the winters of 1962-63 and 1963-64

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Summary

Hard weather during January and February 1963 concentrated most of the population of Dark-bellied Brent Geese into England and France, making a good estimate of numbers possible. The population in mid-January 1963 was between 23,000 and 25,000. Less comprehensive counts during the winter of 1963–64 suggest that the numbers were then much the same. Very few young were recorded from any areas during 1962–63, but during 1963–64 counts from all areas lay within the range 30–40% first-winter.

The Pale-Bellied Brent wintering in Ireland have had two successful breeding seasons in succession, with about 39% young in sample counts in 1962–63, and about 33% in 1963–64.

Introduction

Although the winter of 1962–63 was exceptionally severe throughout Europe, the counts made of Brent Geese were more comprehensive than any obtained pre-