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**Population studies of the grey-lag goose *Anser anser* breeding in the Barycz valley, Poland**

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This study was performed during the period 1972 to 1977. The goose population numbered 280–312 pairs. A similar number was reported before World War II and then after 1960. Between these dates there occurred a sudden drop (of approx. 75%) caused by a sharp increase in the exploitation of geese by man. The population study was performed on 122–154 pairs of geese breeding in one of the fish-pond complexes. The geese nested exclusively on ponds. The time of start of egg laying coincided with the disappearance of ice cover, which could be explained in terms of antipredatory behaviour. The clutch size per breeding female ranged from 2 to 10 (12?) eggs, the mean value in different seasons being 4.9 to 5.6 eggs. No relationship was noted between mean clutch size and time of commencement of the nesting period. The mean clutch size decreased from 6.7 to 3.5 as the season passed. Almost all of the clutches with more than 10 eggs were laid by two females. 44.2% of nests ended in a failure. The main causes were predation by the hooded crow and abandonment of nests, in similar proportions. Other causes accounted for only 0.9%. In successful clutches the rate of hatching success was 90.4%. Mortality of the young (till fledging) was 27.4%. The mean production of young per breeding pair in one season was 2 young. The ratio of actual to potential production was 38%. This was sufficient to ensure stability of the goose population.

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Исследования были проведены в 1972–1977 г. г. Вся популяция насчитывала 280–312 пар. Такой же уровень отмечался до Второй мировой войны и после 1960 года. В промежуточный пе-

риод наступило резкое снижение численности вследствие чрезмерной эксплуатации гусей человеком. Популяционными исследованиями были охвачены гуси, населяющие один из комплексов рыбных прудов, в количестве 122–154 пары. Гуси гнездились только на прудах. Начало кладок было связано с исчезновением ледяного покрова, что является результатом приспособлений против хищников. Величины кладки от одной самки составляли 2–10 яиц (12?) при средней величине 4,9–5,6 в разных сезонах. Не найдено зависимости между величиной средней кладки и сроком начала гнездового периода. В течение сезона средняя величина кладки уменьшалась с 6,7 до 3,5 яйца. Почти все кладки, превышающие 10 яиц, происходили от двух самок. 44,2% гнезд подвергалось уничтожению. Основную роль играло тут хищничество ворон и покидание гнезд. Соотношение потерь, вызванное этими двумя факторами, было почти одинаковое. Потери по другим причинам составили только 0,9%. В удачных кладках птенцы вылупливались из 90,4% яиц. Смертность нелетных птенцов составила 27,4%. Продукция молодых летных птиц составила в среднем 2 особи на пару в течение сезона. Потенциальная продукция всей популяции была реализована в 38%. Этого было достаточно для сохранения численности популяции на стабильном уровне.

Introduction . . . . .	181
Description of the study area . . . . .	181
Methods . . . . .	185
Results . . . . .	187
Population density . . . . .	187
Occurrence . . . . .	189
Circadian rhythm of geese throughout the year . . . . .	189
Distribution and building of nests . . . . .	190
Timing of breeding . . . . .	191
Egg laying and hatching . . . . .	194
Clutch size and egg measurements . . . . .	194
Double clutches . . . . .	197
Duration of the breeding period . . . . .	197
Failures and breeding success . . . . .	198
Proportion and causes of nest failures . . . . .	198
Predation . . . . .	198
Abandonment of nests . . . . .	199
Predation or abandonment . . . . .	200
Other failures . . . . .	201
Successful clutches and production of young . . . . .	201
Hatching success in relation to clutch size and time of laying . . . . .	202
Hatching success in relation to nest-sites . . . . .	203
Survival of young . . . . .	204
Total number of failures and production of young . . . . .	205
Discussion . . . . .	205
Stability of population . . . . .	205
Clutch size . . . . .	208
The importance of egg-size . . . . .	209
Breeding success . . . . .	210
Antipredatory behaviour . . . . .	210
The importance of protection of the grey-lag goose in the Barycz valley . . . . .	212
Acknowledgements . . . . .	213
References . . . . .	213
Streszczenie . . . . .	215

## INTRODUCTION

The population of the grey-lag goose in the Barycz valley has ranked as one of the largest communities of this species in Central Europe for well over 100 years. Certainly it is the most numerous one in Poland. For the last 20 years the number of breeding pairs has been fluctuating around the 300 pairs. The local fish-ponds on which this species breeds, although subject to fairly intensive commercial exploitation, have been a waterfowl reserve since 1949. Up to now there have been no special studies of this population, neither from the biological nor ecological points of view.

The need for initiating such studies has recently become all the more evident because considerable changes have been taking place in the environment as a result of intensification of fish-farming activities. There was concern that this might be detrimental to the habitat, first of all because of the danger of elimination of suitable nesting sites for the majority of waterfowl, including geese, if the works were to continue as planned by the fishery authorities. It was therefore necessary to start a detailed study with a view to determining the conditions that would allow the goose population to remain undisturbed. The present study was performed during the period 1972 to 1977, its objectives being as follows:

- determining the number of breeding pairs in consecutive seasons in order to reveal the extent of any fluctuations and their possible causes,
- evaluating the suitability of the various elements of the pond habitat for the nesting of geese in terms of number of pairs and breeding success,
- determining the pattern of the breeding season in particular years, as well as the factors affecting it,
- determining the clutch size and production of young,
- determining the factors affecting the overall breeding success,
- study of the behaviour of geese during successive stages of the reproduction in order to obtain information on the strategy of life of the population investigated.

Studies of the grey-lag goose of a similar scope have been carried out by YOUNG (1972) and NEWTON and KERBES (1974) in Great Britain. Synthetic reviews of contemporary knowledge about this species have been published by BAUER and GLUTZ (1968), HUDEC and ROTH (1971) and CRAMP (1977).

## DESCRIPTION OF THE STUDY AREA

The Barycz river, a right-side tributary of the Odra, flows in a wide post-glacial valley. In the upper and central parts of this valley there are numerous ponds grouped in six complexes (Fig. 1). The oldest of them were formed as early as the end of the 13-th century by damming off huge overflow arms from

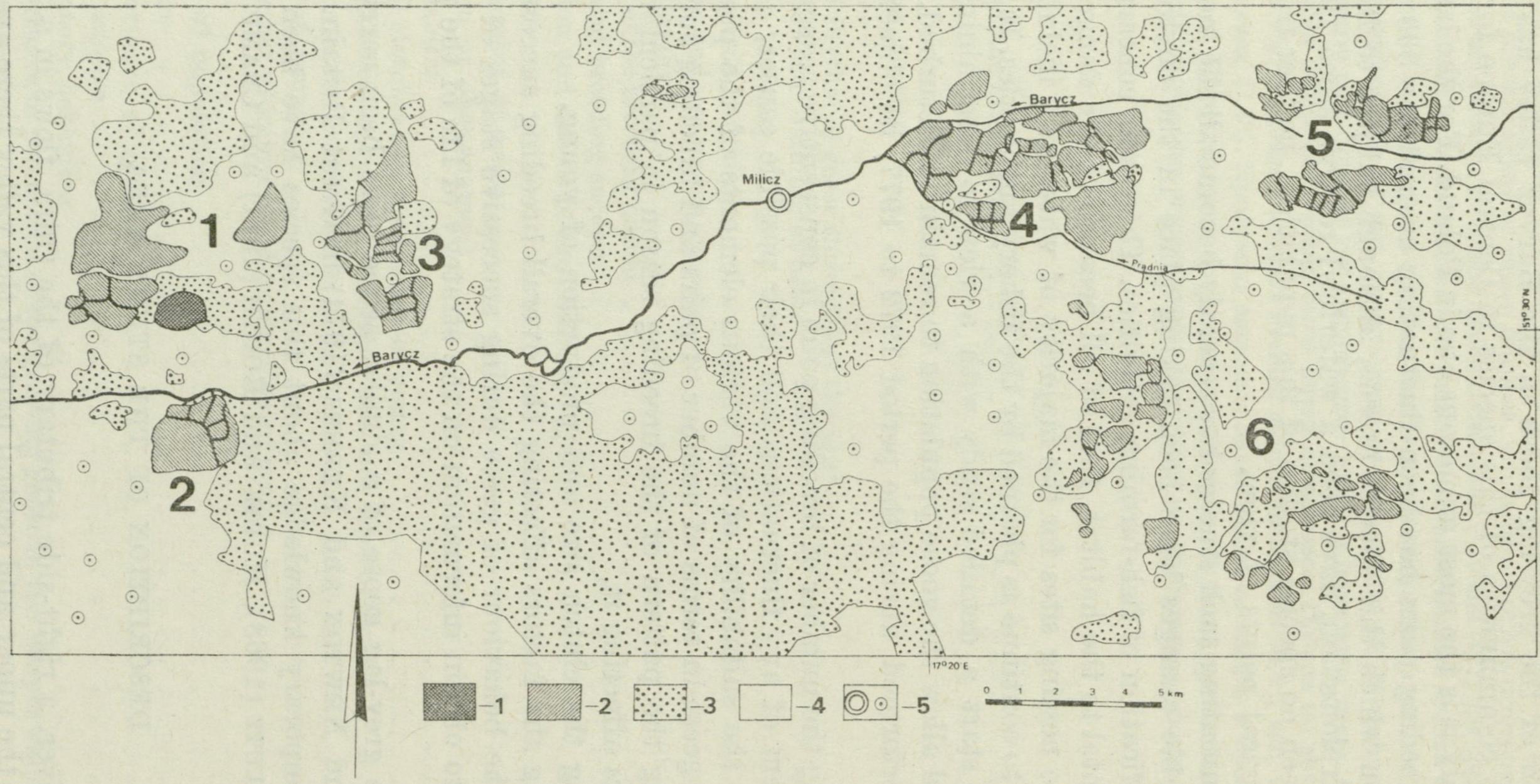


Fig. 1. Barycz valley.

1 — main breeding area of grey-lag geese ("Luge") at least up to 1922; 2 — fish-ponds; 3 — forests; 4 — meadows, pastures, fields; 5 — human settlements. Numbers — fish-pond complexes,

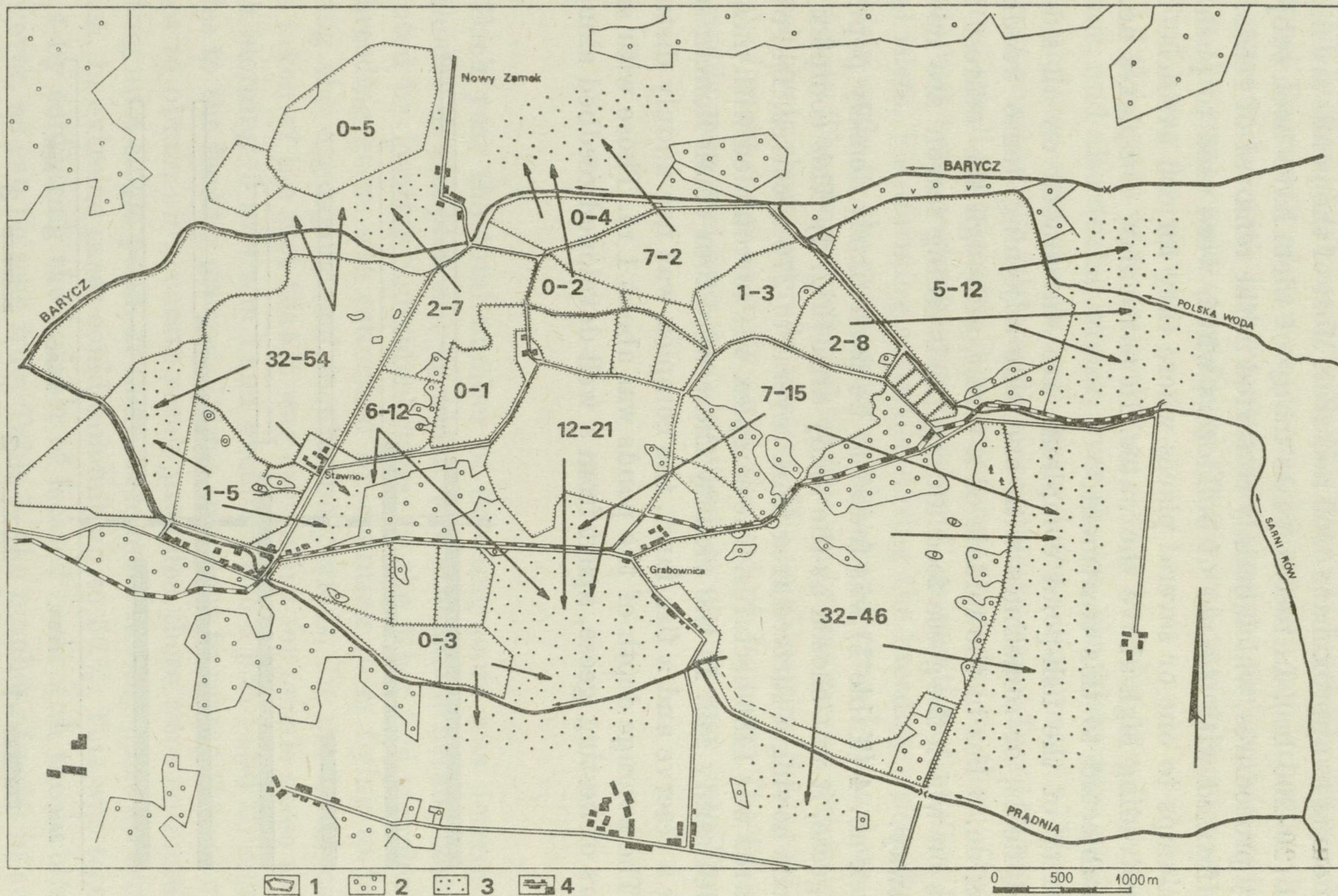


Fig. 2. Area of detailed studies (fish-pond complex No. 4). 1 : 25 000.

1 — fish-ponds; 2 — forests; 3 — meadows, pastures, fields; 4 — human settlements. Arrows show feeding areas of geese breeding in particular ponds. Numbers indicate how many pairs bred in particular ponds.

the river bed. Even today the majority of them have the appearance of shallow lakes with well-developed reedbeds along the dam and numerous islets of reeds in shallower parts of the pond. There are also occasional natural islets with trees growing on their surface. The overall surface area of the ponds in these complexes amounts to approximate 6500 hectares. Most of the ponds are middle- to large-sized (20–200 ha). In recent years many of them have been subjected to renovatory procedures, which mainly consisted in the removal of reeds. This work was performed with the use of bulldozers which were used to push individual reed clumps to one or several places where they formed artificial islets, sometimes protruding high above the water. In particular, complexes no. 1, 2 and 3 were subjected to this treatment.

The majority of the fish-pond complexes are surrounded on all sides by meadows and fields, or sometimes with one side adjoining dense woodlands. Only complex no. 6 lies in the middle of a forest, although the nearest fields and meadows on which the geese feed during the breeding season are no more than 3 km away.

As complex no. 4 (Table 1) was found to be particularly densely populated by breeding geese, it was chosen as the study area (Fig. 2). This complex comprised 30 ponds having a surface area from several to 270 hectares. The overall dammed-off area was 1480 hectares. The complex was surrounded with meadows and fields with sandy soil. In the vicinity there were four small human settlements. Being a reserve and a fish-farm, the complex was not unduly disturbed by humans. The average depth of the ponds was about 1 m. Those with significant numbers of nesting geese, apart from a well-developed reedbed along the

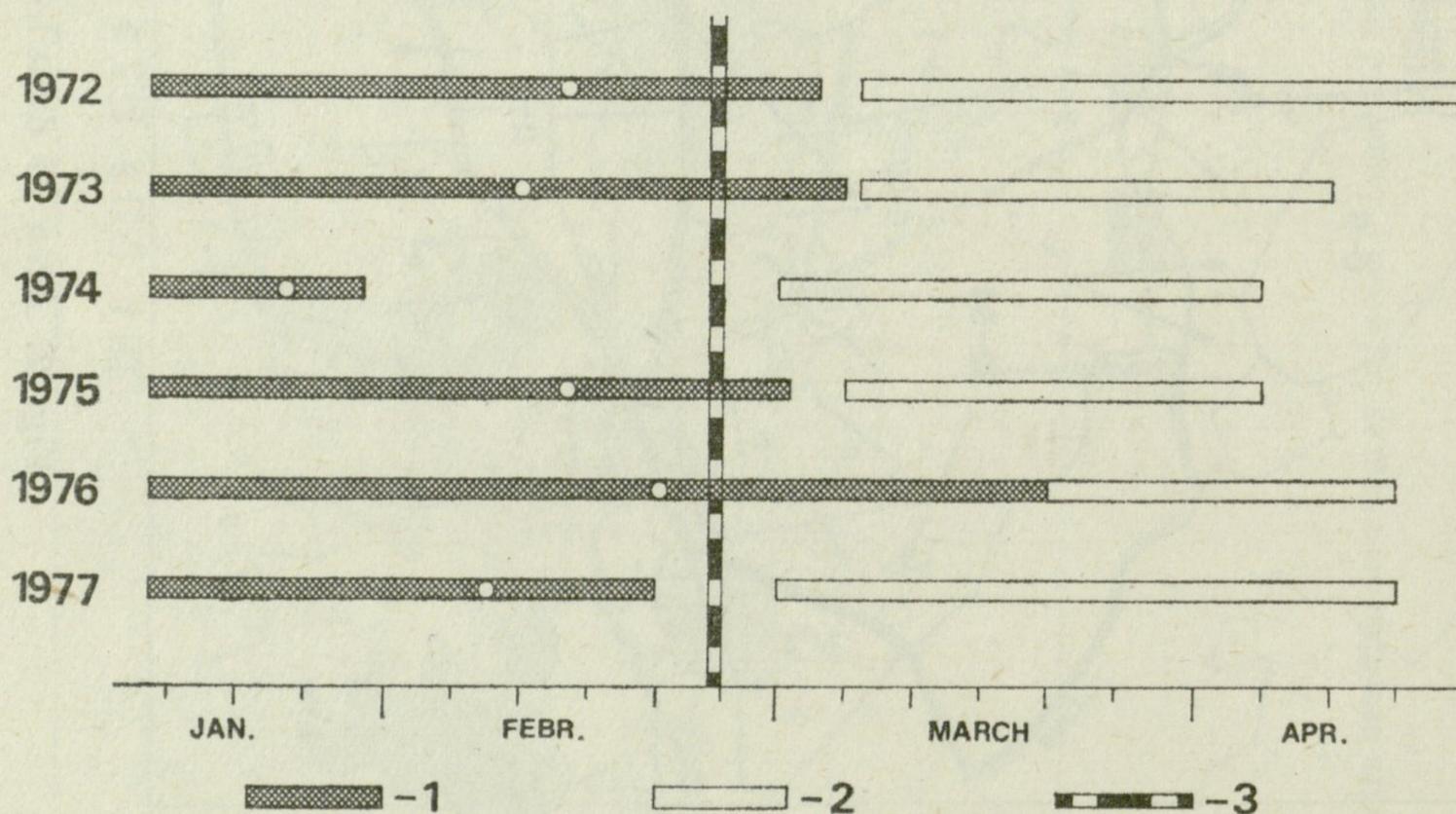


Fig. 3. Ice-cover in relation to laying period.

1 — period when ice-cover exists; 2 — laying period; 3 — time at which the physiological barrier to laying discontinues.

Open circles show the date of arrival of geese from wintering.

dam which sometimes reached a width of 100 m, had numerous islets formed in the shallower parts by *Phragmites communis*, *Typha angustifolia*, *Glyceria aquatica* and *Scirpus lacustris*. The area of such islets ranged from 0.02 to 1 hectare. They had the following structure: the central part was made up of closely packed broken dead reeds with the detritus layer almost touching the water surface. Regrowth of new reeds was practically non-existent there. This part was surrounded with last year's reeds, straight and rather scattered, amongst which the geese could swim freely. There was no detritus layer there, as it was washed away by waves.

All the ponds were drained once a year in order to collect the fish. Because of this, and also during winter, over the ice, the islets were penetrated by wild boar and roe deer which trod many intersecting paths. This made even the deepest parts of the islets easily accessible to geese. In addition, six ponds had natural small islands with shrubs and trees growing on them. Over a half of the ponds had been partially renovated and, as mentioned earlier, had large artificial islets. Fish-farming activities during the breeding season for geese, which is fairly early in the year, were minimal and caused almost no disturbance in the ponds. The years during which this study was carried out were characterized by relatively short and mild winters. The neighbouring fields and meadows were freed of snow cover as early as at the end of January. The time during which the ponds were iced over was also short, as can be seen from Figure 3.

## METHODS

Each year the total number of breeding pairs was determined using two methods: in complex no. 4, which was studied in detail, nesting pairs were counted by locating individual nests; in the other five complexes the number of breeding geese was estimated by counting pairs flying to feeding grounds during the egg-laying and incubation periods. In the latter case, advantage was taken of the fact that it was customary for female geese to leave the nest each morning (5 to 9 a.m.) and evening (4 to 8 p.m.) and fly together with the males to the feeding ground. It was sufficient to repeat the count three to four times to obtain an accurate result provided there were no more than 15 pairs nesting on a single pond. If there were more nesting pairs an error could result which, in extreme cases could amount up to 50%. This was tested in complex no. 4 by comparing the number of located nests with the results of the count. However, as can be seen from Table 1, the number of pairs in complexes other than no. 4 was so small that the possibility of making a significant error could be ignored. Locating of individual nests was begun whenever the behaviour of certain pairs indicated that the females might have started laying eggs. A sign of this was when one of the partners remained in the reeds for longer periods

of time, as the other swam keeping an attentive eye on the surroundings, or when, upon return from feeding grounds, one of the birds disappeared in the reeds while the other remained on the nearby water for some time and then flew back to the feeding ground.

All places that were suitable for goose nesting were searched so many times over as was necessary to locate all nests built during a given season. The likely places were determined by frequent observations from the dam. In my opinion, no more than 5 nests could have been missed in any season.

All nests with successful clutches were inspected at least four times. This made it possible to obtain all the necessary data in the case of nests found when the clutch had not yet been completed. The date of commencement of egg laying was determined by subtracting the number of eggs found from the data of finding the nest. The next visit was scheduled on the day when the clutch was expected to be completed, with the assumption that a single female can lay up to 12 eggs. This visit made it possible to determine the final clutch size and the probable date of commencement of incubation (assuming that the female lays an egg every day and commences incubation on the day of laying the last one). The next visit was scheduled on the 27-th day of incubation. Its aim was to determine the date of hatching (cracks or holes in the egg-shell or audible cheeps indicated the precise date of hatching). The last visit was made on the day of hatching. The chicks were weighed and marked with wing-tags. Unhatched eggs were first tested to see if there was a live embryo inside (shaking of the egg would result in the chick either moving or cheeping) and then broken in order to determine whether the failure was due to infertility or death of the embryo.

In the case of nests found with an already completed clutch (being incubated) the number of visits was increased so as to permit prediction of the date of hatching with the aid of water testing of the eggs. When the eggs started to float the nest would be inspected every three days until the day of hatching. The date of commencement of egg laying was calculated by subtracting from the date of hatching the 28 days of incubation and the same number of days as there were eggs in the nest.

Abandoned or predated nests, if the clutch had not been completed, were included in the final analysis of results only in the construction of the diagram of the egg-laying pattern for the whole population, and in the analysis of nest failures. In the case of nests with completed clutches which were subsequently abandoned or predated, the approximate date of commencement of egg laying was determined from embryo growth, where the loss of the clutch was assumed to have occurred in the middle of the period between the last but one and the last visit. As the unit of time used in the description of the egg-laying cycle was a five-day period, the calculations described above seem to reflect the real situation.

In the majority of cases the causes of nest failures could be determined from the condition of the nest and clutch. Three categories of nest failures were dis-

tinguished: predation, abandonment and flooding or washing away of the nest.

Included in the first category (predation) were nests in which the whole clutch had been destroyed as well as those in which after the loss of one or more eggs during the period preceding the visit incubation was continued until a further loss (not always total) would finally result in abandonment.

Nests were considered abandoned if there had not occurred a loss of eggs since the last visit but incubation had been discontinued. The third category is self-explanatory.

In a considerable number of cases it was difficult to determine the primary cause of the loss. This happened if between successive visits a nest had not only been abandoned but also partially predated, with the consequences of both these events being unknown. Such nests were classified in the mixed category "failed due to predation or abandonment".

As a result of these visits it was possible to determine the pattern of commencement of egg laying by individual females, the relationship between clutch size and date of commencement of egg laying, potential production of the population, extent and causes of clutch losses and actual production in terms of hatching success.

The specific strategy adopted by the population investigated during the period from the day of hatching to the day of fledging, which consisted in carrying out the whole cycle within the territory of the pond, in places with particularly thick growth, made it impossible to follow the pattern of further losses by counting the average number of young of a given age per one leading pair. The number of traced birds was too small to make the results meaningful. The author therefore limited himself to several counts of fledged young (with the aid of 40x binoculars), which at the end of June began to flock together with adult birds at 2-3 fixed places during the break between the morning and evening feedings. These counts were discontinued on 25 July due to the fact that after that date one could expect visits of geese from nearby complexes. The highest count was taken as the final production. By comparing these results with the number of hatched young as determined from nest inspections it was possible to calculate the rate of losses during the stage of chick growth.

From the arrival of geese from wintering until their departure observations were made concerning their behaviour, circadian rhythm and feeding habits. These studies were intensified during the nesting season.

## RESULTS

### Population density

According to KALUZA (in MAYR 1926), in 1815 there were over a hundred pairs of geese nesting on ponds in the western part of the valley. At the turn of the 19-th century the main breeding place was a wetland area overgrown

with shrubbery and alders near Niezgoda, called by the German name "Luge". 300 to 400 geese bred in that area as compared to just several pairs nesting on each of the pond complexes (KOLLYBAY 1905). From the literature published later (PAX 1920, 1925; PAMPEL 1922) one may conclude that the situation described by KOLLYBAY remained unchanged until the 1920's.

In the 1940's there occurred a sudden drop in the number of nesting geese and SZARSKI (1950) observed only several dozen pairs. In a later conversation with me he put their number at 60-70 pairs. Already by that time geese had

Table 1. Number of breeding pairs in particular fish-pond complexes in the Barycz valley

Years	1972	1973	1974	1975	1976	1977
Complex 1 (Radziądz)	31	35	30	26	30	33
Complex 2 (Jamnik)	5	7	5	8	6	10
Complex 3 (Ruda Sułowska)	29	40	38	38	40	45
Complex 4 (Stawno)	132	154	136	145	122	141
Complex 5 (Potasznia)	24	32	31	35	29	28
Complex 6 (Wierzchowice)	35	38	40	42	48	55
Total	276	306	280	294	275	312

discontinued nesting at "Luge" and the whole population was breeding only on ponds. In the 1950's, after the ponds and their surroundings were declared a protected zone, the number of breeding pairs gradually increased until in the 1960's the breeding population again attained its original size, *i.e.* approximate 300 pairs (MRUGASIEWICZ and WITKOWSKI 1962).

The numbers of breeding pairs in the consecutive years of the present study are shown in Table 1. The data presented in the table concerns geese breeding exclusively within the six fish-pond complexes shown on Figure 1. In addition to these complexes, the part of the valley studied contains single ponds or groups of small ponds with another 5-12 pairs nesting on them each year (MRUGASIEWICZ pers. comm.). It can be seen from that data that the goose population during the period concerned was stable and oscillated around the 300 pairs. This number was almost identical with that observed in the 1960's.

It is seen from Table 1 that the largest number of geese nested each year in complex no. 4. On comparing these data with the surface area of individual complexes (see Fig. 1) one can see that this situation could not have been caused solely by the relationship between the pond area in the complexes and the number of pairs nesting in them. The observed disproportions in the numbers of breeding birds in complexes other than no. 4 were caused by the lack of substantial reed growth in the former, particularly by the lack of rushes and islets in complexes no. 1, 2 and 3, where the reeds had been removed during renovation works. It should be noted that in complex no. 3 all the geese were nesting

on only one, largest pond which had not been renovated and contained a considerable area overgrown with reeds. Therefore, the main factor responsible for the disproportions in the distribution of the goose population in the Barycz valley seemed to be the availability of optimal nest-sites, *i.e.* reeds, particularly growing in the form of islets.

Each year one could observe in complex no. 4 forty six to 68 non-breeding geese, always flocking together and haunting those ponds which were occupied by the greatest number of nesting pairs. No such flocks were seen in the other complexes, although this could have been the result of insufficient observation.

### Occurrence

The goose population investigated consisted of migratory birds. Marking of approximately 100 birds with neck collars showed that first departures to wintering grounds started as early as the second half of September with last birds disappearing between 15 November and 10 December. Spring arrivals were noted in the third 10-day period of February at the latest, the actual dates of arrival in particular years being shown in Figure 3. Therefore, the period from departure to arrival ranged from 50 to 75 days. In the years 1974 and 1977, twelve and sixteen birds, respectively, were sighted as late as 15 January. Thus, attempts at wintering in the valley were sporadic and were undertaken by individuals whose origin could not be established due to the fact that from the end of September alien geese of unknown origin began to appear in the Barycz valley, so that by October the total number of local and alien geese ranged from 2 to 2 and a half thousand.

In the spring the returning geese would arrive in groups of 8 to 60 individuals. The period between the arrival of the first and the last group of the local breeding population averaged 25 days.

### Circadian rhythm of geese throughout the year

With the exception of the breeding season the circadian rhythm of the grey-lag goose was as follows:

— at daybreak, departure from ponds to feeding grounds situated on local fields and meadows, where they fed till 8–10 a.m.,

— return to the ponds, drinking water, bathing and resting till 3–5 p.m. The geese rested on artificial islets or in shallow water overgrown with short vegetation,

— departure to feeding grounds, where they remained till dusk in the spring, or even till midnight in the autumn,

— return to the ponds, where they settled for the night.

During the egg-laying season the cycle described above did not change to any significant degree, the nest building and egg-laying activities being done either before the morning departure to feeding grounds or during the mid-day

break in feeding. During brooding the feeding periods occurred at the same time of the day as usual, except that their length was cut down to 1.5 to 2.5 h. During the period of leading their young and moulting the circadian rhythm could not be observed because of the secretive behaviour of the geese.

### Distribution and building of nests

In the fish-pond complex that was investigated in detail (Fig. 2) only 16 out of 30 ponds had geese nesting on them. Geese did not nest on ponds with a surface area below 10 hectares. Each year 60–68 % of breeding pairs nested on the largest two ponds of this complex. These ponds had numerous islets of reeds and a wide reedbed along the dam. They had not been renovated and therefore there were no artificial islets there.

Table 2. Distribution of nests (%)

Year	1972	1973	1974	1975	1976	1977	Total
Reedbeds along the dam	14	22	21	26	17	24	21
Islets of reeds	80	68	69	63	78	65	70
Artificial islets	6	10	10	11	5	11	9
No. of nests	132	154	136	145	122	141	830

In spite of the fact that 14 ponds in the said complex had artificial islets and on the remaining ponds the total surface area of reedbeds was almost twice as high as that of the islets of reeds, it is seen from Table 2 that most of the breeding pairs nested each year on natural islets of reeds, rather than on artificial islets. Nesting on trees was never observed (KUX 1963) despite the existence of suitable conditions on at least two ponds.

The number of nests built on the reed islets was not necessarily proportional to their size. The highest number was observed on islets of 1.5 are which had three nests, the shortest distance between two of them being 5.5 m. The number of nests built on particular islets was not the same from year to year. Differences in nest density could be as high as 66 %.

On natural islets with trees growing on them and on artificial islets the nests were located in such a way as to enable the brooding goose to watch the surroundings in all, or at least in three directions. Unlike ducks, which also nested in considerable numbers on the same islets, the geese never built their nests in dense thickets, under thick-set shrubs or under overhanging edges of the dam.

In reed the nest-sites always afforded easy access by swimming or on foot.

Like reedbeds along the dam, the islets of reeds (see page 185) had such a structure that a considerable number of nests was built at the border-line of the closely packed, broken reeds of the central part of the islet, *i.e.* up to 10 metres

from open water. However, as mentioned earlier, the paths trodden by animals often enabled the geese to penetrate deep into the islets and reedbeds. Table 3 shows the observed distances from open water for a sample of 359 nests in the Barycz valley, compared with data obtained in Czechoslovakia on ponds similar to those in the Barycz valley (HUDEC 1971). It seems that in the Czechoslovak sample the geese tended to build nests close to open water. It is difficult to say whether this difference between the two populations had anything to do

Table 3. Distances of nests located in reeds from open water

Distance (m)	Barycz valley		Czechoslovakia (%)
	no. of nests	%	
1-10	136	38	71
11-20	124	35	26
21-30	61	17	3
31-40	29	8	—
> 40	9	2	—

with adaptation, or whether it was caused solely by some structural differences which, for example, made it physically impossible for geese to penetrate deeper into the reeds. In the Barycz population the rate of breeding success was found to be independent of nest distance from open water.

Nests were normally built on small "eyes" of open water in reeds, and if no such "eyes" could be found the geese would clear reeds from an area measuring 2-5 m in diameter and use the material collected to build their nest. A nest built in this manner would be quite conspicuous from the air. The depth of the water under nests situated in reeds ranged from 10 to 90 cm, the majority of nests being built at 20-50 cm. The dimensions of 140 nests were found to be within the limits reported by HUDEC and ROTH (1970).

The majority of the females started laying eggs before the nest had been completed. They would finish the nest during the egg-laying period, or even during the first few days of brooding. If there occurred a moderate rise in water level, the geese would build up the nest to the required height provided the incubation was not at an advanced stage. They would do this only occasionally if the rise occurred in the last days of brooding. If not flushed the geese would often cover the eggs when leaving the nest, but not as a rule. Both during the egg-laying and brooding period the male and the female would fly together to feeding grounds, leaving the nest unattended.

#### Timing of breeding

Figure 4 shows the egg-laying pattern in consecutive seasons. It is seen that in each season the shape of the curve is normal and that there are no curves with two peaks. It has been reported that on the average 44% of nests fail

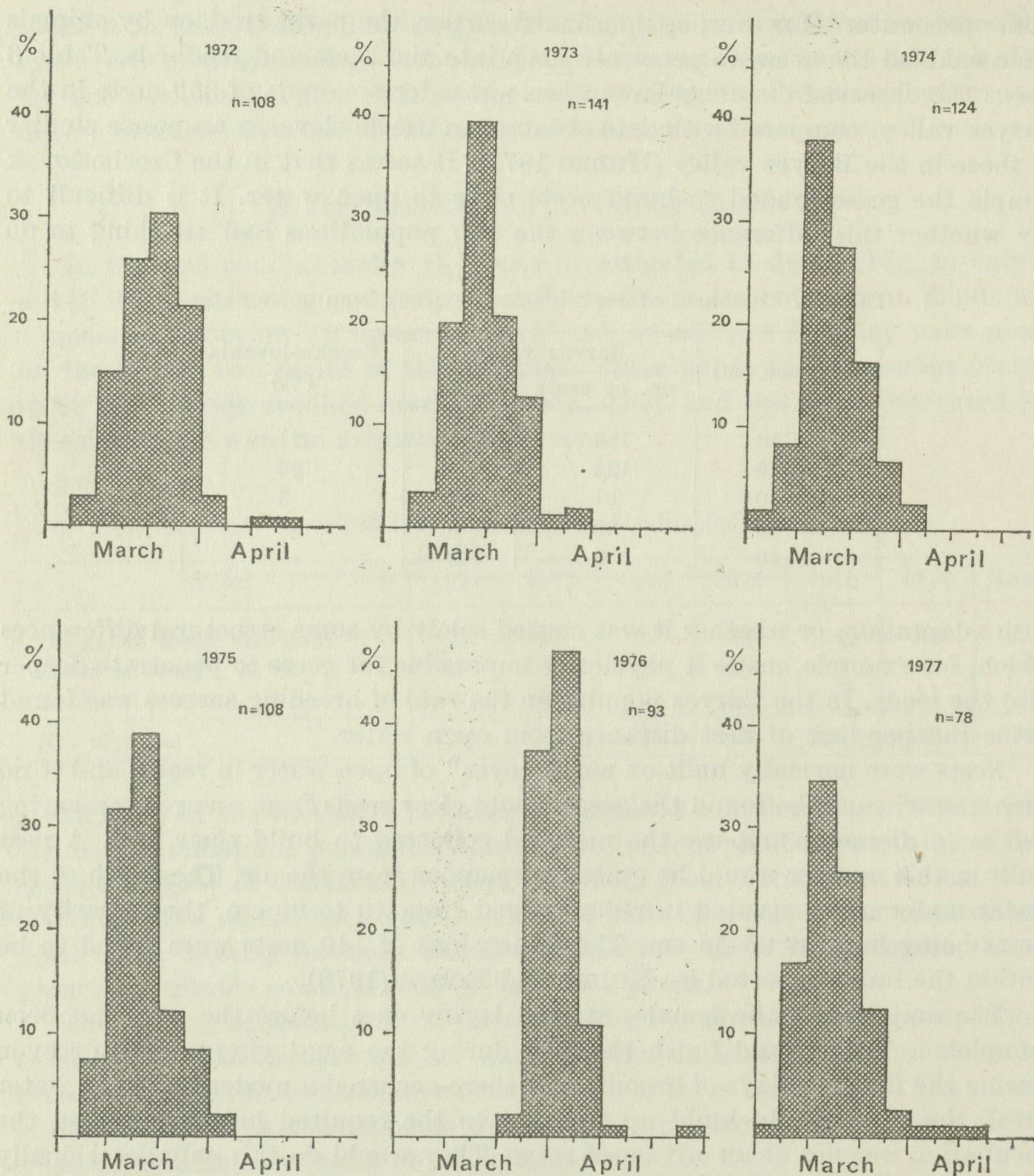


Fig. 4. Chronology of laying (%). Columns show the percentage of females beginning to lay in particular pentades.

during the brooding period (*cf.* Table 10). If geese were to build new nests and lay new clutches after the loss of the first one then one would expect this to be reflected in the shape of the egg-laying curve. As the above-mentioned curves seem to be quite regular we may conclude that at least in the majority of cases last clutches are not replaced with new ones in a given season. This conclusion is also supported by some observations in the field, such as the formation of

flocks of geese, the number of which increased with the passage of the season, as if in proportion to the number of lost clutches. Accordingly to PAAKSPUU (1964), YOUNG (1972) and other authors (in BAUER and GLUTZ 1968) geese lay replacement clutches.

The period between the commencement of egg laying by the first and last female in the population investigated ranged from 30 to 45 days, but the fact that each year 87–97% of geese commenced laying within 20 days of each other confirms the high synchronisation of this process. If the egg-laying season started later than usual then its duration would be reduced (*cf.* the 1976 season with the other ones, Fig. 4).

The egg-laying curves in Figure 4 even if combined into a single diagram (upper diag. in Fig. 5), do not indicate the potential length of the laying season in the Barycz valley due to the fact that all the seasons during this study were

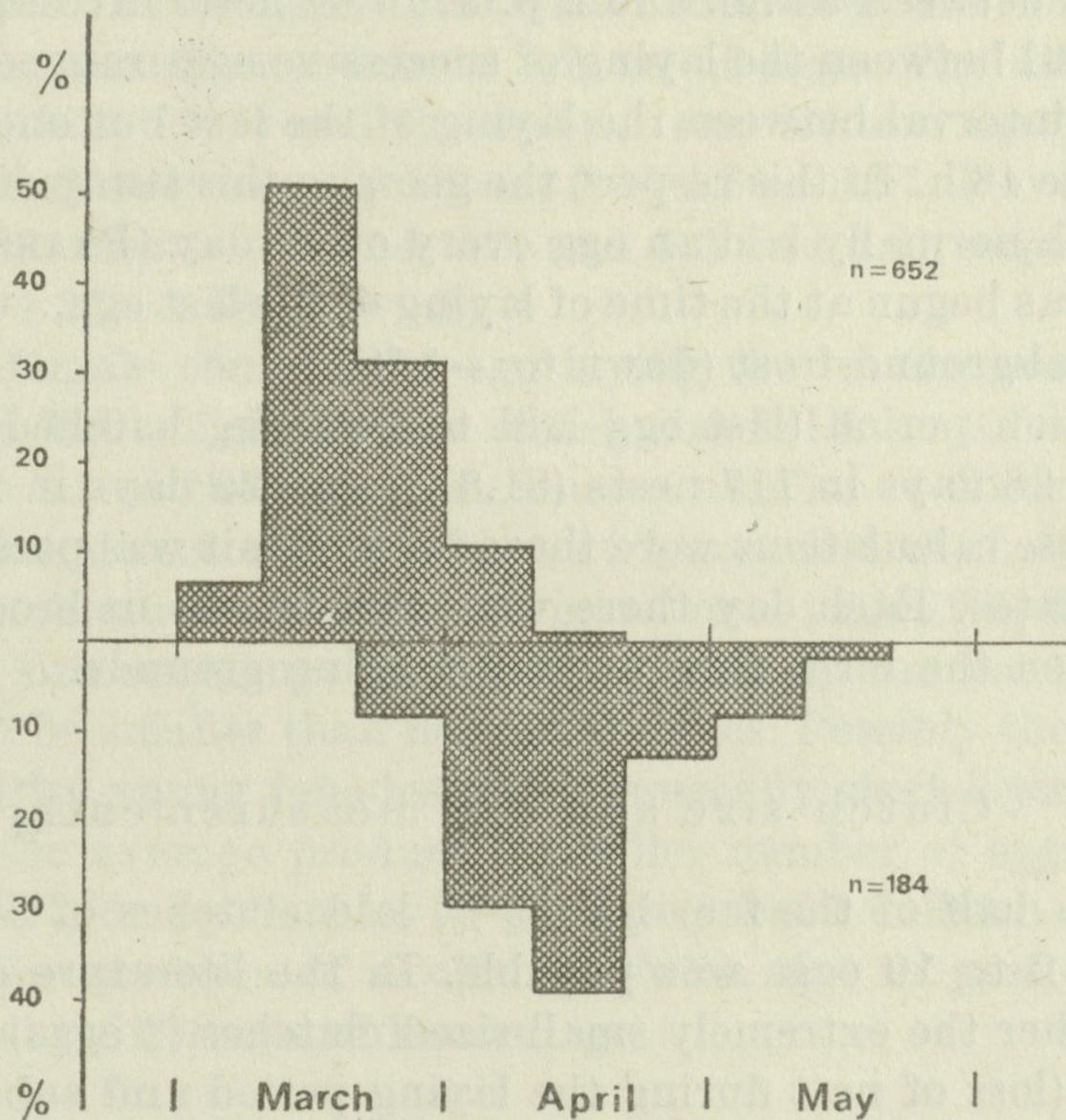


Fig. 5. Potential laying season in Barycz valley.

Columns show the percentage of females beginning to lay in particular pentades. Upper diagram: the overall picture for years 1972-1977. Lower diagram: the beginning of laying in years with relatively severe winters. For other explanations see text.

characterized by relatively mild winters. In order to obtain a more accurate picture of the potential laying season, the author analysed data which he had collected in years characterized by relatively severe winters during which the ponds were ice-bound for a longer period. The results are shown in the lower diagram of Figure 5.

The data collected by the author during the period 1959 to 1979 show that there were only 4 cases (out of a sample of 980) of geese commencing egg laying as early as 26–29 February. Also in Czechoslovakia the earliest date of commencement of egg laying was 26 February (KUX 1963). Thus, it seems that egg laying cannot commence at an earlier date due to the existence of some kind of physiological barrier, perhaps connected with daylength (KENDEIGH 1941). Figure 3 shows the relationship between ice cover and egg laying in consecutive seasons. It is seen that after the disappearance of the physiological barrier the start of egg laying coincided with the melting away of the ice cover. This coincidence will be discussed on page 210.

### Egg laying and hatching

Out of 154 analysed cases in 49 instances eggs were laid before 7 a.m. and in 105 instances between 9 a.m. and 2 p.m. In 64 nests investigated in different years the interval between the laying of successive eggs ranged from 24 to 30 h. In 14 nests the interval between the laying of the last but one and the last egg was approximate 48 h. In this respect the geese in this study differed from those in Estonia which normally laid an egg every other day (PAAKSPUU 1964). Incubation of eggs was begun at the time of laying of the last egg, even if there occurred an occasional ground-frost (down to  $-4^{\circ}\text{C}$ ).

The incubation period (last egg laid to first egg hatched) was 27 days in 2 nests (1.4%), 28 days in 117 nests (81.8%) and 29 days in 24 nests (16.8%). The nests in these calculations were those for which it was possible to determine the necessary dates. Each day there were two breaks in brooding lasting two hours each, when the birds flew to their feeding grounds.

### Clutch size and egg measurements]

More than a half of the females (55%) laid clutches of 5–6 eggs, although anything from 2 to 10 eggs was possible. In the literature doubts have been expressed whether the extremely small-sized clutches (2 eggs) are not the result of an accident (loss of nest during the laying period and subsequent continuation of laying in a new nest), and the extremely large clutches (10–12 eggs) are not laid by two females. In this study, in two nests with 10 eggs each there was no doubt that the eggs had been laid by single females. This finding was based on the following facts: frequent observations from hiding never revealed more than two birds at each of these nests; inspection of the nests every second or third day during the egg laying period always showed the correct number of eggs, *i.e.* one new egg per day; the shape and size of the eggs were within the range of individual variation; 9 and 10 eggs were hatched, respectively, in each case on the same day. Similar data were obtained in the case of another clutch of 12 eggs.

Table 4. Clutch size in different seasons

Year	No. of nests	Frequency of clutches containing the following number of eggs:												Mean clutch size	
		2	3	4	5	6	7	8	9	10	11	12	13		14
1972	108	6	13	18	42	17	7	3	1	1	—	—	—	—	4.9
1973	139	4	9	22	42	23	20	11	1	5	—	2	—	—	5.6
1974	119	2	6	19	40	35	11	2	1	2	—	—	1	—	5.4
1975	106	—	9	22	35	27	7	3	1	1	1	—	—	—	5.2
1976	80	1	11	18	26	15	7	1	1	—	—	—	—	—	4.9
1977	77	1	5	10	26	19	11	4	—	—	—	—	—	1	5.5
All years	No. 629 % 100	14 2.2	53 8.4	109 17.3	211 33.5	136 21.6	63 10.0	24 3.8	5 0.8	9 1.4	1 0.2	2 0.3	1 0.2	1 0.2	5.3

Table 4 gives the frequency of particular clutch sizes in consecutive seasons. Despite the rather considerable individual differences, the overall mean clutch size in particular years ranged from 4.9 to 5.6 eggs. The differences between the means 4.9 (1972, 1976) and the means from 5.4 and up (1973, 1974, 1977) were found to be statistically significant ( $t = 3.69 - 3.97$ ,  $P < 0.001$ ). The difference between the means 4.9 and 5.2, and 5.2 and 5.6, respectively, were not significant ( $t = 1.25 - 1.48$ ,  $P > 0.1$ ).

The later a female commenced egg laying the smaller was the clutch size. This is shown in Table 5. The mean clutch size fell from 6.7 at the start of the laying season to 3.5 at the end of it. Since a number of observations furnished the author with indirect evidence that at least most of the geese did not lay replacement clutches after losing the original one (page 192), the observed drop in mean clutch size could not have been caused by the fact that replacement clutches tend to be smaller than normal clutches. Possibly the decline in clutch size was caused by young females which normally start laying later on in the season and on the average produce a smaller number of eggs (COULSON 1963, MYRBERGET 1977), or by females in poor physical condition (ANDERSEN 1957, JONES 1973). The problem of declining clutch size in geese requires further studies of tagged individuals of known age.

Table 5. Declining of mean clutch-size within the season

Laying seasons are divided into 5-day periods: I to V and following. Data refer to period of first eggs laid. Figures in brackets show sample sizes

	1972	1973	1974	1975	1976	1977	All years
I	6.0 (3)	7.6 (5)	6.5 (2)	6.3 (7)	7.0 (2)	7.0 (1)	6.7 (20)
II	5.7 (16)	6.8 (28)	6.1 (9)	5.8 (34)	5.6 (31)	6.6 (13)	6.2 (131)
III	5.2 (28)	5.9 (56)	6.0 (45)	4.8 (41)	4.4 (36)	5.7 (29)	5.3 (235)
IV	5.0 (33)	4.9 (28)	5.2 (33)	5.0 (13)	4.4 (10)	5.2 (19)	4.9 (136)
V	4.0 (23)	4.3 (17)	4.5 (20)	4.0 (9)	5.0 (1)	4.8 (10)	4.5 (80)
following	3.0 (5)	3.2 (5)	4.4 (10)	4.5 (2)	— (—)	3.8 (5)	3.5 (27)

The dimensions and weight of eggs are given in Table 6. The author weighed only those eggs which had not been incubated for longer than 5 days (Pesola 300). The measurements of the largest and the smallest egg (which hatched later) were  $99 \times 62.5$  mm, 219 g and  $77.5 \times 52.9$  mm, 118 g.

The mean dimensions and weight of eggs did not vary from season to season. Table 7 shows that the mean weight of an egg is almost the same in the three years presented there.

As shown in Table 8, there were no trends and no significant differences in mean egg weight in relation to clutch size.

Table 6. Egg measurements

	Maximum	Minimum	Mean	S.D.	Sample size
Length (mm)	103.0	74.3	86.9	3.19	1903
Breadth (mm)	65.6	50.7	59.3	3.02	1903
Weight (g)	219	118	169.9	11.26	1165

Table 7. Comparison of mean length, breadth and weight of eggs in different years

Year	Length (S.D.)	Breadth (S.D.)	<i>n</i>	Weight (S.D.)	<i>n</i>
1972	87.0 (3.04)	59.1 (4.28)	524	170.1 (11.62)	235
1973	87.2 (3.36)	59.2 (3.43)	729	169.4 (11.52)	493
1974	86.6 (3.03)	59.6 (1.54)	424	170.5 (10.16)	437

Table 8. Mean egg weight in relation to the different clutch-sizes

Clutch size	3	4	5	6	7	8
Mean egg weight (g)	169.2	167.7	171.7	169.4	169.8	167.2
No. of clutches	23	41	52	43	25	17

The weight of chicks at hatching ranged from 91 to 140 g,  $\bar{x} = 114.9$  g, S.D. = 9.13 ( $n = 457$ ).

The data given in Tables 7 and 8 lead one to the conclusion that the mean egg weight in the population investigated is fairly constant and independent of the season or clutch size. Individual deviations from normal are marginal and do not affect the mean values. A larger or smaller production of eggs in individual cases does not affect their size, *i.e.* their quality.

## Double clutches

Two categories of double clutches were observed: one in which two females laid two complete clutches in a single nest, and another where one female laid a complete clutch and another female added just 1–3 eggs to the original clutch.

Out of 629 clutches investigated (Table 5) there were 27 double ones (4.3%), of which only 8 (1.3% of all clutches and 30% of double clutches) were classified in the first category, the remaining ones (19, *i.e.* 3% and 70%, respectively) being classified in the second category.

Table 9. Frequency of double clutches in particular clutch-sizes

	Clutch size								Total
	7	8	9	10	11	12	13	14	
No. of whole clutches	63	24	5	9	1	2	1	1	106
No. of double clutches	10	6	3	4	1	1	1	1	27

Double clutches in clutch-sizes of less than 7 eggs were not found

The frequency of double clutches in different clutch sizes is given in Table 9.

One should qualify the above data concerning double clutches as being only approximate since there certainly could have been other cases of double clutches which went undetected, *e.g.* because of clutch losses *etc.* The main criteria employed in the classification of double clutches (apart from evident, on-site observations) were as follows: significant differences in embryo development in one clutch and addition of new eggs to a clutch at an advanced stage of incubation.

Out of 5 known double clutches with more than 10 eggs only one ended in success. The other ones were lost due to egg chilling, infertility or abandonment.

## Duration of the breeding period

The length of the nesting period, measured from the laying of the first egg to the hatching (or expected hatching in case of failed nests) of young averaged 34 days per pair, or 62 days for the population as a whole, with annual variations in the range 53 to 75 days. The causes of these variations for the population in particular years remain unknown, although it should be stressed that the extension of the mean length of the nesting period was caused by a relatively small proportion of the female population. Most females (*ca* 80%) closed the nesting period in 43 to 53 days. On the other hand, in 1976, when the geese commenced egg laying later than usual, the nesting period for all females lasted only 53 days, *i.e.* it was much shorter than on the average.

From the date of hatching it took another 55–65 days for the young to acquire effective flying capability. Overall, the whole breeding period lasted 108–140 days, with the majority of geese closing the breeding cycle within 95 to 115 days. No unfledged young were seen after 20 July in any year.

### Failures and breeding success

*Proportion and causes of nest failures.* During the nesting period the rate of success was mainly affected by two kinds of losses: predation and abandonment of nests. Losses from other causes were negligible. A detailed list of all causes of nest failures in all seasons is presented in Table 10.

Table 10. Causes of nest failures (%)

	1972	1973	1974	1975	1976	1977	All years
Predation	24	21	18	9	12	12	16.2
Abandonment	20	24	16	9	12	14	16.0
Predation or abandonment	10	6	7	13	16	16	11.1
Flooding	1	1	—	—	3	—	0.9
Total nests failed (%)	55	52	41	31	43	42	44.2
No. of nests	132	154	136	145	122	121*	810

\* 20 remaining nests were not examined later on

*Predation.* On the average 16.2% of nests were destroyed by predators. The highest proportion of losses in this group was caused by the hooded crow *Corvus corone cornix*, (78% of all nests failed due to predation). Within the territory of complex no. 4 there were approximately 50 pairs of the hooded crow breeding there each year, but only 30 of these could have constituted a danger to goose's clutches, the other crows occupying territories too distant from the ponds on which the geese were nesting. Goose's eggs that were predated by crows would normally be eaten at the nest; only on rare occasions were eggs carried off from the predated nest. Crows had the opportunity of predated nests at least twice a day, when the geese were away feeding. They did not find goose's nests by conducting a systematic search of the habitat, but by descrying from tree-tops and noting the places from which geese were swimming or flying out. I think that the above-described strategy of predation predominated, at least with respect to geese. This opinion is based on the finding that in a considerable number of cases crows would not return to a previously predated nest, often left with only one egg destroyed and the others intact, if the nest was abandoned as a result of that event. This could mean that without the "help" of the geese the crows were unable to find the nest for the second time. Since in normal circumstances geese have the habit of leaving their nest very quietly and taking wing at a certain distance from it, the losses due to the hooded crow

were limited. Such losses can increase if for some reason the geese keep getting flushed from their nests.

In the majority of cases (64%) only some of the eggs, not all, were destroyed by a predating crow. However, this would normally result in the goose's abandoning the nest. Only 16% of the females whose nests had been partially predated continued brooding.

The second important predator, which caused 13% of all losses due to predation, was the wild boar *Sus scrofa*. Its pressure was strongest on ponds that were bordered by woodland and had extensive areas of reedbeds at or near the dam. On such ponds the wild boar would occasionally cause losses of the order of 40 to 90%. If a nest was predated by a boar the whole clutch would be eaten and the nest rooted up. The brooding goose would escape unharmed.

The remaining predators, which accounted for a total of 9% of all losses due to predation, were as follows: the marsh harrier *Circus aeruginosus*, numbering approximately 30 pairs in the complex studied, and the red fox *Vulpes vulpes*, at least five pairs.

The losses due to harriers were almost exclusively confined to the period of hatching of chicks, and the most frequent, indirect cause was the flushing of a brooding goose from its nest. These losses accounted for only 5% of all losses due to predation. This relatively low figure was probably due to the habit of female geese to stay at the nest and feed in its vicinity from the moment the chicks start breaking the egg-shell. Nevertheless, there was one observed instance of a marsh harrier carrying off a newly hatched chick in the presence of the adult goose on the nest.

The losses caused by red foxes, although fairly small in number (4% of all losses due to predation), were very dangerous because the fox would not so much destroy the clutch as kill the brooding goose. Most of such losses occurred when during the nesting season the water level in the ponds was reduced, or the pond was drained of water.

There was only one instance of predation by the sea eagle *Haliaeetus albicilla*, which killed a brooding goose. Thus, it is seen that the pressure from this raptor was negligible, despite its frequent haunting of the ponds.

*Abandonment of nests.* Abandonment accounted for a similar proportion of losses as predation (16%). Abandonments must have been caused by a potential or real danger either to the nest only, or also to its owners. It is hard to say precisely which of the two factors was decisive in each case of abandonment. From the inspection data one can only base one's conclusions on guesswork.

One of the causes could have been the plundering by crows, or other predators not dangerous to the life of geese, of neighbouring nests, which could have caused the owner of the nest concerned to sense the imminent danger and abandon the nest.

On some islets with a larger number of nesting geese there seemed to exist a kind of social bond between at least some of the pairs. This was particularly true of the males which showed a specific division of social roles. When the females were brooding some males would stay near the islet, while the remaining ones flew to feeding grounds. In this way the females would at all times be guarded against impending dangers, while part of the males could fly out to feed and also check the safety of the feeding ground before the arrival of the females. Since there was a social group, there certainly must have been some kind of hierarchy. Thus, one can make a supposition that in the case of destruction of a nest belonging to the dominant bird in the group and the resulting abandonment of the nesting place by that bird, other geese ranking lower in the hierarchy might follow suit. A partial confirmation of both the above-mentioned probable causes of abandonment is provided by the observation of more numerous cases of abandonment at nesting places where the clutches of neighbours had already been predated by crows or wild boars. Further studies and experiments are required to explain this problem.

Another cause of abandonment was the appearance of a threat, even if only a potential one, to the life of the brooding goose, *e.g.* possible or real penetration of the nesting site by a fox. This supposition is confirmed by the fact that if a pond was drained all geese nesting on it would immediately abandon their nests.

Finally, abandonments could also have been caused by excessive penetration of nesting sites by human beings (*e.g.* frequent inspections of nests by the author). The number of abandonments due to this could have been particularly high in the first two years of the study. Later the geese clearly got accustomed to the presence of people. However, hides of any kind near the nest, even if very well masked, were always regarded by the geese with great suspicion.

As there was good reason for suspecting that a certain proportion of abandonments was being caused by the investigation itself, the author performed an experiment on the largest pond in the complex. A large part of the pond, densely populated by nesting geese, was left undisturbed during the egg-laying and brooding periods for two consecutive years. Later 47 nests were found there, of which 6, *i.e.* 12.8%, had been evidently abandoned. Since the proportion of abandonments on ponds that were investigated in the usual manner was 16%, it is seen that the abandonments caused by the author accounted for 20% of all abandonments, *i.e.* somewhat more than 3% of all clutches laid.

The effect of abandonments on the total number of clutch failures could have been significantly higher than the above data would indicate. This is because in some cases clutches classified as failed due to predation could have been first abandoned and predated at a later date.

*Predation or abandonment.* This mixed category of losses, which on the average accounted for 11.1% of all losses, was the result of insufficient frequency

of inspections, which made it impossible to determine the real cause of some failure from a knowledge of the sequence of events (details on page 187).

It can therefore be said that as a result of both predation and abandonment 43.3% of all clutches laid ended in a failure.

*Other failures.* The remaining proportion of lost nests (0.9% on the average) was caused by abiotic factors (washing away of nests by waves or flooding).

### Successful clutches and production of young

On the average 55.8% of all clutches ended in the hatching of at least one chick. The mean clutch size in successful nests was 5.5 eggs and was a little larger than the corresponding figure for all nests built (the mean clutch size per nest for all seasons covered by the study was 5.3 eggs). Successful nests had

Table 11. Productivity of successful nests\*

Years	Nests examined	Eggs laid	Eggs unhatched (%)	Eggs predated (%)	Total eggs failed (%)	Eggs hatched	Mean clutch size	Mean brood size at hatching	Mean brood size at fledging
1972	50	263	7.2	3.0	10.3	236	5.3	4.7	3.4
1973	67	381	6.8	5.2	12.1	335	5.7	5.0	3.7
1974	72	401	5.0	3.7	8.7	366	5.6	5.1	3.5
1975	80	439	4.3	4.8	9.1	399	5.5	5.0	3.3
1976	46	237	5.9	—	5.9	223	5.2	4.9	3.8
1977	46	258	5.0	5.8	10.9	230	5.6	5.0	4.0
All years	361	1979	5.6	4.0	9.6	1789	5.5	5.0	3.6

\* The figures presented above do not include those successful clutches for which it was not possible to determine all of the above parameters. The real number of hatched young in the different seasons is given in Table 14.

a very high production of young, the average proportion of all kinds of failures accounting for only 9.6% of the potential production (*i.e.* of all eggs laid). The failures were classified as below:

- unhatched eggs. These constituted 5.6% of all failed eggs. They were either infertile or contained a dead embryo. The corresponding figure for a Scottish population of geese (NEWTON and KERBES 1974) is 6%, *i.e.* both population were similar in this respect.
- eggs predated by hooded crows. The mean value here is 4% of all eggs laid.

A typical pair with a successful nest would produce 5 young. Details are given in Table 11.

### Hatching success in relation to clutch size and time of laying

Hatching success was affected by clutch size. The respective figures are given in Table 12.

It turned out that both small (2-3 eggs) and very large (> 8 eggs) clutches did not differ significantly ( $\chi^2 = 1.53$ ,  $P > 0.1$ ) in hatching success, despite the apparent difference in the proportion of hatched eggs. However, both these categories of clutches exhibit a highly significant difference when compared with the clutch sizes that most frequently occur in geese, *i.e.* 5-7 eggs ( $\chi^2 = 32.9$ ,

Table 12. Hatching success in relation to different clutch sizes (all years combined)

Clutch size	2-3	4	5	6	7	8	> 8
No. of clutches laid	67	109	211	136	63	24	19
% producing young	26.9	53.2	60.2	69.1	63.5	58.3	42.1

$P < 0.001$ ). As regards clutches from 4 to 8 eggs, a statistically significant difference is noted only between 4- and 6-egg clutches ( $\chi^2 = 6.5$ ,  $P < 0.02$ ). The remaining differences were not significant ( $\chi^2 = 3.35$ ,  $P > 0.05 < 0.1$ ).

There were evident differences in hatching success in relation to the date of commencement of egg laying. The respective data is shown in Table 13.

Table 13. Seasonal trends in hatching success

Data refer to period of first eggs laid. Laying seasons are divided into 10-day periods: I, II, III and following.  
*n* - number of clutches laid, *s* - number (%) of successful clutches

Period	Years												Total	
	1972		1973		1974		1975		1976		1977			
	<i>n</i>	<i>s</i>												
I	19	14(74)	33	20(61)	12	11(92)	42	35(83)	37	25(68)	14	12(86)	157	117(74.5)
II	61	28(46)	85	42(49)	81	48(59)	55	32(58)	54	23(43)	49	30(61)	385	203(52.7)
III	28	8(29)	23	5(22)	31	14(45)	11	4(36)	2	1(50)	15	4(27)	110	36(32.7)

The highest rate of hatching success, 74.5%, was noted in clutches commenced in the first 10 days of the egg-laying season. The least successful clutches were commenced at the end of the season (67.3% failed). The differences between successive 10-day periods are statistically significant ( $\chi^2 = 46.8$ ,  $P < 0.001$ ).

Thus, the highest rate of hatching success was noted in clutches of 5-8 eggs, the majority of which were laid in the first half of the season. As mentioned on page 195, small clutches that were commenced late in the season could have been laid by young or physically inferior birds. The same may have been true of breeding success. Lack of experience in the case of a young female, or prolonged stays at feeding grounds in the case of geese in poor physical condition, with the resulting threat of predation of the unattended nests by crows, could

have been the cause of the higher rate of failures of clutches laid by such individuals. Females that commenced laying late in the season had a limited choice of nest-sites, so their nests could have been more exposed. Also, late clutches were found to be more frequently abandoned. This could possibly be linked with the social bonds and hierarchy mentioned on page 200. Young and physically inferior birds certainly did not rank highly in the hierarchical structure of a group.

Relatively high losses were also noted in clutches containing more than 8 eggs. As mentioned on page 197, a considerable number of such clutches were laid by two females. All kinds of perturbations resulting from this fact could have had a detrimental effect on the success of such clutches, *e.g.* inability to warm all the eggs of such a large clutch at the same time, with the resulting chilling of eggs.

It has been suggested that the smaller number of losses observed early in the season is the result of reduced pressure from predators that are just beginning to discover the few nests that have been built, while the relatively lower proportion of losses at the peak of the season compared to its end is caused by the fact that a predator will destroy only as many nests as it has to in order to satisfy its hunger. Since at the peak of the season there are more nests than necessary for this purpose, the excess nests will end in success. At the close of the season there are fewer and fewer nests, and therefore a correspondingly higher proportion of them is predated.

The above-mentioned hypothesis would be acceptable if the goose population in the habitat investigated were the only one that could be preyed upon. In fact, in the second half of the nesting season for geese egg laying is also commenced by numerous coots *Fulica atra*, great-crested grebes *Podiceps cristatus*, and mallards *Anas platyrhynchos*, whose eggs are at least as much prized by the main local predator, the hooded crow, as those of the grey-lag goose. Thus, at the close of the season for geese the pressure from the hooded crow is spread to other species of water-birds that breed in the same habitat.

#### Hatching success in relation to nest-sites

The geese observed in this study nested solely on ponds. Three types of habitat were available for nesting: 1) numerous islets of reeds and some natural islets with trees growing on them (henceforth called natural islets), 2) artificial islets protruding high above the water and overgrown with low vegetation, 3) reedbeds along the dam. The great majority of geese nested on natural islets, the least on artificial ones. The rate of hatching success exhibited a similar pattern. The respective data is given in Table 14. All the differences in hatching success between these three habitats are statistically significant: 1 : 2 —  $\chi^2 = 44.9$ ,  $P < 0.001$ , 1 : 3 —  $\chi^2 = 17.5$ ,  $P < 0.001$ , 2 : 3 —  $\chi^2 = 11.4$ ,  $P < 0.001$ .

The higher rate of losses in reedbeds as compared to natural islets was the

Table 14. Hatching success in relation to nest-sites

	Natural islets	Artificial islets	Reedbeds along dam	Total
No. of clutches laid	581	75	174	830
No. of clutches failed	214	58	95	367
% successful clutches	63	23	45	55.8

result of a stronger pressure from the wild boar as well as incidental penetration of the reedbeds by the red fox.

The highest losses occurred in nests located on artificial islets where brooding geese were very conspicuous, even at a distance, so that crows concentrated their pressure on such islets. This resulted in the highest rate of abandonments of the three habitats. This leads one to the conclusion that the recent changes introduced by the fishermen in the ponds do not spell a good fortune for the goose population there.

### Survival of young

The time from hatching to fledging varied from 55 to 65 days. On the average, 27.4% of all young perished during this period. Details are given in Table 15.

Unfortunately, it was not possible to determine precisely the causes of death in individual cases, although numerous observations indicated that a considerable proportion of losses was caused by predators. In my opinion, terrestrial predators (fox, domestic dog, pine martin *Martes martes*, stoat *Mustella erminea*, polecat *Mustella putorius*) could not have caused significant losses among unfledged young, because they did not haunt the territories where the geese were raising their young. The greatest proportion of losses was certainly caused by predatory birds. Again the hooded crow was among the main culprits, particularly in relation to goslings of several days of age. Crows were even seen to catch swimming goslings from the air. The marsh harrier, hunting not only over open water but also in reeds, now became much more dangerous than during the nesting period. Crows and harriers would be particularly likely to strike when a family of geese was suddenly forced to flee and the young were left

Table 15. Survival of young

Year	1972	1973	1974	1975	1976	1977	Total
No. of young hatched	287	360	407	498	340	410*	2302
No. of young fledged	207	272	280	331	258	324	1672
Young mortality %	27.9	24.5	31.2	33.5	24.1	21.0	27.4

\* For unchecked 20 nests the number of hatched young was calculated on the basis of mean hatching success.

somewhat behind their parents. This situation was most often caused by humans, but also by the mute swan *Cygnus olor*. Certain male swans had the habit of violently attacking every pairs of geese appearing in the vicinity of their nests.

In addition to the killing of goslings, such incidents had another consequence, particularly if several families of geese swimming close to one another got scattered. In such cases goslings from different families would often get mixed. The extent of this phenomenon could have been quite considerable since in 41 cases of trapping several-days-old goslings there were eleven groups consisting of young birds originating from two or even four different nests (as determined from wing-tags that had been affixed to hatched chicks)\*.

During the whole period from hatching to fledging the geese stayed on the ponds, though not necessarily on those on which they had nested. For example, on the pond marked by the number 32-54 on Figure 2 almost all geese moved after the hatching of their young to neighbouring ponds that were less suitable for nesting but more abundant in plants which the geese fed on.

#### Total number of failures and production of young

The most important factor limiting the overall breeding success was the losses suffered during the nesting period, particularly losses of complete clutches as a result of predation and/or abandonment. The proportion of nest failure caused by physical factors was very small (Table 10).

The percentage losses in the case of successful nests were fairly small, averaging 9.6 % of all eggs laid in such nests (Table 11).

The proportion of losses from the time of hatching to fledging averaged 27.4 % of hatched young (Table 15), which is less than one third of the number of losses suffered during incubation (Table 16).

The overall rate of failures in relation to potential production averaged 61.7 %, with one breeding pair producing an average of two fledged young (Table 16). The mean brood size at fledging per successful breeding pair averaged 3.6 (Table 11). The average ratio of actual to potential production was 38.3 %.

### DISCUSSION

#### Stability of population

The population data up to the 1940's and from the beginning of the 1960's show that the population of the grey-lag goose in the Barycz valley has been very stable (page 187).

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\* It results from this finding that one has to be very careful when determining the mean brood size between hatching and fledging by the method of counting the total number of young and dividing it by the number of leading pairs, since it could happen that during such incidents as described above some pairs might lose all their young to other pairs, as seen by the author in two instances.

Table 16. Total failures and actual production of young as a percentage of potential production

Years	Eggs failed due to predation or abandonment (%)	Eggs failed to hatch (infertile, dead embryo) (%)	Eggs failed due to weather conditions (%)	Total eggs failed (%)	Young mortality (%)	Total failures (eggs + young) (%)	Young fledged (actual production) (%)	Mean brood size at fledging per breeding pair
1972	51.1	3.6	0.9	55.6	12.4	68.0	32.0	1.6
1973	53.0	3.3	1.4	57.7	10.8	68.5	31.5	1.8
1974	41.3	3.1	0.0	44.4	17.4	61.8	38.2	2.1
1975	30.3	3.4	0.0	33.7	22.4	56.1	43.9	2.3
1976	35.9	3.6	4.8	44.3	12.5	56.8	43.2	2.1
1977	44.6	3.1	0.0	47.7	10.5	58.2	41.8	2.3
Total	43.0	3.3	1.1	47.4	14.3	61.7	38.3	2.0

During World War II and the years directly following it there occurred a disastrous drop in population to only one quarter of the previous number of geese. Since during the period concerned there were no significant changes in the habitat and there was no increase in the number of local predators endangering clutches or adult geese, this drop must have been caused by man who at that time was the main and the most dangerous of all the potential predators. One can get an idea of the scale of pressure exerted by man from accounts of local fishermen. The lack of food and the prevailing laxity in law enforcement resulted in the killing of geese at all times of the year. There were many fire-arms in the hands of civilians who used them for poaching. Shooting parties were organized that from the view-point of proper game management were nothing else but common poaching, since even brooding geese fell victim to these hunts. In any case, right after the war, as a result of bad blunders in the fixing of close seasons, it was quite legal to shoot geese during the nesting season until mid-May. The local populace frequently laid all sorts of traps at goose's nests. It was a common practice to take eggs for home breeding. It is therefore not surprising that in a situation where not only many clutches were being destroyed but, more important, reproducing geese were shot at the goose population began to decline rapidly. So the decline was caused by excessive mortality rather than abandonment of the imperilled habitat, though it should be mentioned that almost all of the European goose populations at that time were exhibiting a tendency towards decline. Within 10 years from the introduction in 1950 of bird preservation laws in the Barycz valley the goose population there was back to normal.

The facts described above, together with the data presented in this study (Table 16) concerning losses in the process of reproduction, which although as high as 61.7% permitted the maintenance of the goose population at a high and stable level, justify the hypothesis that it is the mortality of breeding geese rather than the rate of breeding success that is the decisive factor affecting the stability of the population.

Despite the discontinuation of pressure from man, the goose population, after attaining a level similar to that before the war, stopped rising, or if there were any rises they occurred as a result of geese settling on unoccupied ponds or on ponds that had not been utilized to the full. For example, such a level was attained by that part of the population which was breeding in fish-pond complex no. 4. Thus, there must have existed some kind of a limiting factor. It seems that this factor was food, the availability of which was limited during an important period in the life of geese as a result of pressure from terrestrial predators. The period concerned is the time of raising young until fledging. On the average this period lasted for 55–65 days and coincided with the moulting season. Throughout the whole period the local geese would never leave their ponds (apart from possible changes of residence), despite the fact that the nearby meadows and fields offered an abundance of suitable food. There could be only one reason for this behaviour — the danger involved in leaving the pond

was too high to take the risk. If one notes that both the adults and the young were unable to fly during that period and that the area surrounding the ponds was haunted by numerous terrestrial predators dangerous to the life of both goslings and adult geese (see page 204), the reluctance to take the risk seems to be justified. Thus, the limited availability of food in the ponds and along their dams during the period of rearing young seems to be one of the main factors limiting the population to a certain size. There may have been other factors, but the lack of nest-sites certainly was not among them.

A possible excess in the number of geese that resulted from this situation may have been the initial cause of the appearance of breeding geese on water bodies outside of the Barycz valley. This view is supported by the observation of several new breeding sites in the Śląsk and Wielkopolska regions (GROMADZKI and WIELOCH 1983).

### Clutch size

The mean clutch size in particular seasons was relatively stable, ranging from 4.9 to 5.6 eggs. However, the observed differences were found to be statistically significant (page 195). Relatively small means were noted in 1972 and 1976. The weather conditions (mainly temperature), which affect the growth of gramineous plants constituting the staple food of the local geese before the start of egg laying, were best in the 1974 season, worst in 1976, and more or less the same in other seasons. If the availability of food just before the start of egg laying had had an effect on clutch size (LACK 1967), then the lowest mean would have occurred in 1976, the highest in 1974, and in the remaining years the means would have been intermediate and more or less the same. However, with the exception of 1976, this was not so (see Table 4).

Also, no distinct relationship was observed between mean clutch size and time of commencement of egg laying. One can see this by comparing the means in Table 4 with the egg-laying curves on Figure 4. Such a relationship, consisting in the fact that the later a given population commences egg laying the smaller is the mean clutch size, has been reported in Czechoslovakia (HUDEC and KUX 1971). No relationship of this kind was seen in a Scottish goose population (NEWTON and KERBES 1974), although the time of commencement of nesting did have a significant effect on the final breeding success.

Thus, in the population investigated the mean clutch size was found to be unaffected by the weather, mean temperature or time of commencement of the nesting season. It is possible that the differences noted in different seasons were affected by the magnitude of bodily energy reserves accumulated by the females at wintering grounds. This factor has a considerable effect on clutch size, *e.g.* in geese breeding far in the north (RYDER 1970, NEWTON 1977).

According to CODY (1966), the size of clutches has evolved depending on the stability of the habitat: the more stable the habitat the smaller the clutch size.

Stability decreases with increasing latitude. The available data concerning this problem are presented on Figure 6. Although one cannot perform statistical tests on this material, the picture obtained throws doubt upon the validity of this hypothesis in relation to the grey-lag goose.

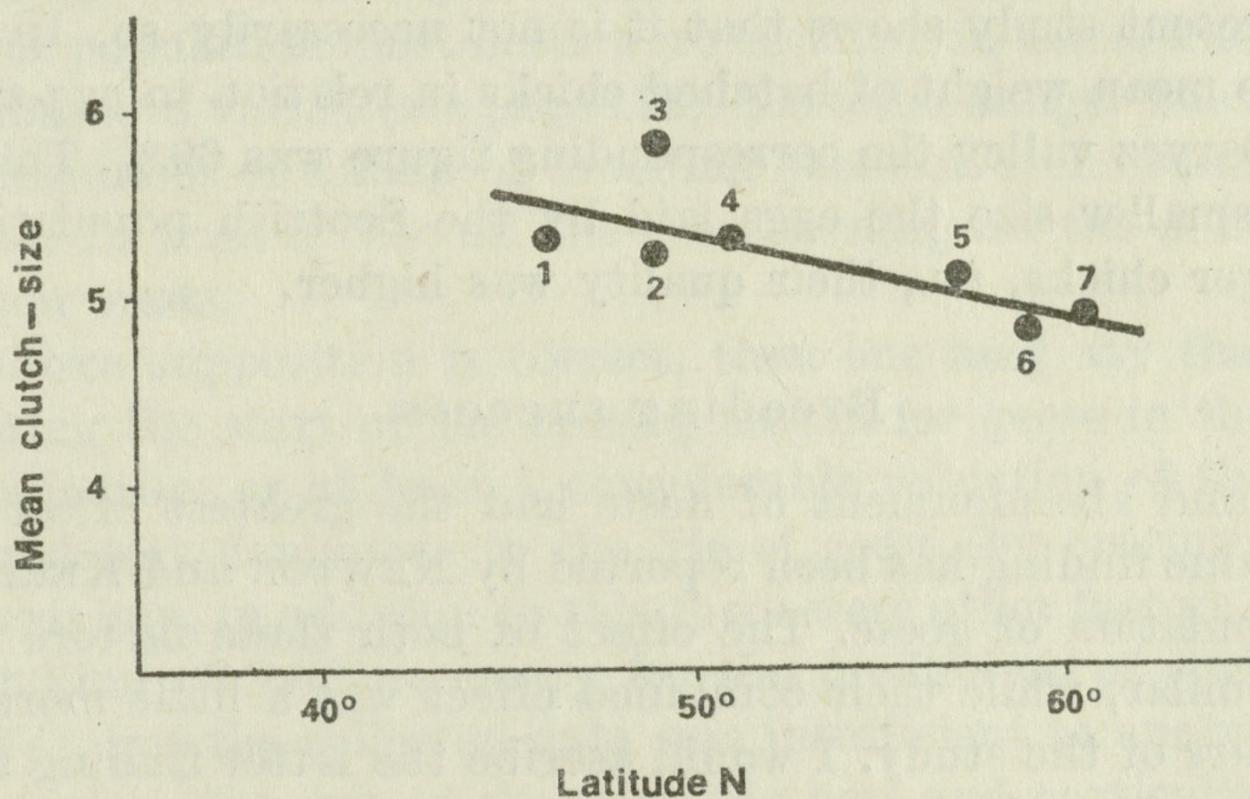


Fig. 6. Mean clutch-size of the grey-lag goose in relation to latitude.

Data after: 1 - KRIVENKO 1970 (Volga Delta); 2, 3 - HUDEC and KUX 1971 (southern Moravia, southern Bohemia); 4 - present paper (western Poland); 5 - NEWTON and KERBES 1974 (Outer Hebrides, Scotland); 6 - PAAKSPUU 1964 (Matsalu Bay, Estonia); 7 - HAARTMAN: in HUDEC and ROTH 1970 (Finland).

### The importance of egg-size

In members of the *Anatinae* family, relatively larger eggs are laid by northern species (LACK 1967). This is a result of natural selection. The bigger the egg the greater the energy reserve of the hatched chick which is therefore more likely to survive sudden climatic changes. Young Swedish mallards, which have a bigger yolk-sac than the English variety, can survive much longer spells of extremely bad weather (MARCSTRÖM 1966). Do populations of grey-lag geese inhabiting different geographical latitudes exhibit a tendency to lay bigger eggs at higher latitudes?

The parameter used in the comparison was the mean weight of eggs laid by different populations. The respective data are given in Table 17. It is seen

Table 17. Egg-size in relation to the latitude

Areas investigated	Weight (g)	Authors of studies
Southern Czechoslovakia	164.4	HUDEC and ROTH 1970
Western Poland	169.9	present paper
South-western Scotland	165.0	YOUNG 1972
Estonia	166.6	PAAKSPUU 1964

that there is a slight trend towards increasing egg-size with increasing latitude. The population discussed in this paper shows a deviation from this tendency, having the heaviest eggs despite its intermediate geographical location.

Thus the question arises whether larger egg-size always means higher quality of the eggs. A comparison of the data given by YOUNG (1972) with the results of the present study shows that it is not necessarily so. In the Scottish population the mean weight of hatched chicks in relation to egg-size was 79%, while in the Barycz valley the corresponding figure was 69%. This means that despite their smaller size the eggs laid by the Scottish population produced relatively bigger chicks, *i.e.*, their quality was higher.

### Breeding success

Predation and abandonment of nests had the greatest effect on breeding success. The same finding has been reported by NEWTON and KERBES (1974) for a Scottish population of geese. The effect of both these factors in individual seasons was similar, while their combined effect was a little more pronounced in the first years of the study. I would ascribe the latter finding to my disturbing the geese until such time when they became accustomed to my activities. The disturbances caused by the study could have increased both the pressure from the hooded crow and the rate of abandoning. Other losses during incubation did not have a significant effect on the rate of nest failures (Table 10, 11).

The losses during the growth of young were relatively small and similar from year to year, with the exception of the years 1974 and 1975 when the number of hatched chicks was relatively high (over 400). This could have induced certain predators to specialize in preying on geese, so that the initial high hatching success was subsequently reduced by higher-than-normal mortality of the young (Table 15).

No significant relationship was noted between breeding success and time of commencement of the breeding season. NEWTON and KERBES (1974) have reported for the Scottish population that the sooner the geese started egg laying the lower was the rate of failures. Owing to the fact that during the period of study of the Barycz valley population the time of commencement of egg laying was almost the same every year (with the exception of 1976), the above-mentioned relationship could not be detected.

### Antipredatory behaviour

The commencement of egg laying coincided with the disappearance of the ice cover on the ponds. In some years (1963, 1969) the geese would start egg laying as late as the middle of April (see Fig. 5) only when the ponds were freed of ice. This coincidence (*cf.* Fig. 3) can only mean one thing — that the existence of the ice cover constituted some kind of barrier stopping the geese from starting the breeding season. This could not have been caused by the ice

in the reeds which always melted away later than that covering the open water (shading by reeds, no waves): the geese would build nests on ice in the reeds as soon as the ice cover on the open water disappeared. Thus one is led to the conclusion that the existence of the ice cover enabled terrestrial predators dangerous to the life of brooding geese to gain access to their nests, since in the case of the Barycz population most nests were situated on islets. The local predators were numerous and varied (see page 198). That the danger was real, was shown by several instances of killing of brooding geese or even swans on ponds that were drained. In such a case all the geese nesting on the pond would always abandon their nests.

If the above supposition is correct, then one may say that an important factor affecting the start of the nesting season for geese in the Barycz valley was the elimination or at least a considerable reduction of the pressure from terrestrial predators dangerous to the life of geese (by cutting off their access to nests). Certainly, in addition to this there were other factors, *e.g.* availability of the right kind of food necessary for the production of eggs (NEWTON and KERBES 1974), but the collected data was insufficient to analyse this problem.

In my opinion, the way of situating the nest and particularly its construction are in themselves characteristic of antipredatory behaviour in the sense that the life of the brooding goose should be saved, even at the cost of its clutch. The clearing of reeds around the nest may be interpreted in terms of collecting material for the nest. However, in most cases the amount of material collected in this way was insufficient and the goose was forced to collect more material elsewhere. Why did it not do it right from the start so as not to deprive the nest-site of its natural concealment? The existence of clear space around the nest may have been crucial in the case of attack, *e.g.* by a fox, which would betray itself as soon as it entered the clear space of water between the nest and the wall of reed at some distance from the former. If the nest had been situated in dense reeds the goose would have had to make its escape on foot, for it would not have been able to take wing, or else its wings would have got entangled in the dense reeds. The clear space around the nest enabled the goose to take wing straight away and thus avoid, at least in some cases, being caught by the attacking predator.

Another example of antipredatory behaviour is, in my view, the behaviour of geese during the brooding period. As mentioned earlier, a considerable number of clutch losses was caused by crows. These losses could have been avoided if the male had stayed at the nest when the female flew to feed (*cf.* page 189). However, the male would always accompany its partner. One of the reasons could have been the fear of breaking the bond between the two partners, but in view of the permanent marital ties in this species it seems improbable. Thus, the more likely reason for this behaviour seems to be concern for the safety of the female which had to feed hurriedly in order to get back to the nest before the eggs got chilled. Pressed for time the female was unable to pay attention to possible dangers. The behaviour of the male accompanying the feeding female showed

that the former's task was to watch over the safety of the female. Measurements made at feeding grounds showed that the female spent 80 % of the time feeding and 20 % watching the surroundings. The reverse was true of the male — it spent only 15 % of the time feeding. The male made up for this later on when it returned to the feeding ground after escorting the female to the nest. In these observations the brooding bird was taken as the female.

The above-described antipredatory behaviour of geese shows how important it is for the survival of the Barycz population, if not for the whole species, to protect not so much the clutch itself as the life of the reproducing female. The evolution of behaviour of geese must have proceeded in accordance with the rules of K-selection (MACARTHUR and WILSON 1967, PIANKA 1970) which is only possible in a stabilized environment. Living in such a habitat and being a potentially longlived species the grey-lag goose finds advantage in breeding only under conditions of maximum safety to the adult bird. With the prospect of many breeding cycles in the future, the goose can produce more young by not risking its life and breeding only when the conditions are maximally safe. This strategy is obviously very effective, as can be seen from the ability of the population studied to maintain its number at a stable level.

#### The importance of protection of the grey-lag goose in the Barycz valley

Losses during the nesting season had the greatest effect on the overall breeding success of the geese. The hooded crow was an important culprit during that season, as it predated both the eggs and the young. Different real or potential hazards resulted in the abandonment of nests by geese, which caused losses of a similar order of magnitude as in the case of predation. Abandonment of a nest could be caused by both the presence of predators and penetration of the nesting area by man who, though not doing any direct damage, was frightening enough for some geese to abandon their nests. It is therefore clear that the overall breeding success of the grey-lag goose can be improved by leaving the nesting sites undisturbed and by partially reducing the population of the hooded crow.

The renovation works that have been going on in the ponds of the Barycz valley for many years now might, if continued to the end, produce a harmful effect on the goose population. By comparing the number of geese breeding in the different fish-pond complexes (Table 1) with the surface area of the ponds in these complexes (*cf.* Fig. 1) one can see that there exists a considerable disproportion in the distribution of breeding pairs in favour of complex no. 4. If one looks at the condition of the different habitats in these complexes then it becomes obvious that an important reason for this disproportion has been the removal of naturally growing reeds, particularly islets of reeds. The artificial reed-heaps formed as a result of this activity, protruding high above the water,

were only reluctantly used by the geese as nest-sites and were also characterized by the highest rate of nest failures (Table 14). Thus, if some of the naturally growing reeds must be removed they should be pushed to form low-profile heaps protruding less than 1 metre above the water level. With fresh reeds growing round them, such heaps would be a much safer place to nest on, at least as far as protection from the hooded crow is concerned. This conclusion is based on observations made on one pond with such low heaps of reeds. Although the losses there were still high, they were lower than in the case of heaps protruding high above the water.

The last remark that comes to mind after the several years of observation of geese breeding in the Barycz valley concerns the spring open season for geese. In its choice of a nest-site the grey-lag goose is very sensitive to all kinds of dangers, above all the danger of losing its life. The presence of a human being, even unarmed, is alone sufficient to frighten it. If a hunting district is left in peace in the spring, geese might start breeding there or, if they are already doing so, their number is likely to rise. The latter situation was observed in pond complex no. 6 which was the only complex within the limits of a hunting district. After the banning of spring shooting in that complex the number of pairs breeding there started to rise (Table 1).

Thus, the tendency to allow spring shooting of geese in regions where they are not yet breeding is based on error, that is, if one wants to have breeding geese on the hunting grounds.

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## STRESZCZENIE

[Badania nad populacją gęgawy *Anser anser* gnieźdzącej się w dolinie Baryczy, Polska.]

Badania przeprowadzono w latach 1972–1977. Populacja gęsi liczyła, w różnych sezonach, 280–312 par. Podobna liczebność utrzymywała się przez ostatnie 80 lat, a jedyne gwałtowne jej załamanie, będące skutkiem nadmiernego pozyskiwania gęsi i to głównie podczas sezonu lęgowego, nastąpiło w latach 40-tych.

Populacja zasiedlała 6 oddzielnych kompleksów stawowych (ryc. 1), na których prowadzona była hodowla ryb. Największa jej część gniazdowała w kompleksie stawowym, oznaczonym na ryc. 1 jako no. 4. Plan sytuacyjny tego kompleksu przedstawiony jest na ryc. 2. Ta część populacji, licząca 122–154 par, była przedmiotem szczegółowych badań. Badana populacja była całkowicie wędrowna.

Termin rozpoczynania sezonu lęgowego zbiegał się z zanikaniem na stawach pokrywy lodowej (ryc. 3). Gęsi gnieździły się wyłącznie w obrębie stawów napełnionych wodą, najliczniej na wyspach (tab. 2). Wspomnianą zbieżność tłumaczy się unikaniem przez gęsi presji drapieżników naziemnych (lis, pies, kuna i tchórz), które, w razie istnienia między brzegiem a wyspami trzciny pomostu, jakim był lód, mogły zagrozić życiu wysiadujących samic.

Skrajne wartości średniej wielkości zniesienia wynosiły w poszczególnych latach 4,9–5,6 jaja, a średnia za cały okres badań 5,3 jaja (tab. 4). Nie stwierdzono istotnych różnic średniej wielkości zniesienia w zależności od terminu rozpoczęcia okresu lęgowego w danym sezonie. Średnia wielkość zniesienia malała w ciągu sezonu z 6,7 jaja na jego początku, do 3,5 pod jego koniec (tab. 5). Zniesienia pochodzące od jednej samicy zawierały 2–10 (12?) jaj. Prawie wszystkie zniesienia zawierające powyżej 10 jaj pochodziły od dwóch samic. Nie zdobyto dowodów świadczących o tym, by po utracie gniazda z kompletnym zniesieniem gęsi powtarzały lęgi w tym samym sezonie. Średnia wielkość jaj była stała w różnych sezonach (tab. 7). Nie znaleziono też różnic średniej wielkości (masy) jaja w zależności od liczby jaj w zniesieniu (tab. 8), a więc większa produkcja jaj niektórych samic nie odbywała się kosztem jakości tych jaj.

Sukces lęgowy ograniczany był w stadium gniazdowym dwoma głównymi czynnikami: drapieżnictwem i porzucaniem gniazd (głównym drapieżnikiem była wrona). Straty kompletnych zniesień z powodu tych dwóch czynników wyniosły w różnych sezonach 31–53%, przeciętnie 44,2% (tab. 10). Straty z powodu zatopienia lub rozmycia gniazda wyniosły zaledwie 0,9%. Udatność lęgów była wyższa w gniazdach założonych na początku sezonu (74,5%), by pod jego koniec spaść do 32,7% (tab. 13). W lęgach udanych, w stosunku do liczby zniesionych w nich jaj, wykluwało się 87,9–94,1% młodych (tab. 11). Na niskie straty (przeciętnie 9,6%) złożyły się zaziębione i niezapłodnione jaja

(5,6%) oraz pojedyncze jaja zniszczone przez wrony (4,0%). W gnieździe jednej pary, której lęg się udał, wykluwało się przeciętnie 5 młodych.

Przeżywalność młodych (od wyklucia do uzyskania zdolności latania) wynosiła 66,5–79,0% (tab. 15). Straty były największe w latach 1974 i 1975, kiedy wykluło się najwięcej młodych. Mógł to być efekt specjalizacji niektórych drapieżników, szczególnie latających, bowiem wychowywanie młodych odbywało się wyłącznie w obrębie stawów i ich grobli, gdzie presja drapieżników naziemnych była znikoma. Ponieważ gęsi z nielotnymi jeszcze młodymi nigdy nie wychodziły na żer na okoliczne pola i łąki, obfitujące w tym czasie w pokarm, przypuszcza się, że powodem tego było zagrożenie życia nielotnych ptaków ze strony drapieżników naziemnych. W związku z tym wysunięto hipotezę, iż czynnikiem ograniczającym wzrost liczebności gęsi ponad pewien pułap, który przypuszczalnie został już osiągnięty w kompleksie 4, była presja drapieżników, blokująca w okresie nielotności gęsi dostęp do zasobów pokarmowych, znajdujących się poza stawami.

Produkcja lotnych młodych, przypadająca na jedną parę lęgową wynosiła przeciętnie 2 młode w sezonie. Zatem produkcja potencjalna realizowana była w 38%.

Zwrócono uwagę na niektóre sposoby zachowania wskazujące na przystosowania antydrapieżnicze (sposób budowy gniazda w trzcinach, zachowanie się samców i samic w okresie wysiadywania). Świadczą one, iż strategia lęgowa gęsi polega na utrzymaniu przy życiu dorosłej, reprodukującej już samicy, a nie na wydaniu w danym sezonie potomstwa za wszelką cenę.

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Redaktor pracy — Przemysław Majewski

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