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Colonial versus territorial breeding of the great crested grebe *Podiceps cristatus* on Lake Drużno*

Goc M. 1986. Colonial versus territorial breeding of the great crested grebe *Podiceps cristatus* on Lake Drużno. Acta orn. 22: 95-145.

The data collected in the years 1975-80 cover 2502 clutches. Grebes were found to nest: in mixed colonies with the *Laridae* primarily *Larus ridibundus* (A), in monospecific colonies (B), singly (C). Mixed colonies arise when grebes aggregate in *Laridae* colonies. In such colonies grebes synchronize their breeding with that of the gulls and start laying eggs at an earlier date than do pairs nesting under different conditions.

Clutches of 3 and fewer eggs included eggs that were on an average narrower than those found in 4-egg clutches or bigger, and they probably belonged to females lacking breeding experience. Their late breeding causes a gradual, seasonal decrease in clutch size and egg measurements. This decrease occurs in each of the groups: A, B and C independently. In the different years the average clutch size varied between 3.6 and 3.8 eggs. Clutch size was correlated with nest success probably due to the activity of egg-predators. This explains why average clutch size in B was smaller than in A and C. On the basis of egg-size variation within clutches intraspecific nest parasitism was found in colonially nesting grebes.

Egg-covering behaviour appears to be more strongly developed in the middle incubation phase, whereas newly-laid, light-coloured eggs often remain uncovered. It is supposed that this is a breeding strategy element. Exposing the first eggs as a bait to predators would be the final test for the safety of a nest site. Its choice is a factor determining the nest success. The highest nest success was found in A (58%) and in grebe nests located near nests of *Fulica atra* (c. 50%), and the lowest in B (18%). The most important function of the territorial behaviour in the great crested grebe is a passive defence resulting from nest dispersion, of the clutch against predators.

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Колониализм и гнездовая территория *Podiceps cristatus* на озере Дружно.

Материал собранный в 1975-80 годах насчитывает 2502 кладки. Гнездование чомги констатировано: в смешанных колониях с *Laridae* (главным образом с *Larus ridibundus*) (A), в самостоятельных колониях (B), одиночно (C). Смешанные колонии образуются путем скопления чомги в колониях *Laridae*. В этих колониях чомга синхронизирует свой цикл размножения с размножением обычно-

*Praca została wykonana częściowo w ramach Problemu MR II/15: Przyrodnicze podstawy gospodarki środowiskiem.

венной чайки, и кладка у чомги начинается тут раньше чем у пар, гнездящихся в иных условиях.

Кладки насчитывающие 3 и менее яиц состояли в среднем из более удлиненных яиц чем кладки из 4 и более яиц и были снесены, по-видимому, менее опытными самками. Наблюдающееся у этих самок опоздание в приступлению к кладкам вызывает постепенное снижение числа снесенных яиц и их величины на протяжении сезона. Причем это явление наблюдалось в пределах всех трех групп А, В и С. Средние величины кладок колебались по отдельным годам от 3,6 до 3,8 яиц. Величина кладки коррелировала с успехом гнездования, что, видимо, было связано с прессом хищников яиц. Этим объясняется, почему кладки В были в среднем меньше чем в А и С. На основании изменчивости величины яиц в пределах одной кладки у чомги гнездящейся колонияльно был констатирован внутривидовой гнездовой паразитизм.

Инстинкт прикрывания яиц более сильно выражен в средней фазе насиживания, в то время, как свежеснесенные светлые яйца часто остаются открытыми. Можно предположить, что этот факт является элементом стратегии гнездования. Выставление первых яиц как приманки для хищников могло бы служить в качестве теста безопасности места гнездования. Избрание места гнездования является решающим фактором его успеха. Наиболее эффективно было гнездование в А (58%) и в гнездах, лежащих поблизости гнезд *Fulica atra* (ок. 50%); наименее эффективно в В (18%). Наиболее существенной функцией территориального размещения гнезд у чомги является пассивная защита кладок от хищников путем распрощения гнезд.

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INTRODUCTION

The great crested grebe has a well-developed territorial-behaviour system (SIMMONS 1955, MELDE 1973). However, the territories defended by it vary considerably in size, and the species even nests in colonies (VENABLES and LACK 1934, McCARTAN and SIMMONS 1956). Its colonies are usu-

ally formed on larger water bodies where a suitable nesting habitat is limited or unevenly spread (HUDEC and ČERNÝ 1972, SIMMONS 1974). Only very recently, detailed studies of the grebe colonies have been carried out (KOSHELEV 1977, MIELCZAREK 1980, ŁAWNICZAK 1982, MARSZAŁEK — unpublished data).

On Lake Drużno the great crested grebe nests in large numbers, both singly and in colonies. It forms monospecific colonies and mixed colonies with *Larus ridibundus*. The aim of the present study is to analyse factors related to the nesting of grebes in large densities, and to compare the breeding success of territorial and colonial pairs.

STUDY AREA

Lake Drużno is a partial nature reserve where birds are protected. It is situated at the north-eastern edge of the Vistula delta near Malbork, south-east of Elbląg. The physical conditions of the lake are unstable. Lake Drużno is a through-flow water body with a wide amplitude of water level variation (up to 1 m). Due to this, the size of flooded-area varies between 12.6 and 29.8 km² (CYBERSKI and MIKULSKI 1976). The former value approximately defines the area of the lake proper, the latter — the lake and the swamps surrounding it. The shore-line is subject to frequent changes. Lake-edge fragments break off and, depending on the water level, form islets, drifting or resting on the bottom. Because of its large surface area and small depth (average 0.8 m, maximum 1.5 m — RICHLINGEROWA 1952, quoted after KLUSZCZYŃSKA and SZMEJA 1979), Lake Drużno is from the limnological point of view treated as a pond-lake (MIKULSKI 1955). Since the waters of this lake are little transparent and shallow, they are easily warmed, but they also lose heat at a fast rate. The circadian temperature amplitude may come up to 8°C (GROMADSKA 1955).

The study area was about 10.8 km². It covered the main part of the lake without two northernmost bays (Fig. 1).

The vegetation biomass of the lake is characteristically high, with only a few dominant plant species. In the growing season, *Nuphar luteum* and *Nymphaea alba* cover a considerable proportion of the lake surface area. *Nymphoides peltata* also forms vast patches, especially at deeper sites. Most important among the emergent species is *Typha angustifolia*. Only in several places are small clumps found of *Phragmites communis* growing in the water. Typical to Lake Drużno large reed-beds are found on the swamp tracts surrounding the lake, being thus of no importance to the great crested grebe. A detailed description of the vascular vegetation of Lake Drużno can be found in the paper by KLUSZCZYŃSKA and SZMEJA (1979).

Little is known about the diet of the great crested grebe on Lake Drużno.

Most numerous among the fish caught in this lake are: *Abramis brama*, *Rutilus rutilus*, *Blicca björkna*, *Perca fluviatilis* and *Esox lucius*.

The breeding success of the great crested grebe may be affected by about

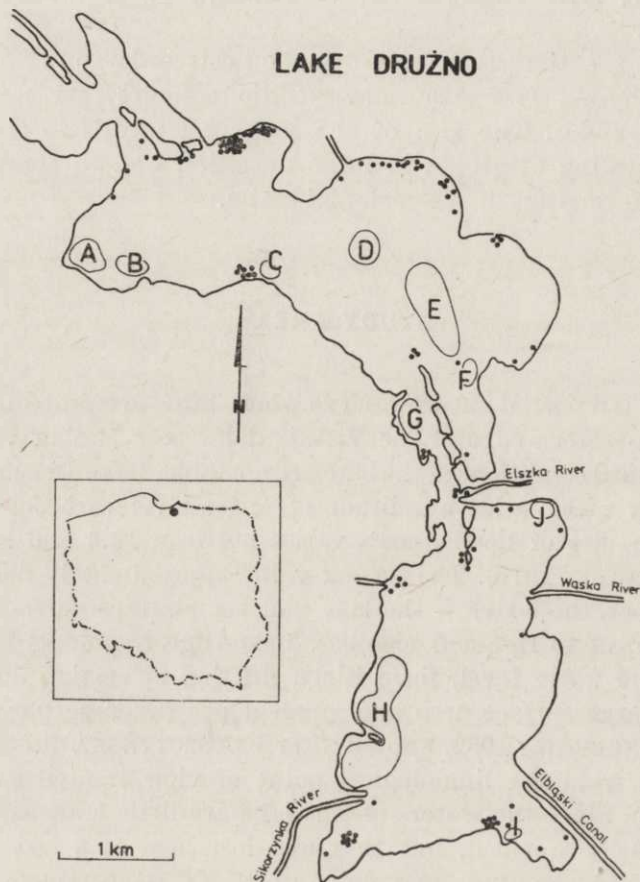


Fig. 1. Lake Drużno — a map of the study area

The regions designated with letters are described in the text; points — grebe nests localization outside these regions in 1978

Ryc. 1. Jezioro Drużno — szkic terenu badań

Regiony oznaczone literami zostały opisane w tekście; kropkami oznaczono lokalizację gniazd perkozów poza tymi regionami w 1978

a dozen bird species which nest or visit the reserve. The most important among them are: *Circus aeruginosus*, *Milvus migrans*, *M. milvus*, *Haliaëtus albicilla*, *Fulica atra*, *Corvus corax*, *C. corone cornix*, *Pica pica*, *Larus ridibundus*, *L. argentatus*, *Sterna hirundo*, *Ardea cinerea* and various duck species. No other grebe species nested in the reserve area under study.

Several predatory mammal species were found to occur on Lake Drużno:

Nyctereutes procyonoides, *Lutra lutra*, *Vulpes vulpes* and *Mustela erminea*. *Onatra zibetica*, which occurs in the study area in large numbers, may also have an effect on the breeding results of the great crested grebe.

MATERIAL AND METHODS

Methods of field work

I collected the data for the study for six breeding seasons, in the years 1975–80. My field work was usually started at the end of April and beginning of May, and ended at the end of June. In 1979, I additionally checked part of the area in mid-July, and carried out an observation in mid-August. In 1980, following a break at the beginning of July, I continued regular studies in the second 10-day period of the month.

I have collected most of the data myself. In 1980, part of the study area, the so-called Gęsia Bay (Goose Bay) was regularly checked by Jerzy MIKIANS. Owing to a great numbers of the grebes in this part of the lake and frequent checks he was able to collect a considerable part of the data of that year.

Field work consisted in detecting great crested grebe nests, recording their location, clutch size and egg size. For this purpose I travelled along the lake shores, island edges and around emergent-vegetation clumps in a rowing-boat trying to reach all nests. It was not always possible. Some nests located on floating islands far from their edges, or on slimy clumps could not be accessed from boat or on foot. Furthermore, if the water level was low, it was impossible to reach some of the bays and islets. As a large proportion of the lake was covered by plants with floating leaves, the speed of the boat was low. To minimize the effect of my presence near the nests on the results of the clutches observed, I restricted my stay in one area to 1-1.5 hours, and did not carry out checking during a rainy weather and high winds. Due to such restrictions, I could not repeat observations at the same sites at regular and adequately short time intervals. I tried not to allow the intervals between successive checking visits to exceed 20-25 days, but this was often impossible. Such a frequency would have allowed to record at least once each of those nests which had persisted through the incubation period. Since I have not been able to do this, the data that have been collected must be treated as a large, random sample. The total number of found nests (Table 1) is lower than the total number of built nests, and probably higher than the number of pairs in the lake part under study.

From 1976 on I marked nest positions on rough sketches of the area in a notebook. If a great crested grebe nest was near another nest belonging to the same species, or to *Fulica atra*, I recorded the estimated distance between them. I arbitrarily adopted a distance of 10 m between two neighbouring nests of grebes as the upper limit of colonial nesting.

Table 1. Number of nests found during the study
 Tabela 1. Liczba gniazd znalezionych w trakcie badań

Year — Rok	1975	1976	1977	1978	1979	1980	Total Razem
No. of nests Liczba gniazd	352	386	480	389	419	476	2502

Only those platforms were treated as nests on which I found eggs, or eggshells indicating that eggs had been laid there. This reservation is important because grebes often build several platforms, only one of which is used as the true nest (SIMMONS 1974).

During each nest checking I wrote down a note stating whether a nest was covered or uncovered. I also took into account a third possibility — poorly covered. This somewhat subjective category referred to nests which were covered, but the clutches were clearly visible, and it was hard to consider them covered. They were finally included among the covered nests for the aim of the analysis was to estimate the frequency of the egg-covering behaviour.

I measured the eggs with a slide calliper to the nearest 0.1 mm. At the time of measuring I wrote the sequence number on each egg, corresponding to egg laying sequence in the clutch. If there was no ground for establishing the laying sequence, the number only denoted the order in which information about eggs was written in the notebook. Egg numbering in conjunction with egg size was sometimes helpful in nest identification during subsequent check visits. It enabled also to find out if any eggs had disappeared between successive checkings.

Clutch age estimation

In the nesting phenology analysis I adopted the dates of the laying of the first egg in the nests examined as a criterion for ordering the data. I calculated the starting date of a clutch on the basis of its age, assuming that eggs are laid at 2-day intervals, and incubation begins after the laying of the first egg (MELDE 1973, SIMMONS 1974) and lasts on an average 27 days (ONNO 1960). The basic method used for clutch age determination was the water test (*e.g.* HAYS and LeCROY 1971). It consists in submerging the egg in water and observing its position. In this test a new laid egg lies horizontally on the bottom of the vessel, and as its specific gravity decreases with age due to the loss of water, the egg changes its position. A detailed description of the changes is presented in Table 2.

For egg-age estimation I also used, to some extent, the phenomenon of egg-shell colour change during incubation. The rate of these changes varies

Table 2. A key to egg-incubation stages
Tabela 2. Klucz do oznaczania stadium inkubacji jaj

Stage Stadium	Water test Test wodny	Other characteristics Inne cechy	Egg age (days) Wiek jaja (dni)
1	the eggs sink, the angle between egg axis and the horizon is: jaja toną, ich długa oś tworzy z poziomem kąt: 0°	the shell bluish-white barwa skorupy niebieskawo-biała	1-2
2		the shell white or slightly dirty skorupa biała lub przybrudzona	2-4
3	30°		4-5
4	45°		5-6
5	60°		6-9
6	90°		8-17
7	the eggs float submerged jaja pływają w toni		16-19
8	the eggs float on the surface, partly emerged jaja pływają na powierzchni częściowo wynurzone		17-24
9		peeping and knocking of the chick can be heard through the shell słysać przez skorupę piski i stukanie pisklęcia	23-26
10		hatching — klucie	25-29

Note: The key has been worked out on the basis of repeated checking of the same clutches. Overlapping age-ranges correspond to the natural variation in the duration of the particular stages.

between nests, depending on the kind of the nest building material and its moisture. For this reason, this is a better basis for establishing the egg laying sequence than for the estimation of the absolute egg age. Nevertheless, if the shell was bluish-white in colour, it was easy to establish that it was an egg laid during the last 24 hours. The water test was not applied if pipping of chicks could be heard through the shell, or when hatching had already begun. In such cases the age of a clutch was estimated on the basis of these symptoms.

Below I am going to illustrate the method of clutch age calculation with an example. If all the eggs of a clutch, *e.g.* a 4-egg clutch, subjected to the water test sink vertically (stage 6 in Table 2), then the last of them must have been laid no later than 8 days ago, and thus the first one at least 14 days ago

and not earlier than 19 days ago. I assumed that the first egg had been laid before about 17 days, and on this basis I calculated the clutch starting date. In the paper the clutch starting dynamics has been presented in a 5-day (pentade) scale. The accuracy of clutch-age determination by the method just described is sufficient, for the error does not exceed time unity.

The water test was used from 1976 on. For this reason, data from 1975 have not been used in many comparisons, because they lack the phenological reference.

Clutch completeness assessment

I considered a clutch to be complete, when egg-laying was finished and there was no traces suggesting egg-loss caused by predators. If all the eggs in a nest had attained stage 3, or a later stage (Table 2), I assumed that egg-laying had been completed. In the subsequent analyses I eliminated all those clutches which I considered incomplete on the basis of the above criteria. I also left out clutches, the eggs of which clearly differed in size or age, which may have indicated that they derived from two females.

Data analysing methods

Elaboration of ovimetric data. The units used for most ovimetric comparisons in the paper are the mean values of clutches, and not the measurements of particular eggs. To avoid a possible effect of the laying sequence on the egg size, the means were only calculated for complete or probably complete clutches. The latter category comprises clutches with a size equal or greater than the mean for "their" pentade which on the checking day did not yet fulfil the completeness criterion.

Nesting success estimation. In the analysis of clutch losses during incubation I used a method which, to the best of my knowledge, had not been used for this purpose before. It is similar to the construction of a life table on the basis of the frequency of recorded individuals of different age (CAUGHLEY 1979). On account of this similarity I am going to use the terms: survival and mortality rate when referring to clutches.

The method for clutch-age determination has been described above. I assumed that the study covered a representative part of the breeding season, and my recording of nests was random in the sense that it was independent of their age. If an adequately large sample is used, the distribution of the frequency of finding nests of a particular age reflects the survival. In this case, sample size

means all the nest-checkings; it is larger than the number of detected nests since some of them had been checked several times. I grouped the data in 2-day age classes, and restricted the analysis to the first 14 classes, i.e., till the 28th incubation day, the time when the first chick should hatch. Due to accidental errors, the survivorship curves thus obtained were irregular. From the biological point of view, a situation where in a life table an older age group is more numerous than the group preceding it is senseless. For the "smoothing" of the survivorship curve I have used a logarithmic-polynomial equation of the format:

$$\log f_x = a + bx + cx^2 + dx^3 \dots,$$

where f_x — interpolated frequency of record of age- x clutches, and a, b, c and d — constants (SNEDECOR and COCHRAN 1967 quoted after CAUGHLEY 1979). The analysis is gradual. At first the $\log f_x = a + bx$ is evaluated. It defines a constant, age-independent survival. If this function does not sufficiently satisfy a distribution under study, then the equation is augmented by adding the next element: $\log f_x = a + bx + cx^2$, and evaluated, and the curve fitting is checked again. The evaluation of the equations of a higher and higher degree is continued until it ceases to significantly affect the accuracy of the fitting. The measure here is the total of the squares of deviations of the calculated frequencies from the observed frequencies. The evaluation of the equation, up to and inclusive of the fifth degree, for 10 frequency distributions (successive years, nest groups differing in location) has been done at the Computer Centre of the Institute of Mathematics of the University of Gdańsk, on an ODRA 1204 computer, using a linear regression analysis program called KUPP. Only equations 1° and 2° were in fact used. It would be hard to expect higher-degree equations to be adequate for describing the clutch survival. Having selected the equation, I calculated the f_x for all age classes. Then I replaced f_x with l_x — a theoretical number of clutches that had survived to attain age class x per each 100 nests built. The values of l_x , set out in the life table, were used in the calculation of the mortality rate q_x (e.g. CAUGHLEY 1979) and in the plotting of the survivorship curves. For a graphical representation of the distribution of the frequencies, found in the field (F_x), around the curve interpolating them, I also calculated them proportionately to $F_1 = 100$. In several cases the theoretical frequencies (l_x) increased towards the end of the incubation period. If this concerned the last age class, or the last two age classes, and these changes were small, whereas the overall curve fitting was good, then as the total survival I adopted an approximate value defined by the last segment of such a curve, and not the last l_x . In such cases the clutch mortality rate q_x drops below zero, which is senseless from biological point of view and must be considered an artefact resulting from the mathematical approximation and non-representativeness of the initial data.

RESULTS AND DISCUSSION

Nest distribution

Presented as an example on the map (Fig. 1) is the distribution of the nests of the great crested grebe on Lake Druzno in 1978. In the breeding seasons of the remaining years the distribution was in general similar. The colonial nesting in areas marked with letters on the map deserves a more detailed discussion.

"A". In this area there are several partly emergent *Typha angustifolia* clumps with an admixture of other plant species. In those clumps I found the following numbers of nests in the successive years: 1976 — 21, '77 — 31, '78 — 13, '79 — 8 and '80 — 5. The fall in numbers observed after 1978 may have been caused by a long-lasting low water level in this season, or by high losses of clutches in the preceding year: between two checkings done by me — on May 28 and 30 1977 — 23 out of the 31 nests previously detected had been destroyed. Judging from the traces found and the observed behaviour of *Fulica atra*, some of the losses may have been caused by the latter. A concurrence of the date of mass losses in the nests of the grebes and the spawning-season of *Abramis brama* may indicate yet some other causes of the destruction. Fish flouncing near the clumps attracted various predators which could at the same time rob nests or destroy them mechanically when using them as watching or hunting platforms. During my checking visit on May 30 I flushed about 20 *Ardea cinerea*. I do not know if they can feed on eggs, but a mechanical destruction of clutches by them seems very likely.

"B". Two *Typha angustifolia* clumps several hundred metres east of "A". From 1978 on, I noticed there a clear increase in the number of nests (1975 — 2, '76 — 3, '77 — 4, '78 — 12, '79 — 23, '80 — 12 nests).

"C". A small *Phragmites communis* clump growing in the water. In 1978, I found there 17 nests of the great crested grebe. The distances between nests ranged from 1.5 to several metres. I have not got complete information, but judging from the nest destruction found four days after my first checking visit, I may presume that the losses here were considerable. No colonial nesting was found in this area in the remaining years (1976 — 4, in 1975, '77, '79, '80 — 0 nests).

"D"*. A fairly large *Typha angustifolia* bed situated at a considerable distance from the lake edge. Before the study was begun I had in 1974 found a mixed colony there, numbering about 100 pairs of *Larus ridibundus* and 70 pairs of great crested grebes. The following year I found 41 nests of grebes, and only over a dozen nests of gulls. In the years 1976-80, I found 13, 4, 3, 16 and 24 (respectively) nests of the great crested grebe. In the years 1976-79, *Larus ri-*

*Areas "D" and "E" will hereinafter be referred to as "Clumps".

dibundus did not nest in this area. In 1979, *Sterna hirundo* built several nests there, and in 1980, also 7 pairs of *Larus ridibundus*.

"E". Three large and several smaller clumps of *Typha angustifolia* growing in the water. In the successive years I found the following numbers of nests: 1976 — 3, '77 — 16, '78 — 49, '79 — 48 and '80 — 58. Inside the clumps the nests were on the whole evenly distributed, which may indicate a territorial tendency even in high densities.

On a small clump, included in this area, relatively near (about 300 m) to a *Larus ridibundus* colony in area "F", 3 gull pairs and 17 great crested grebe pairs nested in 1979. In other years there were no gulls, nor such a concentration of grebe nests there.

"F". A mixed colony of *Larus ridibundus*, *Sterna hirundo* and the great crested grebe near the village of Janowo. *Larus ridibundus*, 500–1000 pairs, and about a dozen pairs of *Sterna hirundo* usually nested there on two larger islands and rarely also on small clumps near by. Grebes built nests in the same patches as the gulls and terns, but the distribution of the nests was different in the different years, due to changes in the water level. At medium and low water states the island located farther to the north was above the water, and the great crested grebes mainly nested on the other, the lower clump. If the water level dropped during the breeding season nests of grebes in the part of the colony thus brought to the surface were still used, and to each of them led a separate, trodden, or more precisely, belly-worn, muddy path. The numbers of great crested grebe nests found in this area in the successive years were similar: 1976 — 37, '77 — 34, '78 — 39, '79 — 36 and 1980 — 38.

"G". A bay near a waterway; in 1976 and 1977, a *Larus ridibundus* colony was found there on numerous clumps and islets. In 1978, gulls moved about in this area in early spring, but after the first nest had been built they left the colony. In 1976 — 13, and in 1977 — 48 great crested grebe pairs nested there among gulls. In the remaining years I only found a few dispersed grebe nests in this bay.

"H". This area is at the entrance to the Geşia (Goose) Bay which has disappeared due to its filling. On some of the islets and *Typha angustifolia* beds, which are numerous there, 1000–1800 *Larus ridibundus* pairs nested. The number and distribution of their nests varied from year to year, so there always was a number of unoccupied clumps. The majority (over 90%) of the great crested grebe nests present in this area, were at sites actually occupied by gulls. The distances between some great crested grebe nests here were very small (minimum 0.8 m, as estimated between nest centres), whereas gull nests and grebe nests often touched one another. In sporadic cases (1–4 cases a year) in the Goose Bay I found mixed clutches in nests of one of the species. In 1975, I found 92 great crested grebe nests there, and in the next years 104, 142, 122, 125, and 164 nests, respectively.

"I". In this area there existed throughout the study period, an island overgrown with *Phragmites communis*, ferns and several scrub willows. In 1977, at this site *Larus ridibundus* set up a compact colony of over 500 pairs. The same year 13 great crested grebe nests were found there. Gulls did not nest there in the subsequent years, nor was colonial nesting of grebes seen in this region thereafter.

"J". In some years (1975, '76, '78, '79) there existed there a loose colony* of *Chlidonias niger* and the great crested grebe, with several up to about a dozen nests of both species. Apart from them, there also nested, though sporadically, *Sterna hirundo* and in 1978 1 pair of *Larus ridibundus*. This area is in essence devoid of emergent vegetation, and great crested grebe nests were found among *Nuphar luteum* and *Nymphaea alba* leaves, without any cover from above. Parts of these plants constituted almost the only building material of nests built there late, usually in June, after the plants had attained a size and closure a suitable to screen nests and protect them against waves. *Chlidonias niger* often built their nests on platforms abandoned by great crested grebes. Distances between grebe nests ranged from 6 to 25 m. Sporadically, I also found similar, unsheltered nests in other parts of the lake, but they never formed colonies.

Apart from the above-described aggregations, in different years and in various places there appeared small colonies of several or about a dozen grebe nests, but a large proportion of pairs nested singly. In the years 1977-80, I found the following numbers of nests located far apart: 143, 91, 118 and 123.

Local densities of grebe nests in mixed colonies with gulls were higher than in monospecific grebe colonies (Table 3). Thus nesting among gulls is con-

Table 3. Distance between great crested grebe nests in colonies, in 1979

Tabela 3. Odległości między sąsiednimi gniazdami perkoza dwuczubego w koloniach, w 1979 r.

Distance between nests (m) Odległości między gniazdami (m)	Number of nests in colonies: Liczba gniazd w koloniach:		% of nests in mixed colonies % gniazd w koloniach z mewami
	mixed with gulls z mewami	monospecific bez mew	
0-3.9	43	23	65.1
4-6.9	39	28	58.2
7-10	23	49	31.9

nected with a stronger than in monospecific colonies reduction of the territorial tendencies of this species. This can be interpreted in the following way: The

*Only some of the nests fulfil the colonial-nesting criterion described (page 99) earlier. They form, however, a clear aggregation in a generally poorly inhabited area. For this reason, I have treated it as a colony.

territorial reaction is evoked by a visual or auditory contact with another individual. In a dense, mobile and noisy gull colony the sight of another individual is, in spite of the small absolute distances between grebe nests, only one of many strong stimuli reaching a bird. Thus gulls play the role of a shield neutralizing and limiting the territorial reaction of grebes.

Synchronized changes in the colonizations of some areas by *Larus ridibundus* and great crested grebe (area "D", "E", "G" and "I") indicate that the formation of mixed colonies by these species is not based on similar habitat requirements, but results from the fact that grebes aggregate in gull colonies.

In 1978, the disappearance of the colony from area "A" coincided with the beginning of a more numerous nesting in "B" and "C". In 1979, there occurred a further growth in number of nests in "B", whereas in area "C" grebes did not breed. This suggests that there was at least partial movement of birds between the clumps concerned, which might indicate that there are individual tendencies to nest in colonies.

The cause of disappearance of mixed colonies and their formation in new areas is the tendency of grebes towards association with *Laridae*. If gulls abandon an area, grebes follow them. It must be emphasized, however, that in not all *Larus ridibundus* colonies on Lake Družno do great crested grebes nest in high densities. In large gull colonies on flooded polders in the southern part of the reserve, outside my study area, grebes nest singly. I suppose this is connected with the small surface area of these water bodies, and thereby limited food supplies for grebes.

Disappearance of monospecific grebe colonies may be connected with high clutch losses in previous years (e.g. area "C", and perhaps "A" as well), and water level changes. The latter probably was the cause of great differences in location between 1977 and 1978. In 1978, almost throughout the breeding season, the water state was below the average level (Fig. 4), which made it difficult for grebes to reach some traditional breeding sites.

Nesting phenology

The dynamics of nesting of the great crested grebe on Lake Družno in the breeding seasons of the years 1976–80 has been presented in Figures 2–6.

The main laying period (MLP — for explanation see Fig. 2) in all the breeding seasons, except 1978, lasted 35 days. In 1978, this period was longer by as many as 20 days, probably because some breeding sites were inaccessible due to a low water level (Fig. 4).

Both the median and MLP indicate that the breeding season of 1980 was delayed by 1.5-2 pentads, relative to the breeding seasons of the remaining years. This cannot be related to variations in the water level, or temperature

in the period preceding the egg laying (Fig. 6). The mean air temperatures for 10-day periods in April '80 were similar to or higher than in the preceding years.

The shape of the histograms representing the number of started clutches (Figs 2–6) indicates that the sample was not homogeneous. For all breeding seasons, except that of 1979, two peaks can be distinguished in the main block, and usually a third one, small — at a later time. Such differences are connected with nesting sites and conditions. I have distinguished four nest groups:

1. Nests located in a mixed colony near Janowo (area "F" in Fig. 1);
2. Nests in the Goose Bay — also in a *Larus ridibundus* colony;

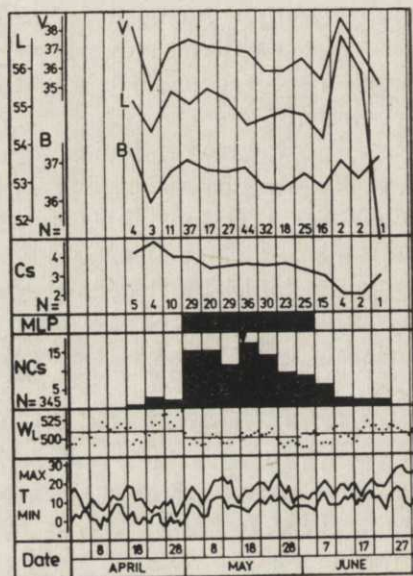


Fig. 2. Seasonal variation in the average egg length (L), breadth (B) volume (V), average clutch size (C_s), number of clutches started (NC_s) on Lake Drużno in 1976

Maximum and minimum daily temperatures (T_{max} and T_{min} and the water level (WL line — monthly average water level for the years 1976–80) are shown.

V — cm^3 ; L and B — mm ; MLP — main laying period — the smallest group of pentads in which about 80% of clutches have been started (VÄISÄNEN 1977); NC_s in % of total number, the median is represented by the triangle; T — $^{\circ}C$; Date — the middle pentad's day.

For other explanations of the symbols V , B and L — see Table 5.

Note: water table data for Zukowo, temperatures for Elbląg. Standard division of the year is used (BUSSE 1973)

Ryc. 2. Zmienność sezonowa średnich długości (L), szerokości (B) i objętości (V) jaja, średnia wielkość zniesienia (C_s), liczba zniesień rozpoczętych (NC_s) na Drużnie w 1976

Zaznaczono maksymalne i minimalne temperatury dzienne (T_{max} i T_{min}) i poziom wody (linia WL — miesięczny średni poziom wody w latach 1976–80); MLP — średni okres znoszenia — najmniejsza liczba pentad, w których rozpoczętych zostało ca 80% zniesień; NC_s — w % ogólnej liczby zniesień, trójkątem oznaczono medianę; data — środkowy dzień pentady. Dalsze objaśnienia symboli V , B i L podano w tabeli 5

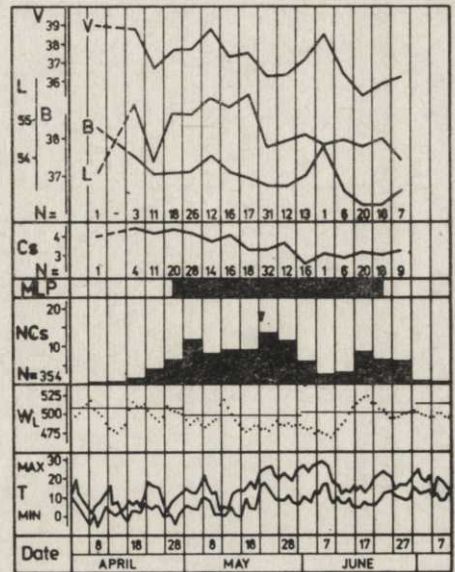
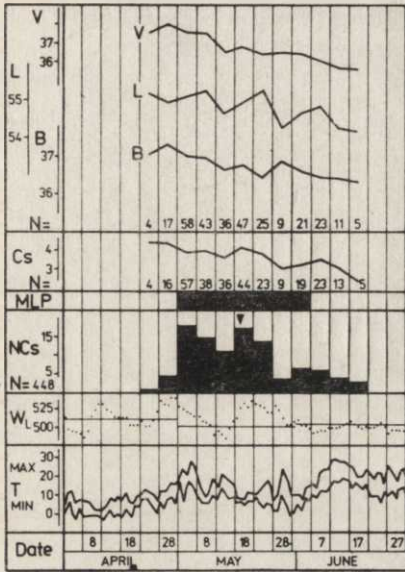


Fig. 3. As in Fig. 2 — data for 1977
Ryc. 3. Jak na ryc. 2 — dane dla 1977

Fig. 4. As in Fig. 2 — data for 1978
Ryc. 4. Jak na ryc. 2 — dane dla 1978

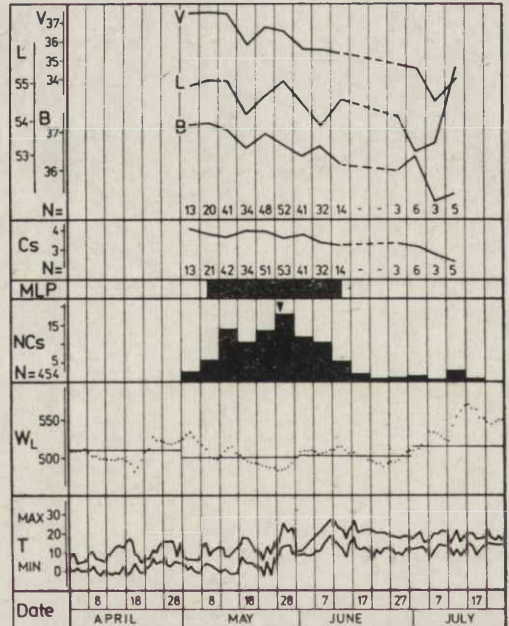
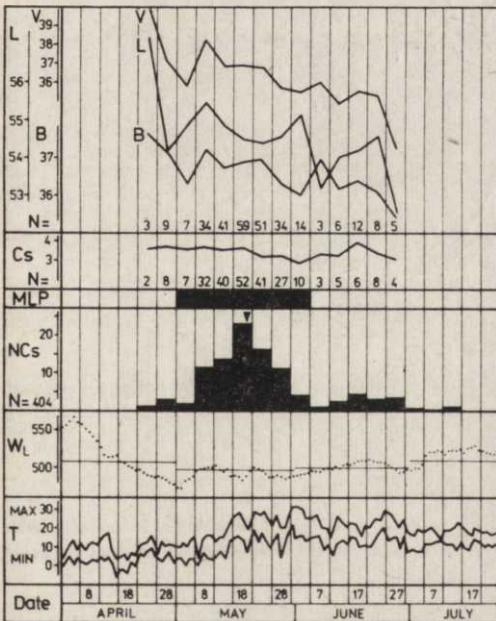


Fig. 5. As in Fig. 2 — data for 1979
Ryc. 5. Jak na ryc. 2 — dane dla 1979

Fig. 6. As in Fig. 2 — data for 1980
Ryc. 6. Jak na ryc. 2 — dane dla 1980

3. "Clumps" — nests in principle in colonies without gulls (areas "D" and "E" in Fig. 1);

4. Other nests.

Presented in Figure 7 is the dynamics of start of laying in nests belonging

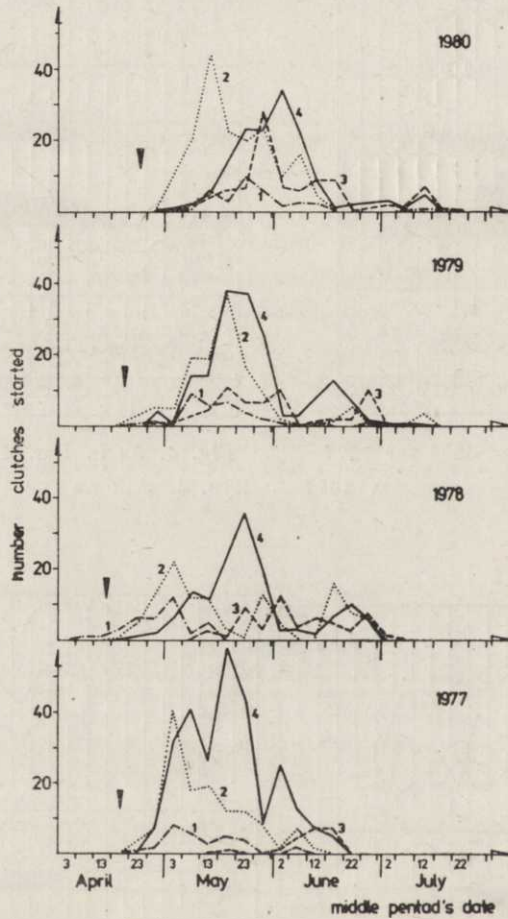


Fig. 7. Start of laying

1 — a mixed breeding colony with black-headed gulls near Janowo village; 2 — a mixed breeding colony with black-headed gulls in Gęsia Bay; 3 — monospecific breeding colonies in "Clumps" (regions D and E in Fig. 1); 4 — other nests. Black triangle — the date of laying of the first eggs by the black-headed gulls in the breeding colony near Żółwiniec (C. NITECKI unpubl. data)

Ryc. 7. Początek znoszenia jaj

1 — kolonia mieszana koło Janowa; 2 — kolonia mieszana w Zatoce Gęsoj; 3 — kolonie jednogatunkowe w „Kępach” (regiony D i E na rycinie 1); 4 — inne gniazda. Czarnym trójkątem oznaczono datę zniesienia przez śmieszkę pierwszych jaj w kolonii koło Żółwińca

to these categories in the years 1977-80. Grebes nesting in *Larus ridibundus* colonies start breeding at a clearly earlier time than other grebes. My observations, which I cannot document quantitatively, indicate that the first nests

of grebes and gulls in mixed colonies are built at the same time. To illustrate this phenomenon I have marked in Figure 7 the dates of laying the first eggs by *Larus ridibundus* in a large colony outside my study area in the "Lake Drużno" reserve (Cz. NITECKI — unpublished data). They can approximately be regarded as the beginning of the breeding season of *Larus ridibundus* also in other parts of the lake. Synchronous is not only the beginning of egg laying, but there is also a synchronized mass start of breeding. This phenomenon is often seen in colonial birds (e.g. PATTERSON 1965, STEMPNIEWICZ 1981), and has less often been described for mixed colonies (BURGER 1974). In other areas of Lake Drużno great crested grebes, outside *Larus ridibundus* colonies, begin to breed at a later date, so the synchrony observed cannot be accidental. Its biological function is obvious — taking advantage of the active defence of colonies, ensured by gulls. FUCHS (1977) has found that *Sterna sandvicensis* also begin breeding at an earlier date in *Larus ridibundus* colonies than when they nest among other species. The synchrony of breeding in connected with the so-called social or group stimulation (DARLING 1938, quoted after IMMELMANN 1971). This phenomenon can also be observed in interspecific systems (interspecific stimulation — IMMELMANN 1971). Apart from several cases checked experimentally (e.g. COLLIAS *et al.* 1971a, 1971b), it is not known what factors cause this stimulation. I think that in the case of interspecific stimulation these factors must be little specific, and the whole phenomenon may be based, on, e.g. a tendency to imitate.

I also observed synchronous breeding in monospecific grebe colonies. An extreme example of this can be one of the clumps in area "E", where all 8 clutches were started within 3 days.

There is good reason to think that it is the second, rather than the first peak on the curves representing the start of egg laying on Lake Drużno that falls on a period typical for the geographical position of this water body. This

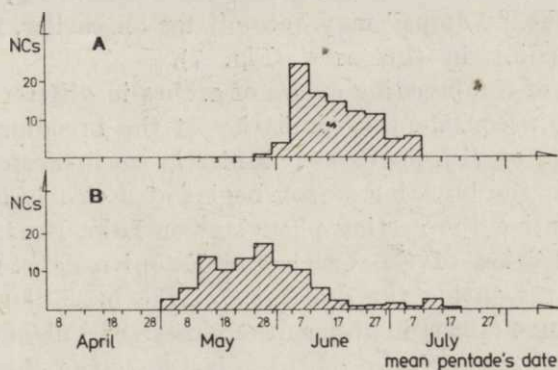


Fig. 8. Start of laying

A — Lake Żarnowieckie, 1980, $N = 467$ (P. MARSZAŁEK unpubl. data); B — Lake Drużno, 1980, $N = 454$;
 NC_s — see Fig. 2

Ryc. 8. Początek znoszenia jaj

is indicated by the comparison of the course of the breeding season on Lake Družno and on Lake Żarnowieckie located about 120 km to the north-west of the study area (Fig. 8). Some unpublished data, made available to me by JEZIERSKI, on the course of the breeding season on Lake Żarnowieckie in 1979, also show that it started later than on Lake Družno. My irregular observations carried out on Lake Choczewskie in 1978, and on Lake Ptasi Raj indicate that this delay is not a local character of the population on Lake Żarnowieckie. The two lakes concerned differ significantly in the trophic status, but I do not think this could have a significant effect on the starting dates of breeding. In this case I base my opinion on the results reported by FJELDSÅ (1973a), who did not find any phenological differences in the breeding of *Podiceps auritus* on water bodies differing in fertility. To be precise, I must add that the climate of the environs of Lake Družno slightly differs from that in the near sea area of Żarnowiec. The many-years' mean of May temperatures for Družno is higher by 2°C (WISZNIĘWSKI 1973). Phenological maps (MOLGA 1973-78) indicate, however, that the associated speeding up of plant growth does not exceed 5 days.

A comparison of the histograms (Figs 2-6) and the curve representing the phenology of great crested grebe pairs breeding twice (Fig. 9c), suggests that the third nesting peak, noticeable on Lake Družno in some years, may be connected with the production of two clutches. However, I have no direct evidence to prove this.

It has been known from studies of other species that the start of laying is often related to the age and breeding experience of the bird pair (e.g. COULSON and WHITE 1956, FJELDSÅ 1973a). In *Podiceps auritus* new breeding areas are mainly occupied by young and inexperienced birds, whereas older pairs tend to return to the sites of their previous nesting (FJELDSÅ 1973a). If this is the case also in the great crested grebe, the statistical growing older of the birds inhabiting the "Clumps" may account for an earlier, from year to year, beginning of breeding in this area (Fig. 7).

A comparison of the breeding cycles of grebes in different parts of the species range reveals a considerable similarity of the breeding starting dates in Czechoslovakia and on fish ponds near Milicz in south-western Poland (Fig. 9a and b). In Estonia the breeding season begins at a clearly later time, whereas the curve representing the nesting phenology on Lake Družno seems to be, as it were, a combination of the Czech and Estonian data. Of a similar shape is the polygon representing the dynamics of the beginning of breeding, studied by MIELCZAREK (1980) in the southern part of Poland. Figure 9c, taken from ZANG'S (1977) paper shows the breeding season of the great crested grebe in Lower Saxony. Taking into account the different ways of data presenting, we find that nesting begins there 10-15 days earlier than in Czechoslovakia or Milicz. The differences in laying dates between the environs of Milicz and Lake Żarnowieckie can be attributed to the fact that in the north of

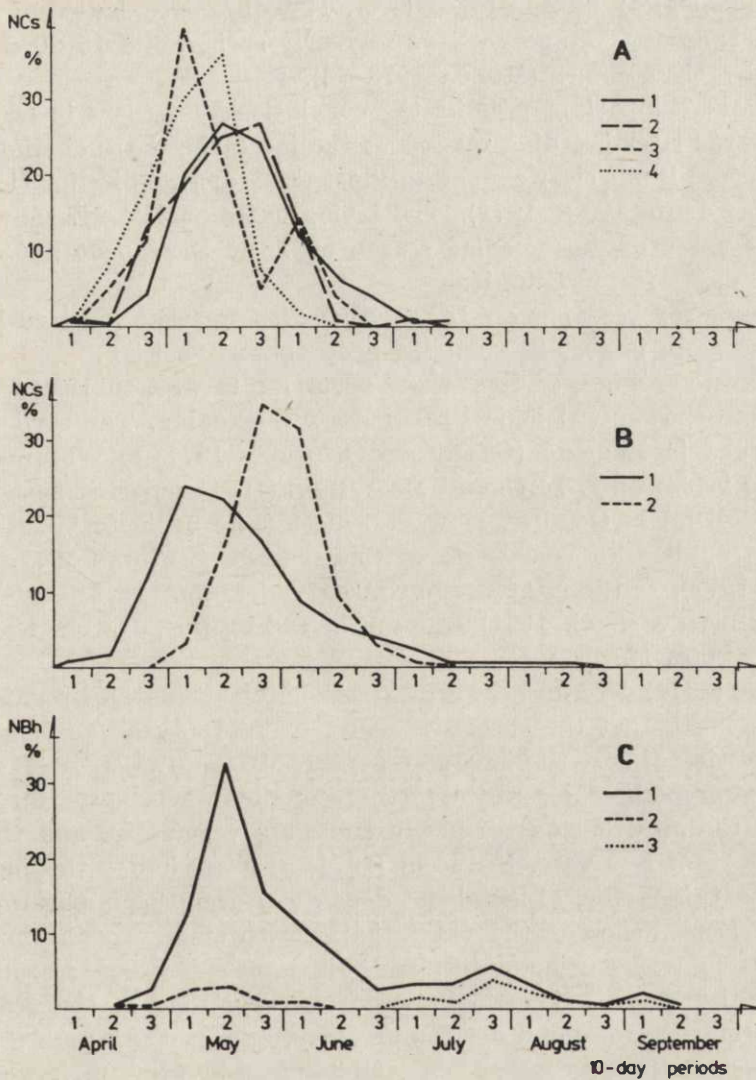


Fig. 9. The timing of breeding of the great crested grebe

A. Polish data — start of laying; 1 — Lake Drużno, $N = 2003$; 2 — water bodies in southern Poland (MIELCZAREK 1980), $N = 216$; 3 — Milicz fish-ponds, 1972 (ŁAWNICZAK 1982), $N = 203$; 4 — Milicz fish-ponds in the years 1956, 1959 and 1960 (WITKOWSKI 1967), $N = 105$

B. Start of laying: 1 — Czechoslovakia (HUDEC and ČERNÝ 1972), $N = 291$; 2 — Estonia (ONNO 1960), $N = 41$

C. The timing of hatching in Lower Saxony (ZANG 1977), $N = 203$; 1 — all nests; 2 — first broods of pairs with two broods; 3 — second broods of these pairs. *NCs* — see Fig. 2. *NBh* — number of broods hatched (in % of total number)

Ryc. 9. Fenologia lęgów perkoza dwuczubego

A. dane z Polski — początek znoszenia; 1 — Drużno; 2 — Polska południowa; 3 — Stawy Milickie, 1972; 4 — Stawy Milickie 1956, 1959 i 1960. B. Początek znoszenia. C. Fenologia wylęgania się piskląt w Dolnej Saksonii. 1 — wszystkie gniazda; 2 — pierwsze lęgi par przystępujących do drugiego lęgu; 3 — drugie lęgi tych par; *NCs* — patrz ryc. 2. *NBh* — liczba gniazd, w których wylęgły się pisklęta (w % liczby ogólnej zniesień)

Poland phenological seasons begin later. The difference between the regions compared is on an average 15 days for early spring, and 15–20 days for full spring and early summer (MOLGA 1973–78).

The above comparison permits the conclusion that there is a general tendency towards later breeding related to the increasing latitude and longitude, but the picture is not clear enough to illustrate HOPKINS bioclimatic rule (1938 quoted after IMMELMANN 1971). The laying dates on Lake Żarnowieckie and the second phase of the breeding season on Lake Družno do not clearly differ from data from Estonia.

The course of breeding on Lake Družno shows that local ecological factors can be more important than the geographical position.

Great crested grebes, at least those occurring in western Europe, for a very long time show physiological readiness for breeding. The earliest clutches were recorded in England (CRAMP and SIMMONS 1977) and France (KERAUTRET 1976) in January. LEYS and De WILDE (1971) reported nests with eggs found in Holland in October. However, most pairs begin to breed in May or June. This applies to both western (CRAMPS and SIMMONS 1977, LEYS and De WILDE 1971), central (BAUER and GLUTZ 1966, MELDE 1973), eastern (ONNO 1960, DEMENTIEV *et al.* 1951) and southern Europe (MAKATSCH 1950, quoted after MELDE 1973).

SIMMONS (1974) describes the great crested grebe as an opportunistic nester, which may mean that the species is ready to take advantage of good conditions for nesting almost throughout the year. TACZANOWSKI (1882) relates the beginning of grebe breeding to the presence of sites where nests can be hidden, that is, to the growth stage of newly emerging vegetation, and the state of its remains from last year. SIMMONS (1974) also attributes the most important role to this factor, although he does not reject the importance of food conditions. Dependence on the vegetation growth stage accounts for the geographical trends of nesting dates, and differences between seasons. MELDE (1973)* studied the relationship between the beginning of the great crested grebe breeding season and water temperature, and gave a number of reasons indirectly proving its existence. The examples given by him can, however, be explained by plant growth dependence on water temperature. If the presence of a suitable site to hide the nest is as a condition understood more broadly, we can accept that this condition can be satisfied by the presence of *Laridae* ensuring the feeling of safety. The direct factor stimulating oocyte development and egg laying would thus be of a psychological nature, dependent on various external circumstances. If we take into account the known comple-

*He also quotes DEMENTIEV *et al.* (1951), wrongly attributing to him the statement that for the start of their breeding grebes require a water temperature above 7.5°C.

xity of the relationship between physical and social stimuli, and physiological and behavioural reactions leading to the start of breeding (HINDE 1975), we cannot *a priori* reject such a possibility.

Clutch size

Figures 2-6 show variation in the average clutch size during the breeding seasons 1976-80. A general tendency is seen towards a decrease in the number of eggs as the breeding season progresses. These differences are small; in some years only, *e.g.* in 1978 earlier clutches were larger by about 1 egg than the late ones. The slowest decrease in the average number of egg in a clutch was recorded for 1979. A seasonal decrease in clutch size was found in the great crested grebe also by other authors (MELDE 1973, MIELCZAREK 1980). In Holland the number of eggs laid in nests from April to June is more or less constant, on an average 3.5-3.6, but only 2 in July clutches (LEYS and Dm WILDE 1971). There have also been reports indicating absence of a noticeable seasonal trend (SIMMONS 1974), and even growth of clutch size, from 4.1 in May to 4.5 in July (BAÜER and GLUTZ 1966). In general, the seasonal decrease in clutch size is attributed to the fact that young females, which lay fewer eggs, start breeding at a later date. This phenomenon is found *e.g.* in *Podiceps auritus*, but apart from the age-dependent clutch size variation, in this species also a seasonal

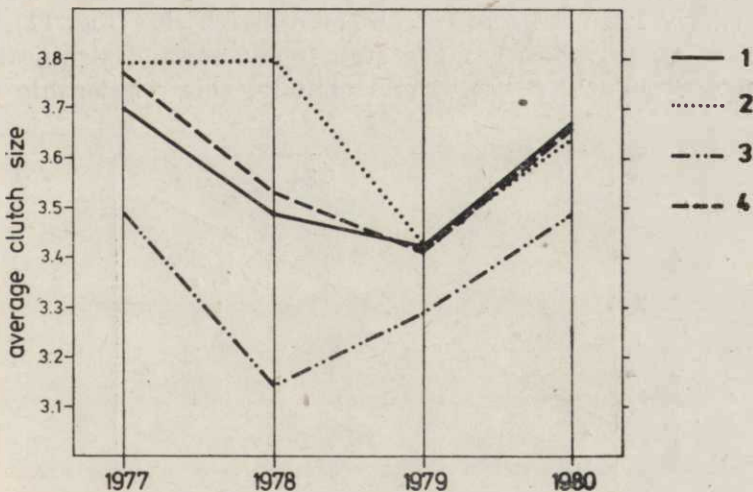


Fig. 10. Average clutch size on Lake Drużno in the years 1977-80

1 - territorial pairs; 2 - mixed grebes-black-headed gulls breeding colonies; 3 - grebes breeding colonies; 4 - all pairs

Ryc. 10. Średnia wielkość zniesienia na Drużnie w latach 1977-80

1 - gniazda rozproszone; 2 - kolonie mieszcane; 3 - kolonie jednogatunkowe; 4 - wszystkie pary

fall was found in the number of eggs laid by both young and experienced females (FJELDSÅ 1973a).

Average clutch sizes in nests located at different sites in the years 1977–80 are presented in Figure 10. A certain similarity noticeable in the course of the curves suggests that at least in some years there was a common factor affecting the clutch size of all great crested grebes in the study area, but in addition to this the influence of local factors could be seen, or factors connected with the way and conditions of nesting. Their effect is seen, *e.g.* in the clutch size of birds nesting in monospecific colonies, lower ($p < 0.002$ Student's *t*-test) than that found for the remaining groups. Since a large part of the data concerning nesting in monospecific colonies has been recorded for the "Clumps", where grebes start breeding at a relatively late time, it is difficult to separate the effect of the site or density from factors causing seasonal variation in clutch size.

One of the phenomena affecting the observed clutch size is usually ignored or underestimated, although its role can be significant. The factor in question is the reduction of clutch size by predators. On Lake Družno such cases are frequent in great crested grebe nests, but I cannot precisely estimate the level of losses on the basis of my data. The probability that a clutch will be reduced or entirely destroyed depends, among other things, on predator pressure. If at any place, time or conditions it becomes stronger or more efficient, the clutches then found will be smaller than the real ones. In a further part of the paper the results are presented from an analysis of nest losses. Some of the results I am going to present at this point to illustrate the relationship between the survival of nests and the observed clutch size (Fig. 11). The correlation between these values is fairly high ($r = 0.84$) and significant statistically ($p < 0.01$ Student's *t*-test). Unfortunately, this relationship does not

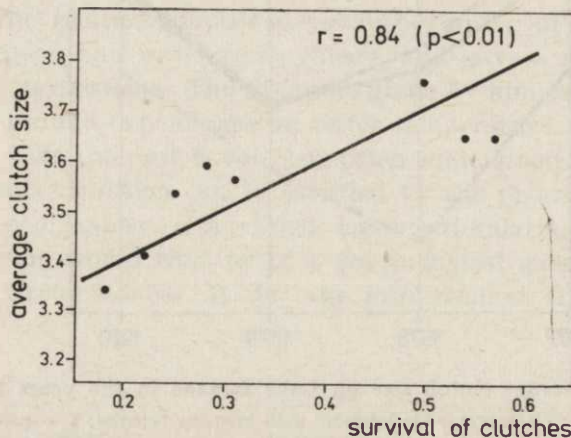


Fig. 11. The relation of the average clutch size and the survival of clutches
Ryc. 11. Zależność średniej wielkości zniesienia od przeżywalności zniesień

help estimate the number of eggs really laid by the birds. The difference in survival between nests in monospecific colonies and dispersed nests is small while clutch sizes differ considerably. One may, therefore, conclude that smaller were not only the observed but also the real clutches of birds in colonies. Of course, predation is not the only cause of nest destruction (see page 129), but it is the most important one, as far as the reduction of the number of eggs in a clutch is concerned.

Clutch size in *Podicipedidae* is not physiologically determined (FJELDSÅ 1973a, FUGLE and ROTHSTEIN 1977). It may therefore be presumed that a loss of some eggs before the termination of laying need not necessarily lead on to a reduction in clutch size. In several cases I even found a growth in number of eggs in small, probably reduced clutches which I had considered completed on the basis of the adopted criterion. One of the cases deserves a detailed discussion. In 1977, I found a nest with one egg that had been incubated for 8 or more days (stage 6 in Table 2). The size of the egg was 55.1×40.9 mm. 18 days later there were 3 other eggs, of the size 52.1×40.5 , 55.0×40.0 and 55.7×34.4 mm, in the nest. The oldest of the additional eggs was 6–7 days old, *i.e.*, was laid about 20 days after the preceding one. The probability of finding a clutch containing an egg with a breadth above 40 mm is of the order of 0.001. The possibility of two females encountering in one nest and laying eggs of such breadths is highly unlikely. One may thus say that the reduced clutch was completed by the same female. In other cases, where the egg-size did not differ so much from the mean for the population, it is hard to rule out mixed clutches. In the relevant literature I have not found any information on clutch replenishment in the successive ovulatory cycle. Such a capability may possibly be of survival value in the great crested grebe, as one of the parents can take care of the young hatched earlier while the other parent continues to incubate later eggs.

J. MARSZAŁEK (unpublished data) found that on Lake Żarnowieckie in nests forming a dense colony the number of eggs was higher than in clutches of pairs nesting in dispersal. The results — 4.73 eggs per nest in a colony is very high not only in comparison with the values found on Lake Družno, but also with those in the literature (*e.g.* MELDE 1973, MIELCZAREK 1980, BAUER and GLUTZ 1966). By analysing egg size in colonial nests on Lake Żarnowieckie I have found that the standard deviations of the breadths of eggs in some clutches are comparatively high and on an average increase with the increasing clutch size (Fig. 12, Table 4). In the equation used for the calculation of the standard deviation:

$$s = \sqrt{\frac{(x - \bar{x})^2}{N - 1}}$$

(PARKER 1978) the denominator is the number of degrees of freedom $N - 1$. For small N , with a homogeneous set assumed, the value of s should decrease

with an increase in sample size. Data from Lake Żarnowieckie indicate a non-homogeneous sample, which means that to large clutches more than one female contributed. On Lake Drużno among nests built in colonies I also found

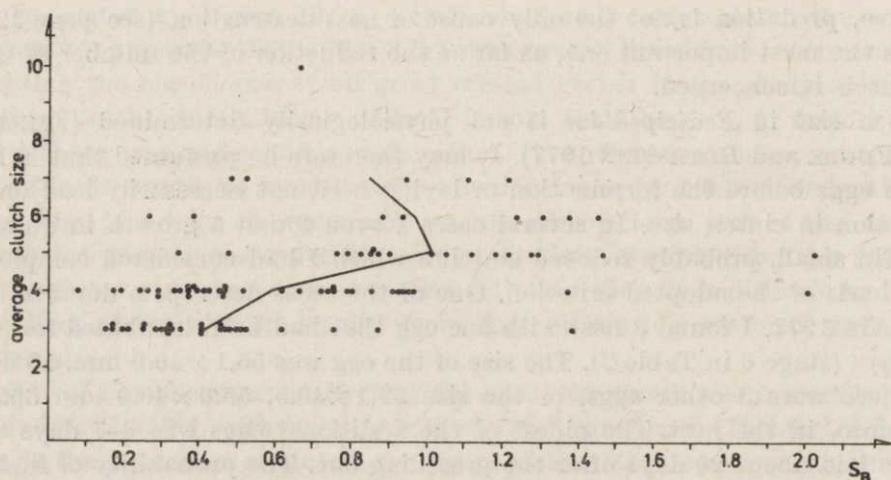


Fig. 12. The relation of the standard deviation of the average egg breadth (s_B) and the average clutch size on Lake Żarnowieckie in 1980

The line connects average values

Ryc. 12. Zależność odchylenia standardowego średniej szerokości jaja (s_B) od średniej wielkości zniesienia na J. Żarnowieckim w 1980

Table 4. Mean standard deviations of egg breadth (s_B) in variable size clutches

Tabela 4. Średnie odchylenia standardowe szerokości jaj (s_B) w zniesieniach różnej wielkości

Origin of data Pochodzenie danych		Clutch size — Wielkość zniesienia				
		3	4	5	6	7
A colony on Lake Żarnowieckie in 1980*	s_B	0.42	0.59	1.01	0.97	0.85
	N	23	36	19	8	5
Kolonia na J. Żarnowieckim w 1980*						
Lake Drużno 1980, colonies without gull	s_B	0.48	0.64	0.84		
	N	27	31	8		
Kolonia bez mew						
L. Drużno 1980, a colony mixed with gulls (Gęsia Bay)**	s_B	0.50	0.51	0.70		
	N	44	64	13		
Kolonia z mewami (Zat. Gęsia)						
L. Drużno 1980, dispersed nests	s_B	0.55	0.50	0.48		
	N	20	47	10		
Gniazda rozproszone						

* Difference between 4-egg and 5-egg clutches: $p < 0.001$;

— Difference between 3-egg + 4-egg clutches and all others: $p < 0.001$;

**Difference between 4-egg and 5-egg clutches: $p < 0.05$;

All: Student's t -test.

a clear growth of s_B in bigger clutches (Table 4). So here also different females lay eggs in one nest. In my opinion, this phenomenon must be considered a density-caused behavioural mistake, detrimental to the breeding results. To be precise, I must add that the distances between nests in the colonies compared, were on Lake Żarnowieckie much smaller (J. MARSZALEK unpublished data) than on Lake Drużno.

In dispersed nests on Lake Drużno I found a slight decrease, as expected, in the mean s_B as the clutch size increased (Table 4). This to some extent confirms the correctness of the above reasoning.

It has been found that in many bird species the egg breadth in a clutch, and even in different clutches of the same female varies less than the length (*e.g.* MYRBERGET 1977). The same is also found in the great crested grebe, at least within one clutch (the average variation coefficients $\bar{v}_B = 1.5\%$, $\bar{v}_L = 2.6\%$). So the egg breadth, and not length, better characterizes the female. The analysis of standard deviation s_B can be used for checking whether a clutch sample contains multiple clutches, or for comparing the relative frequency of their occurrence in different groups, but it should not be used uncritically for identifying such clutches.

In particular clutches the cause of considerable variation in egg size may be different, and a small s_B is not a proof that all the eggs have been laid by one female. There is a considerable probability that two randomly selected females will lay eggs of a breadth similar to the mean for a population, and then also in mixed clutches the s_B will be small.

The observed clutch sizes depend not only on the number of eggs really laid by a female, but also on other factors, to a large extent independent of the female. For this reason considerable caution is required when conclusions are drawn.

Egg size

The mean egg dimensions and the volumes calculated from them are presented in Table 5. I have not found any permanent egg size differences dependent on nest location. Differences between breeding seasons do not reach the level of statistical significance either. It has been found that in many bird species females lacking breeding experience lay smaller eggs than older females (*e.g.* FJELDSÅ 1973a, MYRBERGET 1977). Due to the attachment of experienced females to the site of their previous nesting, new sites are usually occupied by young individuals breeding for the first time (FJELDSÅ 1973a). As there occurred considerable habitat changes between the breeding seasons, I did not in general differentiate between traditional and new nesting sites. It was, however, possible in a few cases. Included among new breeding sites in 1977 were the "Clumps". The mean egg size for 19 clutches was in this case

Table 5. Mean parameters of eggs in clutches (mm)

Egg length (L) and egg breadth (B) were measured to the nearest 0.1 mm with a slide calliper;

$$V = \frac{0.947 \pi LB^2}{6000} \quad (\text{REYNOLDS 1974}); s - \text{standard deviation}$$

Tabela 5. Średnie parametry jaj w zniesieniach (mm)

Długość jaja (L) i jego szerokość (B) mierzone suwmiarką z dokładnością do 0.1 mm; s – odchylenie standardowe

Location – Lokalizacja		1977	1978	1979	1980
Colonies without gulls Kolonie bez mew	N	58	81	61	73
	B	36.64	36.92	36.84	36.54
	s_B	1.09	0.93	1.00	1.11
	L	54.88	54.71	54.93	54.86
	s_L	2.33	2.20	1.87	2.11
	V (cm ³)	36.53	36.98	36.60	36.32
A colony near Janowo (with gulls) Kolonja z mewami	N	22	28	24	28
	B	37.16	37.27	36.80	36.78
	s_B	0.91	0.96	1.08	1.14
	L	55.17	55.34	54.33	54.24
	s_L	2.18	2.18	2.93	2.82
	V (cm ³)	37.77	38.11	36.48	36.38
A colony in Gęsia Bay (with gulls) Kolonja z mewami	N	128	113	122	134
	B	36.69	36.55	36.74	36.63
	s_B	1.11	1.15	1.18	1.06
	L	54.93	54.49	53.03	54.46
	s_L	2.67	2.37	2.02	2.86
	V (cm ³)	36.66	36.09	36.83	36.23
Dispersed nests Gniazda rozproszone	N	91	45	69	82
	B	36.77	36.62	36.93	36.87
	s_B	1.08	1.01	1.12	1.06
	L	54.58	54.72	54.77	54.41
	s_L	1.92	2.34	2.05	2.21
	V (cm ³)	36.59	36.39	37.04	36.67
Lake Drużno Total Ogółem	N	312	236	282	313
	B	36.78	36.88	36.75	36.71
	s_B	1.07	1.07	1.07	1.13
	L	54.89	54.81	54.62	54.61
	s_L	2.05	2.13	2.11	2.15
	V (cm ³)	36.81	36.96	36.56	36.49

35.89 × 54.62 mm. The mean egg breadth there was smaller ($p < 0.05$ Student's t -test) than the mean for all clutches in whole breeding season of 1977, and the mean for the "Clumps" in the following year. In 1978, another site newly occupied by great crested grebes was area "C". The mean egg size for 15 clutches was 36.64 × 54.50 mm and did not significantly differ from average parameters for all clutches in that year. This can to some extent confirm the presumption that the birds nesting in area "C" had abandoned their former sites in area "A".

The mean length and breadth of great crested grebe eggs on Lake Drużno decrease during the breeding season. This obviously is accompanied by a decrease in the mean volume calculated from them, the seasonal changes in the latter reaching a value of 2–3 cm³ (Figs 2–6). The egg size decrease occurs, with some shift in time, independently in the clutch groups distinguished on the basis of nest location (Fig. 13). Here changes in \bar{B} are much more regular

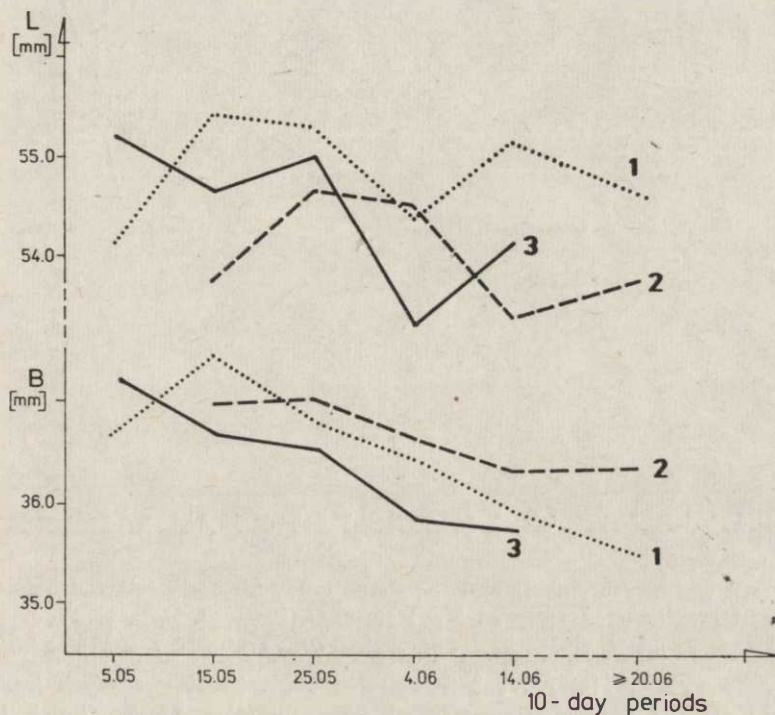


Fig. 13. Average egg measurements in 1980

1 – dispersed nests; 2 – nests in monospecific grebes breeding colonies; 3 – nests in mixed black-headed gull-grebes breeding colony

Ryc. 13. Średnie wymiary jaj w 1980

1 – gniazda rozproszone; 2 – gniazda w koloniach jednogatunkowych; 3 – gniazda w koloniach mieszanych

than changes in \bar{L} . These seasonal variations, and the asynchrony of their course in groups permit the methodical conclusion that any ovimetric data that are to describe a population must be representative for the whole breeding season.

Some of the late clutches are characterized by egg sizes below the range found in the initial period (Fig. 14). Thus the seasonal decrease in mean values is the result of a delayed start of breeding by birds laying clearly smaller eggs. These probably are females breeding for the first time. If it really is the case, the date of their nesting does not depend on calendar dates, since in each

of the different nest categories the decrease in egg size occurs at a different time (Fig. 13). Grebes nesting under specific conditions, e.g. singly or in colonies probably reach the ready-for-breeding status at different dates.

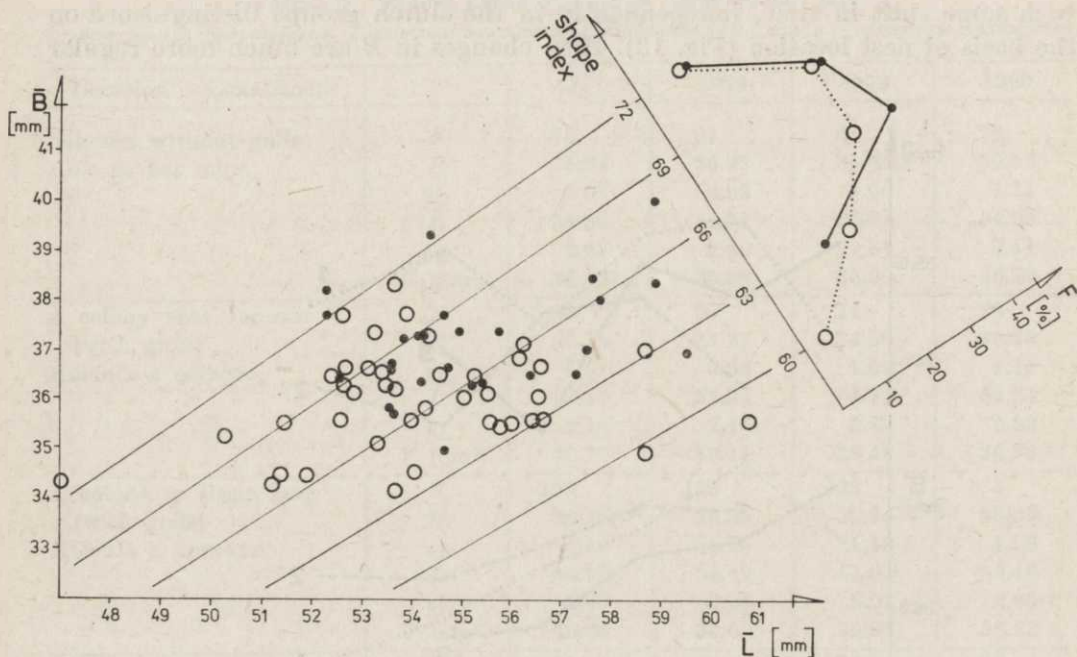


Fig. 14. Average egg measurements and the shape index for early (started before 11 May) and late (started after 25 May) clutches, in Gęsia Bay, in 1980

Periods are chosen arbitrarily. Black dots - early clutches ($N = 27$), circles - late clutches ($N = 43$)

Ryc. 14. Średnie wymiary jaj i wskaźnik kształtu dla zniesień wczesnych (rozpoczętych przed 11 maja) i późnych (rozpoczętych po 25 maja) w Zatoce Gęskiej, 1980

Okresy wybrane dowolnie. Kropki - zniesienia wczesne; kółka - zniesienia późne

A seasonal egg-size decrease in great crested grebe was also found by MIELCZAREK (1980). This tendency was also reported for many other bird species (e.g. BLUMS 1973, FJELDSÅ 1973a), but it is not a rule, for some birds lay the largest eggs in full breeding season, e.g. *Plautus alle* (STEMPNIEWICZ 1981). A seasonal decrease in egg size is most often related to delayed breeding of young and weaker females, or to the appearance of replacement clutches (BLUMS 1973). It seems that in *Podicipedidae* the latter phenomenon has no effect on the seasonal egg-size decrease. This is suggested by results from experiments carried out by FUGLE and ROTHSTEIN (1977) on *Podilymbus podiceps*, and data reported by FJELDSÅ (1973a) on the lack of significant egg-size differences between the primary and secondary clutches of the same *Podiceps auritus* females.

An analysis of the relationship between the egg size and the sequence of

their laying is far more complex in the case of the great crested grebe than *e.g.* in *Laridae* which are characterized by a fairly determined clutch size (*e.g.* LUNDBERG and VÄISÄNEN 1979). Apart from this, because of the irregularity and low frequency of my checking, only for few clutches was I able to determine the laying sequence. As I had more data for the first two and the last two eggs in clutches, I made comparisons only for these egg pairs. The first egg is smaller than the second one: in breadth on the average by 0.25 mm, in length by 0.30 mm, and in volume by 0.69 cm³. The differences are statistically significant ($p < 0.003$, $p < 0.05$, $p < 0.003$, respectively, Student's *t*-test; calculated for 228 clutches). The last egg in a clutch is on an average longer by 0.06 mm, narrower by 0.12 mm, and smaller in volume by 0.16 cm³ than the last but one. Calculated on the basis of 101 clutches, the differences appeared not to be statistically significant. The relationship between the size of the eggs and the sequence of their laying may be energy- or physiology-dependent. It is unlikely for the small size of the first egg to be the result of food conditions, so there remains the physiological agent, which could be interpreted, *e.g.* in the following way: due to a certain level of hormones, the completion of the development of the reproductive system is only reached after the first egg has been laid. MIELCZAREK (1980) also found out that in the great crested grebe the second egg is larger than the first one. Unfortunately, the analysis he carried out of the successive eggs in clutches is hard to interpret, because the author combined data from clutches of different sizes.

A comparison of the mean breadths of eggs in clutches differing in size indicates that there are differences in this respect between small clutches, of up to 3 eggs, and large ones (Table 6). The growth in the mean egg breadth

Table 6. Mean egg breadths (\bar{B}) in variable size clutches
Tabela 6. Średnie szerokości jaj (\bar{B}) w zniesieniach różnej wielkości

Clutch size Wielkość zniesienia	1	2	3	4	5	6
<i>N</i>	25	132	425	553	129	15
<i>B</i> (mm)	36.66	36.59	36.62*	36.84*	36.90	37.10
<i>sd</i>	1.42	1.16	1.07	1.02	0.95	1.08
<i>B</i> (mm)		36.61**			36.86**	
<i>sd</i>		1.11			1.00	

*Difference: $p < 0.003$

**Difference: $p < 0.001$

All Student's *t*-test

with an increase in clutch size can to some extent be accounted for by a statistical decrease of the effect of the first egg, a slightly smaller one. However, if the value is taken into account of the mean difference of \bar{B} between the first egg and second egg of a clutch (0.25 mm), it can be calculated that this factor

cannot account for the whole variation observed. Besides, if this were the only cause, we would have to expect a more or less even growth of \bar{B} , and not any step variation. The similarity to the results from studies of other species (e.g. BLUMS 1973, FJELDSÅ 1973a, MYRBERGET 1977) suggests that the seasonal decrease in clutch size and egg size, and the relationship between \bar{B} and clutch size are connected with age differences of the females. Surely, the limit between the clutch and egg sizes typical of young females, and those characteristic of experienced females is not sharp. The mean egg breadth difference between clutches laid by "primiparae" and older females is probably greater than between small and big clutches in Table 6. This is due to the fact that some of the small clutches arose as a result of the reducing of bigger ones. The real mean egg breadth difference between clutches of beginners and experienced females is better shown from Figure 14. It seems that of the egg dimensions \bar{B} is more suitable for the identification of clutches probably belonging to young females. The egg shape index, sometimes used for this purpose, does not seem adequate (Fig. 14). In order to relate the phenological variation of the different parameters, presented in Figure 15 is the relationship between the clutch

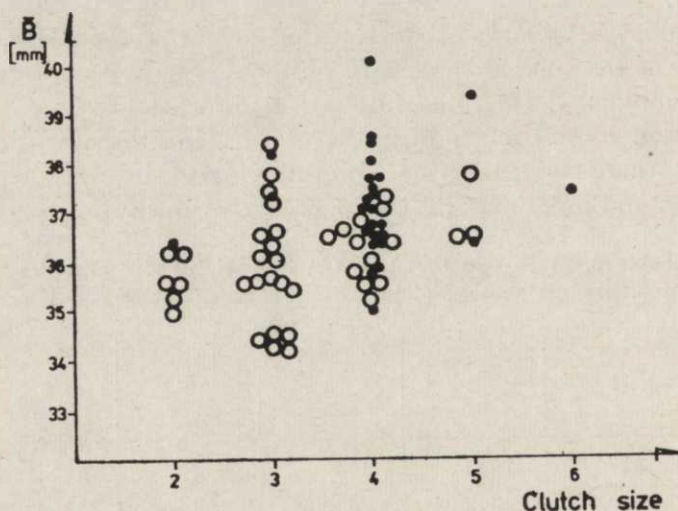


Fig. 15. Average egg breadth in a clutch (\bar{B}) and the clutch size in early and late clutches. Gęsia Bay, 1980

For explanation — see Fig. 14

Ryc. 15. Średnia szerokość jaja w zniesieniu (\bar{B}) i wielkość zniesień wczesnych i późnych
Objaśnienia — patrz ryc. 14

size and \bar{B} for groups of early breeders and late breeders, the egg sizes of which have been used for the preparation of Figure 14. By comparing both figures and taking into account the above-mentioned points and reservations, late

clutches containing up to 3 eggs, with a \bar{B} below 36 mm, can be ascribed to females-beginners. The "lateness" of a clutch must, of course, be estimated in relation to the phenology of nesting in a given area or conditions. Unfortunately, it is impossible to estimate the degree of overlapping of the ranges of the parameters to be used for ageing the females, especially on account of the complexity of the factors on which the clutch size found in the field depends. The results presented above indicate that there occur variability in phenology, clutch size and egg size related to the age of the female. These parameters could be used for the estimation of the age structure of a population only after carrying out a similar analysis for a sample of clutches laid by females of known age.

The fact that larger clutches contain larger eggs indicates that the number of eggs laid is not directly limited by the actual food factor*. This is confirmed by the results of FUGLE and ROTHSTEIN (1977). By regularly removing eggs, these authors obtained a 13-egg clutch from one *Podilymbus podiceps*, but they did not find any significant decrease in egg size or shell thickness. In some species, or under certain conditions the role of food factors and the associated energy reserve of the female may be important, but they influence first of all the clutch size (PINOWSKA 1979).

Egg-covering behaviour

In check whether the tendency to cover nests is equally strong throughout the incubation period, I divided it into four phases, easy to identify by the water test:

- I. Egg-laying phase (stages 1-2 in Table 2);
- II. Early incubation phase (from stage 3 to the attainment of stage 7 by first egg);
- III. Late incubation phase (from the completion of the preceding phase to the appearance of a hole in the first hatching egg);
- IV. Hatching phase (till the end of the nesting period).

The summarized data indicate that in the main incubation phases nests are covered more often than in the initial period and the terminal period (Table 7).

One of possible explanations to this phenomenon is based on the assumption that in the great crested grebe there is individual variation in the development of the egg-covering instinct. Since egg-covering increases the safety of a clutch (MIKIANS 1980), the probability of its survival till later incubation phases would also vary. Natural selection would favour the persistence of

*There may be an indirect effect through a hunting efficiency which can be associated with age.

Table 7. Covering of eggs. Lake Drużno, 1976 and 1979
Tabela 7. Przykrywanie gniazd. Jezioro Drużno, 1976 i 1979

Nesting stage Faza lęgu	Nests — Gniazda			total for stage (100%) suma (100%)
	covered przykryte	poorly covered słabo przykryte	uncovered odkryte	
I	200 (54.4%)	31 (8.4%)	137 (37.2%)	368
II	198 (72.3%)	17 (6.2%)	59 (21.5%)	274
III	144 (73.1%)	19 (9.6%)	34 (17.3%)	197
IV	20 (35.7%)		36 (64.3%)	56
Total — Razem	562	67	266	895

Differences in proportions: I-II $p < 0.001$; I-III $p < 0.001$; I-IV $p < 0.001$; II-IV $p < 0.001$; III-IV $p < 0.001$; II-III $p < 0.5$.

All: chi-square test.

Nests defined as poorly covered were for further comparisons included among those declared as covered.

this behaviour. This explanation can be rejected because often nests which I had found uncovered in phase I were found covered during later checking visits. It follows that the tendency to cover eggs really increases in phases II and III, and is not only a statistical effect of the action of predators. This does not, of course, rule out individual variation in this respect. Further on (page 137) I shall try to explain these changes as a specific breeding strategy.

The above presented results describe all the great crested grebe nests found on Lake Drużno. The only group that appeared to be different included nests in a mixed colony near Janowo (area "F"). The differences in the proportions of covered eggs are significant only between phase IV and all other phases (Table 8). A comparison of Tables 7 and 8 permits the statement that in the colony near Janowo the percentage of uncovered eggs is significantly

Table 8. Covering of eggs in a mixed, black-headed gulls-grebes breeding colony. Lake Drużno, the years 1977-80, area "F" in Figure 1
Tabela 8. Przykrywanie jaj w kolonii mieszanej

Nesting stage Faza lęgu	Nests — Gniazda			total for stage (100%) suma (100%)
	covered przykryte	poorly covered słabo przykryte	uncovered odkryte	
I	26 (44.1%)	3 (5.1%)	30 (50.8%)	59
II	36 (56.3%)		28 (43.7%)	64
III	35 (59.3%)	2 (3.4%)	22 (37.3%)	59
IV	2 (11.8%)	1 (5.9%)	14 (82.3%)	17
Total — Razem	99	6	94	199

Only the proportion difference I+II+III-IV is statistically significant ($p < 0.01$, chi-square test).

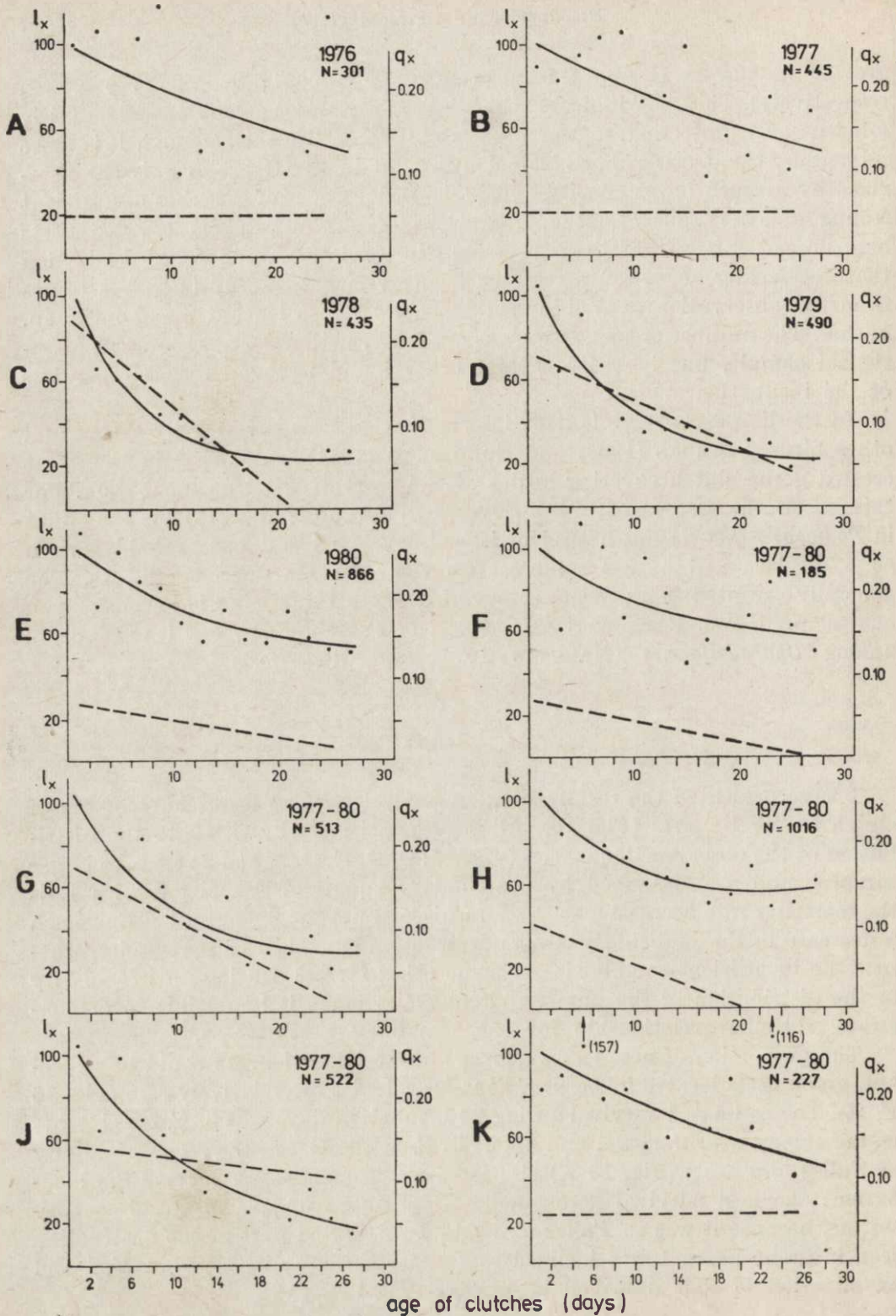
greater in phases II and III ($\chi^2 = 12.26$, $p < 0.001$; $\chi^2 = 9.51$, $p < 0.01$, respectively). This may indicate that a compact *Laridae* colony ensures a fairly efficient nest protection, and grebes are able to realize this. Though it is more numerous, the *Larus ridibundus* colony found in the Goose Bay is characterized by a much lower density and perhaps does not offer grebes a sufficient feeling of safety, because the proportions of uncovered and covered nests here do not differ from those presented in Table 8. Another fact indicating that the feeling of safety affects the nest-covering tendency in grebes comes from the observation of well-hidden nests, e.g. those located under *Salix* sp. bushes. The number of such cases was not large, so they cannot represent a statistical sample, but in those nests I often found uncovered eggs regardless of the incubation stage.

In the literature there is little information on nest covering by grebes and other birds. SIMMONS (1955) and GORDIENKO (1981) found that in the great crested grebe clutch covering begins at the start of the true incubation. For this reason, the first egg often is uncovered. BROEKHUYSEN (1973) has found that in *Podiceps ruficollis* this behaviour is well developed and has probably arisen as a displacement a nest-building behaviour under stress conditions. The generally accepted function of the covering of eggs by grebes is to mask them against predators. Egg covering is typical of *Podicipedidae*, but it also occurs among *Charadriiformes* (MACLEAN 1974) and *Anseriformes*.

Nest losses

I have presented the results from an analysis of nest losses in the form of clutch survival curves (Fig. 16). All curves satisfactorily fitted to the distribution of the observed frequencies (Fig. 16: C, D, E, G, H and J) concern larger samples, and are described by a secondary equation. Associated with it is the mortality rate decreasing with age. This permits the presumption that such a decrease in the probability of nest destruction is typical of the species, whereas the insufficient sample size or some other factors causing an irregularity in the distribution of the observed frequencies make it impossible to demonstrate a similar relationship for the remaining nest groups.

The proportion of nest losses depends on nest location. As could be expected, grebe nests located in *Larus ridibundus* colonies are relatively safe (Fig. 16 F, H). The estimated survival during 28 incubation days was 58 % for clutches in the colony near Janowo, and about 57 % in the Goose Bay. The proximity of *Fulica atra* nests (Fig. 16 K) also increases the chance to survive the incubation; the nest survival here amounted to about 50 %. This result surprises me, because it was to *Fulica atra* that I attributed part of the destruction seen in grebe nests. I was inclined to suspect this by direct observation and examination of eggs damaged in a way typical of the coot.



In nest located far from *Larus ridibundus* and *Fulica atra* the losses are far greater. The survival of dispersed nests came up to 28 % (Fig. 16 G), and in monospecific colonies — 18 % (Fig. 16 J). In the latter case the mortality rate drops very slowly with age.

It is more difficult to analyse survival differences between different breeding seasons. In the first two years (Fig. 16 A and B) the curve is poorly fitted to empirical data. On this basis it can only be estimated that about 50 % of nests survived incubation. The well fitted curves of the years 1978 and 1979 indicate a low survival — about 22 %. The result for 1980 requires a cautious interpretation. In that breeding season data from the Goose Bay represented 59 % of all data. In the preceding seasons they constituted only 37 % of all data (differences between successive years did not exceed 1 %). Since nesting among *Larus ridibundus* ensures a greater safety, I suppose that this change resulted in an over estimation of the result for the whole year. The effect of this factor can be estimated. Assuming that in 1980 about 60 % of the data came from nests located in gull colonies, where the survival rate was about 55 %, and the remainder from nests in less favourable locations with a survival of about 22 %, we obtain a total result of 42 % ($60\% \times 0.55 + 40\% \times 0.22 = 41.8\%$). The value determined by the regression equation is over 10 % higher, thus the survival of clutches in 1980 was indeed better than in the two preceding years.

I did not compare the survival of nests built at different dates, because nesting phenology is connected among other things with nest location. There is some reason for thinking that towards the end of the breeding season losses are higher than in the earlier phases. In 1980, I found 24 nests in which egg laying started in July. 22 of those nest were destroyed, and I have not been able to find out what happened to the remaining 2.

The method I have used for clutch loss estimation is not based on an analysis of the fate of particular nests, but it estimates the survival probability of clutches from a sample under study. For this reason I am unable to present the relative importance of the different factors causing clutch destruction. On Lake Drużno such losses were caused by the following:

1. Water level changes. Though grebe nests are included among floating

Fig. 16. % surviving clutches (l_x — continuous line) and their mortality rate (q_x — dashed line) on Lake Drużno

A, B, C, D, E — all data for the consecutive years 1976–80; F — mixed black-headed gulls-grebes breeding colony, at Janowo village in the years 1977–80; G — dispersed (territorial) nests in the years 1977–80; H — mixed black-headed gulls-grebes breeding colony in Gęsia Bay in the years 1977–80; J — monospecific breeding colonies in the years 1977–80; K — nests in the vicinity of coots nests in the years 1977–80

Ryc. 16. % zniesień przeżywających (l_x — linia ciągła) i ich wskaźnik śmiertelności (q_x — linia przerywana) na Drużnie

A, B, C, D, E — wszystkie dane dla kolejnych lat 1976–80; F — kolonia mieszana koło Janowa w latach 1977–80; G — gniazda pojedyncze; H — Kolonia mieszana w Zatoce Gęziej w latach 1977–80; J — kolonie jednogatunkowe w latach 1977–80; K — gniazda założone w sąsiedztwie gniazd łysek w latach 1977–80

nests (GOTZMAN and JABŁOŃSKI 1972) they are like those of other waterfowl species, sensitive to water level oscillations (HUDEC 1979). The cause of destruction in this case is not always the flooding of nests. They are usually anchored, and a water level drop can cause their tilt. At a low water level nests located on islands and in shallow places become difficult to access. However, grebes are persistent in overcoming such obstacles, and I have never found grebes having abandoned their nest only because they had to walk to it. Information about great crested grebes using a nest located on dry ground has also been reported by LEYS and DE WILDE (1968). The lack of a noticeable relationship between water-level oscillation amplitude and frequency during the breeding season and the survival of nests during that season indicates that this oscillation does not cause high clutch losses.

2. Waves. On Lake Drużno, the role of this factor may be more important at the beginning of the breeding season when both plants with floating leaves and emergent vegetation, is still poorly developed. Its later growth efficiently lessens waves, but at the beginning of May this factor can make difficult and delay the building of nests at sites that are less sheltered, *e.g.* in the "Clumps". More exposed to the action of waves are new, low and unbeaten nests. Since nest building often continues during the egg laying and later, the effect of waves on the mortality rate of nests may depend on their age.

3. Predation. Of the potential predators enumerated in this paper (page 98), capable of causing losses to grebe clutches, I observed the action of *Fulica atra* several times, of *Circus aeruginosus* on two occasions, and of *Pica pica* once. I cannot rule out the possibility that in these cases my presence enabled the predators to access nests. On one occasion I saw a *Circus aeruginosus* female attacking an incubating great crested grebe: the latter jumped off its nest and while on the water it tried in vain to keep the predators off the nest. During none of my nest-checkings did I observe grebe egg destruction by *Larus ridibundus*. Nor did BUJNOWICZ (1978) and MIKIANS (1980) who watched birds in the Goose Bay. PTASZYK (1981) found one great crested grebe chick in *Larus ridibundus* food samples. In several cases I found gnawed remains of adult grebes in nests or near them.

The role of *Fulica atra* in the destruction of great crested grebe eggs requires a detailed discussion. Many authors have noted the fact that nests of these two species are found in close proximity (BLUMS 1973, ŁAWNICZAK 1982, MELDE 1973, ONNO 1959). It was usually found that *Fulica atra* started breeding first (MELDE 1973, ŁAWNICZAK 1982), but this is not a rule on Lake Drużno. In the literature information on grebe egg destruction by *Fulica atra* is rarely found. However, MIKIANS's (1980) observations, as well as mine, indicate that they may cause serious losses. A relatively high survival rate of grebe nests built near *Fulica atra* indicates that more important is the safety they

ensure to the nest and neighbourhood. It may be assumed that there are four mutually non-excluding causes of this contradiction:

A. The belief, based on frequent detection of traces of its feeding, that *Fulica atra* plays a big role in the destruction of great crested grebe nests is exaggerated. *Fulica atra* eats eggs in the nests in which it finds them, and leaves shells pierced in a fairly characteristic way. Detection of traces of feeding of *Pica pica* or *Corvus corone cornix* is less likely as these birds as a rule carry away intact, or only punctured eggs in the bill (LOMAN and GÖRANSSON 1978).

B. Feeding on eggs of other birds may be the specialization of few individuals of *Fulica atra*, while others do not destroy clutches, and since all of them actively defend their territory against predators and conspecifics, they may on an average raise the survival of nearby nests. An example of such a specialization in ransacking *Podiceps nigricollis* nests was observed by FJELDSÅ (1977a) in *Gallinula chloropus*.

C. *Fulica atra* can access eggs only when the great crested grebe moves away. Such situations are rare unless the incubating bird has been flushed. These two species differ in their response to man approaching the nest. Grebes leave it when the threat is still far, and they swim away, if the depth of the water permits this — under water, to a considerable distance. This is a kind of passive nest protection; the birds avoid to attract the attention of a potential predator to the nest. *Fulica atra* runs away to a much shorter distance. If it leaves the nest at the last moment, it does so ostentatiously, running on the water. If it leaves the nest quietly, it hides near by and remains in hiding so persistently that sometimes I was able to catch a coot with my hand. On other occasions, staying near the nest it moves invisible in dense vegetation, giving off luring or warning calls. During my checking visits, *Fulica atra*, staying near by, were able to ransack grebe nests. The fact that I often found traces of such an activity in several neighbouring nests may indicate a temporal and causal relationship between the destruction and my presence. If this interpretation is true, the relatively high survival of nests located near *Fulica atra* is the result, in a way, of a low frequency of my checking visits. On the other hand, foraging in a situation when the bird's own nest is in danger seems, from the point of view of behaviour, little probable and suggests that it may be some kind of a displaced activity connected with inhabited aggression.

D. From my notes I am unable to restore the facts and decide whether the observed cases of grebe egg destruction by the coot took place in the immediate vicinity of its own nest. Perhaps the nest neighbourhood is a protected area and not a feeding ground, as can sometimes be observed in other predators.

4. Other causes. I include here the destruction caused by other animal species which used a nest as a resting or feeding place. Among these can include ducks (males of *Anas* sp. just beginning to moult like particularly to sit on clumps

and islands), *Ardea cinerea* (page 104) and *Ondatra zibetica*, the activity of which was indicated by *Anodonta cygnea* shells accumulated in old nests. In grebe nests located in *Larus ridibundus* colonies a similar role is played by gull nestlings, and particularly the fledgelings. When flushed, young gulls run away into the water and then get on dry places to dry. They do so in groups, and I noticed that grebe nests are as attractive to them as other clumps and islets. In mixed colonies I several times encountered such trampled great crested grebe nests, but I cannot tell whether their condition was the cause or the result of clutch abandonment. If it was the cause, then the observed synchronized egg-laying by grebes and *Larus ridibundus* could be regarded as a kind of protection. In several cases I found gull nests built on old great crested grebe nests. In this case, too, the gulls may have used platforms destroyed or abandoned for other reasons. Anyway, this is not a frequent phenomenon. Maybe, *Larus ridibundus* get some benefits by using as a nest base platforms built by grebes.

The cause of destruction and losses in grebe clutches on Lake Družno may also be the activity of fishermen who regularly set up nets of various types in places densely inhabited by birds. I must stress the fact that I never found a deliberate nest destruction. However, accidental damage, caused directly or indirectly due to bird flushing seems unavoidable. Adult grebes often get entangled in nets set up near their nests, which can probably be tantamount to clutch loss or abandonment, even if the birds are freed later on. Among the other causes of losses I must also include my presence near the nests, as it flushed the birds and enabled the predators to access the eggs.

I have found that nest mortality rate decreases with nest age, and one might try to decide which of the loss causes enumerated can change their intensity in this way. Obviously, none of them itself depends on nest age, but the effect of some of them can be modified by changes in the behaviour of grebes. The risk connected with predation decreases as a result of the increasing tendency to cover nests (page 125). The importance of this behaviour has been demonstrated experimentally by MIKIANS (1980). In the course of incubation, eggs take a more cryptic colour; adult birds show a stronger attachment to the nest, and when flushed, they return to it earlier (BUJNOWICZ 1978). The shield provided by emergent vegetation growing near a nest becomes more efficient as time passes. In addition to all these factors we must mention the selective factor. Some of the newly built nests have a less favourable location, are not well hidden and their construction is poor. These nests are the first ones to be eliminated by both predators and physical factors. The ability to choose a proper nest site may depend on the breeding experience of birds.

Grebes are not the best object for studies of the breeding success. Their relatively inaccessible nests, their being precocial, difficult to identify — both individuals and families on the water, aggravated by frequent division of offspring between the parents make it difficult to gather representative data.

The easiest, comparatively, to obtain are data on the size of clutches and broods led by adult individuals. As it is difficult to determine the number of non-breeders, or unsuccessful breeders, to age chicks at a distance, and as there are other problems, as mentioned above, information on the breeding efficiency of the great crested grebe must be considered with caution.

Quantitative data in the literature indicate considerable variation in the breeding success. WITKOWSKI (1967) has reported low nest losses — 24 % from ponds near Milicz. ŁAWNICZAK (1982) found in 1972, also on Milicz Ponds, that only 31 % of 201 clutches ended with at least one chick hatched. Predation accounted for 50 % of the nest losses there, whereas 19 % of nests got lost for unknown reasons. On the ponds under study 115 nests formed a colony located in flooded *Salix* sp. scrub. In that colony only 26 % of nests survived till the end of the incubation period. A much higher survival has been found for nests built in thick reeds.

MIELCZAREK (1980) found that in great crested grebe colony on a dam reservoir on the Czarna Przemsza river near Siewierz (southern part of Poland) in at least 27 % of nests no chick hatched.

On Lake Żarnowieckie MARSZAŁEK (unpublished data) found nest losses amounting to 50 % in two great crested grebe colonies. In dispersed nests in *Schoenoplectus lacustris* and *Phragmites communis* thickets a 34 % clutch survival was found, and in clumps of *S. lacustris* alone — 21 %.

LEYS *et al.* (1969) inform that on a polder in Holland 111 out of 263 nests (42 %) survived till hatching. Towards the end of the breeding season greater losses were recorded.

PREST and JEFFERIES (1969) say: "it could be expected that of 100 pairs of great crested grebes on lakes in England in 1965, 79 would attempt to breed and of these 67 would fledge young". This gives a very high survival rate, 84 %, the more so as it comprises not only the nest period, but the long parental care as well.

ONNO (1959) has stated generally that though eggs are covered, *Corvus corone*, *C. corax* and *Circus aeruginosus* destroy a large proportion of them, especially when grebes, flushed by people, leave nests. More destruction is then done to new clutches, which birds cover more carelessly and leave more often. This opinion fully agrees with my observation, and even though it is not supported by quantitative data, it suggests a decrease in nest mortality rate with age.

Artificial nest experiments carried out by MIKIANS (1980) have shown, similarly to my data, a favourable effect of the proximity of *Fulica atra* and *Larus ridibundus* on the fate of grebe clutches.

Apart from the incomplete comparability of these data, it may be stated that the proportion of losses is mainly dependent on local factors and may vary considerably even within the same water body. The effect of colonial nesting, at least in monospecific colonies, has no unequivocal effect on the

result of breeding. Important in this case seems to be the kind of environment, offering a better or worse shelter for the nest and accessibility to predators. It seems to me that *Salix* sp. scrubs highly favour the penetration of a colony by *Corvidae*, whereas thick reeds make the activity of the latter slightly more difficult. I think that even the thickest vegetation cannot completely hide a dense colony of grebes consisting of over a score pairs. For this reason, it is only owing to the location of a colony under the "umbrella" of birds actively protecting nests (*Laridae*, *Fulica atra*), or in habitat, where not so much the finding as penetration is made difficult, that in colonies losses are sometimes lower.

GENERAL DISCUSSION

The great crested grebe is a species showing, at least in Europe, a growth in numbers and range. A short but full, and fairly up to date review of literature data on this subject has been presented by CRAMP and SIMMONS (1977). The growth in numbers is very fast. In Holland, for instance, in 1932 the number of pairs was estimated at 300 or less, whereas the 1967 census estimated the numbers at 3300-3400 pairs (LEYS and De WILDE 1971). In the years 1946-65, in Great Britain there occurred almost a two-fold growth in numbers (PRESTT and MILLS 1966). In Scotland a relative population size stability was observed after the increase in numbers (SMITH 1974). There can be various causes of the growth in numbers. In the middle of the last century the level of numbers was low, due to, among other things, a mass killing of grebes for their skins. At the turn of the 19 century hunting for great crested grebes was forbidden, but there is no evidence to prove that the species has been growing in numbers since then (CRAMP and SIMMONS 1977). In Holland the growth began about 1925 (LEYS and De WILDE 1971). Grebe hunting continues, but this does not significantly affect the overall numbers of the species, although it can be considerable locally. JACOOBY *et al.* (1970 quoted after MELDE 1973) report that in the years 1961-68, 4721 individuals were shot on Lake Constance.

Other factors which may favour the growth in numbers of the great crested grebe also depend on man. They include water eutrophication, the rate of which has increased in the recent several score years. Unless a water body attains the polytrophic state, eutrophication increases primary and secondary production (KAJAK 1979). As a result, there are more suitable nesting sites for grebes and more food. Building new dam lakes and impoundments may also to some extent favour population growth (CRAMP and SIMMONS 1977). Of considerable importance may also be a decrease in the number of predators. Some great crested grebe pairs show a surprising habitat plasticity, owing to which they can use water bodies little suitable for nest building (ZANG 1976).

A case has also been reported of successful breeding of grebes at a site frequently visited by people, 2-3 m from a busy path (Van ESBROECK and DEVILLERS 1981).

Great crested grebe breeding density is primarily controlled by territorialism. This can be illustrated by Figure 17 based on my unpublished data

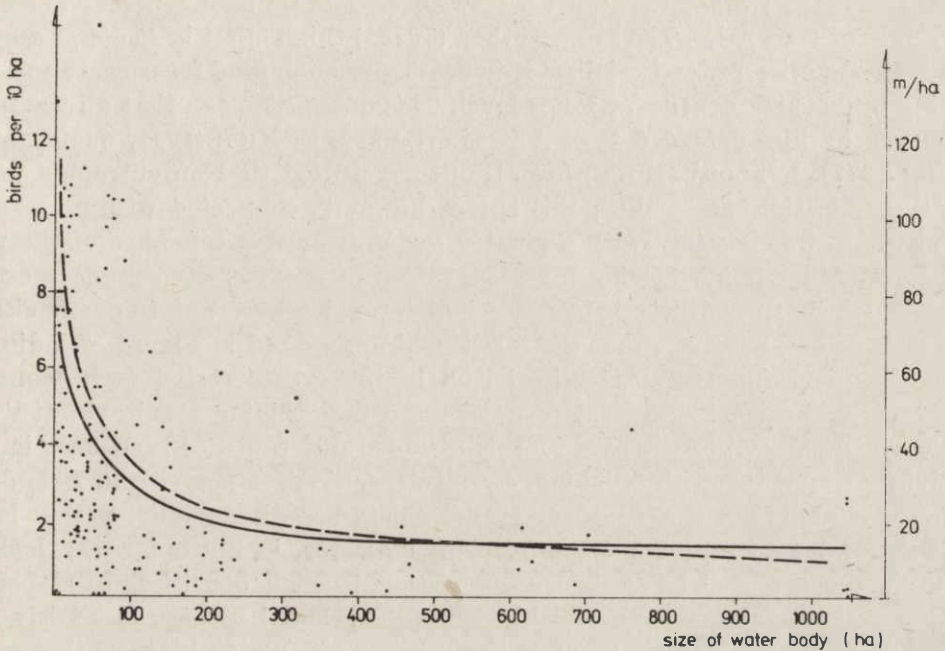


Fig. 17. Relation of the density of grebes and the surface area of the water body

Thick line connects the average values. Dashed line – relation of the circle perimeter to its area (right scale)

Ryc. 17. Zależność zagęszczenia perkozów od powierzchni zbiornika wodnego

Linia gruba łączy wartości średnie. Linia przerywana – stosunek obwodu koła do jego powierzchni (prawa skala)

from Poland, collected by means of a questionnaire. Grebe density drops on an average from 6.3 individuals /10 ha on lakes of 1-20 ha, to 1.2 individuals/10 ha on lakes of over 1000 ha; this decrease shows a considerable similarity to the change of the ratio of the perimeter of the circle to its area. A similar decrease in density with increasing surface area of water bodies was found in Holland by LEYS and De WILDE (1969). The amount of food for the great crested grebe, which hunts for small fish in open water (FJELDSÅ 1977b), depends on the area of the water surface, whereas the density of this species shows some relationship to the length of the shoreline, and thus depends to a large extent on nest habitat than on food habitat. On large lakes where the shoreline to surface area ratio is small, or on smaller water bodies very rich in food (e.g. the Milicz Ponds – ŁAWNICZAK 1982) grebes can form

colonies. There does not therefore occur a gradual decrease in territories, but a rapid, step-like change in their size and in behaviour of the birds. A similar phenomenon has been observed in Denmark in *Cygnus olor*. This species has a well developed territorialism, but at sites with very good food conditions it nests in large colonies (BLOCH 1970). A different way of using an habitat with suitable food conditions has been seen in *Fulica atra*. FJELDSÅ (1973b) found that the same territories were used twice during the same breeding season by different coot pairs. The same author (1973a) thinks that in *Podiceps auritus* the main function of territorialism is to provide enough food for parents and offspring by keeping density at a low level. This does not mean that all the pairs observed by him defended type A territories acc. to NICE (1941, quoted after ODUM 1977). FJELDSÅ (1973a) has also demonstrated that on eutrophic water bodies territories are smaller; this is not, however, connected with a stronger competition but possibly with a greater *Podiceps auritus* tolerance of the proximity of other pairs. During my observation of great crested grebes nesting in colonies sharp conflicts between neighbour pairs were not frequent either. It seems to me, however, that the relationship presented in Figure 17 indicates that the main function of territorialism in the great crested grebe consists in a passive protection against predators and maintaining a suitable distance from other pairs. A shortening of this distance can cause disturbances in the activities connected with breeding, e.g. intraspecific nest parasitism. It is difficult to imagine that this could be indifferent to breeding results. It thus leads to the wasting of reproductive effort and indicates, in my opinion, a lack of behavioural and social adaptation to nesting in high densities. Intraspecific nest parasitism seems to be rare in typically colonial species, but fairly frequent in ducks (WITKOWSKI 1967). There is no evidence to indicate that great crested grebes nesting in colonies experience a kind of stress due to overcrowding, or that colonies include pairs which were unable to gain territories for themselves because of their age and weakness, or because of hierarchical reasons. Clutch size differences between pairs nesting singly and in monospecific colonies can be attributed to a stronger predator activity in the latter. I must add that I did not find any unequivocal relationship between the distance from a neighbour nest and the clutch size. Another point to support the view that density is not by itself the cause of stress is the synchrony of egg laying in colonies, indicating a social stimulation.

Nests and clutches are in great danger of destruction or partial robbing by predators. Since adult birds cannot ensure efficient nest defence nest location plays a very important role. The presence near nests of species which actively defend clutches against predators can be regarded as a feature that makes a site suitable for nesting. GÖTMARK and ANDERSSON (1980) quote many papers dealing with similar adaptations in other defenceless species. At traditionally common nesting sites there can occur a clear synchrony of egg laying of different species. Short distances between grebe nests in *Larus ridibundus*

colonies provide another point to prove the statement that nest protection against predators is the most important function of the territorialism of this species.

If in a neighbourhood no *Laridae* colony or *Fulica atra* nest, both playing a similar, protective role, can be found, the great crested grebe must choose the nesting site by itself. It can be the place used the previous year (especially when with success) or a new one. It seems that occupation of new nesting sites is followed by delayed laying. The construction by great crested grebes of several platforms within a territory, and the subsequent pretended incubation on them, often for a number of days prior to the laying of the first egg (SIMMONS 1974), can be important as a way of checking whether the initially selected site really is safe. Then grebes start laying eggs, at the selected site, but in my opinion, they do not stop testing it. It is almost a rule that the first one or two eggs remain uncovered in the nest (the respective values in Table 7 do not indicate this clearly, because phase I comprises the period of laying all the eggs). This is a surprising behaviour, considering the brightly white colour of the shell; such eggs can be seen from a long distance. If nest covering has developed as a displaced nest-building behaviour (BROEKHUYSEN 1973), I see* no reason why this behaviour should be more intensified in the middle incubation phase than at the beginning. MIKIANS (1980) has demonstrated that the covering of a nest increases its chance to survive. A white, uncovered egg can be considered a bait for a possible predator and a final test for nest safety. If it really is so, the destruction of the first egg should cause nest abandonment, because once found, the nest would be even more in danger (MIKIANS 1980). I have no immediate proof that it is the case indeed. The nest loss assessment method I used is not sensitive enough to reveal changes in mortality rate during the first several days. Nevertheless, the very fact that this rate decreases with age may partly prove this supposition. It is likely that such a seemingly wasteful tactic can efficiently contribute to the choice of the safest place. If such really is the role of leaving the first egg uncovered, my checkings may to some extent have had an effect on the recorded clutch survival, even though I did not destroy eggs, but only flushed adult birds. Unfortunately, it is impossible to assess this effect. If a nest has been abandoned in the initial egg laying phase, subsequent eggs may be laid on a different platform prepared during the prelaying period. I relatively often found newly laid eggs on very low and wet platforms. Perhaps these were cases of continuation of laying after the loss or abandonment of the first nest. In grebes the clutch size is not precisely determined, so the number of eggs in such nests need not be on an average lower than in other nests. The slightly smaller size of the first egg in a clutch may be an economic adaptation to its more probable loss.

*The reason can be a weaker, initially, attachment to the nest (GOTZMAN 1967), in which case flushing would not cause stress and displacement activity.

Varied egg size within a clutch may also play some other adaptive role. O'CONNOR (1978, quoted after OJANEN *et al.* 1981) thinks that the growing size of each successive egg lessen the body-size differences among the offspring due to non-simultaneous hatching. This would be an adaptation to relatively constant food conditions and would indicate a clutch-size adjustment to them. Clutches bigger than the number of offspring permitted by food conditions in average years would be an adaptation to unpredictable trophic conditions. Then in exceptionally favourable years the birds could "make up" for poor breeding results in other years. In this case a decreasing egg size in a clutch, or a lack of relationship between egg size and laying sequence would be of advantage. It would favour a quick reduction in the number of chicks under difficult food conditions. The great crested grebe can be included among species characterized by adaptations enabling it to reduce the brood size at the stage of chick raising. Due to their asynchronous hatching there arise age-related size differences which often grow with time. There arises a clear hierarchy based not only on the age structure, but also on the favouring of selected chicks by the parents. Such a differentiation makes possible the elimination of the weakest chicks under difficult food conditions. On the other hand, as the second egg is bigger than the first one, and the actual incubation often begins only after the second egg has been laid, the difference between the first two chicks is less evident than that between the next ones. Besides, the splitting up of the offspring between the parents favours the raising of the largest possible number of young (SIMMONS 1974).

Generally speaking, data on the breeding success of great crested grebes show that it is low. According to FUCHS (1978), there were 1.8 up to 2.1 young per pair of successful breeders. If all pairs present in the study area were taken into account, the rate was only 0.18 up to 0.74 young/pair. On ponds studied by FIALA (1974) only 33 % pairs reared at least one young (on an average 1.19 fledgeling per a successful pair). With such a low production of young it is rather difficult to understand the rapid growth in numbers of the European grebe population, and changes in its range. This could be attributed to longevity and a high survival rate, but there is practically no information on this subject, because mass catching and ringing of this species are difficult. Data reported by MELDE (1973) suggest that at least in the first year of life the mortality rate is high. Noteworthy are, however, the high ecological and ethological plasticity of the species during breeding, and its opportunistic attitude towards nesting site, time and environment. This elasticity is surprising, especially if we consider the advanced morphophysiological specialization of the great crested grebe as a diving fish-eater.

Environment pollution constitutes a potential threat to great crested grebes. Concentrations of PCB, DDT, DDT-derivatives and other pesticides detected in them are among the highest found in birds (PRESTT and JEFFERIES 1969, SCHIFFERLI 1978; data from Poland: ŁUKOWSKI 1976, DUBRAWSKI

and FALANDYSZ 1980). This results from the fact that as a fish-eater, the great crested grebe represents the last link in the food chain and accumulates these noxious substances. However, no pesticide effect on its numbers and breeding success has so far been noted, although such an effect has been found in other bird species, also in *Acchmophorus occidentalis*, a North American grebe (PRESTT and MILLS 1966). Because of othis unexpected resistance, the great crested grebe is not suitable for aquatic environment pollution monitoring. The long-planned all-European census of this species (FLEGG 1973) has not fully materialized, but it aroused interest and caused studies to be started in many countries. This paper can also be included among the results of this interest.

CONCLUSIONS

1. Great crested grebes nest singly or in colonies. Colonies can be monospecific or mixed with *Laridae*.
2. Mixed colonies are formed as a result of the aggregating of grebes in gull colonies, and they disappear as soon as the latter cease to nest at a given site.
3. Many colonies, both monospecific and mixed, stay in the same place for a number of years, others disappear. The cause of their disappearance can be breeding failures or habitat changes.
4. Grebes show an individual tendency to nest in colonies or singly. There is no evidence to indicate that pairs nesting in colonies are pairs which because of their age and weakness could not gain a territory of their own.
5. Grebe pairs breeding in mixed colonies, monospecific colonies and dispersed nests were found to differ in laying dates. In mixed colonies egg laying of grebes and gulls was synchronous. This was because grebes started breeding at an earlier time than they do under different conditions. Laying synchrony was also seen in monospecific colonies. This indicates that grebes are sensitive to social stimulation.
6. The general geographic tendency to start breeding at a later time as the longitude and latitude increase can be — as it was the case on Lake Družno, disturbed by local ecological factors. The start of breeding depends on the presence of sites ensuring safe nesting.
7. As the breeding season progresses, the average clutch size and egg size decrease. The cause of these changes is the same, because smaller clutches contain smaller eggs. It is belived that late, small clutches, consisting of small eggs, belong to young females without breeding experience.
8. A correlation found between the average clutch size values and nest success indicates that egg predators have an effect on both parameters.
9. It has been found that nesting in large aggregations favours the occurrence of intraspecific nest parasitism in the great crested grebe.

10. The egg-covering behaviour of the bird leaving a nest is the weakest at the beginning and at the end of the incubation period. Egg covering considerably increases egg safety. Egg-covering behaviour was found to be weaker in grebes on a mixed colony, where egg safety depends on active colony defence by gulls.

11. In *Larus ridibundus* colonies or near *Fulica atra* nests grebe nests are more safe than are dispersed nests or nests in a monospecific colony.

12. Prelaying "incubation" and leaving the first newly laid eggs uncovered may serve the purpose of testing for nest site safety. It is very important to the breeding success.

13. The main role of territorialism in the great crested grebe is to passively protect the nest against predators. The food-ensuring role is of secondary importance.

ACKNOWLEDGEMENTS

I am grateful to Stefan STRAWIŃSKI and my Colleagues at the Department of Vertebrate Ecology and Zoology, University of Gdańsk for help with the preparation of the paper and continued readiness to discuss problems emerging throughout the study and elaboration of data. I gratefully acknowledge the valuable assistance of Maciej GROMADZKI and Andrzej DYRCZ who offered many useful comments in their reviews of my paper (Goc 1982). My thanks are also extended to Jerzy MIKIANS for help in field investigations, and to Józef ŻURADA for computer processing of the data in the section Nest Losses.

The kindness is appreciated of members of the Student Ornithological Group of Gdańsk University who gave me the permission to use the great crested grebe egg measurements collected on Lake Żarnowieckie.

REFERENCES

- BAUER K. M., U. N. GLUTZ VON BLOTZHEIM. 1966. Handbuch der Vögel Mitteleuropas. Vol. 1. Frankfurt am Main.
- BLOCH D. 1970. Knopsvanem (*Cygnus olor*) som kolonifugel i Danmark. Dansk Orn. Foren. Tidsskr. **64**: 152-162.
- BLUMS P. 1973. The coot (*Fulica atra*) in Latvia. (In Russian). Riga.
- BROEKHUYSEN G. J. 1973. Behavioural responses of Dabchicks *Podiceps ruficollis* to disturbance while incubating. Ostrich **44**: 111-117.
- BUJNOWICZ G. 1977. Wpływ ingerencji człowieka na zachowanie się perkoza dwuczubego (*Podiceps cristatus* (L.)) w okresie lęgowym. Unpublished M. Sc. Thesis. University of Gdańsk.
- BURGER J. 1974. Determinants of colony and nest-site selection in the Silver Grebe (*Podiceps occipitales*) and Rolland's Grebe (*Rollandia rolland*). Condor **76**: 301-306.
- BUSSE P. 1973. Przedstawianie dynamiki wędrówek ptaków. Not. orn. **14**: 68-75.
- CAUGHEY G. 1979. Analysis of vertebrate populations (In Russian). Moskva.
- COLLIAS N. E., J. K. VICTORIA, R. J. SHALLENBERGER. 1971a. Social facilitation in Waeverbirds: importance of colony size. Ecology **52**: 823-828.

- COLLIAS N. E., M. BRANDMAN, J. K. VICTORIA, L. F. KIFF, C. E. RISCHER. 1971b. Social facilitation in Weaverbirds: effects of varying the sex ratio. *Ecology* **52**: 829-836.
- COULSON J. C., E. WHITE. 1956. A study of colonies of the Kittiwake *Rissa tridactyla*. *Ibis* **100**: 40-51.
- CRAMP S., E. L. SIMMONS (eds) 1977. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 1. Oxford.
- CYBERSKI J., MIKULSKI. 1976. Stosunki hydrologiczne. In: B. AUGUSTOWSKI (ed.) Żuławy Wiślane: 239-288. Gdańsk.
- DEMENTIEV C. P., R. N. MEKLENBURCEV, A. M. SUDILOVSKA, E. P. SPANGENBERG 1951. Birds of the Soviet Union. Vol. 2 (In Russian). Moskva.
- DUBRAWSKI R., J. FALANDYSZ. 1980. Chlorinated hydrocarbons in fish-eating birds from the Gdańsk Bay, Baltic Sea. *Mar. Pollut. Bull.* **11**: 15-18.
- FIALA V. 1974. Populationsdynamik und Brutbiologie der Lappentaucher *Podicipedidae* im Teichgebiet von Náměšt n Osl. (ČSSR). *Anz. Orn. Ges. Bayern* **13**: 198-218.
- FJELDSÅ J. 1973a. Territory and regulation of population density and recruitment in the Horned Grebe *Podiceps auritus* BOJE, 1882. *Vidensk. Meddr. Dansk Naturh. Foren.* **136**: 117-189.
- FJELDSÅ J. 1973b. Territorial regulation of the progress of breeding in a population of Coots *Fulica atra*. *Dansk. Orn. Foren. Tidsskr.* **67**: 115-127.
- FJELDSÅ J. 1977a. The Coot and the Moorhen. Copenhagen.
- FJELDSÅ J. 1977b. Grebes. Copenhagen.
- FLEGG J. J. M. 1973 Single species censuses. In: Standarization in European ornithology. *Auspicium* **5** (suppl.): 9-10.
- FUCHS E. 1977. Predation and anti-predation behaviour in a mixed colony of terns *Sterna sp.* and Black-Headed Gulls with special reference to the Sandwich Tern *Sterna sandvicensis*. *Ornis Scand.* **8**: 17-32.
- FUCHS E. 1978. Zum Bruterfolg des Haubentauchers *Podiceps cristatus* auf dem Sempachersee. *Orn. Beob.* **75**: 33-37.
- FUGLE G. N., S. I. ROTHSTEIN. 1977. Clutch size determination, egg size, and eggshell thickness in the Pied-billed Grebe. *Auk* **94**: 371-373.
- GOC M. 1982. Ekologia gniazdowania perkoza dwuczubego *Podiceps cristatus* (L.) na jeziorze Družno Unpublished Dr. Thesis. University of Gdańsk.
- GORDIENKO N. S. 1981. Note on ecology of grebe (*Podiceps*) in North Kazakhstan (In Russian). *Ornitologia* **16**: 33-40.
- GÖTMARK F., M. ANDERSSON. 1980. Breeding association between Common Gull *Larus canus* and Artic Skua *Stercorarius parasiticus*. *Ornis Scand.* **11**: 121-124.
- GOTZMAN J. 1967. Remarks on ethology of the Red-backed Shrike. *Lanius collurio* L. — nest defence and nest desertion. *Acta orn.* **10**: 83-96.
- GOTZMAN J., B. JABŁOŃSKI. 1972. Gniazda naszych ptaków. Warszawa.
- GROMADSKA M. 1955. Stosunki fizyko-chemiczne wody. In: J. S. MIKULSKI (ed.). Jezioro Družno — próba charakterystyki limnologicznej. *Ekol. Pol. A.* **3**: 5-8.
- HAYS H., M. Le CROY. 1971. Field criteria for determining incubation stage in eggs of the Common Tern. *Wilson Bull.* **83**: 425-429.
- HINDE R. A. 1975. Animal behaviour (Russian ed.). Moskva.
- HUDEK K. 1979. Der Einfluss der Schwankungen des Wasserspiegels auf die Nester der Wasservogel. *Folia zool.* **28**: 269-282.
- HUDEK K., W. ČERNÝ. 1972. Fauna ČSSR 19: Ptáci — Aves. Vol. 1. Praha.
- IMMELMANN K. 1971. Ecological aspects of periodic reproduction. In: D. S. FARNER, J. R. KING (eds). *Avian biology*, Vol. 1. New York: 342-389.
- KAJAK Z. 1979. Eutrofizacja jezior. Warszawa.
- KÉRAUTRET L. 1976. Notes sur la reproduction du Grèbe huppé *Podiceps cristatus* dans le nord de la France. *Alauda* **44**: 181-186.

- KLUSZCZYŃSKA K., J. SZMEJA. 1979. Współczesny etap w przemianach roślinności jeziora Drużno. Zesz. Nauk. Biol. U.G. Gdańsk **1**: 35-49.
- KOSHELEV A. J. 1977. The colonial nesting habits of the great crested grebe (*Podiceps cristatus* L.) in the northern part of Lake Menzelinskoe (Western Siberia) (In Russian). Bull. Mosk. O-va Isp. Prirody. Otd. Biologii **82**: 5-9.
- LEYS H. N., J. MARBUS, J. J. F. E. de WILDE. 1969. Waarnemingen bij een broedpopulatie van Futen (*Podiceps cristatus* L.) in Oostelijk Flevoland. De Levende Natuur **72**: 133-141.
- LEYS H. N., J. J. F. E. de WILDE. 1968. Nestplaatskeuze en nestmateriaal bij Futen. De Levende Natuur **71**: 265-272.
- LEYS H. N., J. J. F. E. de WILDE. 1969. Broed-populatie-dichtheden van de Fuut, *Podiceps cristatus* (L.), in Nederland. De Levende Natuur **72**: 201-208.
- LEYS H. N., J. J. F. E. de WILDE. 1971. Het voorkomen van de Fuut *Podiceps cristatus* L. in Nederland. Limosa **44**: 133-183.
- LOMAN J., G. GÖRANSSON. 1978. Egg shell dumps and Crow *Corvus cornix* predation on simulated birds nests. Oikos **30**: 461-466.
- LUNDBERG C., R. A. VÄISÄNEN. 1979. Selective correlation of egg size with chick mortality in the Black-headed Gull (*Larus ridibundus*). Condor **81**: 146-156.
- ŁAWNICZAK D. 1982. Z ekologii i biologii perkoza dwuczubego (*Podiceps cristatus* (L.)), perkoza rdzawoszyjego (*Podiceps griseigena* (BODD.)) i zausznika (*Podiceps nigricollis* C. L. BREHM) na stawach rybnych koło Milicza. Acta Univ. Wratisl. Pr. zool. **12**: 63-81.
- ŁUKOWSKI A. 1976. Uwagi o krażeniu insektycydów i ich wpływie na ekosystemy. Wiad. Ekol. **22**: 26-41.
- MACLEAN G. L. 1974. Egg-covering in the *Charadrii*. Ostrich **45**: 167-174.
- MCCARTAN L., K. E. L. SIMMONS. 1956. Territory in the Great Crested Grebe *Podiceps cristatus* re-examined. Ibis **98**: 370-378.
- MELDE M. 1973. Der Haubentaucher. Wittenberg Lutherstadt.
- MIELCZAREK P. 1980. Studia porównawcze nad dynamiką zniesień czterech gatunków rodzaju *Podiceps* (LATHAM 1787). Unpublished M. Sc. Thesis. Jagiellonian University, Kraków.
- MIKIANS J. 1980. Eksperymentalne badania nad stratami w zniesieniach ptaków wodnych jeziora Drużno. Unpublished M. Sc. Thesis, University of Gdańsk.
- MIKULSKI J. S. 1955. Teren badań i metodyka pracy. In: J. S. MIKULSKI (ed.). Jezioro Drużno - próba charakterystyki limnologicznej. Ekol. Pol. **3**: 2-5.
- MOLGA M. 1973-1978. Początek fenologicznych pór roku. Mapa nr 24. In: S. LESZCZYŃSKI (Chief Editor). Narodowy Atlas Polski. Wrocław.
- MYRBERGET S. 1977. Size and shape of eggs of Willow Grouse *Lagopus lagopus*. Ornith. Scand. **8**: 39-46.
- ODUM E. P. 1977. Podstawy ekologii. Warszawa.
- OJANEN M., M. ORELL, R. A. VÄISÄNEN. 1981. Egg size variation within passerine clutches: effect of ambient temperature and laying sequence. Ornith. Fennica **58**: 93-108.
- ONNO S. 1959. Comparative ecology of grebes species in Estonia (In Russian). Tartu.
- ONNO S. 1960. Zur Ökologie der Lappentaucher (*Podiceps cristatus*, *griseigena* und *auritus*) in Estland. Proc. XIIth Int. Ornith. Congr. Helsinki 1958: 577-582.
- PARKER R. E. 1978. Wprowadzenie do statystyki dla biologów. Warszawa.
- PATTERSON I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. Ibis **107**: 433-459.
- PINOWSKA B. 1979. The effect of energy and building resources of females on the production of House Sparrow (*Passer domesticus*) populations. Ekol. Pol. **27**: 363-396.
- PREST I., D. J. JEFFERIES. 1969. Winter numbers, breeding success and organochlorine residues in the Great Crested Grebe in Britain. Bird Study **16**: 168-185.
- PREST I., D. H. MILLS. 1966. A census of the Great Crested Grebe in Britain 1965. Bird Study **13**: 163-185.

- PTASZYK J. 1981. Pokarm mewy śmieszki, *Larus ridibundus* L. Prz. zool. **25**: 267-272.
- REYNOLDS A. 1974. Measurements made on Great Crested Grebe eggs during the incubation period. Rep. of the Rye Meads Ringing Group **7**: 28-34.
- SCHIFFERLI A. 1978. Rückstände von Pestiziden und PCB bei schweizerischen Haubentauchern, *Podiceps cristatus*. Orn. Beob. **75**: 11-18.
- SIMMONS K. E. L. 1955. Studies on Great Crested Grebes. Avic. Mag. **61**: 3-13, 93-102, 131-146, 181-201, 235-253, 294-361.
- SIMMONS K. E. L. 1974. Adaptations in the reproductive biology of the Great Crested Grebe. Brit. Birds **67**: 413-437.
- SMITH R. W. J. 1974. S.O.C. Great Crested Grebe enquiry 1973. Scot. Birds **8**: 151-159.
- STEMPNIEWICZ L. 1981. Breeding biology of the Little Auk *Plautus alle* in the Hornsund region, Spitsbergen, Acta orn. **18**: 1-26.
- TACZANOWSKI W. 1882. Ptaki krajowe. Vol. 2. Kraków.
- VAN ESBROECK J., P. E. DEVILLERS. 1981. Un cas d'adaptation du Grèbe huppé (*Podiceps cristatus*) à la présence humaine. Aves **18**: 36-47.
- VÄISÄNEN R. A. 1977. Geographic variation in timing of breeding and egg size in eight European species of waders. Ann. Zool. Fenn. **14**: 1-25.
- VENABLES L. S. V., D. LACK. 1934. Territory in the Great Crested Grebe. Brit. Birds **28**: 191-198.
- WISZNIEWSKI W. (ed.). 1973. Atlas Klimatyczny Polski. Warszawa.
- WITKOWSKI J. 1967. Badania nad lęgowym zespołem ptaków stawów rybnych w Miliczu (Unpublished Dr. Thesis). University of Wrocław.
- ZANG H. 1976. Bestandsaufnahme des Haubentauchers (*Podiceps cristatus*) in Niedersachsen und Bremen 1974. Vogelkundliche Berichte aus Niedersachsen **8**: 1-8.
- ZANG H. 1977. Zur Frage der Häufigkeit von Zweitbruten beim Haubentaucher (*Podiceps cristatus*). J. Orn. **118**: 261-267.

STRESZCZENIE

[Kolonialne i terytorialne gniazdowanie perkoza dwuczubego na jeziorze Drużno.]

Badania prowadzono w latach 1975-80 w rezerwacie przyrody Jezioro Drużno koło Elbląga. Obejmowały one zasadniczą część sezonu lęgowego perkoza dwuczubego (maj-czerwiec). Wyszukiwano gniazda, zaznaczano ich lokalizację na planach terenu, długość i szerokość jaj mierzono z dokładnością do 0,1 mm, określano ich stadium inkubacji na podstawie testu wodnego (tab. 2). Stadium inkubacji służyło do oceny wieku zniesienia i określenia daty jego rozpoczęcia. Rejestrowano, czy zniesienie było w chwili znalezienia lub kontroli przykryte. Liczby gniazd znalezionych w kolejnych sezonach zawiera tabela 1. Sukces gniazdowy szacowano własną metodą, opartą na analizie częstości spotkań zniesień w kolejnych klasach wieku. Wynik interpolowano metodą logarytmiczno-wielomianową.

Stwierdzono gniazdowanie perkozów dwuczubych w koloniach jedno-

gatunkowych, w koloniach mieszanych ze śmieszką i rzadziej z innymi *Laridae*, oraz pojedynczo. Rozmieszczenie gniazd w 1976 r. przedstawia rycina 1. W koloniach mieszanych ze śmieszką lokalne zagęszczenia gniazd perkozów były wyższe niż w koloniach jednogatunkowych (tab. 3). Na podstawie zmian lokalizacji kolonii mieszanych wykazano, że ich powstawanie oparte jest na skupianiu się perkozów w koloniach *Laridae*. Są wskazówki, że istnieje indywidualne zróżnicowanie skłonności do gniazdowania kolonijnego.

Dynamikę zakładania gniazd w sezonach 1976–80 i związane z nią zmiany wielkości zniesienia i wymiarów jaj przedstawiono na rycinach 2–6. Nie stwierdzono związku terminów przystępowania do lęgów z temperaturą powietrza w okresie poprzedzającym, ani ze zmianami poziomu wody. Początek sezonu lęgowego był w 1980 r. wyraźnie późniejszy niż w pozostałych latach, a gniazdowanie w 1978 r. znacznie bardziej rozciągnięte w czasie. Wykazano, że początek gniazdowania perkozów w koloniach śmieszek jest zsynchronizowany z rozpoczęciem rozrodu przez mewy i znacznie wcześniejszy niż w innych okolicach na Drużnie. Synchronizacja ta przypuszczalnie pozwala na lepsze wykorzystanie antydrapieżniczej obrony kolonii i zmniejsza niebezpieczeństwo uszkodzenia gniazda i zniesienia przez podloty mew. Terminy rozpoczynania lęgów przez perkozy gnieźdzące się poza koloniami mew na J. Drużno są zbliżone do obserwowanych na J. Żarnowieckim (Płn. Polska, około 120 km na płn.-zach. od Drużna). Zestawienie danych o fenologii gniazdowania w różnych rejonach Europy świadczy o coraz późniejszym rozpoczynaniu lęgów przez perkozy w miarę wzrostu szerokości i długości geograficznej (ryc. 9a, b, c). Zróżnicowanie terminów rozpoczynania rozrodu na Drużnie wskazuje jednak, że lokalne czynniki ekologiczne mogą być istotniejsze od położenia geograficznego.

Wielkość zniesienia w różnych latach i miejscach jest skorelowana z przeżywalnością zniesień (ryc. 11). Drapieżniki dekompletując zniesienie wpływają na jego obserwowaną wielkość. Tym można tłumaczyć istotnie mniejsze niż w innych okolicznościach zniesienia perkozów w koloniach jednogatunkowych.

Stwierdzono sezonowy spadek wielkości zniesienia.

Analizując odchylenia standardowe szerokości jaj w zniesieniach, wykazano, że w koloniach dochodzi niekiedy do powstawania jednogatunkowych zniesień mieszanych. Jeżeli są one częste, mogą wpływać na podwyższenie średniej wielkości zniesienia, tak jak to stwierdzono w kolonii na J. Żarnowieckim.

Perkozy dwuczube składają w ciągu sezonu średnio coraz mniejsze jaja. Wykazano, że spadek wymiarów zachodzi niezależnie w grupach gniazd różniących się lokalizacją, nie jest więc związany z datą kalendarzową, a raczej z względnym opóźnieniem w obrębie tych grup. Część późnych zniesień charakteryzuje się wymiarami poniżej zakresu stwierdzonego w początkowej fazie sezonu lęgowego (ryc. 14). Te wyróżniające się małymi wymiarami jaj

późne zniesienia są zwykle niewielkie, zawierają do 3 jaj (ryc. 15). Pochodzą one prawdopodobnie od młodych, niedoświadczonych lęgowo samiec. Tym związanym z wiekiem samicy różnicowaniem tłumaczy się sezonowy spadek wielkości zniesień i wymiarów jaj, a także związek między średnią szerokością jaj w zniesieniu a jego wielkością (tab. 6). Stwierdzono, że pierwsze jajo w zniesieniu ma szerokość średnio o 0,25 mm, a długość o 0,30 mm mniejszą niż drugie. Nie ma natomiast istotnych różnic wielkości między przedostatnim i ostatnim jajem. Porównanie współczynników zmienności dla szerokości i długości jaj zarówno wewnątrz zniesienia, jak wewnątrz- i między populacjami, wskazuje na większą przydatność szerokości jaj jako parametru różnicującego.

Wykazano, że skłonność do przykrywania jaj przez opuszczające gniazdo perkozy jest silniejsza w środkowym okresie inkubacji niż podczas składania jaj i w okresie wykluwania się piskląt. Ptaki gnieźdzące się w obrębie gęstej kolonii śmieszek wykazywały mniejszą tendencję do przykrywania gniazd. Przypuszcza się, że zarówno to zjawisko, jak wcześniejsze rozpoczynanie lęgów w tych rejonach, związane jest z większym poczuciem bezpieczeństwa.

Straty gniazdowe są najwyższe w koloniach jednogatunkowych (82 %) i wśród gniazd rozproszonych (72 %). Sąsiedztwo śmieszek zmniejsza straty do około 42 %, a lokalizacja w pobliżu gniazd łysek do około 50 %. Krzywe przeżywalności zniesień w różnych sezonach i okolicznościach przedstawia rycina 16. W większości przypadków wskaźnik śmiertelności zniesień — prawdopodobieństwo zniszczenia w jednostce czasu, maleje z ich wiekiem. Dyskutowana jest rola łysek w niszczeniu zniesień perkozów oraz inne możliwe przyczyny strat.

Wysunięto hipotezę, że strategia gniazdowa perkoza dwuczubego polega na wypróbowywaniu bezpieczeństwa gniazda we wstępnym etapie okresu gniazdowego. Składa się na to budowanie przez parę kilku platform, z których jedna zostaje przekształcona w prawdziwe gniazdo, „próbne” wysiadywanie, jeszcze przed zniesieniem pierwszego jaja, oraz pozostawianie świeżych jaskrawo białych jaj bez przykrycia. Skuteczność tej metody prób zwiększona jest przez brak ścisłego zdeterminowania wielkości zniesienia, pozwalający na odtworzenie go mimo utraty części jaj. Możliwe jest również uzupełnienie zdekompletowanego zniesienia w kolejnym cyklu owulacyjnym.

Funkcja terytorializmu u perkoza dwuczubego polega głównie na ochronie gniazda przed drapieżnikami oraz na zapobieganiu zakłóceniom w rozrodzie, takim jak zniesienia mieszane. Pokarm ma raczej mniejsze znaczenie, bowiem zagęszczenia perkozów są lepiej skorelowane z długością linii brzegowej zbiornika niż z jego powierzchnią (ryc. 17). Są więc silniej uzależnione od siedliska gniazdowego niż od żerowiska.

Ogólnie niska efektywność rozmnażania, stwierdzona na Drużnie i wykazywana w literaturze, utrudnia zrozumienie obserwowanego od kilkudziesięciu lat wzrostu liczebności i zasięgu perkoza dwuczubego w Europie.