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# Long-term reproductive performance in White-fronted Geese *Anser a. albifrons* and Tundra Bean Geese *A. fabalis rossicus* wintering in Zeeland (The Netherlands)

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*The reproductive performance of White-fronted Geese and Tundra Bean Geese was surveyed during 1964/65 to 1994/95 in southern Zeeland (the Netherlands). The proportion of first-year birds was higher on average in the White-front than in the Tundra Bean Goose (29 ± 10% and 25 ± 5%) and mean brood-size was also higher (2.5 ± 0.3 versus 2.1 ± 0.2). During the first five years of the survey, more than 15% of broods in both species were single-parent, this proportion dropped to 5–10% in the course of the 1970s. No trend in time in reproductive parameters of either species was found. The proportion of first-year birds was significantly correlated with mean brood-size in both species. In the White-fronted Goose both parameters show a pattern of poor breeding every three years and the proportion of first-year birds is strongly correlated with those of the Dark-bellied Brent Goose. No cyclical variations were found in the Tundra Bean Goose, perhaps because its breeding range is more southerly than that of the White-front.*

Two basic indices are available to assess reproductive performance in Arctic breeding geese on their wintering grounds: the proportion of first-year (juvenile) birds, and the mean brood-size (number of juveniles per family) in randomly sampled flocks. These techniques were first used in Europe by Boyd[1–2] in Great Britain and by Lebret[3] in The Netherlands but they are fraught with problems and shortcomings.[4–7] However, with experience, errors made in the field can be reduced to an acceptable level.[8–10]

Assessment of reproductive success on the winter quarters is necessary for several reasons. Fieldwork in remote subarctic tundra areas remains difficult and expensive, and visibility bias in aerial surveys may overlook high nesting success.[11]

The importance of tundra areas in north-east European Russia for breeding White-fronts and Tundra Bean Geese was formerly underestimated, although densities of up to 15–20 breeding White-front pairs/km² occur in good years.[12] Also between 250 000 and 400 000 Tundra Bean Geese stay here during summer and are presently increasing.[12,13] Ringing recoveries show that most White-fronts and Tundra Bean Geese wintering in The Netherlands originate from the north-east of Europe.[14,15]

The aims of this study are to present long-term trends in proportions of young and brood-size in both species and to assess cyclical variation in their breeding performance.

## STUDY AREA AND METHODS

Wintering flocks of both geese were mainly examined in the eastern polders of Zeeuws-Vlaanderen and of Zuid-Beveland, (Zeeland, The Netherlands). Virtually all geese observed roost on the 'drowned land of Saeftinghe' (04°13′E, 51°23′N). During the winters 1984/85 to 1988/89, fortnightly survey of that roost revealed peaks of 18 000 White-fronts and 5200 Tundra Bean Geese.[16]

The distinction between adult and juvenile Tundra Bean Geese was described in earlier papers.[17,18] The assessment of percentage young and brood-size among White-fronted Geese and Tundra Bean Geese started in 1964/65 and 1969/70, respectively. The earliest winters provided insufficient material on the Tundra Bean Goose. More confident assessments of age-group ratios and of family size began in 1970/71 and 1975/76, respectively (Table 1). Care was taken to minimize bias in field counts. Elevated proportions of first-year birds occur on the edge of flocks. The proportion of first-years is higher amongst flocks foraging on high-quality food (e.g. residues of potatoes or sugar beets), compared to flocks feeding on pastures. Small (<100 geese) and/or medium-sized flocks (100–500 geese), also tend to contain greater numbers of first-years (pers. obs.).[19] We always tried to examine about the same proportions of each of these categories.

Caution is needed when sampling brood-size amongst White-fronts. First, the method of observation strongly influences the results. An observer who looks from successive observation spots at families on the ground ($n$ = 2831) finds on average 0.55 ± 0.06 more juveniles per family than a stationary observer who is studying only flying families ($n$ = 2905).[20] The

**Table 1.** Proportions of first-year birds and mean brood-sizes among White-fronted Geese and Tundra Bean Geese in flocks wintering in the south of the province of Zeeland (The Netherlands) (personal counts)

| | *White-fronted Goose* | | | | *Tundra Bean Goose* | | | |
|---|---|---|---|---|---|---|---|---|
| *Winter* | n | *% First-year* | n | *Mean brood -size* | n | *% First-year* | n | *Mean brood -size* |
| 64/65 | 3 505 | 25 | 61 | 2.2 | | | | |
| 65/66 | 3 629 | 28 | 127 | 2.2 | | | | |
| 66/67 | 2 074 | 36 | 131 | 2.7 | | | | |
| 67/68 | 3 160 | 35 | 152 | 2.7 | | | | |
| 68/69 | 4 513 | 14 | 91 | 1.8 | | | | |
| 69/70 | 6 010 | 44 | 552 | 2.6 | | | | |
| 70/71 | 6 024 | 45 | 471 | 3.0 | 1184 | 29 | | |
| 71/72 | 6 022 | 10 | 127 | 2.3 | 1024 | 19 | | |
| 72/73 | 8 358 | 46 | 723 | 2.9 | 1412 | 17 | | |
| 73/74 | 14 337 | 36 | 413 | 2.8 | 2140 | 22 | | |
| 74/75 | 15 805 | 19 | 433 | 2.5 | 3047 | 17 | | |
| 75/76 | 14 067 | 39 | 979 | 2.7 | 2234 | 22 | 39 | 2.2 |
| 76/77 | 12 871 | 42 | 1026 | 2.7 | 2155 | 23 | 69 | 1.8 |
| 77/78 | 3 659 | 28 | 81 | 2.5 | 1877 | 26 | 83 | 1.8 |
| 78/79 | 6 066 | 20 | 85 | 2.2 | 2601 | 34 | 172 | 2.2 |
| 79/80 | 1 354 | 26 | 106 | 2.6 | 2234 | 32 | 100 | 2.3 |
| 80/81 | 6 369 | 25 | 156 | 2.6 | 3234 | 29 | 115 | 2.4 |
| 81/82 | 5 286 | 29 | 147 | 2.7 | 5572 | 27 | 181 | 2.2 |
| 82/83 | 10 522 | 26 | 337 | 2.3 | 3700 | 20 | 84 | 1.9 |
| 83/84 | 7 603 | 31 | 265 | 2.5 | 4301 | 24 | 78 | 2.2 |
| 84/85 | 7 400 | 23 | 68 | 2.8 | 3895 | 20 | 67 | 1.9 |
| 85/86 | 13 818 | 45 | 614 | 2.8 | 3469 | 26 | 106 | 2.1 |
| 86/87 | 18 815 | 17 | 293 | 2.0 | 4105 | 14 | 83 | 1.6 |
| 87/88 | 16 068 | 26 | 648 | 2.4 | 4834 | 25 | 104 | 2.0 |
| 88/89 | 13 602 | 40 | 964 | 2.7 | 2917 | 31 | 102 | 2.3 |
| 89/90 | 16 572 | 23 | 380 | 2.3 | 2683 | 27 | 86 | 1.9 |
| 90/91 | 16 308 | 32 | 618 | 2.4 | 2788 | 27 | 56 | 2.1 |
| 91/92 | 17 235 | 41 | 394 | 3.0 | 3850 | 33 | 134 | 2.6 |
| 92/93 | 14 703 | 12 | 148 | 1.8 | 2864 | 22 | 56 | 1.9 |
| 93/94 | 11 473 | 28 | 318 | 2.5 | 3150 | 28 | 129 | 2.2 |
| 94/95 | 18 222 | 21 | 548 | 2.2 | 4553 | 22 | 102 | 2.2 |
| *n* winters | 31 | | 31 | | 25 | | 20 | |
| Mean (sd) | | 29 (10) | | 2.5 (0.3) | | 25 (5) | | 2.1 (0.2) |
| cv ± se as % | | 34 ± 4 | | 12 ± 2 | | 21 ± 3 | | 11 ± 2 |

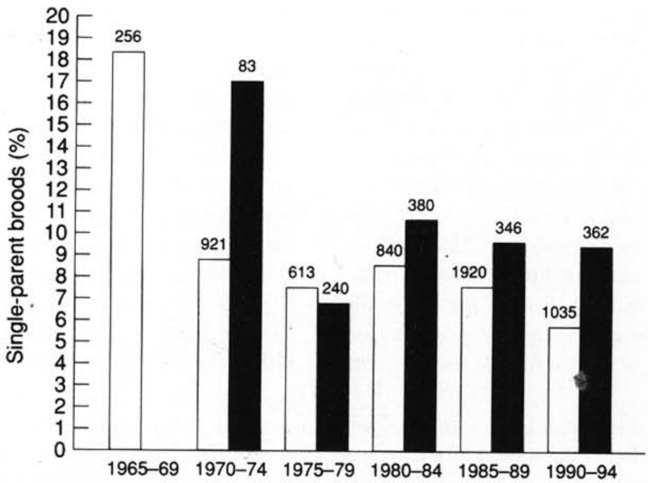


**Figure 1.** Percentage of single-parent broods among White-fronted Geese (1965/66 to 1994/95) and Tundra Bean Geese (1970/71 to 1994/95) per five-year period. Records before 31 December. Unshaded columns, White-fronted Goose; black columns, Tundra Bean Goose. Numbers above columns indicate sample sizes of broods.

first method was used throughout this investigation. Secondly, to eliminate amalgamated broods as much as possible, only one or two adults with a maximum of eight first-year birds were considered. Thirdly, there is strong evidence that, in this species, family cohesiveness breaks up in the course of the winter.[20] For example, Holz and Sellin[21] observed flocks of 3000 White-fronted Geese on spring migration in East Germany, consisting nearly exclusively of first-year birds. For that reason we examined brood-sizes before 15 January.

For convenience, years are defined as 'good' if in the succeeding winter the reproductive parameters exceed the value of the long-term mean plus one standard deviation ($\bar{x} > +1$ sd). Years are recognized as 'poor' if these parameters fall below the long-term mean minus 1 sd ( $\bar{x} < -1$ sd).

Statistical procedures follow Sokal and Rohlf.[22] Occurrences of significant deviations around the linear regression are examined according to the general trends test of von Neumann *et al.*[23] For correlation and regression analyses, the mean proportions of first-year birds are converted into their corresponding arcsine values. Testing for periodicity in data has been achieved by the Mann–Whitney *U* test and by the Kruskal–Wallis test, in which the years in Table 1 were successively labelled 1, 2 and 3, and the mean of the parameter in each set of years has been tested to find if they are the same.[24]

## RESULTS

### Proportion of first-year birds and brood-size

The percentage of first-year birds within winter flocks was significantly higher in White-fronts (29 ± 10%) than in Tundra Bean Geese (25 ± 5%) ($t_{54} = 2.256$; $P < 0.05$, Table 1). The mean family-size was also higher but was not statistically different: 2.5 ± 0.3 versus 2.1 ± 0.2 ($t_{50} = 0.619$; ns).

The mean proportion of first-year birds was more variable in the White-front (coefficient of variation cv = 34 ± 4%) than in the Tundra Bean (cv = 21 ± 3%). There was no difference in mean brood-size between the two species: cv = 12 ± 2% (White-front) and 11 ± 2% (Tundra Bean).

Table 2 lists the years of 'good' and 'poor' reproduction. There were more good and poor years for only one parameter than for both: seven based on one parameter to six based on both parameters in the White-front compared with nine and two in the Tundra Bean, there being no statistical difference ($\chi^2_{corr} = 1.028$; df = 1; ns).

The distribution of single-parent broods per five-year period exceeds 15% for the White-fronted Goose during the second half of the

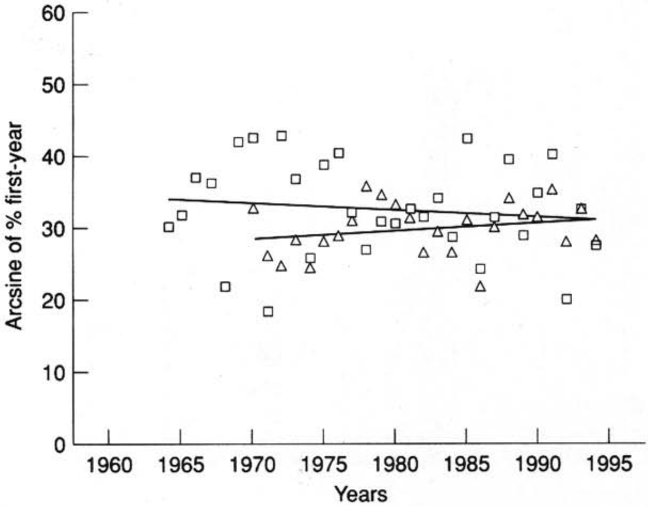


**Figure 2.** Regression lines of proportions of first-year birds (arcsine transformed) among White-fronted Geese (squares, 1964/65 to 1994/95) and Tundra Bean Geese (triangles, 1970/71 to 1994/95) on years. The linear regression equations of the arcsine transformed percentage of first-year birds upon time are: White-fronted Goose: $Y = 40.6 - 0.102X$; $t_{29} = 0.761$; $P > 0.4$; Tundra Bean Goose : $Y = 21.4 + 0.100X$; $t_{23} = 1.019$; $P > 0.3$.

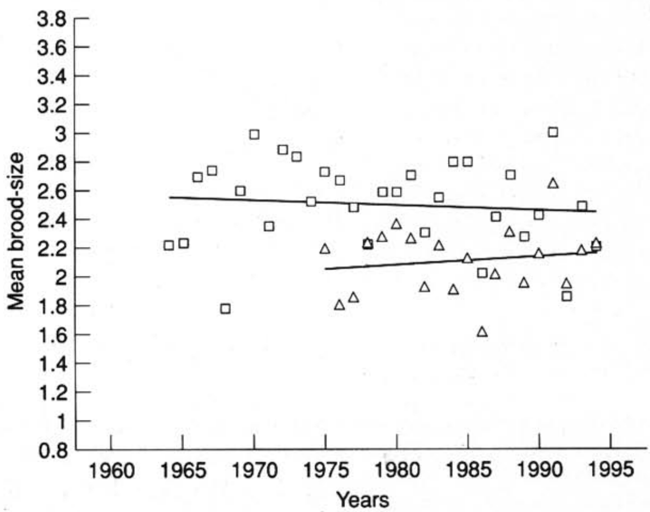


**Figure 3.** Regression lines of mean brood-sizes among White-fronted Geese (squares, 1964/65 to 1994/95) and Tundra Bean Geese (triangles, 1975/76 to 1994/95) on years. The linear regression equations of the mean brood-sizes upon time are: White-fronted Goose: $Y = 2.78 - 0.004X$; $t_{29} = 0.587$; $P > 0.5$. Tundra Bean Goose: $Y = 1.61 + 0.006X$; $t_{18} = 0.631$; $P > 0.5$.

1960s and for the Tundra Bean Goose during the first half of the 1970s. Later on, the percentages in both species fell to between 5% and 10% (Fig. 1).

## Trends of reproduction parameters

In both geese, a regression of the arcsine transformed proportions of first-year birds (Fig. 2) and of the mean brood-sizes (Fig. 3) on years was best fitted by a linear relationship. However, the regression coefficients of both equations did not differ significantly from zero, hence there were no trends in reproductive parameters for the period which we have investigated.

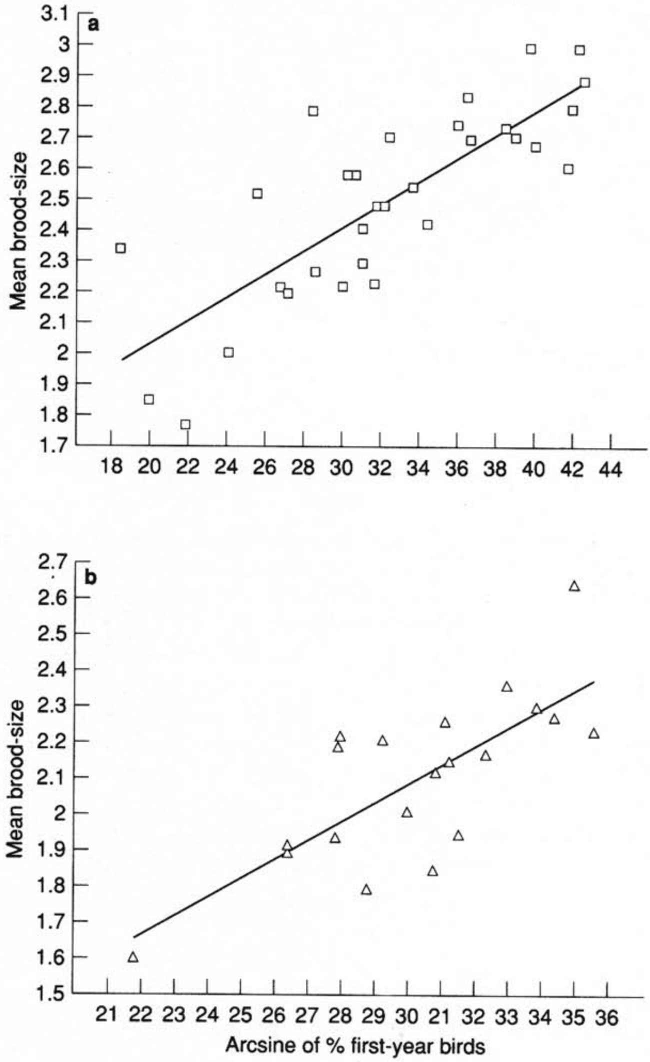


**Figure 4**. Correlation between the mean brood-sizes and the arcsine transformed proportions of first-year birds among (a) White-fronted Geese, 1964/65 to 1994/95 and (b) among Tundra Bean Geese, 1975/76 to 1994/95. The correlations and linear regression equations of the mean brood-sizes upon the arcsine transformed percentage of first-year birds are: White-fronted Goose: $r = 0.800$; $t_{29} = 7.444$; $P < 0.001$; $Y = 1.30 + 0.036X$. Tundra Bean Goose: $r = 0.749$; $t_{18} = 4.807$; $P < 0.001$; $Y = 0.53 + 0.051X$.

## Relationships between reproductive parameters within and between geese

In both species, there was a highly significant positive correlation between the mean brood-size and the arcsine transformed mean proportion of first-year birds (Fig. 4). The correlation coefficients of the variables in these figures can be considered homogeneous ($t_s = 0.416$; $n_1 = 31$ and $n_2 = 20$; $P > 0.76$).

The proportions of first-year birds in the two species were closely related (Fig. 5). The arcsine-transformed percentages of first-year birds show an absence of correlation when all winters (1970/71 to 1994/95, $n = 25$) are considered: $r = 0.315$; $t_{23} = 1.591$; ns), due mainly to the anomalous data from 1972 (Spearman rank correlation reveals a large difference in ranking: 25/25 for *A. albifrons* and 3/25 for *A. f. rossicus*, Table 2). In the winter of 1972/73,

**Table 2.** Years with reproductive parameters above ('good') and below ('poor') the limits of the long-term mean ± 1 sd

| | *White-fronted Goose* | | | | *Tundra Bean Goose* | | | |
|---|---|---|---|---|---|---|---|---|
| | *% First-year* 31[a] (19.4–39.4) | | *Brood-size* 31 (2.19–2.79) | | *% First-year* 25 (19.5–29.7) | | *Brood-size* 20 (1.86–2.32) | |
| | *Above* | *Below* | *Above* | *Below* | *Above* | *Below* | *Above* | *Below* |
| | 1969 | 1968 | 1970 | 1968 | 1978 | 1971 | 1980 | 1976 |
| | 1970 | 1971 | 1972 | 1986 | 1979 | 1972 | 1991 | 1977 |
| | 1972 | 1974 | 1973 | 1992 | 1988 | 1974 | | 1986 |
| | 1976 | 1986 | 1991 | | 1991 | 1986 | | |
| | 1985 | 1992 | | | | | | |
| | 1988 | | | | | | | |
| | 1991 | | | | | | | |
| Sum of 'good' and 'poor' years | 12/31 | | 7/31 | | 8/25 | | 5/20 | |
| % | 38.7 | | 22.6 | | 32.0 | | 25.0 | |

[a] Number of winters and mean ± 1 sd.

White-fronts had a good year (45.9% first-year birds) the Tundra Bean Geese had a poor season (17.3%). Removal of the 1972/73 winter ($n$ = 24 winters) attains a significant correlation coefficient (Fig. 5). Furthermore, there was a highly significant correlation based on data from the last 14 winters (1981/82 to 1994/95) ($r = 0.710$; $t_{12} = 3.493$; $P < 0.01$).

There was a close relationship ($n$ = 20) between mean brood-sizes in both goose species (Fig. 6). Based on the last 14 winters, the correlation again becomes highly significant ($r = 0.682$; $t_{12} = 4.188$; $P < 0.01$).

No statistically significant difference was found between the correlation coefficients of Fig. 5 and of Fig. 6: ($t_s = 0.254$; $n_1 = 24$ and $n_2 = 20$; ns).

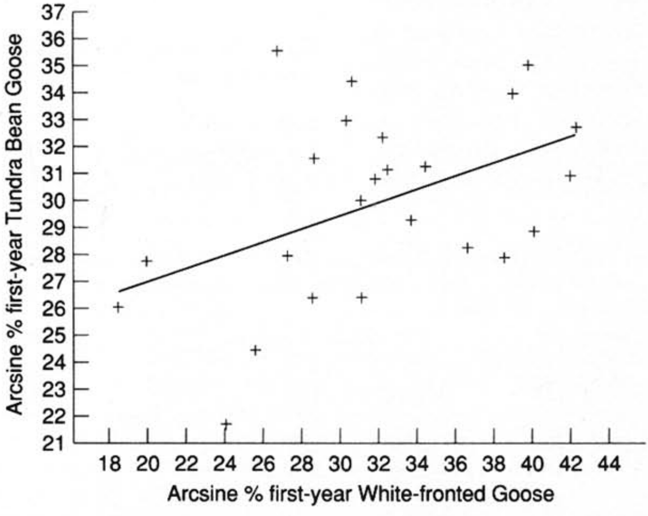


**Figure 5.** Correlation between the proportions of first-year birds (arcsine transformed) among Tundra Bean Geese and White-fronted Geese (1970/71 to 1994/95, the winter 1972/73 discarded). Correlation: $r = 0.452$; $t_{22} = 2.376$; $P < 0.05$. The linear regression equation of the arcsine transformed percentage of first-year birds in Tundra Bean Goose upon these in White-fronted Goose is: $Y = 22.2 + 0.239X$.

**Table 4.** Mean brood-sizes of White-fronted Geese (WG) and of Tundra Bean Geese (TBG) in different sets of years: same procedure as in Table 3

| | *Mean brood-size in 2 years* | | | *Mean brood-size in 3 years* | | | *Mean brood-size in 4 years* | | |
|---|---|---|---|---|---|---|---|---|---|
| | *Position* | *WG* | *TBG* | *Position* | *WG* | *TBG* | *Position* | *WG* | *TBG* |
| | 1 | 2.42 | 2.16 | 1 | 2.25 | 1.97 | 1 | 2.61 | 2.25 |
| | 2 | 2.52 | 2.03 | 2 | 2.58 | 2.12 | 2 | 2.42 | 2.05 |
| | | | | 3 | 2.63 | 2.17 | 3 | 2.54 | 2.06 |
| | | | | | | | 4 | 2.41 | 2.02 |
| $U_s$ | | 88 | 39 | | | | | | |
| $H_{adj}$ | | | | | 8.196 | 1.499 | | 2.223 | 2.208 |
| $P$ | | ns | ns | | <0.05 | ns | | ns | ns |

1972/73, these measures were highly dissimilar (Table 2). This may be the result of a different choice of moulting grounds, with unequal degrees of hunting pressure or other causes of heavy mortality. Zubtsovskiy & Ryabitsev,[26] for example, observed large flocks of moulting Bean Geese in the Kanin Peninsula in August 1968, whereas the White-front does not show mass moult migration to that area.[27]

In general, both geese have been reported to share the same breeding range in north-east Europe but recent information suggests otherwise.[27] White-fronts breeding in the western part of their range, from the Kanin Peninsula east to the Pechora Delta, are restricted to a coastal fringe (Timan coast) along the Barents Sea, rarely more than 40 km inland. In their distibution maps, Dement'ev & Gladkov,[28] Voous,[29] and Cramp and Simmons[30] showed a breeding range for White-fronts at least twice as large as that confirmed by recent Russian research.[27] Mineyev[13] indicated 15 locations of high breeding densities of the Tundra Bean Goose on the mainland. Four of them are entirely or mostly south of the southern limit of the breeding range of the White-front. This more northern breeding range distribution and the suggestion that Tundra Bean Geese are less vulnerable to Arctic Fox *Alopex lagopus* predation[31] may explain the significantly greater variation in the proportions of first-year birds in White-fronts than in the Tundra Bean Geese (Table 1).

In the White-front, the proportions of first-year birds as well as the mean brood-sizes are characterized by a three-year cycle (Tables 3 & 4). It seems possible that breeding success in this species is related to lemming cycles and prey-switching of predators as decribed by Summers[32] and Summers & Underhill[24] in the Dark-bellied Brent Goose *Branta b. bernicla* at the Taimyr Peninsula. For the period 1964–1994 ($n$ = 31 years) there was a good agreement between 'good' and 'poor' years in the proportions of first-year birds amongst White-fronts (Table 2) and Brent Geese, using the criteria of Summers[32] (> 32% first-year birds = 'good' and < 13% = 'poor'). Thus the Brent Goose shared six of the seven 'good' years with the White-front, and all of the five 'poor' years. For the whole period, the proportions of first-year birds were significantly correlated (Spearman rank correlation, $r_s = 0.686$; $n = 31$; $P < 0.01$). During the years 1986–1988, Syroechkovskiy *et al.*[31] argued that annual variation in reproductive rate in the White-front on Vaygach Island was explained by the prey-switching theory.

In the Tundra Bean Goose, no cyclical fluctuations of the breeding parameters can be found in three sets of two-, three- and four-year cycles (Tables 3 & 4). There was no significant correlation between the proportion of first-year birds in this species and in the Dark-bellied Brent Goose over the period 1970–1994 ($r_s = 0.231$; $n = 25$; $P > 0.05$).

## Reliability of long-term trends in breeding parameters

In neither species did the slopes of the regression equations of the breeding parameters against years deviate significantly from zero (Figs 2 & 3).

In the case of the White-front, however, some caution may be needed in accepting the absence of a significant trend. Figure 1 shows that in both species the proportion of single-parent families decreased through the 1970s. Since 1970, general restrictive measures have been imposed on shooting, especially in the White-fronted Goose.[33] A link between both features seems probable. Shooting is by far the most important cause of death among adult wild geese[34] and adult survival rates increase when hunting mortality is reduced.[34–37] Because in wild geese many investigations have confirmed that hunting mortality is heavier in first-winter birds than in adults,[38,9,34] it can be suggested that average brood-size may have been larger in Zeeland before the start of this investigation.

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