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POOR BREEDING SUCCESS IN NORTHERN WILD GEESE IN 1986. DESCRIPTION AND ANALYSIS OF POSSIBLE CAUSES

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INTRODUCTION

The breeding performance of wild geese is known to vary largely year by year, and this is the reason why every autumn the wildfowler wonders whether these birds, wintering in his observation area, will bring a large number of young from their breeding grounds. In the fall of 1986, on arrival of the first wild geese in the southern Netherlands, it was obvious that the northern breeding season must have been very adverse, and seemed to have affected all controlled populations. Because their reproduction haunts are vast and mostly inaccessible, the analysis of possible causes is complicated but nonetheless a fascinating subject for investigation for the sedentary observer in the remote winterquater. Generally, only one cause is attributed to explain poor breeding performance, whereas interaction between several causes has rarely been considered. Up till now, an indisputable and irrefutable mechanism to clear up this matter has not been put forward.

For the winter period 1986-1987, an analysis of the poor breeding success was complicated by the reactor accident at Chernobyl, which happened at the end of April 1986. Official reports informed us that in Scandinavia radiation levels due to this accident came close to the danger level (Rich, 1987). This event involved the forced slaughtering of hundreds of Reindeer (*Rangifer tarandus*) and of Mooses (*Alces alces*). However, detailed mapping in these countries of the fall-out of nuclids learned their northernmost districts remained mainly saved (Backe *et al.*, 1986; Bennerstedt *et al.*, 1986; Finnish Centre for Radiation and Nuclear Safety, 1986). The levels of cesium-137 did not exceed those reported by Hvinden and Lillegraven (1961) during the end of the 1950's, following nuclear experiments. Hence, acute effects from the Chernobyl fall-out upon the wild geese, such as infertility in parents or embryonal death, are to be regarded as highly improbable.

The aim of this study is threefold:

- to give a description of the reproduction failure of 1986 in the southern Netherlands, by means of comparative data collected in that area during.

former winters;
- to prospect the impact of weather conditions in the reproduction areas and in the wintering areas upon the breeding success;
- finally, to present a critical review of the causes of breeding failure, as investigated by many authors and on the basis of personal considerations.

MATERIALS AND METHODS

Ever since the 1960's, the breeding performances of five species or subspecies of wild geese in the winterquarters of the southern Netherlands have been examined annually; namely the White-fronted Goose (*Anser albifrons*), the Taiga and the Tundra Bean Goose (*A. f. fabalis* and *A. f. rossicus*), the Barnacle Goose (*Branta leucopsis*) and the Dark-bellied Brent Goose (*B. b. bernicla*). During the winter 1986/1987, the Svalbard population of the Pink-footed Goose (*A. brachyrhynchus*) was also included in the investigation, but comparative data of preceding winters of this species were lacking, in literature as well as in personal records.

The entire breeding range of the populations under analysis is situated in the northern Eurasian Continent, extending from Lapland in the west to the Taimyr Peninsula in the east. Even several Arctic Islands are included in the investigation, so the breeding range is wide. In all populations the annual study on the breeding success was done by scanning feeding flocks and by discovering the proportions of juvenile (first-winter) birds. In three of them (*A. albifrons*, *A.f. fabalis* and *A. f. rossicus*) the yearly mean brood size was also determined. These standard methods, although widely used, show two shortcomings:

- First with regard to the adult/juvenile ratio. Because our estimates originated from a restricted part of the entire wintering area, important biases concerning the evaluation of this parameter may be expected. *A. albifrons* and *A.f. rossicus* were only assessed in the southern parts of the province of Zeeland, whereas the reproduction performances of *B. leucopsis* and *B. b. bernicla* were checked in the whole of this province. The data concerning *A.f. fabalis* came from the border region between the provinces Noord-Brabant and Limburg. *A. brachyrhynchus* was studied at Damme (province of West-Flanders, Belgium) because only a small number of this species winters in Zeeland. However, observations from previous winters showed that the percentages of juveniles we collected in these rather limited areas did not differ substantially from those, presented by the Ganzenwerkgroep Nederland (1980 -1987) over the whole country. Furthermore estimates of the adult/juvenile ratio may differ considerably because juvenile birds are not mixed randomly through the flocks. This is especially the case for the Dark-bellied Brent, because its young birds are often at the front and edges of the feeding flock. This difficulty can be avoided by taking samples from different parts of each flock.

- Second, with regard to the brood size. A long-term study on the durability of family cohesion in the White-fronted Goose revealed that the number of unaccompanied juveniles increased exponentially throughout the winterseason. This was an important factor for the decreasing trend of the mean number of juveniles per family during winter (Van Impe, 1978). Therefore, we finished the investigation on the brood size before 15 January.

To examine whether weather conditions at the breeding grounds influenced the wide fluctuations in the yearly breeding performance, mean monthly summer values of temperature and of precipitation (rain + snow) were supplied by the Bulletins of the Monthly Climatic Data for the World (MCDW), from which 32 northern weather stations were selected. Only those stations presenting complete or nearly complete long-term records were included in this selection. The Bulletins do not give any information about the amount of snowfall. Firstly, all stations were mapped and we examined whether they belonged to the tundra or to the taiga zone. Because the transition between both belts is not sharply demarcated, we classified the southernmost subzones of the tundra, *i.e.* the southern tundra and the forest tundra (terminology of Gorodkow *in* Berg, 1958) under the taiga zone. These subzones of the tundra are situated almost exclusively upon podsolic soils, which are characteristic of the taiga zone (Dewdney, 1971). The Ural mountains were considered to be the classic boundary between an European (''western'') and an Asiatic (''eastern'') part of both belts. Apart from the four regions delimited in this way, we considered also a fifth and a sixth, both well circumscribed: the Lapland-Kola region and the Arctic Islands region. Finally, all selected stations were distributed into one of the six regions, with reference to the position of the above mentioned boundaries. The names of the stations per region and their position are listed in Table 7. That their spread is not equal over the six regions remains a major source of criticism. However, this bias was unavoidable, especially since only a part of the Soviet stations publish their records in the MCDW Bulletins. An inquiry to receive supplementary data, mainly concerning Novaya Zemlya where two important weather stations are situated, was left unanswered. So we were obliged to compare the breeding performance of *B. leucopsis* with data from two stations situated in the Frantsa Iosifa Archipelago.

The data from the weather stations were used as follows:

- For each population, one-to-one correlations were set up between the yearly proportion of juveniles in the winterquarters running over the census period 1970/1971 - 1986/1987, and the mean monthly temperature and precipitation during the preceding northern summer. Firstly, the correlation analyses considered the data from each separate station laying within the breeding area and secondly, the mean value of combined data from pooled stations, covering the breeding area, were taken into account. The populations versus the regions were chosen as follows:

for the months May, June and July separately:

A. albifrons *A.f. rossicus*	western tundra, 2 stations;
A.f. fabalis	Lapland + Kola Peninsula + western taiga, 16 stations.

for the months June and July separately:

A.albifrons *A.f. rossicus* *B.b. bernicla*	eastern tundra, 3 stations;
A. albifrons *A.f. rossicus*	western + eastern tundra, 5 stations;
B. leucopsis	Arctic Islands, 2 stations.

- In another confirmatory study, for each of the 32 stations a comparison was made between on the one hand the mean of their monthly summer temperatures and precipitations during four years with overall low breeding performance, and on the other hand during four years with overall high breeding performance.

- Finally, we compared the overall ''bad'' years with the overall ''good'' years with regard to the proportion of stations x years having a negative departure for temperature and a positive one for precipitation from their long-term means. Long-term means covering the period 1931 - 1960 were taken from the Report n° 117 (1982) of the World Meteorological Organization. Because this report did not include the means of all stations under examination, we calculated the missing long-term means from the individual MCDW Bulletins throughout the period 1970-1985. In another set of correlation analyses we tried to demonstrate amongst the five populations the possible relationship between mean monthly temperatures and precipitations in their winterquarters and their subsequent breeding success. The weather data registered at the Koninklijk Meteorologisch Instituut (K.M.I.) in Uccle (Belgium) were used for this investigation.

Concerning the statistical analysis, we followed the procedures described by Sokal and Rohlf (1969). If nonparametric statistics were imposed, Siegel (1956) was consulted.

RESULTS

THE PERCENTAGES OF JUVENILES AND THE MEAN BROOD SIZES

Tables 1 and 3 illustrate respectively the mean proportions of juveniles in the five examined populations and the mean brood sizes in *A. albifrons*, *A.f. fabalis* and *A. f. rossicus*. These data collected throughout a long-term period were set out against the records from the last winter 1986/1987. Tables 2 and 4 give a more detailed outline of these two pivot points of population dynamics, by comparing these every winter with their long-term reference mean, and by paying special attention to the negative deviations. These data clearly illustrate the failure of the breeding season of 1986 for all populations wintering in the study area. All brought a low percentage of juveniles from their breeding grounds and in four of them, the negative departure exceeded minus one standard deviation (-1 S.D.) from the long-term mean of the reference period (Table 2). The same failure was found in the Pink-footed Goose at Damme: there were only 7.3% juveniles on 659 controlled birds during January-February 1987. Although comparative data of this Svalbard population were not available, this poor result may be explained if we look at the reproduction performance of the Icelandic population of this species. In the period 1951-1976, Ogilvie (1978) calculated a minimum value of 5.6% juveniles in only one winter. All other seasons gave at least 11% juveniles and 19 out of 27 winters gave a proportion of more than 20%. The brood size of the three examined populations leaded to the same conclusion of failure in the breeding season of 1986 (Tables 3 and 4). Here the Taiga Bean Goose seemed the least affected, with 1.5 juveniles per family, against a long-term mean of 1.6. However, there is little doubt that also this goose followed the general trend of failure, because Mrs Otsu (pers. comm.) counted less than 10% juveniles within flocks wintering in Great-Britain. It is likely that Taiga Bean Geese wintering in this country are of the same origin as those wintering in the Netherlands (Huyskens, 1986).

If we sum up all negative deviations in the controlled populations per winter-season (Table 2 and 4), one may discern generally "bad" from generally "good" breeding seasons for a substantial part of the wild geese breeding in the northwestern Palearctic. This analysis again views the breeding performance from two angles: the adult/juvenile ratio and the mean brood size.

- Concerning the proportion of juveniles (Table 2), except for a few data lacking, only one overall successful breeding season was recognizable in a series of eighteen. In 1985 the proportion of juveniles exceeded the long-term reference mean value in all populations. However, most breeding seasons procured a percentage below their long-term mean in two or three populations. Moreover, ten of them demonstrated a negative deviation exceeding -1 S.D. for one or more populations. The summers of 1971, 1974 and 1986 were to be regarded as very unsuccessful. Their sums of negative departures were considerable, respectively -69% (1986), -65% (1971) and -60% (1974). No

Table 1. Mean percentages of juveniles among wild geese wintering in the southern Netherlands compared with the results of the winter 1986/1987 (Personal observations).

	Area of observation (°)	Period	Numbers of winters	Mean percentage (± 1 S.D.)	Mean percentage winter 1986/1987.
A. albifrons	Z	1964/1965 - 1985/1986	22	30.5 (±10.3)	16.2
A. f. fabalis	NB/L	1970/1971 - 1985/1986	16	16.4 (± 5.8)	12.3
A. f. rossicus	Z	1969/1970 - 1985/1986	17	24.5 (± 5.1)	13.7
B. leucopsis	Z	1969/1970 - 1984/1985	16	22.0 (±14.3)	3.1
B. b. bernicla	Z	1969/1970 - 1985/1986	17	20.1 (±18.8)	0.0

(°) Z: southwestern part of the province of Zeeland.
NB/L: border region between the provinces Noord-Brabant and Limburg.

Table 2. Negative departures from a long-term reference mean (1969/1970 - 1985/1986) of the percentages of juveniles among wild geese wintering in the southern Netherlands.

	Anser albifrons	*Anser f. fabalis*	*Anser f. rossicus*	*Branta leucopsis*	*Branta b. bernicla*	Σ negative departures
Long-term reference mean (± 1 S.D.)	31.4 (±10.8)	16.4 (± 5.8)	24.5 (± 5.1)	22.0 (±14.3)	20.1 (±18.8)	
1969/1970	+	- (°)	+	-7.5	+	-7.5
1970/1971	+	*-8.1*(°°)	+	+	+	-8.1
1971/1972	*-21.4*	-4.3	*-5.2*	*-17.5*	-16.7	-65.1
1972/1973	+	*-6.4*	*-7.2*	+	+	-13.6
1973/1974	+	-3.2	-2.2	+	+	-5.4
1974/1975	*-12.8*	*-9.3*	*-7.4*	-10.3	*-20.1*	-59.9
1975/1976	+	*-9.1*	-3.1	+	+	-12.2
1976/1977	+	+	-1.4	+	-8.7	-10.1
1977/1978	-3.5	+	+	*-17.0*	*-20.1*	-40.6
1978/1979	*-11.1*	+	+	*-17.0*	-3.3	-31.4
1979/1980	-5.3	+	+	-4.0	+	-9.3
1980/1981	-5.9	+	+	-0.9	*-19.4*	-26.2
1981/1982	-2.5	+	+	+	-17.8	-20.3
1982/1983	-4.7	+	-4.8	-4.0	+	-13.5
1983/1984	-0.5	+	-0.7	+	-17.9	-19.1
1984/1985	-8.6	+	-4.8	*-16.0*	-17.2	-46.6
1985/1986	+	+	+	- (°)	+	+
1986/1987	*-15.2*	-4.1	*-10.8*	*-18.9*	*-20.1*	-69.1

(°): insufficient data.
(°°): departures > or = - 1 S.D. from long-term reference mean are in italics

Table 3. **Mean brood sizes in *Anser albifrons, A. f. fabalis* and *A. f. rossicus* in the southern Netherlands compared with the results of the winter 1986/1987 (Personal observations).**

	Area of observation (°)	Period	Numbers of winters	Mean brood size (± 1 S.D.)	Mean brood size winter 1986/1987
A. albifrons	Z	1964/1965 - 1985/1986	22	2.55 (± 0.28)	2.00
A. f. fabalis	NB/L	1973/1974 - 1985/1986	12 (°°)	1.67 (± 0.39)	1.56
A. f. rossicus	Z	1973/1974 - 1985/1986	13	2.10 (± 0.18)	1.60

(°): see Table 1.
(°°): winter 1984/1985 with insufficient data.

Table 4. **Negative departures from a long-term reference mean (1973/1974 - 1985/1986) of the mean brood sizes among *A. albifrons, A. f. fabalis* and *A. f. rossicus* wintering in the southern Netherlands.**

	A. albifrons	*A. f. fabalis*	*A. f. rossicus*	Σ negative departures
Long-term reference mean (± 1 S.D.)	2.58 (± 0.19)	1.67 (± 0.39)	2.10 (± 0.18)	
1973/1974	+	*-0.40* (°°)	+	-0.40
1974/1975	-0.07	*-0.67*	+	-0.74
1975/1976	+	*-0.55*	+	-0.55
1976/1977	+	-0.03	*-0.31*	-0.34
1977/1978	-0.11	-0.17	*-0.26*	-0.54
1978/1979	*-0.37*	+	+	-0.37
1979/1980	-0.01	+	+	-0.01
1980/1981	-0.01	+	+	-0.01
1981/1982	+	+	+	+
1982/1983	*-0.29*	+	*-0.19*	-0.48
1983/1984	-0.05	+	+	-0.05
1984/1985	+	- (°)	*-0.21*	(-0.21)
1985/1986	+	-0.06	+	-0.06
1986/1987	*-0.58*	-0.11	*-0.50*	-1.19

(°): insufficient data.
(°°): departures > or = - 1 S.D. from long-term reference mean are in italics

statistical difference between these values emerged ($F_S = 0.054$; $n_1 = 2$; $n_2 = 12$; $P > 0.75$). In the subsequent winters, the proportion of juveniles in none of the five populations reached the value of the long-term reference mean, and in the winters of 1974/1975 and 1986/1987, the departures in four populations out of five were as severe as > -1 S.D..

- These findings are largely confirmed when we examine the negative deviations concerning the mean brood sizes among three populations (Table 4). Again the successful season 1985 gave no obvious departure from the long-term reference mean. On the contrary, 9 out of 14 seasons revealed departures > or = -1 S.D. for one or more populations. Here also the poor breeding season of 1986 was largely confirmed, with a sum of negative departures of -1.2 juveniles per family.

Fig. 1 shows the yearly summed negative departures for the two parameters during the period 1973/1974 - 1986/1987. Both values are correlated ($r = 0.66$; $P = 0.01$) and the generally poor seasons of 1974 and 1986 are distinctly separated from the others. The failure of the third general poor year, 1971, could not be illustrated, because the brood size was not yet investigated during this early period.

We may conclude that for wild geese wintering in the southern Netherlands, a yearly overall reproduction success is rather rare. Concerning the proportion of juveniles, it occurs only once in eighteen years, and concerning the mean brood size, only five seasons out of fourteen could be regarded as overall successful. Reproduction seasons causing a departure from the long-term reference mean as important as -1 S.D. in two or more populations are not uncommon at all. It happens in six out of eighteen seasons concerning the percentage of juveniles and in two out of fourteen concerning the brood size. But the latter value remains largely underestimated, because the mean brood size was only examined in three populations instead of five. If we sum up all negative departures for the two parameters, 1986 shows the least successful season, especially by its deviation from the mean brood size. In 1986 the heaviest departures obviously came from the northernmost populations, as it was the case for *A. brachyrhynchus*, *B. leucopsis* and *B.b. bernicla*. Geese breeding more inland, such as *A. albifrons* and *A.f. rossicus*, are less affected, and the southernmost taiga-breeding *A.f. fabalis* demonstrates the smallest negative departure. The latter deviates only -4% from the long-term mean of the proportion of juveniles, and demonstrates no negative departure from the long-term mean of the brood-size.

BREEDING SUCCESS AND SUMMER WEATHER DATA

Many authors attribute breeding failure in northern wild geese in first instance to adverse weather conditions during a part or the whole of their

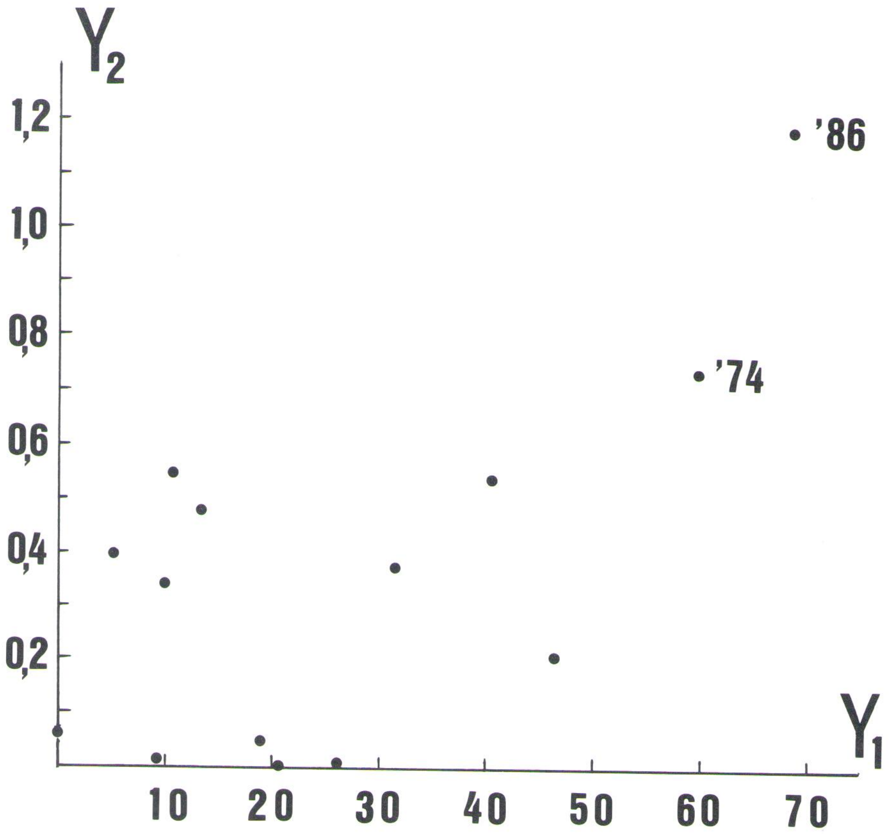

Fig. 1. Scatter diagram of the sum of negative departures in the winters 1973/1974 - 1986/1987, southern Netherlands.
Y1 : $\sum$ negative departures of the percentages of juvenile birds, 5 populations.
Y2 : $\sum$ negative departures of the mean brood sizes, 3 populations.

reproduction cycle. By means of the weather data which were at our disposal, we examined whether such a link could be made.

As a first step in this examination, we hoped to find a good number of year-by-year correlations between the winterly percentage of juveniles of each population and the mean monthly summer values of temperature and precipitation from each station situated within their respective breeding range. Some relationships were found indeed, but the general picture of strong dependence was far from convincing and even confusing. Secondly, we looked for correlations between the percentages of juveniles and the mean monthly

Table 5. **Correlation coefficients between the percentages of first-winter birds among wild geese wintering in the southern Netherlands and the mean monthly temperatures (°C) from pooled stations in their breeding area. Absence of significant positive correlation.**

	Western tundra, 2 stations			Eastern tundra, 3 stations		Western + Eastern tundra, 5 stations		Lapland + Kola Peninsula + Western taiga, 16 stations			Arctic Islands, 2 stations	
	May	June	July	June	July	June	July	May	June	July	June	July
A. albifrons												
n	16	17	17	16	17	15	16					
r	-0.05	0.20	0.12	0.26	-0.33	0.30	-0.07					
A. f. rossicus												
n	16	17	17	16	17	15	16					
r	0.16	-0.21	-0.33	0.21	-0.08	-0.12	-0.44					
A. f. fabalis												
n								17	17	17		
r								0.35	0.36	-0.39		
B. leucopsis												
n											15	16
r											-0.15	-0.27
B. b. bernicla												
n				16	17							
r				-0.02	-0.04							

weather records from pooled stations which cover the breeding areas. The outcomings of the latter experiment were even more discouraging. No significant positive (temperature) or negative correlation (precipitation) could be demonstrated (Tables 5 and 6).

This is the reason why we made a thorough comparison between the weather data of four overall bad years, *i.e.* years with low numbers of juveniles in all examined populations and of four overall good years, *i.e.* years with a large, recent offspring. As said above, we considered the seasons 1971, 1974 and 1986 as bad, because the sum of all negative deviations in the examined populations was large in the subsequent winter (Table 2). Also the year 1962 was included in this group, because the winter 1962/1963 was characterised by very low percentages of juvenile White-fronted Geese and of Brent Geese in the wintering

Table 6. Correlation coefficients between the percentages of first-winter birds among wild geese wintering in the southern Netherlands and the mean monthly precipitations (mm) from pooled stations in their breeding area. Absence of significant negative correlation.

	Western tundra, 2 stations			Eastern tundra, 3 stations		Western + Eastern tundra, 5 stations		Lapland + Kola Peninsula + Western taiga, 16 stations			Arctic Islands, 2 stations	
	May	June	July	June	July	June	July	May	June	July	June	July
A. albifrons												
n	16	17	17	16	17	16	16					
r	-0.14	0.25	-0.25	-0.20	-0.15	0.15	-0.41					
A. f. rossicus												
n	16	17	17	16	17	16	16					
r	0.01	0.09	-0.47	0.15	0.27	0.22	-0.06					
A. f. fabalis												
n								17	17	17		
r								0.04	0.19	-0.13		
B. leucopsis												
n											15	16
r											-0.07	-0.06
B. b. bernicla												
n				16	16							
r				-0.08	-0.40							

haunts of western Europe (Doude van Troostwijk, 1974; Prokosch, 1984). From Table 2, good years were regarded as years with a low sum of negative departures, such as 1970, 1976, 1979 and 1985.

Table 7 lists the monthly means of temperature and of precipitation during these four overall bad and four overall good years from all northern stations which provided long-term data. A lot of comparisons did not come up to thė expectation, which means that bad years are characterised by a lower temperature and/or a higher precipitation than good years. The inverse of this preconceived opinion totalised 81 out of 164 comparisons, approximately half of the total. This happened more frequently in the case of precipitation (41 out of 82 comparisons) than in that of temperature (34 out of 82), but without statistical significance ($X^2 = 0.610$; d.f. = 1; $P > 0.3$). Especially the tundra

Table 7. **Mean temperatures (°C) and mean precipitations (mm) from stations in the Northwestern Palearctic during four years with overall bad reproduction success (1962, 1971, 1974,1986) and four years with overall good reproduction success (1970, 1976, 1979, 1985) in wild geese in the southern Netherlands.**

Region	Station	Temperature					
		May		June		July	
		Bad	Good	Bad	Good	Bad	Good
Lapland + Kola Peninsula	Vardo 70°22'N 31°06'E	2.1	2.7^{NS}	6.0	6.0	9.2	9.3^{NS}
	Karesuando 68°27'N 22°30'E	3.5	3.6^{NS}	10.6	11.0^{NS}	12.1	13.6^{NS}
	Haparanda 65°50'N 24°09'E	5.8	5.9^{NS}	12.8	13.3^{NS}	14.6	15.7^{NS}
	Stensele 65°04'N 17°09'E	6.3	6.2°	11.5	12.8^{NS}	12.9	13.5^{NS}
	Ostersund 63°11'N 14°30'E	8.7	7.8°	11.5	13.1^{NS}	12.6	13.3^{NS}
	Harnosand 62°38'N 17°57'E	7.5	7.4°	13.3	13.8^{NS}	15.0	14.7°
	Sodankyla 67°22'N 26°39'E	4.5	4.9^{NS}	12.0	12.0	13.4	14.4^{NS}
	Kajaani 64°17'N 27°41'E	6.4	7.5^{NS}	13.3	13.1°	15.1	15.3^{NS}
	Jyvaskyla 62°24'N 25°41'E	8.0	9.5^{NS}	13.9	13.2°	15.1	14.8°
	Vaasa 63°03'N 21°46'E	8.1	8.4^{NS}	13.7	13.9^{NS}	14.9	15.3^{NS}
	Murmansk 68°58'N 33°03'E	3.0	4.3*	9.8	8.8°	12.6	13.3^{NS}
	Arkhangelsk 64°35'N 40°30'E	5.4	6.4^{NS}	12.5	11.7°	15.9	15.6°
	Reboly 63°49'N 30°49'E	5.2	6.7^{NS}	14.2	12.7°	16.1	15.2°
Western parts of Ural mountains							
Tundra	Kanin Nos 68°39'N 43°18'E	-1.5	-1.2^{NS}	4.0	3.8°	10.2	8.0°
	Narjan Mar 67°39'N 53°01'E	-0.2	-1.1°	7.2	6.3°	13.7	13.1°
Taiga	Vytegra 61°01'N 36°27'E	6.5	9.2^{NS}	14.8	12.7°	16.8	16.1°
	Hoseda-Hard 67°05'N 59°23'E	-3.1	-2.4^{NS}	6.8	6.0°	10.4	12.8^{NS}
	Syktyvkar 61°40'N 50°51'E	8.0	8.5^{NS}	13.1	12.8°	17.1	16.7°

Region	Station	Precipitation					
		May		June		July	
		Bad	Good	Bad	Good	Bad	Good
Lapland + Kola Peninsula	Vardo 70°22'N 31°06'E	21	30°	29	21^{NS}	56	16*
	Karesuando 68°27'N 22°30'E	17	33°	30	40°	84	71^{NS}
	Haparanda 65°50'N 24°09'E	32	25^{NS}	29	24^{NS}	55	54^{NS}
	Stensele 65°04'N 17°09'E	30	33°	43	43	89	110°
	Ostersund 63°11'N 14°30'E	22	30°	70	57^{NS}	104	126°
	Harnosand 62°38'N 17°57'E	39	47°	30	27^{NS}	57	82°
	Sodankyla 67°22'N 26°39'E	30	41°	51	52°	92	60^{NS}
	Kajaani 64°17'N 27°41'E	43	29^{NS}	46	48°	74	73^{NS}
	Jyvaskyla 62°24'N 25°41'E	40	31^{NS}	40	55°	89	103°
	Vaasa 63°03'N 21°46'E	28	26^{NS}	38	24*	58	64°
	Murmansk 68°58'N 33°03'E	31	26^{NS}	26	25^{NS}	66	31^{NS}
	Arkhangelsk 64°35'N 40°30'E	43	45°	52	76°	57	53^{NS}
	Reboly 63°49'N 30°49'E	46	44^{NS}	44	54°	82	70^{NS}
Western parts of Ural mountains							
Tundra	Kanin Nos 68°39'N 43°18'E	13	18°	23	38°	20	26°
	Narjan Mar 67°39'N 53°01'E	18	29°	16	30°	62	32*
Taiga	Vytegra 61°01'N 36°27'E	48	36^{NS}	69	84°	80	55^{NS}
	Hoseda-Hard 67°05'N 59°23'E	29	31°	32	33°	76	29^{NS}
	Syktyvkar 61°40'N 50°51'E	40	43°	42	76°	70	54^{NS}

Table 7. (continued)

Region	Station	Temperature					
		May		June		July	
		Bad	Good	Bad	Good	Bad	Good
Eastern parts of Ural mountains							
Tundra	Mys Celjuskin 77°43'N 104°17'E			-0.7	-1.4°	1.1	1.3^{NS}
	Dikson Island 73°30'N 80°14'E			-1.0	0.7*	4.9	3.9°
	Mys Kamennyj 68°28'N 73°36'E			1.5	1.7^{NS}	8.0	6.8°
Taiga	Salehard 66°32'N 66°32'E			6.8	7.2^{NS}	14.7	13.3°
	Tarko-Sale 64°55'N 77°49'E			8.1	10.0^{NS}	15.6	15.5°
	Hatanga 71°59'N 102°28'E			4.7	6.6^{NS}	12.1	12.6^{NS}
	Njaksimvol 62°26'N 60°52'E			11.8	12.3^{NS}	17.0	16.0°
	Turuhansk 65°47'N 87°57'E			9.4	12.1^{NS}	16.2	16.7^{NS}
	Hanty-Mansijsk 60°58'N 69°04'E			13.0	12.9°	18.3	17.0°
	Surgut 61°15'N 73°30'E			12.5	12.4°	18.1	17.6°
	Sverdlovsk 56°48'N 60°38'E			14.7	14.9^{NS}	19.0	17.3°
	Tobolsk 58°09'N 68°11'E			14.7	15.7^{NS}	19.1	17.4°
Arctic Islands							
	Heysa 80°37'N 58°03'E			-1.3	-1.3	1.0	1.1^{NS}
	Vise 79°30'N 76°59'E			-1.6	-1.1*	0.6	0.6

° : inverse of the prediction: in bad years the mean temperature is higher or the mean precipitation lower as compared to good years.
* : P < or = 0,05.
NS: No statistical difference between bad and good years according to the Mann-Whitney U-test (one-tailed) for n_1 = 3 or 4 and n_2 = 4.

Region	Station	Precipitation					
		May		June		July	
		Bad	Good	Bad	Good	Bad	Good
Eastern parts of Ural mountains							
Tundra	Mys Celjuskin 77°43'N 104°17'E			30	20NS	36	28NS
	Dikson Island 73°30'N 80°14'E			24	38°	16	41°
	Mys Kamennyj 68°28'N 73°36'E			11	26°	35	15NS
Taiga	Salehard 66°32'N 66°32'E			41	41	75	47NS
	Tarko-Sale 64°55'N 77°49'E			53	58°	78	42NS
	Hatanga 71°59'N 102°28'E			28	24NS	29	17NS
	Njaksimvol 62°26'N 60°52'E			43	51°	60	111°
	Turuhansk 65°47'N 87°57'E			59	45NS	71	50NS
	Hanty-Mansijsk 60°58'N 69°04'E			89	92°	83	93°
	Surgut 61°15'N 73°30'E			57	94°	84	73NS
	Sverdlovsk 56°48'N 60°38'E			94	45*	68	73°
	Tobolsk 58°09'N 68°11'E			77	56NS	51	120°
Arctic Islands							
	Heysa 80°37'N 58°03'E			13	16°	11	23°
	Vise 79°30'N 76°59'E			31	11NS	101	16NS

west of the Ural mountains frequently did not meet the prediction, and agreement occurred only once in six comparisons concerning temperature and in six concerning precipitation. Here we have to bear in mind that this area certainly must hold large numbers of breeding *A. albifrons* and of *A.f. rossicus*, wintering in the Netherlands. Concerning the comparisons in agreement with the prediction, *i.e.* 83 out of 164, 91% did not yield statistical difference. In Table 7, the seven statistically different comparisons show a scattered distribution and no distinct pattern emerges concerning significance for a group of stations within a region.

The conditions of difference per region can also be examined by the sign test. Sign "+" was attributed to the statement of the advance prediction and sign "-" to the inverse. Because of the sparsity of stations situated in the tundra west and east of the Ural mountains, we pooled their results respectively with those from the stations in the western and the eastern taiga. No sign test could be made concerning the two stations of the Arctic Islands. On 16 comparisons examined in this way, eight for temperature and eight for precipitation, only one, the mean May temperature in the Lapland-Kola region, was significant ($P = 0.188$), with ten signs in the sence of the prediction and three "-" signs.

Another confirmatory study was as confusing. Here we compared the number of stations x years per region with a negative departure for temperature and a positive one for precipitation between four years with overall bad reproduction success and four years with overall good reproduction success. For the temperature (Table 8), 10 comparisons out of 15 did agree with the prediction, so that in years with low reproduction performance there were more stations x years with negative departures than in good ones. However, only two of these comparisons reached the level of statistical significance by the Fisher's exact probability test. No significance was reached between the bad and the good series of the Lapland-Kola stations, nor between these of the stations in the tundra and the taiga west of the Ural mountains. The Arctic Islands stations followed the prediction very well for June and July, reaching the level of significance once. But as we know, among the five populations studied in the winterquarters, only the Barnacle Goose may depend upon these weather conditions. With regard to precipitation (Table 9), the comparison of generally bad and generally good years was even more confusing. Only 9 out of 15 did agree with the prediction that precipitation is higher in bad years. One of them, the western taiga, was significant for July, but this region can hardly supply important numbers of breeding geese which winter in the examined area.

In conclusion, we can put forward that as far as weather records are available from stations laying within the potential breeding area of northern breeding geese, it is discouraging to find a lack of sustained trends in comparing them with breeding performance. If we tend to work out a more simplified model by which extremes in breeding performance are compared with weather data from the breeding area, the latter are too inconclusive to accept a link between these weather data and breeding success.

Table 8. **Percentage of stations x years with a negative departure for temperature in four years with overall bad reproduction success (1962. 1971. 1974. 1986) and in four years with overall good reproduction success (1970. 1976. 1979. 1985).**

Region (Number of stations)	May Bad	May Good	June Bad	June Good	July Bad	July Good
Lapland + Kola Peninsula (13)	49 (49)(°)	42NS (50)	37 (46)	43° (51)	82 (51)	72NS (51)
Western parts of Ural Tundra (2)	80 (5)	87° (8)	57 (7)	75° (8)	57 (7)	50NS (8)
Taiga (3)	86 (7)	50NS (12)	40 (10)	58° (12)	66 (9)	50NS (12)
Eastern parts of Ural Tundra (3)			55 (9)	50NS (12)	73 (11)	54NS (11)
Taiga (9)			84 (31)	48** (33)	35 (31)	51° (35)
Arctic Islands (2)			50 (6)	12NS (8)	57 (7)	0* (8)

° : Inverse of the prediction.
(°): Number of stations x years.
** : $P < 0{,}01$.
* : $P = 0{,}05$.

NS : No significant difference between bad and good years according to the Fisher's exact test (one-tailed) for $N < 20$ and the X^2 test for $N > 20$, if the conditions mentioned by Siegel (1956) are fulfilled.

Table 9. **Percentage of stations x years with a positve departure for precipitation in four years with overall bad reproduction success (1962. 1971. 1974. 1986) and in four years with overall good reproduction success (1970. 1976. 1979. 1985).**

Region (Number of stations)	May Bad	May Good	June Bad	June Good	July Bad	July Good
Lapland + Kola Peninsula (13)	45 (49)	49° (51)	28 (46)	23^{NS} (51)	57 (51)	49^{NS} (51)
Western parts of Ural Tundra (2)	0 (4)	25° (8)	28 (7)	37° (8)	43 (7)	25^{NS} (8)
Taiga (3)	43 (7)	25^{NS} (12)	40 (10)	41° (12)	55 (9)	8^{*} (12)
Eastern parts of Ural Tundra (3)			33 (9)	41° (12)	50 (10)	30^{NS} (10)
Taiga (9)			53 (30)	40^{NS} (32)	39 (31)	40° (32)
Arctic Islands (2)			33 (6)	28^{NS} (7)	57 (7)	37^{NS} (8)

Same remarks as in Table 8.

BREEDING SUCCESS AND WINTER WEATHER DATA

Because some authors advocate a strong relationship between weather conditions in the winterquaters and subsequent productivity performance in the northern breeding range, we studied this matter in the south of the Netherlands. In a long-term period, we calculated the year-by-year coefficients of the correlation between the percentage of juveniles amongst each of the five populations and the means of monthly temperatures and precipitations registered at the K.M.I. in Uccle during the foregoing winter. Therefore, we used the means from the separate months December, January, February and March as well as those from the entire period December - February. Consequently, the number of correlation analyses for each weather variable amounted to 5 (periods) x ((populations) = 25. In the 26th, supplementary analysis, the yearly mean percentage of the juveniles of all five populations was set out against the mean value of the weather variable for the whole period December - February. Concerning the temperature, the number of pairs of variates ranged from 15 to 22, and the correlation coefficients from +0.20 to -0.48. None of them yielded the level of significant positive correlation. For the precipitation, the same doubtful results were obtained. With the same number of pairs of variates, the correlation coefficients varied here between -0.49 and +0.44. Only the first coefficient reached the level of significant negative correlation. Because in general interdependence between both variables was absent, we may conclude that in the southern Netherlands it was not possible to assign any influence of the winter weather parameters upon the conditions of subsequent breeding perfomance in the five studied populations.

DISCUSSION

In the southern Netherlands as well as in other countries where investigations on the population dynamics of wild geese have been carried out, notable year-to-year changes concerning their breeding success have been noted. Such fluctuations and especially the extent of the overall negative deviations in some years are thoroughly demonstrated in this paper.

For many years, investigators have attempted to explain the possible causes leading to this phenomenom. Hitherto, none of these propositions stands up against criticism. A brief and critical survey of the suggested origins of failure or absence of breeding performance might bring us closer to the elucidation of this fascinating matter. Thus we shall pass in review the most quoted impacts on breeding success, such as: weather conditions on the breeding grounds and in the winterquarters, the female condition on arrival at the breeding place, and the alternative prey theory.

Many authors state that the weather conditions during the reproduction period are the prevailing factor determining breeding success. Inclement weather and late snowfall were thought to be responsible for poor breeding performances (Scalon, 1935; Ogilvie and Matthews, 1969; MacInnes *et al.*, 1974; Ogilvie and St Joseph, 1976; Owen and Norderhaug, 1977; Ogilvie, 1979). These conditions can provoke follicle atresia (Barry, 1962), a delay of breeding (Newton, 1977), or a complete breeding failure (Heyland, 1979). On the other hand, Meltofte *et al.* (1981) observe at the breeding grounds of *A. brachyrhynchus* in North-East Greenland that Arctic Foxes (*Alopex lagopus*) increased predation on the eggs of this species when snow cover was more intense.

However, as we have demonstrated in various ways in this paper, we never found in the five populations in the south of the Netherlands a strong link between on the one hand summer temperature and precipitation and on the other hand breeding success. Other papers are also in disagreement with this rough climate hypothesis. Ely and Raveling (1984) state that Pacific Whitefronts (*A. albifrons frontalis*) were reproductively successful during three seasons with wide varying phenologies. Also Summers (1986) reveals no significant differences between temperature and precipitation in the western Taimyr Peninsula and years with good and poor breeding success in *B.b. bernicla*. A recomputation of Summers' data confirms this opinion. We divide the mean annual June + July temperatures, covering 23 years (1957-1979), at Ostrov Dikson (West-Taimyr) into three classes: summers with a temperature > 30% above the long-term mean of this reference period (n = 8), summers with a temperature 1 - 20% above the mean (n = 4), and summers with a temperature below this mean (n = 11). A model II Anova analysis could not detect any significant difference between the three classes and the corresponding percentages of young counted by the I.W.R.B. - Brent Research Group (Prokosch, 1984) during the subsequent fall ($F_S = 0.23$; $n_1 = 2$ and $_2 = 20$; $P > 0.5$). Moreover, three out of eight very good summers at Ostrov Dikson with mean temperatures > 30% above the long-term mean gave a low percentage of juveniles, such as in 1962 (0.2%), 1965 (6.9%) and 1977 (2.0%). Finally, in a large scale investigation among breeding success of many Arctic-nesting geese species in a large part of the Holarctic, one-to-one correlations between yearly temperature deviations and a total breeding success index is hard to find (Boyd, 1982). This author concludes that for evaluating breeding performance in northern geese populations, temperature data are not necessarily the most informative, and that many more investigations are needed. This opinion is sustained in his recent paper (Boyd, 1987). Here the author points out the difficulty that the summer weather data as used by the investigator in the winterquarters may sometimes be misleading, because a mean monthly temperature has not necessarily a strong linear relationship with the time of snow smelt.

Some authors reveal a significant correlation between the temperature in the winterquarters of Arctic- or Subarctic- breeding Anseriformes and their productivity in the following summer. This seemed true for varying genera, as for Barnacle Geese wintering in Ireland (Cabot and West, 1973) and Whooper Swans (*Cygnus cygnus*) wintering in southern Sweden (Nilsson, 1979).

Cadbury (1975) however, could not demonstrate any significant correlation between the percentages of juvenile Bewick's Swans (*C. bewickii*) in England during the period 1960/1961 - 1974/1975 and temperatures in the preceding winters and springs. Joyner *et al.* (1984) suggest that a reduced food supply in January and February in *B. canadensis interior* did not affect its reproductive potential in May. Also our own investigations in the southern Netherlands contradict the association of mean winter temperatures and precipitations with the proportion of juveniles during the subsequent winter. In that way the hypothesis about the mild winterweather cannot merit full acceptance and is not to be generalised.

Related to the foregoing hypothesis, several investigators advance the argument that female condition on arrival in the breeding area determines her breeding success. Increases in body weight of females in spring of 41 - 53% of winter weight have been documented for Todd's Canada Goose (*B. canadensis interior*) (Hanson, 1962), Ross' Goose (*A. rossii*) (Ryder, 1967 and 1970), Lesser Snow Goose (*A. c. caerulescens*) (Ankney, 1977; Ankney and MacInnes, 1978), Cackling Goose (*B. c. minima*) (Raveling, 1979) and Giant Canada Goose (*B. c. maxima*) (McLandress and Raveling, 1981). These reserves provide the necessary energy for migration and reproduction, and are critical in affecting clutch size. In this respect, the results obtained by Ebbinge *et al.* (1982) on the Dark-bellied Brent Goose in the Dutch Wadden Sea are of great value. Females do not always leave their spring staging areas in the same condition each year. Detailed work on individuals show that females returning in the fall with young have achieved significantly heavier body weights in the previous spring than those failing to do so. Females subsequently found to prove successful have grazed a larger proportion of See Arrow-grass (*Triglochin maritima*) in their spring diet and their males are of a high status, as measured by the number of interactions they have won. Such males can provide their mates with enhanced feeding opportunities, resulting in accumulation of more body reserves in the spring and a heigthened probability of successful breeding (Teunissen *et al.*, 1985). Although as already expressed by Ebbinge *et al.* (1982), these data still ignore some important considerations: Dark-bellied Brents migrate over 4000 km to reach their breeding grounds of the Taimyr Peninsula, and we lack information on body weights upon their arrival there. Moreover, parents arriving in good condition may hatch their eggs successfully, but lose their young to predators or adverse weather conditions. Such parents would be classified by the investigator in the winterquarters as failed breeders.

Summers (1986) suggest an alternative prey theory, namely that the breeding success of the Dark-bellied Brent Goose on the Taimyr Peninsula is in some way related to years of peak lemming (*Dicrostonyx torquatus, Lemmus sibiricus*) abundance. According to a paper of V.F. Dorogov (*in* Summers, 1986), such peaks occurred every three years between 1969 and 1982. In years when lemming numbers are low, their predators (chiefly Stercoraridae and Arctic Foxes) may migrate out of the Arctic, fail to breed, or switch to alternative food, consisting mainly of eggs and goslings of wild geese. Although many authors adhere to this hypothesis, which was corroborated by a recent paper (Summers and Underhill, 1987) and was also hold true for the reproduction success int the Curlew Sandpiper (*Calidris ferruginea*) bij Roselaar (1979), observations from the breeding grounds and statistics indicate that this increased predation cannot be the only reason for poor breeding success at Taimyr (P. Tomkovich *in* Summers, 1986; Dhondt, 1987; Owen, 1987). In some years, the Brent Geese did not attempt to breed, despite favourable conditions of weather and of predation. It may be suggested in this case that their nutrient reserves were too low which could result from feeding conditions prior to migration (Ebbinge *et al.*, 1982). Moreover, the recent conclusions of El'shin and Shubin (1983) on the feeding distribution of the Rough-legged Buzzard (*Buteo lagopus*) and of the Snowy Owl (*Nyctea scandiaca*) in the Yamal tundra during conditions of lemming crashes seem also to contradict the increased predation hypothesis. These two predators did not shift diet to more numerous voles, but changed foraging patterns to concentrate on isolated pockets of high-density lemmings.

In conclusion, no full reliable explanation has been found to solve the problem of the year-to-year changes concerning the breeding success of northern geese. Several separate hypotheses have been put forward, but we have tried to demonstrate that their evidence is rather meagre and the results confusing. There is little doubt that some significant results in this paper could be caused by chance, because a large set of data have been examined. Hence, the interrelationships of several causes become more and more likely.

In the future, restricted maximum likekihood estimation of a lot of variance components, as done by Birkhead *et al.* (1983) for evaluating factors affecting the breeding success in the Mute Swan (*C. olor*), seems a trustworthy analysis for helping to solve the matter. In this way, a causal chain could be produced, taking into account a large number of response variables such as clutch size, laying date, age and genotype of the parents, habitat, year effect, and climatic conditions. Because a large part of the breeding area of wild geese wintering in western Europe remains inaccessible nowadays, the prospect of ever obtaining biological data series on these birds is not brilliant.

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SUMMARY

During the winter 1986-1987 a poor breeding success was observed in five populations of wild geese wintering in the southern Netherlands. This paper describes the extent of this reproduction failure, by means of long-term records on the breeding performance of wild geese collected in this area, and attempts to explore its causes. An overall reproduction success in all controlled populations hardly ever occurs. Concerning the proportion of juveniles in five populations, it occurred only once out ot eighteen years, and concerning the mean brood size in three of them, only five seasons out of fourteen were regarded to be successful. Seasons with large departures from the reference mean in two or more populations are not uncommon. The seasons 1970, 1976, 1979 and 1985 show a small sum of negative departures and are regarded as

overall good, whereas 1971, 1974 and 1986 can be regarded as overall bad. Many authors associate the result of the breeding performance in northern wild geese with weather conditions during their reproduction cycle. However, we failed to demonstrate significant correlation coefficients between these variables in our own research. We have then compared the mean summer temperatures and precipitations of 32 northern stations between four years of overall good breeding performance and four years of overall bad breeding performance. Again, no distinct pattern emerged. Furthermore, the analyses of the correlation between weather conditions in the winterquarters and subsequent breeding performance were inconclusive for all five populations. Up till now, no indisputable mechanism has been found to explain the yearly changes of breeding succcess in wild geese. Several hypotheses have been put forward, but a combination of several causes seems likely. This complex study object needs more data concerning response variables than are available at present.

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RESUME

L'été 1986 fut caractérisé par de mauvais résultats de reproduction chez les oies sauvages, comme il le fut constaté par une enquête effectuée sur cinq populations hivernant dans le sud des Pays-Bas. Cette étude compare les résultats obtenus pendant l'hiver 1986/1987 avec les moyennes de références de longue date et essaie de trouver une explication des échecs de reproduction. Depuis le début des observations, la reproduction fut rarement un succès pour l'ensemble des cinq populations. En ce qui concerne la proportion des exemplaires en plumage adulte / juvéniles, elle fut un succès une fois en dix-huit années. Pour la taille moyenne de la famille dans l'ensemble de trois populations, le succès se déclara cinq hivers sur un total de quatorze. D'importantes déviations négatives par rapport aux moyennes de référence se présentèrent couramment en même temps chez au moins deux populations. Par l'addition de ces déviations négatives dans la proportion adultes / juvéniles, nous avons pu distinguer de bonnes et de mauvaises saisons de reproduction. A cause de leur faible déviation négative, les saisons 1970, 1976, 1979 et 1985 furent considérées comme généralement bonnes. Les années 1971, 1974 et 1986 furent considérées comme généralement mauvaises, leur déviation négative étant élevée. Beaucoup d'auteurs admettent l'existence d'un lien entre les résultats de reproduction des oies sauvages d'origine nordique et les conditions climatologiques durant leur cycle de reproduction. La présente étude n'a pu soutenir cette thèse. Même en comparant les moyennes des températures et des précipitations mensuelles enregistrées en 32 stations climatologiques situées dans l'aire de reproduction, nous n'avons pu constater des différences climatologiques entre les saisons avec une reproduction généralement bonne ou avec une reproduction généralement mauvaise. Aussi nous n'avons trouvé de lien entre les moyennes de température et de précipitation dans le quartier d'hivernage et les résultats de reproduction pendant l'été suivant. Malgré le grand nombre d'études concernant ce sujet, nous ignorons jusqu'ici l'origine des fluctuations des résultats de reproduction. Il est très probable que les différentes hypothèses émises à ce sujet se relient par des rapports complexes. L'éclaircissement de ceux-ci est une étude compliquée, qui nécessite la connaissance d'un nombre de variables biologiques supérieur à celles que nous avons actuellement à notre disposition.

SAMENVATTING

De zomer 1986 was gekenmerkt door slechte voortplantingsresultaten bij wilde ganzen, zoals bleek uit een onderzoek, uitgevoerd bij vijf ganzenpopulaties die in het zuiden van Nederland overwinteren. Door een vergelijking met de langdurige referentie-gemiddelden afkomstig uit vorige winterseizoenen beschrijft deze studie de ernst van dit gering voortplantingssucces en tracht een verklaring te vinden van zulk verschijnsel. Sinds het begin van het onderzoek werd een gemeenschappelijk broedsucces bij alle gecontroleerde populaties slechts zelden waargenomen. Betreffende de verhouding overjarigen / juvenielen bij vijf populaties, kwam zulk gemeenschappelijk succes slechts tijdens één winter voor op een totaal van achttien en betreffende de gemiddelde familiegrootte bij drie populaties, noteerden wij dit succes slechts in vijf winters op veertien. Negatieve afwijkingen ten opzichte van de langdurige referentie-gemiddelden zijn terzelfvertijd bij twee of meer populaties niet ongewoon. Voor wat betreft de verhouding overjarigen / juvenielen, vertoonden de broedseizoenen 1970, 1976, 1979 en 1985 een geringe som van negatieve afwijkingen tegenover de langdurige gemiddelden. Deze seizoenen werden als algemeen «goed» bestempeld. De broedseizoenen 1971, 1974 en 1986 werden door hun aanzienlijke som van negatieve afwijkingen als algemeen «slecht» beschouwd. Volgens vele auteurs bestaat bij de wilde ganzen met een noordelijk broedareaal een verband tussen hun voortplantingsresultaten en de weersomstandigheden gedurende hun voortplantingscyclus. Omtrent deze stelling zijn in deze studie geen signifikante korrelaties aangetoond. Ook werden de gemiddelde zomertemperaturen en -precipitaties van 32 noordelijke weerstations vergeleken tussen vier jaren met algemeen goede en vier jaren met algemeen slechte voortplantingsresultaten. Ook

deze vergelijkingen hebben niet geleid tot een duidelijk onderscheid. Tevens werd bij geen der populaties een signifikant verband gevonden tussen gemiddelde temperaturen en precipitaties in het winterkwartier en de daaropvolgende voortplantingsresultaten. Spijts de vele studies, is tot heden nog geen sluitende verklaring gevonden voor het wisselende broedsucces bij noordelijke wilde ganzen. Zeer waarschijnlijk zijn de daaromtrent verschillende vooropgestelde hypothesen met elkaar verbonden door moeilijk te ontcijferen verbanden. Hun opheldering is een moeilijk onderwerp en behoeft zeker heel wat meer kennis van de biologische variabelen dan tot heden het geval is.

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