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## Breeding biology and ecology of the marsh harrier *Circus aeruginosus* in the Barycz valley, Poland

WITKOWSKI J. 1989. Breeding biology and ecology of the marsh harrier *Circus aeruginosus* in the Barycz valley, Poland. Acta orn. 25: 223–320.

A population of marsh harriers was studied in 1972–75, when it was affected by DDT and shooting, and in 1982–84, seven years after the removal of both pressures. Since the end of the 19th century the population had two periods of growth (during World War II and after stopping the use of DDT) and a period of decline during most intense DDT application (1950–70). The breeding territory of a single pair ranged from 27 to 100 ha in both the study periods. The mean home range in the years of highest numbers was 160 ha. Only 4% of the females mated bigamously. They produced 40% less young than females mated monogamously. Bigynous males produced 30% more young than monogamous males. The average date of initiation of egg laying was 27 April. Females laid 2–8, on an average of 5.0 eggs. The mean clutch size declined from 5.6 eggs early in the season to 4.4 eggs late in the season. The first and the last eggs within a clutch were usually smaller than the eggs laid in between. No difference was recorded in the production of fledglings between clutches made up of larger eggs and those containing smaller eggs. The daily food intake by the young was 1/4 to 1/3 of their body weight. Males started to fly on days 37–39, whereas females on days 41–44 after hatching. Males, which are lighter than females, could catch little mobile prey when 54 days old, but they were still partly fed by parents up to 80 days of age. The sex ratio in the young was 54% in favour of males. Broods containing both sexes predominated but 26% of the broods contained only one sex. In 5-egg clutches, males hatched from relatively larger eggs, typically laid in the middle of the laying sequence, whereas females from smaller eggs laid at the beginning and at the end of the sequence.

In 1972–75, the highest losses were caused by egg breakage and low hatchability as a result of DDT contamination. The index of shell thickness in the Barycz valley was 23% lower than that of European marsh harriers prior to 1945. Losses from DDT were so high that they reversed the typical trend of lower losses at the beginning than at the end of the season. Prolonged rains additionally increased losses from egg breakage and nestling mortality. In 1982–84, the highest losses were due to predation and nest desertion. Nestling mortality accounted for 25%. Nestlings that hatched first survived until fledging in 94%. No one nestling hatched as the sixth survived. Aggression among siblings accounted for negligible losses. In 1972–75, 42% of the eggs laid produced young, whereas in 1982–84, 51%. The production of young in successful nests was the same in the two study periods (3.1 fledglings/pair). The marsh harrier population declined in the period of DDT application because of the elimination of some pairs from reproduction and as a result of the shortening of the life span of adults contaminated with DDT and its metabolites.

The diet of marsh harriers in the breeding season ( $n = 1355$  food items) consisted of birds — 60%, mammals, typically small rodents, — 28%, dead fish in 10%, and frogs — 2%. Males caught 58% of the prey items from land habitats and 24% from aquatic habitats, whereas females caught only 8% of the prey items from land and as many as 83% from aquatic habitats. A clear separation of food niches between males and females in the breeding season was evident within the population studied. On the average, the prey caught by the male was smaller by half than the prey caught by female.

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Биология и экология периода размножения болотного луня в долине реки Барычи, Польша

Представлены результаты исследований популяции болотного луня проведенных в 1972–75 годах, когда еще применяли ДДТ и производился отстрел, и результаты исследований проведенных в 1982–84 годах, когда оба эти фактора не имели места на протяжении уже 7 лет. С конца XIX века численность популяции болотного луня возрастала в двух периодах (II мировая война и когда перестали применять ДДТ). Период регресса наблюдался во время наиболее интенсивного применения ДДТ (1950–1970). Плотность пар в разные периоды составляла 27–100 га/1 гнездовая пара. Площадь гнездового ареала в годы наиболее высокой численности составляла в среднем 160 га. У 4% самок наблюдалась бигамия. Их продукция птенцов была на 40% ниже чем у самок моногамных. У бигамных самцов продукция птенцов была на 30% выше чем у моногамных. 50% самок начинало кладки 27 апреля. Они сносили 2–8 яиц, в среднем 5.0. В начале сезона средняя кладка составляла 5.6 яиц, а под конец 4.4 яйца. Первые и последние яйца в кладке были как правило более мелкие по сравнению с остальными. Не констатировано различий в продукции летающих молодых в зависимости от величины яйца. Птенцы съедали в течение суток порцию пищи, масса которой была равна  $\frac{1}{4}$ – $\frac{1}{3}$  массы их тела. Самцы начинали летать по истечении 37–39 дней с момента выклева, самки по истечении 41–44 дней от выклева. Самцы, более легкие чем самки, были в состоянии схватить мало подвижную добычу на 54 дне жизни. Однако, родители докармливали молодых до 80 дня жизни. Соотношение полов у молодых составляло 54% на пользу самцов. Выводки состояли обычно из птиц обоих полов, но 26% были однополыми. В кладках содержащих 5 яиц из более крупных яиц, откладываемых в середине периода кладки, обычно вылупливались самцы, из более мелких (начало и конец откладывания) — самки.

В период 1972–75 годов самые высокие потери были вызваны раздавливанием яиц высиживающими самками, а также тем, что из значительного количества яиц не выклевывались птенцы — и одно и другое было результатом воздействия на организмы болотных луней ДДТ. Индекс толщины скорлупы болотных луней из долины Барычи был на 23% ниже, чем у этого вида в Европе до 1945 года. Величины потерь по поводу ДДТ были настолько велики, что переменялся нормальный у птиц тренд, согласно которому потери в начале гнездового периода являются меньшими по сравнению с потерями под конец периода. Длительные осадки увеличивали потери вызванные раздавливанием яиц и смертностью птенцов. В период 1982–84 причиной наибольших потерь было хищничество и оставление гнезд. Смертность молодых на гнездах составляла 25%. Птенцы, которые вылупились как первые, выживали до вылета из гнезда в 94%. Из птенцов, которые были вылупились как шестое, не выжил ни один. Потери возникшие в результате агрессии в пределах выводка не имели значения. В период 1972–75 потенциальная продукция была реализована в 42% а в период 1982–84 в 51%. Продукция молоди у пар с удачными выводками была одинакова в обоих периодах (3,1 молодой птицы на 1 пару). Причиной снижения численности болотного луня в период применения ДДТ было исключение некоторых пар из процесса размножения и сокращение длительности жизни взрослых особей вследствие отравления ДДТ и продуктами его обмена.

В гнездовом периоде пища болотного луня в долине Барычи (N = 1355 жертв) состояла в 60% из птиц, 28% из преимущественно мелких млекопитающих, 10% из неживых рыб, а 2% составляли лягушки. 58% жертв добытых самцами происходило из сухопутных биотопов, а 24% из водных. У самок наоборот – 8% было сухопутных и 83% водных. Констатировано четкое разделение пищевых ниш самца и самки у болотного луня в гнездовом периоде. Жертвы самцов были в среднем на половину легче, чем жертвы самок.

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## INTRODUCTION

In the recent 20-year period, birds of prey received a special attention because of a drastic decline in many species, including extinction of some populations.

This group of birds started to be threatened more than one hundred years ago. The highest level of threat was reached in the 1960s as a result of the appearance

of a new, destructive factor such as different toxic substances introduced to ecosystems by man in the form of heavy metals and pesticides, especially DDT. The most affected were the species largely feeding on birds or fish (NEWTON 1979). However, the first signals concerning side effects of DDT leading to a reduction of breeding success due to shell thinning, and indicating also further consequences of this process appeared relatively late (RATCLIFFE 1967, PEACALL 1970).

The marsh harrier has a wide food spectrum (UTTENDÖRFER 1952, SCHIPPER 1973). In some populations, insectivorous passerines account for a large proportion of their diet (HILDEN & KALINAINEN 1966, BOCK 1979). In most European countries, the numbers of marsh harriers considerably declined in the period of DDT application (CRAMP & SIMMONS 1980). This was also the case in the Barycz valley in western Poland. Although at the end of the 1940s their numbers were low (SZARSKI 1950), a decline by 40% was noted in the 1960s, when the harmful effects of DDT were most pronounced.

The studies on marsh harriers in the Barycz valley were started in 1972, when destructive effects of DDT were already known, and many countries ceased using it. At the same time demands for protecting all species of birds of prey were growing.

In those years also the 4th volume of *Handbuch der Vögel Mitteleuropas* (GLUTZ *et al.* 1971) appeared in the European literature, summing up the known facts of the life of marsh harriers. This monumental work reveals many gaps and controversial issues concerning the biology of this species.

The study undertaken in 1972 on a sample involving then about 30 pairs was planned as a standard population study in the breeding season, but its most important purpose was to understand the factors accounting for the population decline in the study area. A special attention was paid to losses caused by the use of DDT, in particular to egg breakage by incubating females.

A relationship was expected between the food composition and the cumulation of DDT in body tissues. Thus, food samples were taken showing not only the diet composition but also the proportions of all prey categories, including those which cannot be detected in the remains left on the nest, or on feeding sites, or in pellets.

The methods used to estimate breeding failures caused by DDT (frequent visits to nests since the initiation of laying) and to analyze food composition on some occasions provided new details on breeding biology, including laying intervals, span of incubation period, division of parental care, food consumption in young of different age classes, growth rate of nestlings, daily activity of young and adult birds, sex ratio in the young generation, etc. Many of these aspects were not known from the literature on the marsh harrier.

Several years ago, it was noted that in some species eggs differ in size according to the sequence of their laying, and it was concluded that these differences are adaptive (HOWE 1976, SLAGSVOLD *et al.* 1984). Some authors found a relationship between egg size, the sequence of laying individual eggs, and the sex of



nestlings hatched from these eggs (FIALA 1981, ANKNEY 1982). Using detailed materials collected for marsh harriers in 1972–75, this problem is also considered in the present paper. This was the period in which DDT was commonly used in Poland. This practice was officially forbidden in 1975, and since that time all birds of prey have been protected by law.

The same population was studied again in 1982–84, that is seven to nine years after the elimination of two important factors reducing population numbers – DDT and shooting. Generally, the study was limited to the breeding success and the causes of breeding failures. Supplementary food samples were also taken and some observations were made on the young after fledging. The main purpose of the study in the second period was to collect data permitting a comparison of reproductive parameters in the two periods.

#### STUDY AREA

The study was carried out in the middle reaches of the Barycz river ( $51^{\circ}27' - 51^{\circ}35' \text{ N}$ ,  $16^{\circ}58' - 17^{\circ}32' \text{ E}$ ), where 6 complexes of fish-ponds are located. Going eastward these are: 1) Radziadz plus Niezgodna (830 ha), slightly to the south, 2) Jamnik (327 ha), 3) Ruda Sułowska (730 ha), 4) Stawno (1730 ha), 5) Potasznia (670 ha), and further to the south, 6) Wierzchowice (798 ha).

Complex 3, 4, and 5 are located in open areas. Complexes 1 and 2 border on a forest to the south, and almost all ponds of complex 6 are located in a forest, but no more than 1 km from open areas.

Soils are poor, sandy-podzolic. The main crop plants are potatoes, rye, and there are meadows and pastures there.

Human population in this part of the valley is low (49 inhabitants per  $1 \text{ km}^2$ ). The largest town Milicz, has a population of 10 thousand people.

All the complexes, except complex 6, are in part nature reserves established in 1949 for the protection of birds.

A detailed study was conducted in complex 4. In the other complexes only numbers of breeding pairs of marsh harrier were estimated.

Complex Stawno (Fig. 1) is made up of 31 ponds of a joint surface area of 1730 ha. Suitable nesting sites occurred on 19 ponds, but marsh harriers nested on only 16 ponds, where the area of reed beds along the shores and on islands represented 14–50%, with a mean of 27% of the pond surface (with one exception). The other ponds, without nesting sites, were used as hunting grounds which offered plentiful nestlings of grebes, coots, black-headed gulls and wild ducks.

The ponds were surrounded by open areas. Cultivated land was slightly predominated by meadows. To the north and south the area was closed by forests growing on either side of the valley.



## ESTIMATE OF FOOD RESOURCES IN THE STUDY AREA

For marsh harriers returning from their winter quarters practically no food existed in the ponds. Sometimes even the ice did not melt. For this reason the main sources of food in this early period were adjacent crop fields and meadows. Since mid-April food conditions improved as goslings were hatching, coots and ducks were laying eggs, and frogs were moving into the ponds.

Among the most abundant bird species nesting in the ponds and being the potential prey of marsh harriers were coots *Fulica atra*, 4 species of grebes *Podiceps* spp., ducks, mostly diving *Aythya* spp., and reed warblers *Acrocephalus scirpaceus*. Also a large colony of black-headed gulls *Larus ridibundus*, consisting of over 3 thousand pairs, was nesting on the ponds, but it was not exploited by marsh harriers.

The majority of these birds raised chicks in June. Marsh harriers produced young and had the highest food requirements in the same period. Thus, the reproduction of marsh harriers was clearly synchronized with a peak prey abundance.

Since mid-July, food resources on the ponds declined again. The young of large water birds were too big to be captured by marsh harriers.

Numbers of small mammals on adjacent crop fields and meadows were not estimated. They could not have been high, however, as soils were poor. No waders were present there, except for scarce lapwings *Vanellus vanellus*. The partridge *Perdix perdix* was very rare and the pheasant *Phasianus colchicus* practically did not occur. The density of hares *Lepus europaeus* was very low, and rabbits *Oryctolagus cuniculus* were not recorded from that part of the valley.

## METHODS

## NUMBER ESTIMATES

Numbers of breeding pairs on all the ponds except Stawno were estimated from 3 censuses between April 15 and May 31. Observations were made from trees and from dikes between lakes. The behaviour of harriers provided cues about the breeding status of birds, and as a result the number of breeding pairs could be estimated. Typically nesting attempts started after May 31 represented replacement nests. In the complex Stawno (4) all the nests were found.

## DENSITY OF BREEDING PAIRS, TERRITORY, NEST SITE

Nest sites were mapped on a 1:10000 map, and distances among nests were calculated from the map. The distances of nests from open water were noted. Changes in the location of nests sites from year to year were observed. At each



nest an attempt was made to determine the direction of most frequent flight directions of the male from the nest and to the nest with prey. The distances covered by hunting males were noted during the nesting period and especially during raising the young to obtain information on the size of hunting territory. The sex of hunting harriers was recorded to determine the expected differences in males' and females' food niches.

#### LAYING PERIOD

If the behaviour of a pair of harriers indicated that egg laying had been started, the nest was located. The eggs were marked with indelible varnish, measured with a slide calliper to the nearest 0.1 mm, and weighed with a 50 g Pesola spring balance. Then the nest was visited every second day until laying was finished. If more than one egg was found in the nest during the first visit, the sequence of their laying was established from the amount of dirt on them. Eggs of complete clutches were not weighed. The weighed eggs were incubated no more than eight days, provided the incubation started on the day following the day of the laying of the first egg.

#### INCUBATION

In the incubation period, nests were visited at about 10-day intervals, and the fates of eggs were recorded. On day 31 after the date of the first egg laid, hatching was checked. The number of days from the laying of an egg to its hatching was noted when these parameters were known. For the first egg the onset of incubation was recorded from the day following its laying date. When no traces of hatching were detected, the nest was visited two days later. The hatched young were weighed and marked with special rings the diameters of which could be regulated. The next visits were planned so that the dates and order of the hatching of successive nestlings could be known. When possible, it was noted which nestling hatched from which egg. Hides were built at two nests to observe incubating females for several days, and to record the time of their feeding, the species of prey, and the approximate weight of prey items brought by the male, in the cases when the female ate them on the nest.

#### PERIOD FROM HATCHING TO BEGINNING OF FLIGHTS

When all the young hatched, the nest was visited every 3–5 days to weigh the young and to identify food remains on the nest and on the plucking platforms. The development of nestlings was observed, including the growth of successive



layers of down and the emergence of flight-feathers. In nestlings of known age, primaries 5 and 6 were measured, and also the length of the tarsus. On remaining days, the nests were observed from hides. The hides were built at a distance of 8 m from nests with nestlings. Four bars were fastened in the ground so that they formed a square with a side length of 130 cm, and they were covered with reed-mats. After its construction such a hide was observed from a longer distance to see if the female returned to the nest. If she did not within one hour, the hide was removed to avoid the abandoning of the nest. Males were much more tame than females, and all of them accepted the presence of hides, returning to the nest soon after their construction, and in this way encouraging females to do the same.

From the hides different kinds of activities of the young were noted throughout the day. They included the time of returning with prey by the parents, approximate weight of prey items, and their repartition among the young. The weight of prey items was estimated by comparing them with a table of mean weights of the species that can be preyed upon by marsh harriers. Mean weights of adult individuals were taken mostly from the literature and in part from the author's measurements. The weight of young individuals, especially ducks, coots, and grebes, was established first by weighing standard individuals of different ages, and then comparing the prey with them, using for example the length of the tarsus. Attention was paid to the labour division between males and females and its changes with the age of the young.

#### SEX OF THE YOUNG

The young were sexed several days prior to their first flights. Three criteria were used jointly:

male – body weight no more than 600 g, tarsus no more than 84 mm long, and iris light brown,

female – body weight over 680 g, tarsus over 88 mm, iris dark brown.

In several cases only two of these parameters were used as the third deviated from the norm. This was either body weight or tarsus length.

#### POST-FLEDGING PERIOD

In six nests, most suitable for observations, the young were marked with white dye prior to fledging. Different parts of the body exposed in flight were dyed. Successive nestlings in the brood were individually marked with coloured plastic rings. The marked birds were observed until they were 90 days old. The dates of learning different skills were noted, also the duration of their dependence for food on the parents, and the division of duties between sexes in this period.

## LOSSES

Frequent visits to the nests during laying and incubation periods permitted the assessment of the kind and size of losses. If a nest was robbed, predators were identified from traces. If a harrier ate the eggs, traces were evident – eggs were on the nest, emptied through a small hole, with traces of claws on the shell. Wild boars *Sus scrofa* broke the eggs into small pieces and tumbled the nest. Eggs predated by polecats *Putorius putorius* or pine martens *Martes martes* had traces of their fangs on the shell.

In the study period of 1972–75, the population of marsh harriers was affected by DDT still used in Poland at that time. The symptoms included shell-thinning and eggs breakage by incubating females. I assumed then that all single eggs that disappeared from a nest during the laying or incubation were broken. The following facts can be reported in favour of this assumption: a) in 25% of the cases this was directly recorded, as during one visit a cracked or dented egg was in the nest, and during the next visit it was found to have disappeared; b) hooded crows *Corvus corone cornix* were the best possible candidates that could steal single eggs. As about 50 pairs of crows were nesting in the study area, a special attention was paid to the interactions between them and marsh harriers. For a long time crows were observed at the nesting territories of marsh harriers but no case of egg robbing was noted. Typically, crows ate the robbed eggs on dikes, leaving their shells. These places were carefully searched, and no shells of harrier eggs were found; c) most harrier eggs disappeared during rainfall. Observations of incubating females on rainy days provided additional evidence that eggs were broken by females showing nervous and incautious behaviour in such situations.

The losses caused by visiting the nests were negligible and limited to the laying period.

## FOOD

There were two groups of samples: 1) whole-day observations at nests from hides, and 2) observations of hunting birds, and prey remains on nests and platforms. Platforms were the places where the male delivered food to the female, and where both birds consumed the prey, or plucked them before feeding to the young. They were located in reedbeds on broken stems and most often on old nests of grey-lag geese *Anser anser* breeding in the nesting territories of marsh harriers.

An important problem was to find out which prey item carried to the nest by female had been captured by herself and which one by the male. The difficulty resulted from the fact that the male often passed the prey to the female and not to the nest directly. This problem was solved in two ways. During the whole study period two nests were found near trees and one near the dike. Thus, hides were

built on these trees and on the dike from which there was a broad view over the nest surroundings, and it was clearly seen which item was passed to the female and which directly to the nest. In the second case, concurrent observations were made by two persons: one from the dike, the other at the nest. Comparing data from the same time period, it was possible to identify the prey and the hunter.

Since during the incubation period the female rarely ate the food brought by the male on the nest, observations from hides near the feeding places of the females were conducted for four days.

## RESULTS

### POPULATION NUMBERS

An attempt was made to estimate population numbers on the pond complex of Stawno in five periods characterized by different population dynamics.

Period I. From the end of 19th century to 1925. In the literature there exist only several general notices on the numbers of marsh harriers in Silesia. According to KOLLIBAY (1906) and PAX (1925), it was a scarce species in the province, permanently occurring and a little more abundant only on ponds in the Barycz river valley and near Niemodlin. Using fragmentary data (PAMPEL 1922, PAX 1925) from those years and the analogy to later recorded tendencies, along with the proportions of densities of breeding pairs on different ponds of the complex Stawno, I attempted to estimate numbers in this period. It may be suggested that no more than 15–20 breeding pairs nested over the whole complex, that is, 35–45% of the present population.

Period II. World War II and first post-war years. From this period there is only one statement that in 1946 and 1947 one pair nested on almost every pond (SZARSKI 1950). At that time, like today, the complex Stawno consisted of 16 ponds on which marsh harriers could nest. The tendencies revealed later suggest that on six of these ponds more than one pair could have bred. On the basis of the above data it can be assumed with a high probability that about 25 pairs were breeding over the complex at that time. Thus, the population increased by about 20% as compared with the preceding period. This could have been due mostly to a decreased hunters' pressure during the war.

Period III. The turn of the 1950s and the 1960s. Already SZARSKI (1950) noticed that numbers of marsh harriers declined in the last years of his study. Data from single large ponds in 1958–60 (WITKOWSKI 1967) indicated that no more than 16 pairs were breeding over the complex Stawno. The estimation of breeding pairs made by the author in 1965 revealed 13–15 pairs. This was thus the most critical period for marsh harriers in the Barycz valley.

Period IV. The first half of the 1970s. In this period the detailed study of the marsh harrier population in the Barycz valley described in this paper was carried out. This period was characterized by a slow increase in numbers as a result of gradually reduced shooting and limitation or total elimination of DDT from many countries in Europe.

Numbers of breeding pairs in the complex Stawno are shown in Table 1. In 1972–75, the mean number of nesting pairs was 31.5 (30–35 pairs), that is, almost twice as many as in the preceding period (Table 2).

Period V. The first half of the 1980s. Marsh harriers in Poland had already been protected for seven years. The use of DDT had been forbidden for the same number of years. As Table 1 shows, the Stawno population continued to increase (from 35 to 50 pairs, with a mean of 44 pairs), being 40% higher than in the preceding period.

To see if the dynamics of the Stawno population was representative of the other five pond complexes in the Barycz valley, an inventory of breeding pairs in these complexes was made in 1973 and 1975. In 1982–84 also the data from the files of the Department of Avian Ecology, University of Wrocław, were used (Table 3). They are compared with the data for Stawno in Table 2. This table also

Table 1. Number and distribution of breeding pairs of marsh harrier in fish-pond complex Stawno

Tabela 1. Liczba i rozmieszczenie par lęgowych błotniaka stawowego w kompleksie stawów rybnych Stawno

Name of pond (hectares) Nazwa stawu (ha)	1972	1973	1974	1975	1982	1983	1984
Grabownica (283)	8	13	11	12	10	12	11
Andrzej (175)	3	3	4	2	3	4	6
Słoneczny G. (164)	5	8	3	6	5	8	10
Golica (119)	— <sup>+</sup>	— <sup>+</sup>	3	— <sup>+</sup>	8	9	— <sup>+</sup>
Gadzinowy D. (90)	—	—	—	—	—	—	—
Henryk (71)	2	—	2	3	—	1	3
Bolko I (70)	3	1	1	2	—	4	3
Przelotny (60)	— <sup>+</sup>	1	— <sup>+</sup>	—	—	—	3
Wilczy Duży (56)	1	1	1	2	1	1	1
Nowy Świat Dolny (50)	2	3	1	1	2	—	—
Polny (45)	—	—	—	—	—	1	1
Nowy Świat Górny (37)	5	1	2	5	3	4	5
Wilczy Mały (35)	—	—	2	1	1	1	2
Bolko II (29)	—	—	—	1	—	1	2
Staś Dolny (24)	—	—	—	—	1	1	1
Słowian (18)	1	—	—	—	1	—	—
Total — Razem	30	31	30	35	35	47	50

<sup>+</sup> That year the pond was dried.

W tym roku staw był nienapuszczony.



Table 2. Comparison of marsh harrier population density between Stawno and other fish-pond complexes in the Barycz valley

Tabela 2. Porównanie liczebności populacji błotniaka stawowego w kompleksie Stawno z innymi kompleksami stawowymi w dolinie Baryczy

Period <sup>+</sup> – Okres	Number of breeding pairs – Liczba par lęgowych	
	Stawno	Other complexes – Inne kompleksy
III 1958–60	ca 16	ca 23
IV 1972–75	$\bar{x} = 31.5$ (97%)	$\bar{x} = 45.5$ (98%)
V 1982–84	$\bar{x} = 44.0$ (40%)	$\bar{x} = 97.5$ (114%)

Figures in parantheses show the percentage increase in relation to previous period.

W nawiasach podano o ile procent wzrosła liczebność par w stosunku do poprzedniego okresu.

\* For period description see pages 233–234.

Table 3. Number of breeding pairs of marsh harrier in all fish-pond complexes of the Barycz valley

Tabela 3. Liczba par lęgowych błotniaka stawowego na wszystkich kompleksach stawowych doliny Baryczy

Name of complex (hectares) Nazwa kompleksu (ha)	1973	1975	1982	1983	1984
1. Radziądź + Niezgodą (893)	13	17	23	32	34
2. Jamnik (327)	2	2	5	5	7
3. Ruda Sułowska (780)	10	12	25	21	18
4. Stawno (1730)	31	35	35	47	50
5. Potasznia (566)	10	9	18	20	22
6. Wierzchowice (797)	7	9	22	25	16
Total – Razem (5039)	73	84	128	150	147

includes extrapolated data for period III, which was the most critical period for the population.

It turned out that the population dynamics at Stawno was similar to that in the other complexes only in period IV, in which number increased by almost 100% as compared with the preceding period. Significant differences occurred in period V, when numbers were higher by only 40% as compared with the preceding period, and they were higher by as many as 114% (90–175%) in the other complexes. Presumably, these differences can be explained by the fact that the Stawno population was close to the exhaustion of habitat carrying capacity already in period IV, and the other populations were not.

In addition to breeding pairs (Tab. 1), the Stawno population included 1–3 territorial single males, most of which were only in partly adult plumage, each year of the two study periods.

Moreover, in each complex there were several (no more than 5) juvenile females, not paired with territorial males.

## OCCURRENCE

The marsh harrier is a migratory species in the Barycz valley. The earliest appearance in spring was observed on March 13, 1982. In other years they returned between 17 and 20 March. Most birds returned from their winter quarters at the turn of March. This is illustrated in Figure 2. By March 25, every

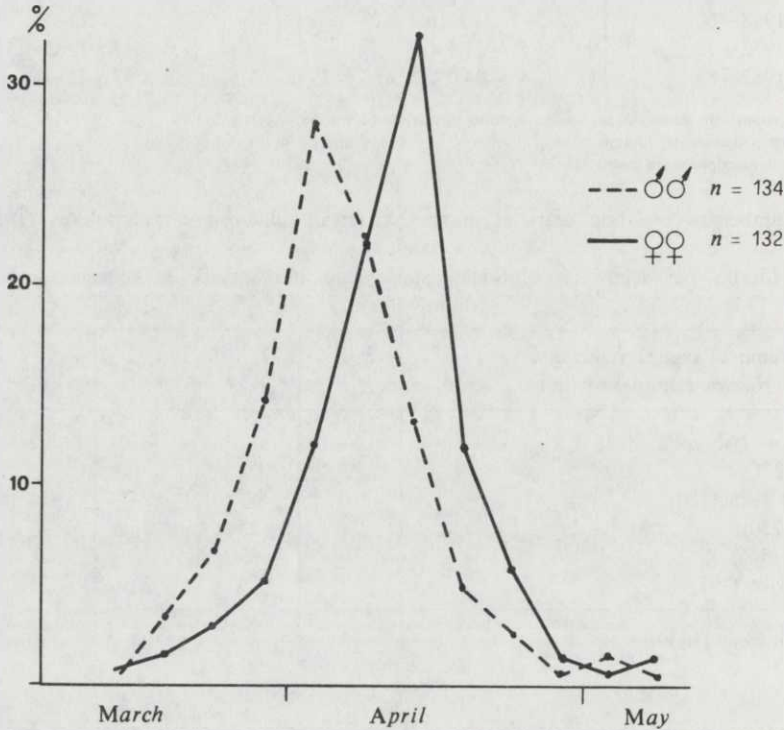


Fig. 2. Timing of the return of marsh harriers from wintering ground  
Points show the percentage of males and females observed in pentads. All years combined

Ryc. 2. Terminy powrotu błotniaków stawowych z zimowisk

Punkty na wykresie wskazują procent samców i samic, które powróciły w danej pentadzie. Dane ze wszystkich lat zsumowano

returning bird was noted. Later on only birds in their territories were counted and only on the ponds where other observations were made so that their presence could permanently be checked. The material collected in this way illustrated only the process of territory establishment, but these two processes went almost concurrently.

The most important phases of the life cycle of marsh harriers from their return in spring until departure are illustrated in Figure 3.

After the breeding season, when the young became capable of independent life, marsh harriers left their breeding grounds very soon (see Fig. 3). Almost 10% of

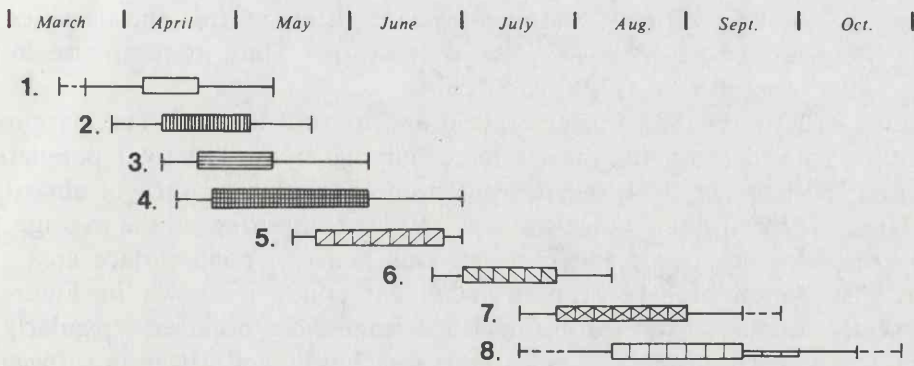


Fig. 3. Phenology of the life-cycle of marsh harriers in the Barycz valley

1 - return, 2 - establishing of territory, mating, nest building, 3 - laying period, 4 - incubation period, 5 - hatching period, 6 - fledging period, 7 - post-fledging period, 8 - post-breeding dispersal and departure. The intensity of the relevant phenomenon is shown as follows: high - bars; low - solid line; trace - dashed line

Ryc. 3. Fenologia cyklu życiowego błotniaka stawowego w dolinie Baryczy

1 - powrót z zimowisk, 2 - ustanawianie terytorium, łączenie się w pary, budowanie gniazd, 3 - okres niesienia jaj, 4 - wysiadywanie, 5 - wykluwanie się młodych, 6 - okres wychowywania młodych w gnieździe, 7 - okres nabywania samodzielności przez młode, 8 - dyspersja połączona, odlot z zimowiska. Słupki oznaczają okres największego, linie ciągłe - niskiego, a linie przerywane - śladowego nasilenia zjawiska

adult males disappeared from the ponds already in the second half of July, leaving to females further care for the young. Most adult males and a large proportion of females started migration in August. After mid-September no more than 15% of individuals remained in the study area. These were adult females and the current-year young. Single females or young were occasionally seen till mid-October. The latest observation (of a young bird) was made on 27 October, 1985.

Marsh harriers returned thus to the Barycz valley for nesting and raising the young, and this took them almost five months. More than half of a year they spent outside the breeding area.

#### DENSITY OF BREEDING PAIRS, TERRITORY, NEST LOCATION, AND TERRITORIAL BEHAVIOUR

In the Stawno complex, marsh harriers nested only on 16 ponds out of 31, although habitat conditions were suitable at least on 19 ponds. Thus, densities were calculated for two variants: a) in relation to the total area of the pond complex (1730 ha), and b) in relation to the total area of the ponds with nesting marsh harriers (1326 ha).

In 1972-75, mean densities were 1 pair/55 ha (a) and 1 pair/42 ha (b). In 1982-84 these densities increased to 1 pair/40 ha and 1 pair/30 ha, respectively. In 1984, when the number of breeding pairs was the highest, the density for variant b was 1 pair/26.5 ha. The maximum density, recorded on one of the ponds in three different years was 1 pair/7.5 ha (see Tab. 1, pond Nowy Świat Górny).

The home range of the marsh harrier, as defined by NEWTON (1979), consists of

the nest site, nesting territory, and hunting area. It seems that the densities for variant b correspond to the size of nesting territories. Thus, its mean size in the Barycz valley was 26.5 ha (1326 ha/50 pairs).

Figure 1 illustrates the complex Stawno and its surroundings. The margins of the outline coincide with the most remote hunting areas. The total population, comprising 50 pairs in 1984, satisfied all the needs within an area of almost 80 km<sup>2</sup>. Thus, the mean home range size was 160 ha, comprising on the average 125 ha of crop fields, meadows, and pastures, and 35 ha of pond surface area.

The distribution of nest sites on individual ponds is shown in Figure 1. Permanently occupied sites are distinguished from those occupied irregularly or only once. The mean distance between nests was 370 m, and 210 m in sufficiently wide reedbed belts along the shore. The smallest distance between nests of two different pairs was 29 m. These nests, however, were separated by a 20 m wide open water stretch.

In contrast to grey-lag geese, marsh harriers showed no preference for nesting on reedbed islets (WITKOWSKI 1983). A rough comparison of numbers of nests on islets and shoreline reedbeds (taking into account the area proportions of the two habitats) revealed no difference in density.

No preference was observed for island size. Typically, marsh harriers did not nest on islets less than 500 m<sup>2</sup>, nonetheless two successful nests were located on islets of 80 and 180 m<sup>2</sup>. 1-ha or larger islands were often occupied by two pairs.

No nest was recorded outside the ponds, although the habitat conditions were suitable. Likewise, dry ponds were avoided, though the same ponds filled with water could have one of the highest densities of nesting pairs (see Tab. 1, pond Golica).

A significant difference in nest location was found between the two study periods. In 1972–75, most nests were located deep in the reedbed, whereas in 1982–84 close to open water (Tab. 4).

All these characteristics of nest location seem to be antipredatory adaptations. Nest located on the ponds filled with water were better protected from mammalian predators than those located on the land or on dry ponds. The new tendency to

Table 4. Distance of marsh harrier nests from open water table in Barycz valley  
Tabela 4. Odległość gniazd błotniaka stawowego od otwartej wody w dolinie Baryczy

Period – Okres	Distance shorter than 10 m Odległość mniejsza niż 10 m No. of nests – Liczba gniazd	Distance longer than 15 m Odległość większa niż 15 m No. of nests – Liczba gniazd	Total Razem
1972–75	35	85	126 (6) <sup>+</sup>
1982–84	81	45	137 (11) <sup>+</sup>

Significance of difference (Chi-square test)

$P < 0.001$

Istotność różnic (test Chi-kwadrat)

<sup>+</sup> Figures in parantheses show the number of nests located between 10 and 15 m.

W nawiasach podano liczbę gniazd zbudowanych w odległości pośredniej.



nest at the reedbed-open water interface developed in response to the increasing impact of wild boars. Foraging wild boars (also on islets) were searching shallower parts of the reedbed, thus situated further from open water. A similar change in behaviour was also recorded for the grey-lag geese nesting on Stawno ponds.

Nesting territory typically contained one or more platforms where marsh harriers plucked and consumed the prey. In most cases these were inactive nests of geese. After establishing his territory, often but not always the male built a nest for himself. He roosted on it, and frequently landed after the so-called aerial dance. On rare occasions this nest was the basis of the later breeding nest. In two cases it was used to finish egg laying when the earlier nest with the first eggs had been abandoned.

Territorial advertisement in males depends on the recipient. The role of aerial dances performed by males (BENSON 1958-59, CRAMP & SIMMONS 1980) is not known. The present observations show that they were triggered in two situations: 1) when the male was unpaired yet, and 2) in the presence of an intruding male. In the first case, males danced frequently, especially during sunny weather, without any noticeable stimulus. This could have been a signal for other marsh harriers passing this area (spring migration was still continued). For males it could signify that the place is already occupied, and for females that a single territorial male is available.

In the second case, the signal was clearly addressed to a sexual competitor, and if it had no effect, more aggressive displays followed such as pursuit, threatening (by stretching the legs with spread claws), and finally an attack.

The response of a male to the approaching female never included dancing. If this was his current or prospective mate, the male pursued her in flight in an attempt to make her hover over his territory, and then land in it. If the female resisted even when the male pushed her in flight, he pretended to attack her. When the female landed, the male often flew to his platform where he stored prey, took an item, and brought it to the female. Sometimes this was only a piece of reed stem or a twig.

The response of paired males to alien females showed individual differences. Some males chased them, but never so vigorously as in the case of alien males. Others were neutral or even friendly. The response of their mates depended on circumstances. If the male was on the spot, they did not respond. If the male was absent, they tried to chase the intruding male or female.

Hunting areas of males extended over neighbouring crop fields and meadows or pastures. As the birds were not marked so that individuals could be identified at a distance, only directions of their hunting flights were noted (Fig. 1), whereas the location and boundaries of their hunting areas could not be observed. This was possible, however, in the case of two males that differed from all the other males in a natural way. One of them held the same nesting territory for four successive years, and all his nests were located within a radius of 40 m. Over two successive years he occupied the same hunting area, the central part of which was

3.5 km from the nest. After four years he disappeared. The other male nested on the same pond for two successive seasons, though on two different islands. His hunting area was 6 km from the nest.

If the nest was lost or abandoned, the birds either renested in the same or in a different territory, or they abandoned their territory, first the female, then the male, depending on time. When the nest was lost late in May or in June, the pair usually did not reneest and left the territory. Of 31 pairs that lost the nests to predators or abandoned them during incubation (see Tab. 16), 17 (55%) renested in the same territory, 8 left the territory, and in 6 territories only males remained. The majority of replacement nests were built in territories occupied year after year.

#### POLYGAMY

Over 7 years only 9 cases of polygamy were recorded, although a special attention was paid to this phenomenon. In all these cases it was bigyny. The nests of the second female mates accounted for less than 4% of all the nests.

In such a case, both the females nested in the same territory, and the largest distance between their nests did not exceed 400 m. The territories held by polygynous breeders must have been more suitable than other territories since in all the study years they were occupied first. They covered either single large reedbed areas, or several neighbouring smaller islets. Within these territories each of the two females had her own nesting site in which she treated the other female as an alien female.

Pair bonds between the male and two females were not simultaneously developed. The second female was accepted when the first was incubating (7 cases) or completing the clutch (2 cases). Three out of the nine mates of bigynous males were first-year breeders, as indicated by their plumage. One of them laid four eggs and raised two chicks. The second one built a nest together with the male but she did not lay eggs. She was "incubating" an empty nest for over 40 days, being fed by the male all this time. The third female occupied an abandoned nest of grey-lag goose with one egg. She added a little nesting material and was incubating for at least 38 days, although she had not laid eggs, and the male provided her with food.

Six adult and one young females, all being the second mates of polygynous males, produced a total of 10 young capable of flying, or 1.4 young per female at reproductive age. Thus, their production was 40% lower than the mean production of females being the only mates (2.3 young). The females paired with polygynous males as their first mates produced a little more offspring (1.9 fledglings) than the second mates of these males (1.4). The mean production of young by polygamous females in the Barycz valley was 1.66 young fledged. Reduction in the number of raised young by polygamous as compared with monogamous birds was related to much higher losses during incubation and in the

first days of brooding. The mates of bigynous males were not adequately supplied with food by the male, so they had to hunt, and this increased the number of chilled eggs and nestlings in their first days.

The production of young in nine bigynous males was 3.3 young per male, and it was higher by 30% than in monogamous males.

#### NEST

At the beginning of nest building the males carried nest material, and the female was building. In the final phase, the female carried more nest material. The nest was lined with the material brought only by female.

There were differences in the behaviour of the two partners during nest building. Females collected materials near the nest site and carried it (in the bill or in claws) directly to the nest. Males often collected materials far from the nest (from the dike or even further), flew with them rather high in the air and often hovered before landing. The behaviour of males seemed to be demonstrative. Perhaps this was a part of the territorial behaviour.

After laying, and especially after hatching of the young, the nest was enlarged, and its lining permanently supplemented, particularly after heavy rains. The nest with chicks was often lined with green grass or twigs with fresh leaves. Grass was brought by the female and twigs mostly by the male.

Four females out of almost 180 having nests with young, built quickly, within one day, an emergency nest. This was a result of the disturbance caused by frequent visits of the observer to the nests. In each of these cases the young were sufficiently grown to move in the reed and walk to the emergency nests (or may be they could have been carried there by the females).

Under active nests of marsh harriers, other species of birds nested. They included two nests of the water rail *Rallus aquaticus*, one nest of the little crane *Porzana parva*, and two nests of the pochard *Aythya ferina*.

#### LAYING PERIOD, INTERVALS BETWEEN SUCCESSIVE EGGS, REPLACEMENT CLUTCHES

Females started laying 12–25 days after their appearance in the territory, on an average of 20 days ( $n = 48$ ). This period was longer for pairs formed at the very beginning of the season, and shorter for delayed pairs.

The distribution of laying dates (without replacement clutches) showed year-to-year variation (Fig. 4). In some seasons (1972, 1974, 1975, 1982, and 1983), the curve of laying dates had a sharp and short-lasting peak, whereas in other years (1973, 1984) the peak was flat, long-lasting with a tendency to bimodality. These differences corresponded to changes in temperature in various seasons, which was particularly clear-cut in 1984.

The laying period did not start prior to April 10, and over 90% of the females



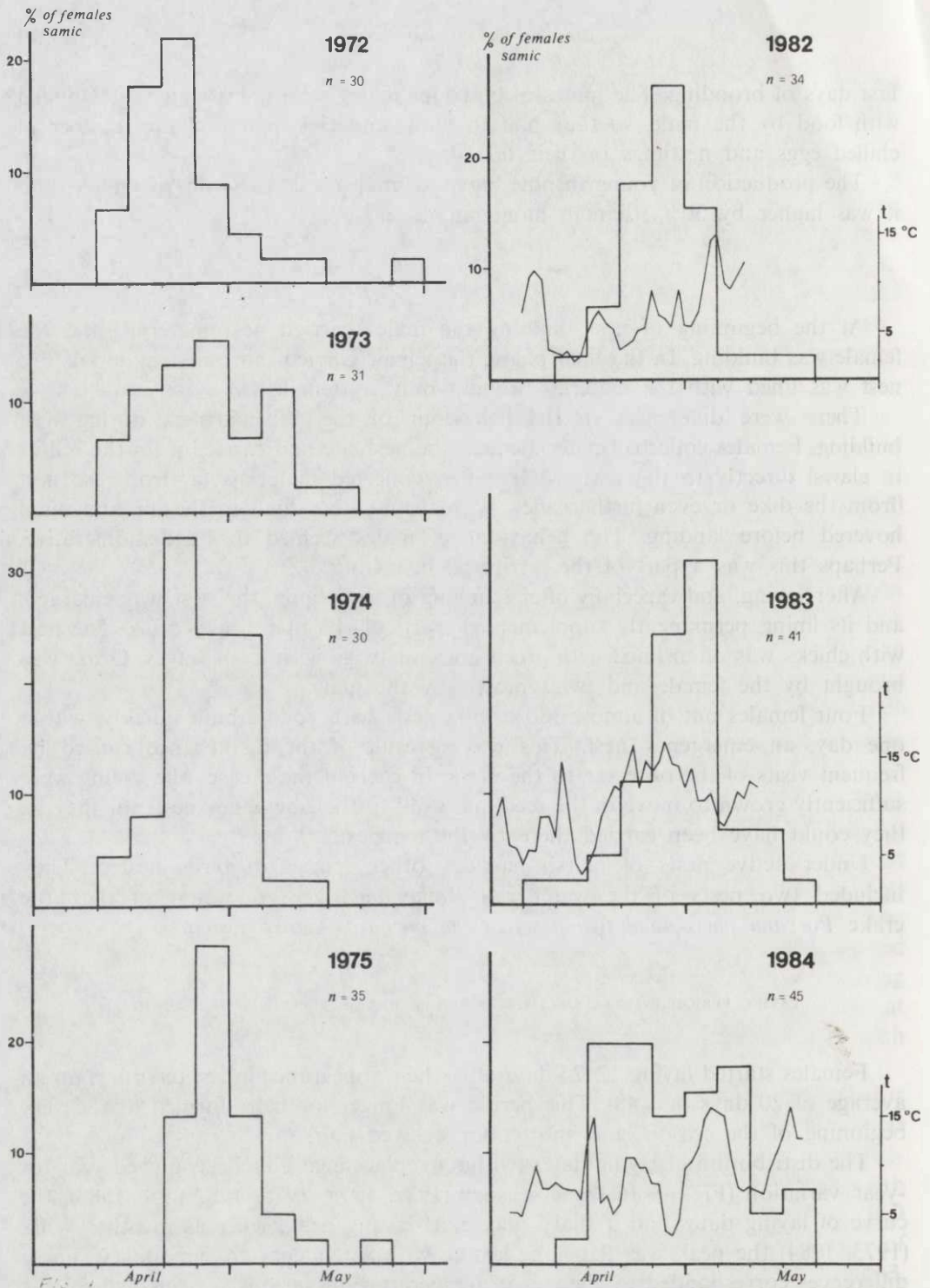


Fig. 4. Timing of the laying period in different years

Columns show the percentage of females starting the clutches in pentads. For the years 1982-84, also average daily temperatures are shown

Ryc. 4. Przebieg rozpoczynania znoszenia jaj w poszczególnych latach

Kolumny ukazują procent samic rozpoczynających się nieść w danej pentadzie. W latach 1982-84 pokazane są również średnie dobowe



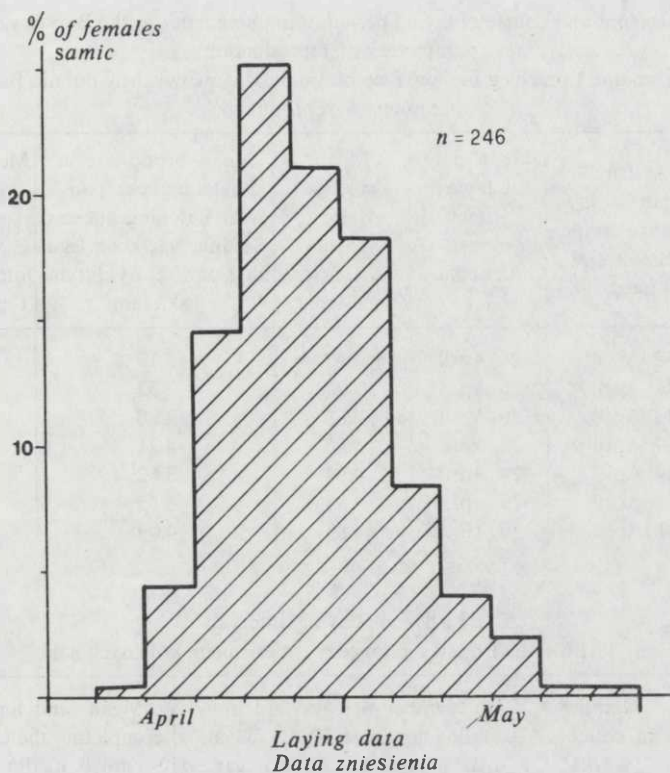


Fig. 5. Laying period of marsh harrier in the Barycz valley  
All years combined

Ryc. 5. Przebieg rozpoczynania znoszenia jaj przez błotniaki stawowe w dolinie Baryczy  
Na podstawie zsumowanych danych z wszystkich lat

started laying prior to May 10 (Fig. 5). Weather conditions in particular seasons had an effect on the rate of laying rather than on the duration of the laying period. Under mean climatic conditions (especially temperature) of the Barycz valley, most females started laying between April 20 and May 5.

The first females started laying between April 8 and 17 in different seasons (Tab. 5). The median date of laying the first egg was between April 24 and 30 (Tab. 5). Differences in the two dates were thus small, and in extreme cases they were 9 and 6 days, respectively.

As many as 94% of the eggs were laid at two-day intervals (Tab. 6). Thus, a completion of an average clutch of 5 eggs (Tab. 7) took 8 days. The period of clutch completion extended from 3 to 15 days, depending on the clutch size (Tab. 6).

Of the 17 replacement clutches (known for sure to be replacement clutches) 8 were started between May 6 and 15, 6 between May 16–25, and 3 between May 26

Table 5. Commencement and course of laying period of marsh harrier in the Barycz valley in relation to parameters of reproduction

Tabela 5. Rozpoczęcie i przebieg niesienia się błotniaków stawowych w dolinie Baryczy, a wielkość parametrów reprodukcji

Year Rok	First female began to lay Pierwsza samica zaczęła się nieść	Mean date of laying Środek okresu niesienia jaj	Mean clutch- -size Średnia wielkość zniesienia	Mean brood-size at hatching per pair with hatching success Średnia wielkość lęgu na 1 parę z wyklutymi pisklętami	Mean brood-size at fledging per successful pair Średnia liczba lotnych młodych na 1 parę z sukcesem
1972	12 April	24 April	5.43	3.19	2.89
1974	12 April	26 April	5.25	3.52	2.74
1973	14 April	26 April	4.68	3.86	3.32
1975	17 April	27 April	5.25	4.21	3.41
1982	14 April	28 April	4.94	3.62	3.24
1984	15 April	29 April	4.84	3.83	2.57
1983	8 April	30 April	4.83	4.09	3.43

Table 6. Laying intervals

Tabela 6. Przerwy pomiędzy zniesieniem kolejnych jaj

Clutch size Wielkość zniesienia	Number of clutches Liczba zniesień	Number of eggs laid in following intervals (in days): Liczba jaj zniesionych w nastę- pujących przedziałach (w dniach):				Mean (and longest) time of completing the clutch (in days): Średni (i najdłuższy) czas kom- pletowania zniesienia (w dniach):
		2	3	4	5	
2	1	—	1	—	—	3 (3)
3	4	7	1	—	—	4 (5)
4	14	41	1	—	—	6 (7)
5	24	93	3	—	—	8 (9)
6	11	51	3	1	—	10 (12)
7	3	15	2	—	1	12 (15)
Total Razem	57	207 94.0	11 5.0	1 0.5	1 0.5	

and June 5. These nests are excluded from histograms and tables. In 1974, an unusual course of one of the replacement clutches was noted. On April 28, the nest contained a complete clutch of 5 eggs. Until May 10 only two eggs remained. The other eggs were broken by the incubating female, this having been directly observed for two eggs. On May 23, one nestling hatched. The second egg contained a dead embryo. On May 29, the nest contained one nestling, and two new, freshly laid eggs. Thus, the female started a replacement clutch on the same nest as a consequence of a significant though not complete loss. It is symptomatic

Table 7. Clutch size  
Tabela 7. Wielkość zniesienia

Period Okres	Clutch size Liczba jaj	2	3	4	5	6	7	8	$\bar{x}$	SD
1972–75	Number of clutches Liczba zniesień	1	5	19	57	22	11	2	5.15 <sup>+</sup>	1.06
	%	0.9	4.3	16.2	48.7	18.8	9.4	1.7		
1982–84	Number of clutches Liczba zniesień	1	3	26	69	19	—	—	4.86 <sup>+</sup>	0.74
	%	0.8	2.5	22.0	58.5	16.1				
Total Razem	Number of clutches Liczba zniesień	2	8	45	126	41	11	2	5.01	0.92
	%	0.9	3.4	19.1	53.6	17.4	4.7	0.9		

<sup>+</sup>  $t = 2.44$ ,  $P < 0.025$

that even the hatching of a nestling did not inhibit the new ovulation. At the end only one chick hatched and left this nest.

Another female, which lost a brood of 4 nestlings 1–5 days old, started relaying on May 29, or 9 days after the loss.

#### CLUTCH SIZE

Female marsh harriers laid 2–8 eggs in a clutch, with an average of 5.0 eggs (Tab. 7). In 1972–75, the mean clutch size was higher by 0.3 eggs than in 1982–84 ( $t = 2.44$ ,  $P < 0.02$ ). This was due to a dozen or so clutches of 7 and 8 eggs, lacking in the second period. In 1972–75, there were also clutches of 9–11 eggs. This was an effect of laying additional eggs to the same nest after breaking many eggs originally laid. These additional eggs are not included in Table 7.

Mean clutch size reached highest values early in the season, and it gradually declined with time (Tab. 8). Differences in mean values between the extreme 5-day periods were 1.2 eggs, and they were statistically significant ( $t = 4.5$ ,  $P < 0.001$ ).

Mean clutch sizes in different study years are shown in Table 5. They are ordered according to the dates by which half of the females started laying in a given season. A weak trend can be seen – the earlier the laying, the higher the mean clutch size. Only in 1973 this was not true. The median date of egg laying was relatively early in that year (26 April) and the mean clutch size was the lowest (4.68). Nevertheless, the relationship was statistically significant (SPEARMAN rank correlation coefficient  $r_s = -0.747$ ,  $P < 0.05$ ).

The number of eggs in 17 replacement clutches laid between 6 May and 5 June varied from 3 to 6 ( $3 \times 1$ ,  $4 \times 10$ ,  $5 \times 5$ ,  $6 \times 1$ ), with a mean of 4.35 eggs.

Table 8. Declining of mean clutch size within the season

Data for all years combined. Laying seasons are divided into 5-day periods: I-V and following (&gt;V)

Tabela 8. Spadek średniej wielkości zniesienia z upływem sezonu

Dane ze wszystkich lat łącznie. Każdy okres lęgowy podzielono na pentady: I-V i dalsze (&gt;V)

5-day periods Pentady	Mean clutch size Średnie zniesienie	SD	N	
I	5.6 <sup>+</sup>	0.94	17	$\bar{x} = 5.4^{++}$ , $SD = 0.85$
II	5.5	0.83	42	
III	5.2	0.82	48	
IV	5.0	0.70	44	$\bar{x} = 4.7^{++}$ , $SD = 0.86$
V	4.7	0.78	37	
> V	4.4 <sup>+</sup>	0.95	47	

<sup>+</sup>  $t = 4.5$ ,  $P < 0.0001$ .<sup>++</sup>  $t = 6.25$ ,  $P < 0.0001$ .

## SIZE AND WEIGHT OF EGGS

Eggs were measured only in 1972-75, and the results are shown in Table 9. Eggs much smaller than the mean are excluded if no embryo developed in them. Very small eggs from which nestlings hatched are included. The smallest size of an egg out of 544 measured was 44.1 × 35.1 mm and its weight was 29 g, whereas the respective figures for the largest egg were 54.7 × 41.4 mm and 51 g.

Table 9. Egg measurements  
Tabela 9. Wymiary i masa jaj

	Maximum	Minimum	Mean Średnia	SD	N
Length Długość (mm)	56.5	42.0	48.90	2.05	544
Breadth Szerokość (mm)	42.0	34.5	38.17	1.39	544
Weight Masa (g)	51.0	29.0	37.86	3.79	561

The number of eggs in a clutch had no effect on their weight. On the average, small clutches (3-4 eggs) contained a little lighter eggs ( $\bar{x} = 37.68$  g,  $SD = 2.8$ ,  $n = 19$ ) than large clutches of 6-7 eggs ( $\bar{x} = 38.19$  g,  $SD = 3.2$ ,  $n = 28$ ), but the difference was not statistically significant ( $t = 1.26$ ,  $P > 0.2$ ).

It has been found that nestlings hatched from extremely small eggs (29-32 g) account for a higher proportion of the egg weight than those hatched from eggs of the mean size, and the latter account for a higher proportion of the egg weight than the nestlings hatched from the heaviest eggs (Tab. 10). These differences, however, were not statistically significant.



Table 10. Relation of the weight of eggs to the weight of hatchlings  
Tabela 10. Masa jaja, a masa wyklutego żeń pisklęcia

Mean egg weight (range) Średnia masa jaja (zakres zmienności)	Mean weight of hatchling (range) Średnia masa pisklęcia (zakres zmienności)	Hatchling weight in relation to egg weight (%) Proporcja masy pisklęcia do masy jaja (%)	<i>n</i> Chi-square test test Chi-kwadrat
31.1 g (29–32 g)	23.1 g (22–24 g)	74.3	4 ← $\left. \begin{array}{l} N. s. \\ N. s. \end{array} \right\} N. s.$ ← 9
37.9 g (33–42 g)	26.5 g (24–28.5 g)	69.9	
44.2 g (43–47 g)	29.9 g (27–32.5 g)	67.6	

The weight of eggs had no effect on breeding success, at least until fledging, and small differences in the production of young between clutches with very light and very heavy eggs were statistically not significant (Tab. 11).

Table 11. Breeding success in relation to the mean size of eggs within the clutch  
Tabela 11. Sukces lęgowy w zależności od średniego rozmiaru jaj w zniesieniu

	Mean egg weight up to 33.5 g Średnia masa jaj do 33.5 g <i>n</i> = 12	Mean egg weight above 43.5 g Średnia masa jaj powyżej 43.5 g <i>n</i> = 11	Significance of difference (Chi-square test, <i>t</i> – test) Istotność statystyczna różnicy (Chi-kwadrat i <i>t</i> – test)
Number of eggs laid Liczba jaj zniesionych	66	55	
Number (%) of broken eggs Liczba (%) jaj zgniecionych	20 (30.3)	15 (27.3)	<i>N. s.</i>
Number (%) of unhatched eggs Liczba (%) jaj niewyklutych	8 (12.1)	6 (10.9)	<i>N. s.</i>
Number (%) of young hatched Liczba (%) młodych wyklułych	38 (57.6)	34 (61.8)	<i>N. s.</i>
Number (%) of young dead Liczba (%) młodych zmarłych	8 (12.1)	5 (9.1)	<i>N. s.</i>
Number (%) of young fledged Liczba (%) młodych lotnych	30 (45.5)	29 (52.7)	<i>N. s.</i>
Mean brood size at fledging per pair Średnia wielkość lęgu przy wylocie na parę	2.5 ± 1.7	2.6 ± 1.6	<i>N. s.</i>

19 nestlings out of 30 hatched from small eggs were males, and 14 nestlings out of 29 hatched from large eggs were males. The difference thus was small, statistically not significant.

Eggs from the same clutch could show large differences in size. The mean difference between the heaviest and the lightest eggs in the clutch accounted for

9.0% ( $n = 107$ ) of the weight of the heaviest egg. This difference ranged from 1.2% to 24%. The mean difference did not exceed 7.5% for 65% of the clutches, and a difference of over 15% was found for 13% of the clutches.

An unexpected relationship was found between the weight of eggs and the sequence of their laying. In most cases, the first and the last eggs in the clutch were smallest, whereas the second and the third eggs tended to be the largest. A complete set of results is shown in Table 12.

Table 12. Variability of egg-weight sequences in 33 five-egg clutches and 9 four-egg clutches  
Eggs within the clutch are ranked from heaviest to lightest

Tabela 12. Rozmaitość sekwencji jaj pod względem ich masy w 33 zniesieniach złożonych z 5 jaj i 9 zniesieniach z 4 jaj

Jaja w poszczególnych zniesieniach zostały uszeregowane od najcięższego do najlżejszego

Sequence — Sekwencja Number of clutches — Liczba zniesień	Consecutive number of egg (and its mean position within the clutch) Numer kolejny jaja (i jego średnia pozycja w zniesieniu)							
Five-egg clutches — Zniesienia złożone z 5 jaj:								
12453	13524	14325	14532					1 (5)
1	1	1	1					
21435	21453	23154	23415	23451	23541	24135	25314	2 (2)
1	1	1	2	1	1	1	1	
32451	34125	34152	34251	34521	35241			3 (3)
2	1	1	1	2	1			
42135	42315	42531	43215	43251	45231			4 (1)
1	1	1	2	1	1			
51423	52143	53421	54321					5 (4)
1	2	1	1					

Four-egg clutches — Zniesienia złożone z 4 jaj: 1234 1243 2341 3124 3214 3421

Consecutive number of egg (and its mean position within the clutch) 1 (2 = 3), 2 (1), 3 (2 = 3) 4 (4)  
Numer kolejny jaja (i jego średnia pozycja w zniesieniu)

#### INCUBATION

Females started incubation after laying the first egg. At the beginning it was not intense but after laying the second or the third egg it was already normal. As a result, in some nests, the hatching of young from the first two (occasionally three) eggs was synchronous. In 32 nests, or 28% of the total of 114 nests checked on the first day of hatching, two nestlings hatched on the same day, and in 5 nests (4.5%) even three nestlings hatched on the same day.

After the completion of clutch, longer breaks in incubation occurred when the male brought food. The ceremony of taking the prey in the air (80% of the cases) or from the feeding platform, eating, and the subsequent hovering over the nest took 5–25 minutes. If the female delayed resuming incubation, the male forced her to return to the nest. While the female was eating on the platform, the male was sitting on the nest or on a nearby tree. There were 4–7 breaks of this type during the day as the female received food with this frequency, on the average. In the meantime, also short breaks took place as if for checking the situation in adjacent areas. The last, longest break occurred at sunset, always in the presence of the male near the nest. It lasted over 20 minutes. Occasionally, during that break the female covered a large distance from the nest.

When it was raining, incubating females frequently got up on the nest to shake the water off. During a heavy rain they were standing over the eggs, bent at an angle of 50°, and the water was running off their backs and tails, beyond the nest cavity. Frequent changes of the position during the rain accounted for most cases of egg breakage. After the rain, the female loosened the surface nest layer with the beak, and when it became partly dry, she brought a fresh lining material.

The male, if not hunting, was resting on a tree near the nest. When he noticed a man approaching by boat, he flew toward the nest and warned the female. The warning signal was a tilt in flight over the nest. It may have been accompanied by a quiet call that could not be heard by the observer because of his distance from the nest. Due to the warning flight over the nest the female was not cheeping upon seeing the male, as she usually does, so she did not disclose her presence. The warning behaviour described above was typical. Some males flew toward the approaching boat, and displayed the behaviour that they demonstrate when a man is at the nest and has flushed the female. There was some indication that these were individuals experienced in earlier years, and they knew that the approaching observer was going to the nest. As a result of this behaviour, the female often did not wait until the last moment but immediately joined the alarming male.

#### Duration of incubation

The duration of incubation was measured from the day following the date of laying of the first egg to the date of hatching of the young from this egg. The duration of incubation of the second and all the other eggs was measured from the dates of laying each of these eggs to the dates of their hatching. It varied between 30 and 36 days. The incubation of the first and the last eggs was a little longer, on the average, presumably due to not so careful incubation at the very beginning and reduced warming of the last eggs, when earlier-hatched nestlings were already in the nest. The time of incubation was assessed for 145 eggs:

30 days – 1.4%	32 days – 17.5%	34 days – 5.6%
31 days – 3.5%	33 days – 69.2%	35–36 days – 2.8%

## HATCHING, ACTIVITY OF THE YOUNG AND PARENTAL LABOUR DIVISION DURING THE NESTLING PERIOD

Hatching. The young hatched asynchronously for 3–12 days, depending on the number of eggs in the nest. Data for 88 nests are shown in Table 13. As the mean clutch size was 5 eggs, hatching lasted 8 days, and the mean difference in age between the oldest and the youngest nestlings was 7 days in a brood of 5 nestlings.

Table 13. Duration of hatching in relation to clutch size  
Tabela 13. Tempo wykluwania się młodych w zależności od wielkości zniesienia

Clutch size Wielkość zniesienia	Duration of hatching (in days) Czas wykluwania (w dniach)			No. of clutches Liczba zniesień
	Mean Średnio	SD	Range Zakres zmienności	
3	4.0	0.7	3–5	9
4	6.4	1.2	4–8	20
5	8.4	1.3	6–11	46
6	10.2	1.2	8–12	13
Mean – Średnio	7.7	2.1	3–12	88

Nestling activity. Typically, a nestling was fed for the first time on the next day after hatching, and no earlier than 8 hours after hatching if on the same day. According to the literature data (e.g. GLUTZ *et al.* 1971) nestlings are fed “from beak to beak”, which suggests a situation similar to that in passerine birds. This was not the case, however. When the female returned to the nest with the food, the young were cheeping and crawling towards her, and then stopped with stretched necks in front of her. They did not open their beaks wide as passerines do. The female tore a small piece, and holding it with the end of her beak, head bent, she was waiting until a chick took it. If no chick took the item, she ate it herself after a short time of waiting.

In the first days of life, the young responded to the movement of the female rather than to her image. They also approached the observer and the objects moved by him. This response was maintained until 7–10 days of age or even longer if the young starved. Between days 10 and 20 the young showed fear response to the observer, and they moved to the edge of the nest. About day 20 they developed defensive-aggressive responses. They opened their beaks wide, lay down on their backs, and struck the intruder with their claws.

At an age of 23–25 days, the young started to tear the prey brought by the parents, provoked by increasing competition with siblings and their increasing aggression, when the best strategy was to seize the whole booty the parent brought instead of fighting with siblings for its pieces. At this age, they used much time for



preening, plucking down, and various exercises such as rapid seizing of nest material with claws, jumping combined with fluttering the wings, and jumping on broken reed stems near the nest. On hot days they left the nest to drink water, bathe, and search for shade in the reed. From the very beginning the young cared for keeping the nest clean. They voided the faeces while standing at the rim of the nest. To void the faeces they crawled backwards to the rim of the nest, and they spurted them out.

Different categories of nestling activity are set in Table 14. This table also shows the percentage of the 16-h. period of their daily activity used for different kinds of activities.

Table 14. Activity of the young in different developmental stages

Particular kinds of activity are shown as a percentage of whole daily activity

Tabela 14. Aktywność młodych w różnych stadiach wiekowych

Poszczególne rodzaje aktywności są podane jako procent całodzienniej aktywności

Kind of activity Rodzaj aktywności	Age of young (in days) — Wiek młodych (w dniach)							
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-42
Slipping, lying Spanie, leżenie	94.0	91	85	74	60	50	38	29
Struggling for food, eating Walka o pokarm, jedzenie	3.5	5	7	7	8	8	8	7
Walking, jumping, wing-fluttering Chodzenie, skakanie, bicie skrzydłami	2.5	3	5	9	12	17	22	20
Preening, down-plucking Pielęgnacja piór, wyskubywanie puchu	+	1	3	10	15	20	25	18
Temporary nest leaving, bathing Wychodzenie z gniazda, kąpiel	—	—	—	+	4	4	4	13
Rising up, hunting exercises Podlatywanie, ćwiczenia w chwytaniu	—	—	—	—	1	1	3	12
Flying Latanie	—	—	—	—	—	—	—	1

Young males, being lighter than females, started flying when 37–39 days old, whereas the heavier females at an age of 41–44 days (see Tab. 15). The beginning of flying is considered as the time when the young bird rose in the air and was flying over the reedbed, rather than the time when it was moving on reed tops while fluttering the wings. In one case, when a mate of a polygynous male had to start hunting very early, she was feeding her only chick almost exclusively with dead carps *Cyprinus carpio*. Although this was a male, he flew out of the nest for the first time only at the age of 51 days.

Labour division between parents. Typically, after the hatching of the young the male passed the prey to the female or left them on the platform. Only when the female was absent or busy with feeding the young, did he occasionally carry food directly to the nest.

Table 15. Daily weights (g) of nestling marsh harriers  
 Tabela 15. Masy ciała (g) młodych błotniaków stawowych w różnym wieku

Age (days) Wiek (dni)	Males — Samce					Females — Samice					
	N	Body weight — Masa ciała				Body weight — Masa ciała				N	Age (days) Wiek (dni)
		min.	max.	mean	SD	min.	max.	mean	SD		
1	25	22	32	26.0	2.8	24	32	27.0	2.5	21	1
2	38	23	35	29.1	3.8	24	38	30.1	3.6	25	2
3	31	28	53	34.6	6.3	31	58	36.0	5.9	24	3
4	27	33	70	46.0	9.2	32	72	52.1	9.5	22	4
5	26	42	86	60.5	9.5	49	91	68.8	11.2	19	5
6	30	46	102	77.3	13.8	53	102	83.7	13.0	22	6
7	23	54	130	95.6	15.5	61	126	106.6	18.7	19	7
8	24	93	140	118.4	11.4	86	200	133.1	27.3	20	8
9	27	104	198	144.1	23.0	82	238	160.9	35.4	23	9
10	20	130	214	171.0	21.0	106	260	195.7	30.6	19	10
11	25	124	262	200.1	37.1	150	340	228.4	38.9	19	11
12	26	140	286	229.2	36.5	164	354	258.5	31.0	17	12
13	26	133	325	257.5	39.8	218	365	298.4	38.8	23	13
14	24	158	340	286.1	40.2	260	420	340.9	51.3	25	14
15	26	208	410	313.0	39.6	264	445	380.7	58.0	19	15
16	27	210	435	340.9	42.8	288	500	426.4	44.5	23	16
17	42	212	460	369.8	46.1	340	525	457.3	60.3	18	17
18	24	265	465	397.0	47.4	365	545	495.7	48.4	22	18
19	24	330	515	421.6	45.0	380	600	519.3	38.3	22	19
20	29	360	520	447.2	34.8	370	650	545.3	62.1	30	20
21	27	360	520	464.2	39.3	415	650	581.5	47.1	23	21
22	26	410	560	485.4	44.3	500	705	610.4	54.5	24	22
23	29	380	580	505.0	43.3	520	725	627.9	55.1	21	23
24	29	400	580	513.6	49.8	520	710	644.7	47.6	18	24
25	28	410	580	519.2	46.9	460	740	668.1	65.8	21	25
26	30	390	600	524.2	55.1	480	820	685.0	70.0	23	26
27	29	430	630	530.5	56.5	490	760	696.8	24.8	11	27
28	32	420	620	537.5	50.5	540	740	700.4	38.9	21	28
29	33	430	660	538.5	47.0	550	780	708.7	47.6	19	29
30	28	450	630	540.5	42.4	565	820	716.2	56.3	19	30
31	34	460	640	540.9	45.2	620	845	725.3	52.2	19	31
32	29	480	620	544.7	32.4	620	860	725.1	48.5	24	32
33	29	460	640	546.9	43.3	600	820	730.9	43.2	27	33
34	23	485	640	552.4	35.1	650	780	733.2	24.8	14	34
35	22	485	620	552.9	36.3	680	820	732.8	45.2	16	35
36	19	470	600	553.4	28.3	650	780	727.7	38.6	15	36
37	15	470	620	551.3	35.8	640	810	725.3	38.9	17	37
38	11	460	580	533.2	34.5	680	790	724.4	37.4	11	38
39	8	490	590	535.6	29.7	670	790	725.0	23.8	14	39
						680	810	725.0	35.8	11	40

Until the mean young in the brood reached an age of about 10 days, only the male provided food. The female was brooding the young, or she protected them from the sunshine or rain. Later the female was hunting as well, and her contribution to providing the young with food was increasing. Even at an age of about 25 days the young could not tear the prey well. They were fed only by the female, never by the male. Under normal conditions, the male was never seen feed the young during several hundred hours of observations. This happened only once, when the female disappeared and three young were 11–17 days old. The male carried to the nest plucked and torn prey. When he started to tear them, the hungry chicks snatched the pieces from his beak and claws. This male successfully raised all the three chicks.

Marsh harriers started to be active at sunrise and continued their activity until half an hour after sunset. After the hatching of the young, the male was hunting practically all this time. Typically, the males did not hunt within their nesting territory. And even if they preyed in the ponds, they did not do this near the nesting territories of other conspecific pairs. The females, on the contrary, hunted almost exclusively within the nesting territory, sometimes a dozen or so metres from the nest, when the young were not fully grown. As the young were growing older, the females hunted not only on neighbouring ponds, but also in crop fields. But on open land they hunted on rare occasions, as indicated by their diet (Tab. 43).

The hunting activity of a male and a female during the nesting season, as measured by the number of prey delivered at different times of the day, is shown in Figure 6. The upper drawing (A) shows the beginning of this period, when females practically did not hunt yet. The lower drawing (B) illustrates the situation typical of the second half of the nesting period, when the contribution of the two birds was similar.

During the day, the male could catch 3–20 prey items. He reached the highest mean of 12 prey (9–15) when feeding not only the young but also the female. Later, when the female was also hunting, this mean value dropped to 8.2 prey per day, ranging 3–20. The reason for this decline is not known. It could have been due to a reduction in the prey density within the hunting area of the male, or due to the fact that the female participated in hunting.

When the female did not brood the young, she was a little more effective than the male, as on the average she caught 9.5 prey per day (4–16), and the additional difference was that she hunted for much heavier prey than the male did.

Figure 7 shows the timing of feeding over the day by males and females for four nests (A, B, C, D). Three of them (A, B, C) contained 4 or 5 young, thus more than the average brood of 3.1 young. Despite this the feeding effort of the males in the period when they supplied food to the whole family was not proportionally higher than the effort of the male rearing a brood of two chicks (D). In nest D, the male almost stopped feeding when the female joined him in this activity.

Figure 8 illustrates a cycle of observations on a brood of two chicks from 17 to

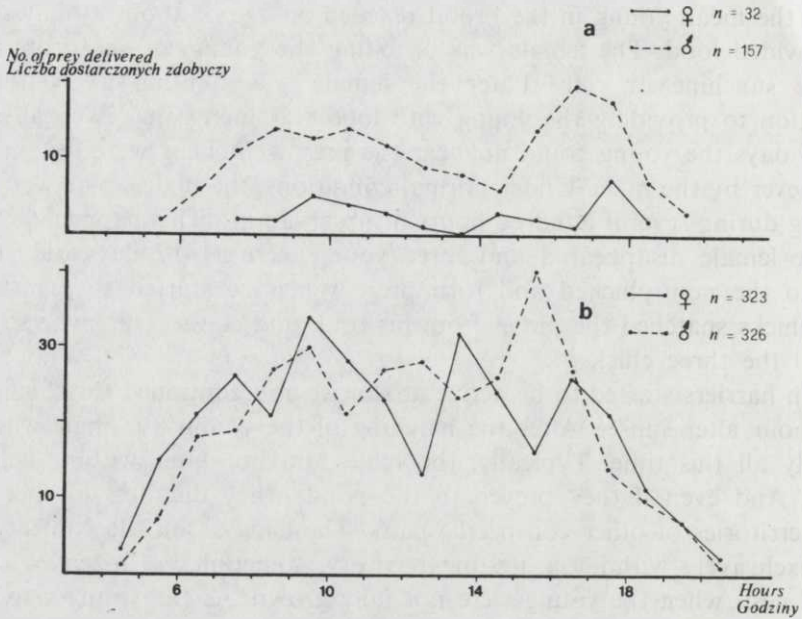


Fig. 6. Daily delivery of prey by males and females of marsh harrier in early (a) and later (b) part of the nestling period

Ryc. 6. Aktywność dobowa dostarczania zdobyczy przez samce i samice błotniaków stawowych w pierwszej (a) i drugiej (b) połowie okresu od wykucia do wylotu młodych z gniazda

55 days of age. In addition to the data on the timing of feeding by parents, different symbols indicate the timing of the development of important skills by the young.

#### GROWTH OF THE YOUNG

Lack of data in the literature (see GLUTZ *et al.* 1971) on the development of young marsh harriers inclined the author to present his results. Some measurements and descriptions can be useful for ageing and sexing the young.

Fig. 7. Prey delivery by the male (marks over the line) and the female (under the line) in four different nests (A, B, C, D)

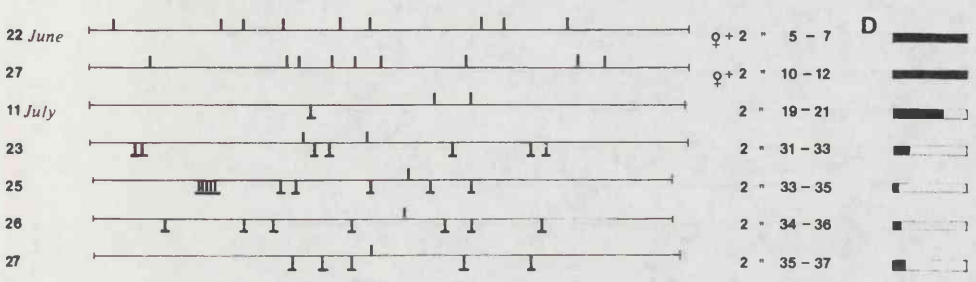
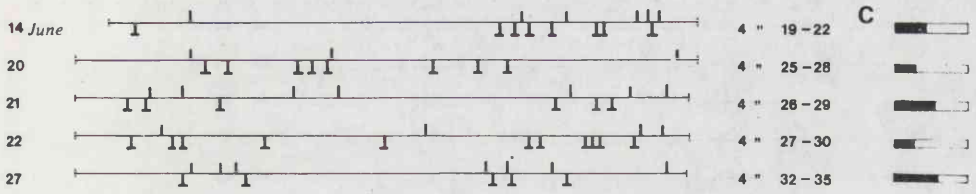
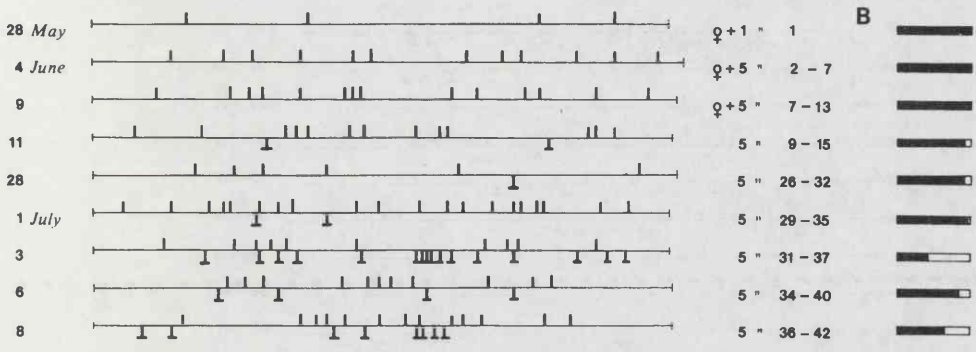
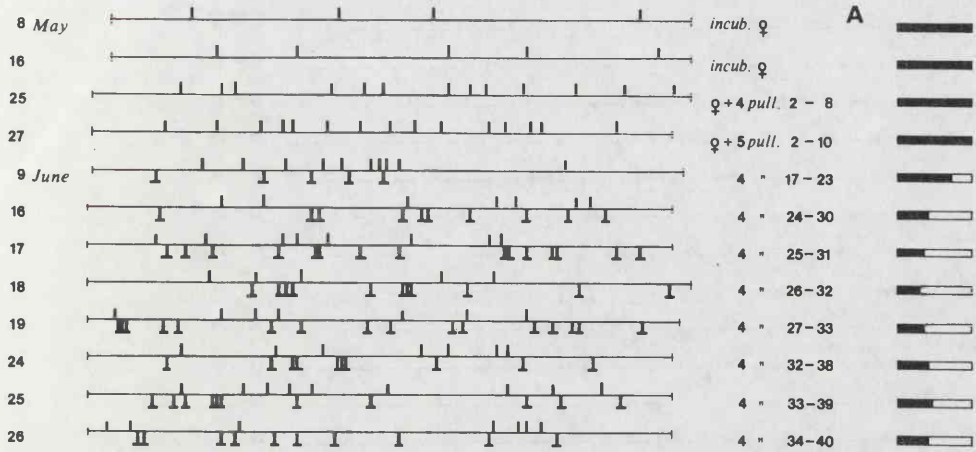
Marks show also the time of delivery. Black areas on the right side show the percentage of male's participation in food supply; white areas – female's participation

Ryc. 7. Dostarczanie zdobyczy przez samce (znaki nad linią) i samice (znaki pod linią) w czterech różnych gniazdach (A, B, C, D)

Znaki wskazują również czas dostarczania zdobyczy. Czarne pola po prawej stronie wskazują na udział samca, a białe – udział samicy w dostarczaniu pokarmu do gniazda



Nest contained: Age of young (days) Participation of male in food supply  
 Gniazdo: Wiek młodych (dni) Udział samca w dostarczaniu pokarmu

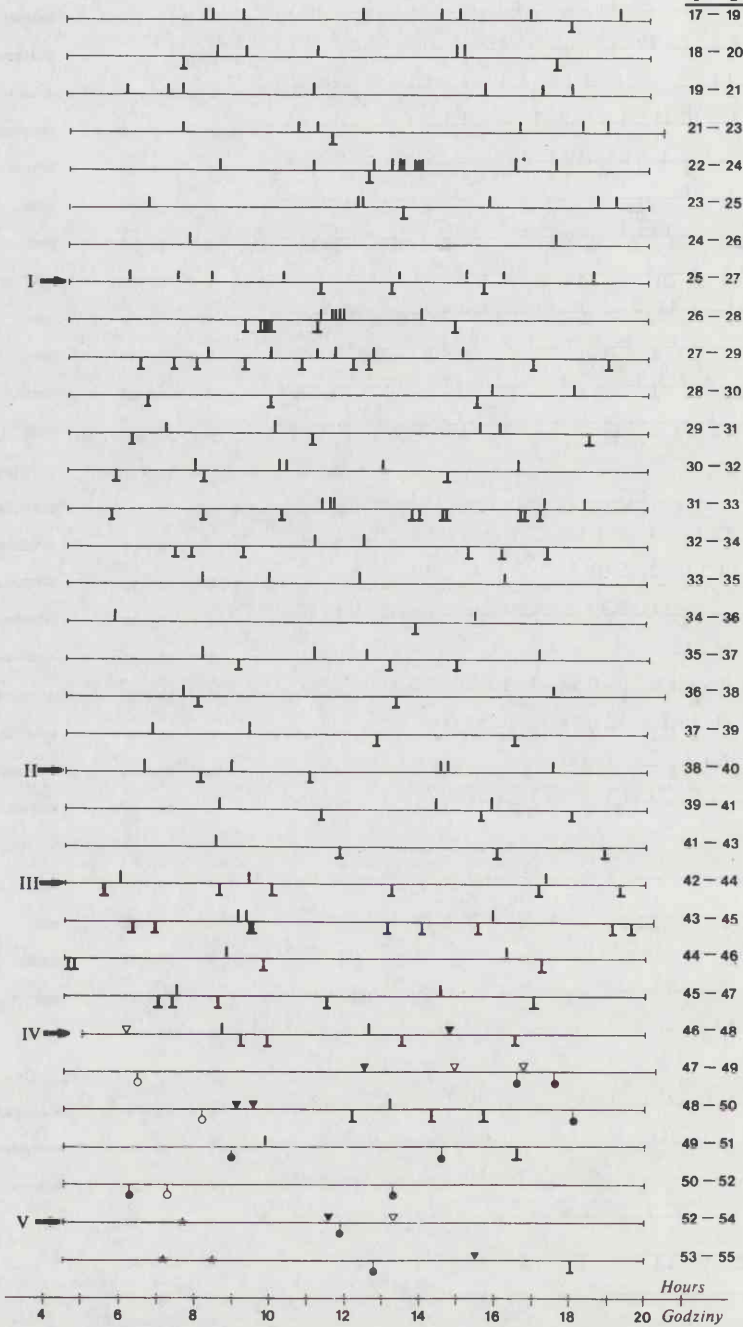


Hour: godzina: 4 6 8 10 12 14 16 18 20

Age of young (2 ind.)  
(days)

Wiek młodych (2 os.)  
(dni)

$\frac{1}{17-19}$   $\frac{2}{20-21}$  young



I - 1   ▽ - 3   ◯ - 5   ★ - 7   I →   III →  
 I - 2   ▼ - 4   ● - 6   II →   IV →   V →

Table 16. Length of the 5th primary and tarsus in nestlings of marsh harrier  
Tabela 16. Długość piątej lotki i skoku u młodych błotniaków stawowych

*N* = 6-28

Age of nestlings (in days) Wiek młodych (w dniach)	Mean length of 5th primary (mm) Średnia długość piątej lotki (mm)	Mean length of tarsus (mm) Średnia długość skoku (mm)	
6	+	27	
7	0.5	32	
8	1.5	36	
9	3.0	40	
10	6.0	43	
11	10	46	
12	15	49	
13	23	53	
14	29	56	
15	35	58	
16	42	61	
17	48	64	
♂♂                      ♀♀			
18	53	66	68
19	59	68	72
20	65	70	75
21	73	72	78
22	83	73	80
23	95	75	82
24	106	78	84
25	117	80	85
26-27	126-135	81	86
28	143	81	87
29-30	150-157	82	88
31-32	165-173	82	88
33-34	182-189	82	88
35-36	196-205	83	89
37-38	213-218	83	89
39-40	221-223	83	90

Fig. 8. Timing of prey delivery by the male and the female to a nest with two chicks

Different marks show the time of developing new skills by the young. 1 – male's prey, 2 – female's prey, 3 (5) – failed air food-pass between the male (female) and a young, 4 (6) – successful air food-pass between the male (female) and a young, 7 – first hunting attempts by young. I – young begin to tear up the prey on their own. II – beginning of flights, III – flying to meet the parent bringing the prey, IV – beginning of aerial food-passes between the parents and the young, V – young try to hunt

Ryc. 8. Dostarczanie pokarmu przez samca i samicę do gniazda zawierającego dwa pisklęta

Za pomocą różnych znaków wskazano na czas uzyskiwania nowych umiejętności przez młode. 1 – pokarm samca, 2 – pokarm samicy, 3 (5) – nieudane przekazanie ofiary młodem w locie przez samca (samicę), 4 (6) – udane przekazanie ofiary w locie przez samca (samicę), 7 – próby samodzielnych polowań. I – młode zaczynają same rozrywać ofiary, II – młode zaczynają latać, III – loty ku rodzicom niosącym pokarm, IV – przekazywanie młodym ofiar w powietrzu, V – młode próbują łowić samodzielnie

Newly hatched young were covered with white-cream down. They kept the eyes closed, though they could open them. On day 5 the second down was growing in the region of scapula, on the forearm, and at the sides of the tail. It was denser and longer, camel-wool-coloured. On days 8–10, this down formed thick cushions in these places. Pin feathers of primaries and secondaries started to emerge concurrently at an age of about 7–8 days. Their growth is illustrated in Table 16, using primary 5 as an example. This table also illustrates the growth of the tarsus. First, primaries 7 and 6 were growing at the highest rate, but at an age of more than 30 days primary 5 showed the highest growth rate. The highest growth rate of 10–12 mm/day was observed between days 21 and 27. On days 13–14 the primaries burst forth, and 5 days later so did coverts. At an age of about 30 days the young started losing the down, and then they spent much time plucking and removing the down by energetic shaking. They were totally feathered at an age of 35 days, when only single down remained on the head and the nape.

There was a clear difference in the growth rate of the tarsus between males and females from day 18 (Tab. 16). On day 40 it reached 6 mm on the average. In females at this age the length of the tarsus always exceeded the range of individual variation of the tarsus length in males, and was an additional diagnostic feature for sex determination.

#### INCREASE IN BODY WEIGHT AND DAILY FOOD CONSUMPTION IN THE YOUNG

Newly hatched young weighed 22–32 g. Typically, they did not take food on the day of hatching. On the next day they ate 6 g of meat, on the average, gaining 3 g of body weight. This means that 50% of the food weight was converted into body tissues. The corresponding values from hatching to fledging are shown in Table 17. Data for nestlings 1–10 days old were collected from two nests containing two and four young. Data for older nestlings were collected from 7 nests with 2–5 young.

The daily food intake per young increased until 26–30 days of age (Tab. 17, columns b and c). The relative growth rate (ratio of the body weight on the preceding day to that on the current day in percentage – Tab. 17, column f) was the highest on day 4 and decreased after day 5. Also from that day on the percentage conversion of food into body weight decreased (Tab. 17, column e). This was related to the increasing activity of the young, growth of down, and increasing homeothermy. The growth of body weight was stopped between days 26 and 30 (see also Tab. 15), although the mean food intake was still increasing. Now food was utilized mainly for the growth of feathers and increased activity of the young (see p. 250–251, Tab. 14). A slight increase in body weight was still noted at an age of about 35 days. 1–2 days prior to the onset of flying, the young consumed clearly less food than in preceding days. Mean values of daily increase in body weight of the young are shown in Table 15. The time of the day when the



Table 17. Daily food intake and its utilization by growing young marsh harriers  
 Tabela 17. Dobowe pobieranie pokarmu i jego wykorzystanie przez rosnące młode błotniaki stawowe

Age of young (in days) Wiek młodych (w dniach)	Mean daily food intake (g/young) Średnia dzienna porcja pokarmu (g/l młodego)	Range of daily food intake (g/young) Zakres zmienności dobowej racji pokarmowej (g/l młodego)	Mean daily growth rate (g) Średni dobowy przyrost masy ciała młodego (g)	Percent of food utilized for growth <sup>+</sup> (b:d) Procent wykorzystania pokarmu <sup>+</sup> (b:d)	Mean daily growth rate (calculated from means in Tab. 15) <sup>++</sup> Dobowe tempo średniego przyrostu masy młodego wyliczone ze średnich w tab. 15) <sup>++</sup>
a	b	c	d	e	f
1	+	0-2	+	+	+
2	6.0	3-10	3.0	50	10.5
3	12.0	3-20	6.0	50	16.5
4	21.0	15-40	11.0	48	28.0
5	32.0	15-45	14.5	45	24.0
6-10	45-80	35-90	18-32	40	15.5-19.5
11-15	80-107	45-120	32-33	31-40	8.5-14.5
16-20	112-127	50-155	27-36	21-31	5.5-8.0
21-25	122-135	5-165	15-26	11-21	1.5-4.5
26-30	123-164	50-240	4-11	2-9	0.0-1.0
31-35	129-162	80-240	0-12	+	0.0-0.5
36-40	123-137	25-190	-2-3	0	0.0

<sup>+</sup> Percentage of mean daily food intake used for mean daily increase in body weight.

<sup>++</sup> Ratio of the body weight on the preceding day to that on the current day in percentage.

<sup>\*</sup> Dobowy przyrost masy ciała młodego jako procent masy pokarmu pobranej w ciągu doby.

<sup>++</sup> Aktualna masa ciała młodego jako procent jego wczorajszej masy ciała.

young were weighed was not the same, and for this reason nestlings in some nests were hungry while in other nests they had already been fed when weighing was done. Despite this, the mean body weight taken in this way was very close to the mean obtained for a small sample of young which were weighed in the morning prior to being fed. Ranges of individual variation and values of standard deviations in weight of the young (Tab. 15) showed large differences of body weight between the individuals at the same age.

At the end of the nesting period, young females were heavier than young males by 190 g on the average (body weight of a male represented for 75% of that of a female), though they were approximately the same at hatching (Tab. 15). This does not imply, however, that females took more food than males. The daily food intake of males and females was identical, and for this reason it is not separated by sex in Table 17. Females reached their higher body weight due to being less

active and growing at a lower rate, rather than by eating more food than males. Males could fly 5 days earlier than females, and they earlier became independent. Thus, parental investment in both sexes was the same. Differences in the body weight between males and females were pronounced already in the nestling period. From about day 25 on, differences in the mean body weights  $\pm SD$  can be used as a diagnostic feature for sexing the young (Fig. 9).

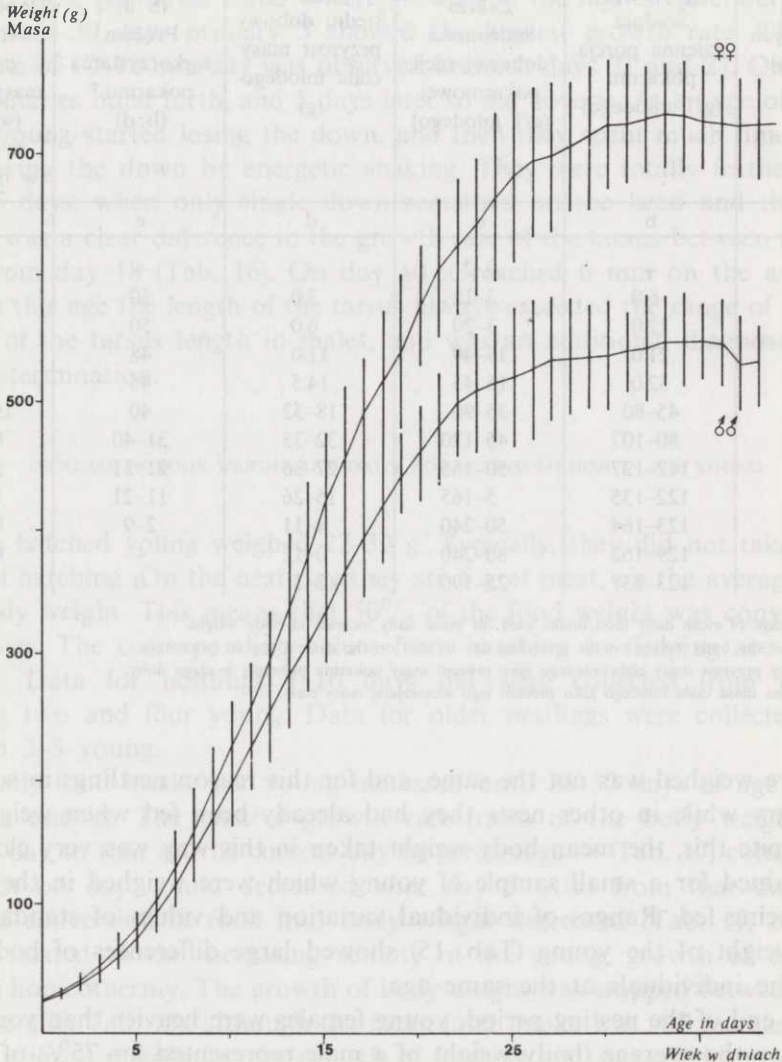


Fig. 9. Mean growth curve of the young marsh harriers

Sample sizes are shown in Table 15. One *SD* is shown on either side of the mean

Ryc. 9. Średni przyrost masy ciała młodych błotniaków

Wielkości prób w tabeli 15. Odłożono jedno *SD* po obu stronach średniej

Figure 10 shows individual growth curves for two males of the same nest. In addition to fluctuations in body weights due to temporary food deficiency, a tendency can be seen towards reaching a maximum body weight between days 28 and 35, and towards a subsequent decline by about 10% until the onset of flying.

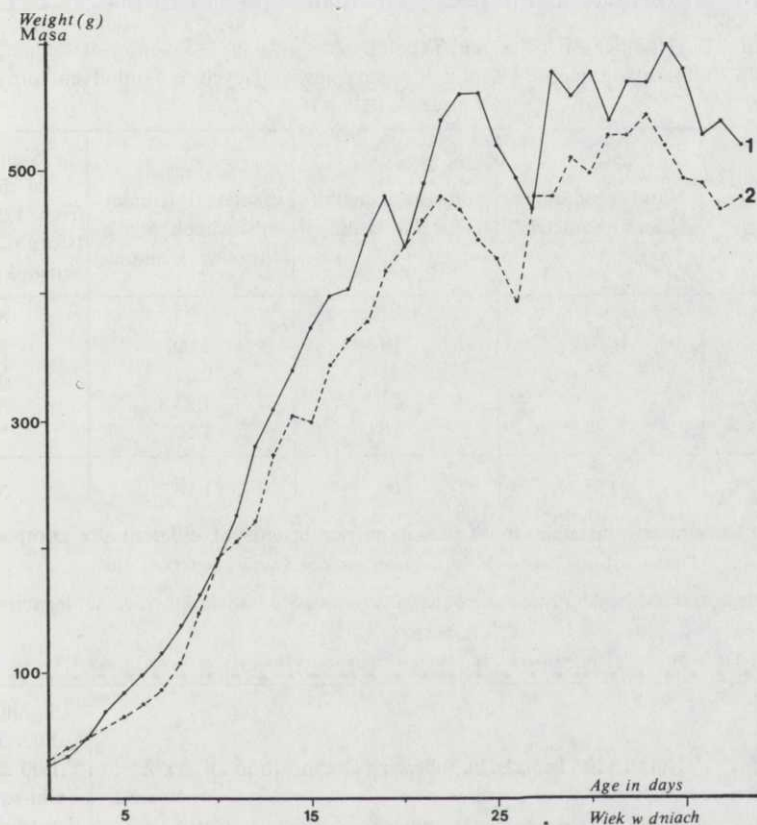


Fig. 10. Individual growth curve of two male chicks  
Ryc. 10. Przyrost masy ciała u dwóch młodych samców

This decline was not caused by shortage of food. The two-day younger chick was rarely discriminated by the older chick, as indicated by observations and almost parallel decreases and increases in their body weights (Fig. 10). Nevertheless, the younger chick never weighed more than the older one, even though the former had been heavier at hatching. Shortage of food for 2–3 days had no adverse effects on the final body weight and activity of the young.

A long-term food deficiency or a food of low value (*e.g.* dead fish) reduced the body weight of chicks by up to 35%, and delayed the onset of flying even by two weeks.

## SEX RATIO IN THE YOUNG GENERATION

Sex ratio was observed in 82 successful nests. The young were sexed at an age of about 30 days, using three parameters (see p. 231).

In four out of five categories of brood sizes males predominated over females (Tab. 18). In all broods combined also males prevailed (54.2%). Differences

Table 18. Number of males and females in broods of 1-5 young at fledging  
Tabela 18. Liczba samców i samic w lęgach zawierających 1-5 młodych lotnych

*N* broods - lęgów = 82

Brood size Wielkość legu	Number of males Liczba samców	Number of females Liczba samic	Sex ratio (males: 1 female) Stosunek płci (samców: 1 samice)	Significance of difference from 1.00 sex ratio Istotność różnic od stosunku płci 1.00
1	5	4	1.25	<i>N. s.</i>
2	20	10	2.00	<i>N. s.</i>
3	35	43	0.81	<i>N. s.</i>
4	53	43	1.23	<i>N. s.</i>
5	24	16	1.50	<i>N. s.</i>
Total - Razem	137	116	1.18	<i>N. s.</i>

Table 19. Frequency distribution of marsh harrier broods of different sex composition

Figures in parentheses show the frequency expected assuming a 1:1 sex ratio

Tabela 19. Częstotliwość występowania różnych kompozycji stosunku płci w lęgach błotniaków stawowych

Liczby w nawiasach wskazują częstotliwość oczekiwaną, wynikającą ze stosunku płci 1:1

Brood size Wielkość legu	Number of broods of following composition of sex <i>N</i> = 82 Liczba lęgów o następującej kompozycji płci M = male - samiec F = female - samica					Significance of difference from 1.00 sex ratio. Chi-square test Istotność różnicy od stosunku płci 1.00. Test Chi-kwadrat	
1	M		F			<i>N. s.</i>	
	5 (4.5)		4 (4.5)				
2	MM		MF	FF		<i>N. s.</i>	
	7 (3.8)		6 (7.5)	2 (3.8)			
3	MMM	MMF	MFF	FFF		<i>N. s.</i>	
	2 (3.3)	8 (9.8)	13 (9.8)	3 (3.3)			
4	MMMM	MMM F	MMFF	MFFF	FFFF	<i>N. s.</i>	
	3 (1.5)	6 (6.0)	9 (9.0)	5 (6.0)	1 (1.5)		
5	MMMMM	MMMMF	MMMFF	MMFFF	MFFFF	FFFFF	<i>N. s.</i>
	1 (0.3)	0 (1.2)	5 (2.5)	2 (2.5)	0 (1.2)	0 (0.3)	



between the number of males and females were not statistically significant, however, neither for different categories of brood size nor in total.

Different proportions of males and females in broods of various sizes are set in Table 19. Broods with both males and females prevailed. Nevertheless, broods made up of only one sex accounted for 26<sup>0</sup>%. Also in this case the differences between the observed and the expected (1:1) sex ratios were statistically not significant for all brood sizes (Tab. 19), thus the numerical prevalence of males over females was due to chance.

## SEX VERSUS RELATIVE EGG WEIGHT WITHIN A CLUTCH

Table 20 shows data that make it possible to check the possible relationship between the sequence of laying eggs and the sex of the young hatched from them. In 5-egg clutches the number of males hatched increased from egg 1 to egg 4, whereas the number of females decreased. In 4-egg clutches a similar tendency was

Table 20. Sex of hatchlings and losses within a sequence of egg laying in 30 five-egg and 9 four-egg clutches

Tabela 20. Płeć piskląt i straty w zależności od kolejności złożenia jaja w 30 zniesieniach złożonych z 5 jaj i 9 zniesieniach z 4 jajami

Egg sequence Kolejność złożenia jaja:	1	2	3	4	5	1	2	3	4
Unhatched eggs — Jaja nie wyklute	5	3	—	1	3	—	1	—	—
Disappeared eggs — Jaja, które znikły	1	3	2	4	6	—	—	—	4
Dead young, unsexed — Młode zmarłe z nie oznaczoną płcią	3	2	5	4	10	—	2	2	3
Total losses — Całkowite straty	9	8	7	9	19	—	3	2	7
No. of hatched males — Liczba wyklu- lonych samców	$\left\{ \begin{array}{cc} 8 & 12 \end{array} \right\}^+$					$\left\{ \begin{array}{cc} 17 & 7 \end{array} \right\}^+$			
N. of hatched females — Liczba wyklu- lonych samic						$\left\{ \begin{array}{cc} 13 & 10 \end{array} \right\}^+$			
	14	9	4	4	5				
						4	2	4	1

\* Chi-square test  $P < 0.025$ .

noted only for males. These clutches were represented by a small sample and this could have accounted for the equivocalness of the results. The results could have been additionally distorted by disproportionately high losses of last eggs in the clutch and of the chicks hatched from them, because it was not possible to sex these eggs or chicks. These losses reached 63<sup>0</sup>% for 5-egg clutches and 78<sup>0</sup>% for 4-egg clutches.

As in most clutches the first and last eggs were smaller than the other eggs (see Tab. 12), and because a relationship was found between the sequence of egg laying

Table 21. Sex relative to egg-weight sequence in 30 five-egg and 9 four-egg clutches

Egg weight is ranked from heaviest (A) to lightest (D or E)

Tabela 21. Płeć w zależności od sekwencji wg masy jaja w 30 zniesieniach złożonych z 5 jaj i 9 zniesieniach z 4 jajami

Jaja uszeregowane od najcięższego (A) do najlżejszego (D lub E) w obrębie danego zniesienia

Egg-weight sequence Kolejność jaj wg ich masy	A	B	C	D	E	A	B	C	D
Number of unsexed eggs/young Liczba jaj/młodych z nieustaloną płcią	7	7	9	15	14	2	3	3	4
Number of males – Liczba samców	17	20	11	4	6	5	5	1	2
Number of females – Liczba samic	6	3	10	11	10	2	1	5	3

Differences between the number of males and females hatched from first two eggs and last two eggs within the clutch are significant. For 5-egg clutches (Chi-square test)  $P < 0.0001$ , for 4-egg clutches  $P < 0.025$  and for both categories together  $P < 0.0001$ . In 5-egg clutches egg C was omitted because of its middle position.

Różnice pomiędzy liczbami samców i samic wykylutych z dwóch pierwszych i dwóch ostatnich jaj w zniesieniu są statystycznie istotne. Dla zniesień złożonych z 5 jaj  $P < 0.0001$ , dla zniesień z 4 jaj  $P < 0.025$ , a dla obu kategorii zniesień razem  $P < 0.0001$  (test Chi-kwadrat). W zniesieniach złożonych z 5 jaj w obliczeniach różnic pominięto jajo C jako pośrednie.

and the sex of chicks hatched from them, it was assumed that females hatched from smaller (lighter) eggs and males from larger (heavier) eggs. This assumption was checked using the same clutches as above. This time the eggs were ordered according to their relative weight within the clutch rather than to the sequence of laying. The results are shown in Table 21 in which eggs are ordered from the heaviest (A) to the lightest (D or E, depending on the clutch size). Now the results were consistent for the two categories of clutches, and they totally confirmed the suggestion that relatively larger eggs produce males, whereas smaller eggs produce females.

## POST FLEDGING PERIOD

For 3–5 days after the young started flying, they still returned to the nest, where adults continued to deliver the prey. Some aspects of this part of the breeding cycle are illustrated in Figure 8, where the timing of the development of new skills in the young is marked along with the kind and range of parental care.

After 6–10 days from the first attempts to fly, the young started to meet the adults approaching with prey. However, the prey were still delivered to the nest, and the young landing on the nest first could take them. If at that time a young which could not fly was in the nest, it took the prey, and in this way its lack of flying skill as a result of asynchronous hatching was compensated for. The young capable of flying with increasing frequency were resting on the reedbed or in trees.

Three days later, the parents encouraged the young to take food from them in

the air. Typically the male did so the first. About half of these attempts failed, that is, the prey fell down in the reed or in water. Many prey were still delivered into the nest (Fig. 8).

15 days after the young had learned to fly, that is, on days 52–56 (depending on the sex) after hatching, the young started hunting on their own. The result was that they only flushed ducks and coots raising young. The only successful attack prior to 60 days of life was made by a male 54 days old, which hunted a frog on a mown reed. At that time the young were flying several hundred metres from the nest, and perched mostly in trees.

Between days 60 and 80, the young hunted on their own, but they were still dependent on their parents for food, and kept staying near the nest. Both parents or only one of them delivered on the average 5 prey items per day for the whole brood. At that time the young occasionally visited nests of their conspecifics with younger offspring, and they robbed food from them when their parents were out. Young harriers most often caught frogs and chicks of waterfowl resting on floating, mown reed. They also took dead fish from the shore or from reed platforms. They were afraid to take prey from the water.

The young became independent of their parents as late as between days 80 and 90. Most male parents broke bonds with the young earlier, sometimes even before they started to fly.

#### NEST LOSSES

Nest with eggs or nestlings lost totally in different stages of the nesting cycle are shown in Table 22, and the causes of failure are set in Table 23.

Table 22. Fate of nests  
Tabela 22. Losy gniazd

Nest categories — Kategorie gniazd	No. of nests (%) Liczba gniazd (%)	
	1972–75	1982–84
Total number of nests Gniazda założone	117	118
Nests lost in incubation period Gniazda stracone w okresie wysiadywania	24 (20.5)	21 (17.8)
Nests in which young hatched Gniazda, w których wykluły się młode	93 (79.5)	97 (82.2)
Nests in which young hatched but did not fledge Gniazda, w których młode się wykluły, ale nie wyleciały	11 (9.4)	2 (1.7)
Nests with fledging success Gniazda, z których wyleciały młode	82 (70.1)	95 (80.5)

## Losses during egg laying

In both study periods, losses in this phase of the nesting cycle were small. Only 10 clutches started (10%) were lost. Three nests were lost due to predators such as the wild boar (2 nests) and probably a marten (1 nest), and seven were abandoned as a result of the disturbance by the observer. All these nests contained no more than two eggs. As it was almost certain that these birds would renest, this category of losses is not included in the total losses.

## Losses during the incubation period

These losses were analyzed for the two study periods separately, and divided into two categories:

- loss of the total clutch,
- partial losses in nests from which at least one young fledged.

Table 23. Causes of failures in nests without fledging success  
Tabela 23. Przyczyny strat w lęgach, z których nie wyleciały młode

Nest categories – Kategorie gniazd	No of nests Liczba gniazd		Total nests Razem gniazd	Percent of total nests % wszystkich gniazd	Percent of total failed % straconych gniazd
	1972-75	1982-84	Both periods – Oba okresy		
Total nests Gniazd założonych	117	118	235		
Nests without success Gniazda bez sukcesu	35	23	58	24.7	
Clutches predated Zniesienia zniszczone przez drapieżniki	5	13	18	7.7	31.0
Broods predated Lęgi zniszczone przez drapieżniki	5	–	5	2.1	8.6
Clutches deserted Zniesienia porzucone	7	6	13	5.5	22.4
Broods deserted Lęgi porzucone	2	1	3	1.3	5.2
All eggs broken in the clutch Wszystkie jaja w zniesieniu zgniecione	4	–	4	1.7	6.9
Some eggs broken, others unhatched Część jaj zgnieciona, reszta nie wykluta	8	–	8	3.4	13.8
All hatched young died Wszystkie wyklute młode zmarły	4	1	5	2.1	8.6
Clutches flooded Zniesienia zatopione	–	2	2	0.9	3.4



Table 24. Unsuccessful nests

Different categories of losses in relation to the number of eggs laid

Tabela 24. Lęgi nieudane

Poszczególne kategorie strat w odniesieniu do liczby zniesionych jaj

Period Okres	Number of unsuccessful nests Liczba gniazd nieudanych	Number of eggs laid Liczba jaj zniesionych	Number (%) of broken eggs Liczba (%) jaj zgnie- cionych	Number (%) of unhat- ched eggs Liczba (%) jaj nie- wyklutych	Number (%) of eggs predated Liczba (%) jaj zniszczonych przez drapieżniki	Number (%) of eggs deserted Liczba (%) jaj porzu- conych	Number (%) of eggs washed off by waves Liczba (%) jaj zmytych przez fale	Number (%) of young dead Liczba (%) młodych zmarłych	Number (%) of young killed by predators Liczba (%) młodych zabi- tych przez drapieżniki	Number (%) of young deserted Liczba (%) młodych porzuconych
1972-75	35	184	57 (31.0)	32 (17.4)	26 (14.1)	34 (18.5)	—	9 (4.9)	17 (9.2)	9 (4.9)
1982-84	23	110	3 (2.7)	—	71 (64.5)	21 (19.1)	8 (7.3)	3 (2.7)	—	4 (3.6)
Significance of difference Chi-square test Istotność różnic test Chi-kwadrat		$P <$	0.0001	0.0001	0.0001	<i>N. s.</i>	0.001	<i>N. s.</i>	0.001	<i>N. s.</i>

Table 25. Losses and production of young in nests with fledging success in relation to the number of eggs laid  
 Tabela 25. Straty i produkcja młodych w gniazdach udanych, w stosunku do liczby zniesionych jaj

Period Okres	Nests successful Gniazda udane	Eggs laid Jaja zniesione	Eggs broken Jaja zgniecione (%)	Eggs addled Jaja nie wyklute (%)	Eggs washed off Jaja zmyte przez fale (%)	Young hatched Młode wyklute (%)	Young dead Młode zmarłe (%)	Young killed by siblings Młode zabite przez rodzeństwo (%)	Young fledged Młode lotne (%)	Mean brood size at fledging Średnia wielkość lęgu przy wylocie
1972-75	82	419	62 (14.8)	45 (10.7)	—	312 (74.5)	59 (14.1)	—	253 (60.4)	3.1
1982-84	95	464	33 (7.1)	61 (13.1)	2 <sup>+</sup> (0.2)	368 (79.3)	74 (15.0)	3 (0.6)	291 (62.7)	3.1

\* Female relaid in the same nest and reared fledglings.  
 Samica zniosła się ponownie w tym samym gnieździe i wyprowadziła młode.

The proportion of nests totally lost was similar in the two periods (Tab. 22), but the causes of losses extremely differed. In 1972–75, most losses were due to the application of DDT (Tab. 23). They include clutches in which all eggs were broken by the incubating female, or in which only some eggs were broken and the remaining eggs did not hatch although the incubation was continued. Such losses did not exist in 1982–84. Instead, the proportion of nests lost to predators increased (Tab. 23).

Losses due to desertion were similar in the two periods (Tab. 23). In 9 of 13 abandoned nests, eggs were spiked and sucked out. The traces unquestionably indicated that this was done by marsh harriers. These losses were not considered as an interspecific predation because on two occasions I saw that the male pecked and ate the eggs from his own nest when the female disappeared. I have never seen even an attack of an alien conspecific on an incubating female, not to mention a robbery. In view of these facts, it seems that desertion of the nest rather than predation was the true cause of the losses, though predation cannot be totally excluded.

In 1982–84, two nests were flooded, the case not recorded in the earlier period. These flooded nests were located very close to the open water, which protects them from wild boars.

Total losses of eggs or young (Tab. 23) were calculated in relation to the number of eggs laid and compared for the two study periods (Tab. 24). Statistically significant difference were found for losses due to DDT and predators.

Partial losses in successful nests are shown in Table 25. In 1972–75, losses were dominated again by egg breakage (column d). They were twice as high as in 1982–

Table 26. Differences in proportion of broken eggs between the two periods of studies  
Tabela 26. Różnice w proporcjach jaj zgniecionych pomiędzy dwoma okresami badań

	1972–75	1982–84	Significance of difference (Chi-square test) Istotność różnic (test Chi-kwadrat)
Number of eggs broken in successful nests Liczba jaj zgniecionych w lęgach udanych	62 (419)	33 (464)	$P < 0.001$
Number of eggs broken in unsuccessful nests estimated up to time of nest loss Liczba jaj zgniecionych w gniazdach nieudanych	57 (184)	3 (110)	$P < 0.0001$
Total number of broken eggs Liczba wszystkich jaj zgniecionych	119 (603)	36 (574)	$P < 0.0001$

In parentheses — total number of eggs laid.

W nawiasach — liczba zniesionych jaj.

84. Addled eggs accounted for a similar proportion of losses (column e). These losses were higher in the second than in the first period, which was unexpected as DDT was no more used. Presumably other poisons were then active, causing even more developmental disorder to harrier embryos than DDT did.

Total losses due to egg breakage in relation to the number of eggs laid are set in Table 26. Differences in the two categories of losses (see p. 267) between the two study periods are highly significant.

#### Chick losses from hatching to fledging

As in the case of eggs, two categories of losses should be distinguished: nests producing no one fledging, and nests in which only a part of the young died.

For the first category there were differences between the two study periods (Tabs 23 and 24): In 1972–75, five broods were predated and in four nests all the young died. In 1982–84, only in one nest did all the young die, and no losses due to predators were noted. Differences in losses due to predators, though statistically significant, seem to have been due to chance. Traces left in nests in the first period indicate that the broods were destroyed by the white-tailed eagle *Haliaeetus albicilla*, the polecat, and the stoat *Mustela erminea*. In the second period fewer traces were left by mustelids, but more by the pine marten and the wild boar.

The desertion of three broods was caused by the loss of the female in two cases, and the construction of hide too close to the nest in one case. In all the three nests the oldest chick was no more than 8 days old, thus the male could not rear them alone as they could not tear up the prey.

Partial losses in successful nests were similar in the two study periods (Tab. 25). They concerned young birds that died in the first days of their lives, mostly due to their poor condition at hatching, and as a result of starvation. At least three young were killed by their siblings (fratricide) in a period of food shortage.

#### Losses in relation to the timing of laying

Clutches lost in total. The data have been divided into three parts representing the beginning of laying (5-day periods I and II), middle part of the laying period (5-day periods III and IV), and the end of laying (5-day periods V and later). They are set in Table 27).

In 1972–75 losses were similar over the whole nesting season (Tab. 27).

In 1982–84, the losses were the lowest at the beginning of the nesting season (6.3%), and the highest at the end of the season (25%). Differences among the three parts of the season were statistically significant (Tab. 27).

The losses were considered in relation to the total number of eggs laid (potential production) in the first and the second parts of the season (Tab. 28). In 1972–1975, the losses in the first and the second half of the season were identical



Table 27. Clutch losses in relation to time of the season in which clutches started  
 Tabela 27. Straty zniesień w zależności od terminu ich rozpoczęcia

	1972-75			1982-84		
	Number of clutches started Liczba zniesień rozpoczętych	Number (%) of clutches failed Liczba (%) zniesień utraconych	Significance of difference (Chi-square test) Istotność różnicy (test Chi-kwadrat)	Number of clutches started Liczba zniesień rozpoczętych	Number (%) of clutches failed Liczba (%) zniesień utraconych	Significance of difference (Chi-square test) Istotność różnicy (test Chi-kwadrat)
Beginning of the season Początek sezonu (I + II pent.)	43	16 (37.2)	} <i>N. s.</i>	16	1 (6.3)	} $P < 0.05$
Middle of the season Środek sezonu (III + IV pent.)	50	11 (22.0)		42	7 (16.7)	
End of the season Koniec sezonu (V + > V pent.)	24	8 (33.3)		60	15 (25.0)	
Total - Razem	117	35 (29.9)	118	23 (19.5)		

(58%). This was due to two facts: higher losses in the category of failed nests in the first half of the season, and a lower production of young in successful nests in the second half of the season. Differences in these two categories of losses between the first and the second half of the season were significant (Tab. 28). In 1982-84, the total losses in the second half of the season were higher by 14.5% than in the first half, and for failed nests this difference was as high as 18.2%. Losses in the category of successful nests were a little higher (by 3.7%) in the first than in the second half of the season. This difference is not statistically significant.

#### The effect of DDT contamination on losses

High nesting losses in the first half of the breeding seasons of 1972-75 were an effect of egg breakage resulting from shell-thinning (Tabs 24, 25, and 26). In this period the index of shell thickness of marsh harrier eggs in the Barycz valley was 1.395 (Tab. 29), and it was lower by 23% than the index for European marsh

Table 28. Losses in clutches started early and later in the breeding season  
 Tabela 28. Straty w lęgach rozpoczętych w pierwszej i drugiej połowie sezonu lęgowego

Period Okres	Nest categories Kategorie gniazd	Clutches started before 25 April Zniesienia rozpoczęte przed 25 kwietnia		Clutches started after 25 April Zniesienia rozpoczęte po 25 kwietnia		Significance of difference (Chi-square test) Istotność różnic (test Chi-kwadrat)
		Number of eggs laid Liczba jaj znie- sionych	Number (%) of eggs/young lost Liczba (%) jaj/młodych utraconych	Number of eggs laid Liczba jaj znie- sionych	Number (%) of eggs/young lost Liczba (%) jaj/młodych utraconych	
1972-75	All nests Wszystkie gniazda	376	218 (58.0)	227	132 (58.1)	<i>N. s.</i>
	Unsuccessful nests Gniazda nie- udane	132	132 (35.1)	52	52 (22.9)	<i>P</i> < 0.025
	Successful nests Gniazda udane	244	86 (22.9)	175	80 (35.2)	<i>P</i> < 0.025
1982-84	All nests Wszystkie gniazda	203	81 (39.9)	371	202 (54.4)	<i>P</i> < 0.05
	Unsuccessful nests Gniazda nie- udane	15	15 (7.4)	95	95 (25.6)	<i>P</i> < 0.0001
	Successful nests Gniazda udane	188	66 (32.5)	276	107 (28.8)	<i>N. s.</i>

harriers (1,823) prior to 1945 (UNDERHILL-DAY 1984). This would indicate that females and the eggs they laid were contaminated with DDT and its metabolites (PEAKALL & PEAKALL 1973).

The content of DDT and its metabolites was analyzed in 14 eggs. Addled eggs were collected for this analysis and also freshly cracked or punctured eggs, as such eggs were always broken by the incubating female and their removal did not effect the level of losses.

High contents of DDT and DDE in the eggs and a low index of shell thickness (Tab. 29) confirmed the suggestion concerning the cause of losses. The mechanism of the reversal of the trend described above (see p. 270-271) could have been as follows: older, most experienced females, starting laying earlier, suffered low losses under normal conditions, accounting for lower losses in the first half of the breeding season. However, these relatively old females had also been subject to

Table 29. Residues of DDT, its metabolites (DDE, DDD) and Lindan in eggs of the marsh harrier in the Barycz valley in 1972–1975

Tabela 29. Zawartość DDT i jego metabolitów (DDE, DDD) oraz Lindanu w jajach błotniaków stawowych w dolinie Baryczy w okresie 1972–75

N(eggs - jaj) = 14

	ppm pp' DDE	ppm pp' DDD	ppm pp' DDT	ppm DDT	ppm rHCH Lindan	Shell thickness index Indeks grubości skorupy
Mean Średnia	8.843	1.847	2.073	12.734	0.322	1.395
SD	3.102	0.517	0.834	3.264	0.268	0.133
Range Zakres zmien- ności	4.230–12.220	1.308–2.834	0.970–3.360	7.218–15.637	0.091–0.750	1.205–1.573

adverse effects of DDT contamination for a longer time than younger females. Thus, the accumulation of DDT in their bodies was high, leading to a heavier disfunction of the shell-producing gland. Consequently, the eggs of older females had a thinner shell and were broken more often than the eggs of younger females, laying later in the season. Because of the scale of contamination, egg losses in older females were so high that they outweighed typically high natural losses of eggs laid late in the season.

In 1982–84, the trend was typical of undisturbed conditions. Nevertheless, 6.3% of the eggs laid were broken (Tab. 33). In this period, egg contamination was not analyzed, so it may be only suspected that marsh harriers of the Barycz valley continue to be in contact with DDT somewhere, or that some other pesticides currently applied have similar effects as DDT. It is also possible that some long-living females (RYDZEWSKI 1962) present in 1972–75 survived through 1982–84 and they continued to lay eggs with thin shell. And finally, a small proportion of broken eggs may be a normal occurrence in marsh harriers.

#### Losses caused by predators in relation to nest location

Losses caused by predators were much heavier in border belts of reeds than on reed islets (Tab. 30). In the former habitat the pressure of pine marten, polecat, stoat and fox *Vulpes vulpes* was likely to be higher; losses due to wild boars were similar in the two habitats. It is striking that marsh harriers did not seem to adapt to the actual species composition and pressure of predators. It is possible that other factors, equally important as anti-predatory behaviour, accounted for this situation. Location of the nesting territory at the border of the pond could have been of greater advantage, making it possible, for example, to hold a better

Table 30. Losses caused by predators in relation to nest location  
 Tabela 30. Straty spowodowane przez drapieżniki w zależności od lokalizacji gniazda

Nest location Usytuowanie gniazda	Reedbed along the dike Przybrzeżny pas trzciny	Islet of reed Wyspa trzciny	Significance of difference (Chi-square test) Istotność różnic (test Chi-kwadrat)
Total number of nests Liczba założonych gniazd	106	129	
Number (%) of nests predated Liczba (%) gniazd zniszczonych przez drapieżniki	17 (16.0)	6 (4.7)	$P < 0.01$
Number (%) of successful nests Liczba (%) gniazd udanych	66 (62.3)	111 (86.0)	$P < 0.0001$
Mean clutch size Średnia wielkość zniesienia	5.1	4.9	
Young fledged per successful pair Młodych lotnych na 1 parę z sukcesem lęgowym	3.5	3.2	

hunting area in terms of its distance from the nest. The true underlying reasons are waiting for explanation. However, the suggestion that better individuals settled on islets, whereas worse individuals were forced to the border of the lake as no empty islets were available can already be excluded. Both these habitats were occupied simultaneously. Moreover, both groups of birds had the same mean clutch size and the same production of young per female in successful nests (Tab. 30).

#### The effect of rainfall on nest losses

The data used for estimating the effect of weather on nest losses do not include the young that died before the age of 2 days, assuming that the mortality in the first days of life could have been due to factors other than weather. Also losses caused by predators, abandonment, and fratricide are excluded. The rainless period is defined as the period with no rain or with occasional rains, and the rainy period is defined as at least one-day continuous rain.

In the rainy periods, losses due to egg breakage were twice as high as during the rainless periods, and chick mortality was three times higher (Tab. 31).

In the first study period, the months of May and June were more rainy in 1972 and 1974 than in 1973 and 1975. In the rainy years, losses of eggs were 24% and losses of young were 21.6%. The respective losses in the rainless years were 15.1 and 16.1%. Only differences in egg losses were statistically significant (Chi-square = 5.8,  $P < 0.025$ ).



Table 31. Effect of rain on nest losses in the breeding season  
Tabela 31. Wpływ deszczu na straty w okresie lęgowym

	In rain		Without rain		Significance of difference (Chi-square test) Istotność różnic (test Chi-kwadrat)
	number liczba	%	number liczba	%	
Eggs broken Jaja zgniecione	106	68.4	49	31.6	$P < 0.001$
Young dead Młode zmarłe	60	74.0	21	26.0	$P < 0.001$

In the second study period only the breeding season of 1984 was rainy. Egg losses in that year accounted for 7.0%, whereas losses of young reached 32%. In the remaining two study years, the respective losses were 5.8% and 13.9%. Differences in the mortality of young were statistically significant (Chi-square = 10.0,  $P < 0.01$ ).

Higher losses of eggs on rainy days were due to the fact that incubating females got up very often, fluffed their feathers, wriggled, walked on eggs, etc. Higher losses of young resulted from cold and shortage of food.

#### Total losses

In the two study periods jointly, most nests were lost due to predators (9.8%). The second cause of losses was nest desertion (6.8%) (Tab. 32). In the period 1972–75 alone, most losses resulted from breakage of all or some eggs in a nest, or from hatching failure. These losses outweighed the losses to predators (Tab. 32).

In 1972–75, total losses (Tab. 33) were 350 eggs or young (58% of total eggs laid). Broken eggs accounted for 34% of the total losses, then unhatched eggs accounted for 22% of the losses. The next two categories of losses included the young that died in the period between hatching and fledging (19.4%), and eggs or chicks robbed by predators (14.6%).

In 1982–84, the total losses (Tab. 33) were 283 eggs or young (49.3%). The highest proportion of losses was represented by dead chicks (27.2%), predated eggs (25.1%), and addled eggs (21.6%). The proportion of broken eggs was reduced to almost one-third (12.7%) as compared with that in the earlier period.

#### Mortality of young

The mortality of young in relation to their age is shown in Table 34. Most of the lost young birds (62%) died before the age of 5 days. These losses were particularly high during prolonged rains and cold weather. After 25 days of age,

Table 32. Causes of nest failures  
Tabela 32. Straty gniazdowe i ich przyczyny

	1972-75			1982-84			Percent of total nests % wszystkich gniazd
	Number of nests Liczba gniazd	Percent of total nests % wszystkich gniazd	Percent of nests failed % gniazd utraconych	Number of nests Liczba gniazd	Percent of total nests % wszystkich gniazd	Percent of nests failed % gniazd utraconych	
	N = 117			N = 118			
Nests predated Gniazda zniszczone przez dra- pieżniki	10	8.5	28.6	13	11.0	60.9	9.8
Nests deserted Gniazda porzucone	9	7.7	25.7	7	5.9	26.1	6.8
All eggs in the clutch broken or addled Wszystkie jaja w zniesieniu stłu- czone lub nie wyklute	12	10.3	34.2	—	—	—	5.1
All young in the nest dead Wszystkie młode zdechły	4	3.4	11.4	1	0.8	4.3	2.1
Nests flooded Gniazda zatopione	—	—	—	2	1.7	8.7	0.9
Total nests failed Razem utraconych gniazd	35	29.9	100.0	23	19.5	100.0	24.7

Table 33. Total failures and actual production of young in relation to the number of eggs laid  
 Tabela 33. Straty całkowite i produkcja zrealizowana, w odniesieniu do produkcji potencjalnej

Period Okres				
1972-74	117	603	5.2	119 (19.7)
1982-84	118	574	4.9	36 (6.3)
				61 (10.6)
				26 (4.3)
				34 (5.6)
				10 (1.7)
				347 (57.5)
				68 (11.3)
				17 (2.8)
				3 (0.5)
				9 (1.5)
				253 (41.7)
				2.5

Significance of difference  
(Chi-square test)  
Istotność różnic  
(test Chi-kwadrat)

$P < 0.0001$

N. s.

$P < 0.01$

N. s.

$P < 0.001$

N. s.

N. s.

$P < 0.0001$

N. s.

N. s.

N. s.

Table 34. Mortality of young  
Tabela 34. Śmiertelność młodych

Age in days Wiek w dniach	0-5	6-10	11-15	16-20	21-25	Over Ponad 25	Total Razem
Number of young dead Liczba młodych zmarłych	110	32	20	11	4	1	178
Proportion of total dead (%) Proporcjonalnie do całości zginęło (%)	61.8	18.0	11.2	6.2	2.2	0.6	100.0
Including – W tym:							
Killed by predators Zabitych przez drapieżniki	1	6	4	4	1	1	17
Deserted Porzuconych przez rodziców	7	6	–	–	–	–	13
Killed by siblings Zabitych przez rodzeństwo	–	–	1	1	1	–	3

practically no dead chicks were recorded. The mortality of the young during the nestling period amounted to 24.7%. Death of starvation must have been a rare event, if the young dead by day 5, predated young, and abandoned young are excluded.

#### Aggression among siblings: fratricide and cannibalism

If both parents reared the young and food was supplied in adequate amounts, practically no aggression was observed among siblings, except for fighting for the prey brought by the parents, which is typical of raptors. If food was in short supply, as during prolonged rains, the youngest chicks starved. But even in these circumstances, the older chicks did not intensify their aggression to the level at which they could kill younger chicks. Only when a further shortage of food led the weakest chicks almost to death, did their poor condition trigger aggression in older siblings. I cannot decide whether the appearance of the dying chick alone was the releasing stimulus, or its behaviour as it uttered twitter calls (shrill erick – erick) signalling conflicting and dangerous situations. Thus, individuals that were killed were as a rule dying individuals. I witnessed four such occurrences, and in no case did the older siblings tear and eat dead chicks. In two cases, the corpses remained on the nest and disappeared on the next day, and in two other cases they were removed from the nest by the female.

My impression is that in the cases described above, the aim of aggression from the older siblings was not to appease hunger but to kill a dying individual with abnormal behaviour. For this reason the losses of chicks effected in this way were not included among those caused by fratricide but in the losses from starvation. There were at least 27 cases of death of this kind during the study period.



Included here are also chicks in the state of agony and with traces of pecking on their body during one visit and absent from the nest during the next visit.

During 85 days of observations of different nests from the hide, only three cases of true fratricide were observed. In all these cases on the day of aggression much less food was delivered to the young than usually. In two nests containing 4 chicks each, the youngest chicks were less than 20 days old. Although they were smaller than older siblings, they were well developed for their not privileged status within the brood. On the day of aggression their behaviour was normal. In all the three nests, the attack occurred late in the afternoon. In one nest it began after a visit of the male, which dropped in flight a very small rodent. The prey was quickly eaten by the third chick in terms of age, and this triggered aggression in the second chick, which started to peck the youngest chick. After a while it was joined by the oldest chick, and by the evening they killed the youngest chick but they did not eat it. On the following day, the female tore it and fed it to the young. In the other two nests, aggression occurred when one of the parent birds appeared over the nest without food. In the above-mentioned nest with four young, the second chick attacked the youngest one, bringing it almost to death by the evening. On the following day it was dead but intact. It was removed by the female, which after feeding a coot to the young brought it to the platform and ate it. In the third case, the nest contained three young, and the youngest was already 24 days old. After the male visited the nest without prey, the oldest chick attacked the youngest one. The middle chick joined it very soon. The passive response of the attacked chick was striking. It could run away in the reed. After receiving many strikes it was forced out of the nest. Than I took it and reared it at home.

The cases of fratricide described above seem to indicate that the killers were not motivated by considering younger siblings as a source of food.

#### PRODUCTION OF YOUNG

Early clutches were larger and, if successful, they produced more fledglings than later, smaller clutches (Tab. 35). Such a trend occurred in both the study periods, although the distribution of losses in 1972–75 differed from that in the second period. Differences in the production of various developmental stages from clutch size to the number of fledglings between the first and the second halves of the two study periods were statistically significant (Tab. 35).

Table 36 shows hatching and fledging successes for different clutch sizes. The most productive clutches contained 4–6 eggs, and in particular 4 or 5 eggs. 80% of the latter nests produced fledglings.

Production of fledglings as a percentage of the number of eggs laid was the highest (over 50%) in nests with 4 or 5 eggs (Tab. 37), and no difference was observed between the two study periods. The productivity of 6-egg clutches was

Table 35. Clutch size (a), brood size at hatching (b) and brood size at fledging (c) early and later in the breeding season

Tabela 35. Wielkość zniesienia (a), wielkość lęgu przy wykluciu (b) i wielkość lęgu przy wylocie z gniazda (c) w pierwszej i drugiej połowie sezonu lęgowego

Period Okres	Clutches started before 25 April Zniesienia rozpoczęte przed 25 kwietnia			Clutches started after 25 April Zniesienia rozpoczęte po 25 kwietnia			Significance of difference (Student <i>t</i> -test) Istotność różnic (test- <i>t</i> Studenta)	
	no. of nests liczba gniazd	mean średnia	SD	no. of nests liczba gniazd	mean średnia	SD		
1972-75	(a)	67	5.61	0.95	50	4.54	0.86	$P < 0.0001$
	(b)	54	4.93	1.33	39	3.46	0.94	$P < 0.05$
	(c)	45	3.51	1.01	37	2.57	1.04	$P < 0.0001$
1982-84	(a)	40	5.08	0.47	78	4.76	0.82	$P < 0.01$
	(b)	37	4.24	0.89	60	3.63	1.16	$P < 0.01$
	(c)	37	3.30	0.91	58	2.91	1.13	<i>N. s.</i>

Table 36. Frequency of different clutch sizes and brood sizes of marsh harrier in the Barycz valley  
Tabela 36. Częstotliwość różnych wielkości zniesień i lęgów błotniaka stawowego w dolinie Baryczy

Clutch/brood size: Wielkość zniesienia/lęgu	1	2	3	4	5	6	7	8	$\bar{x}$	SD	Total Razem
Number of clutches laid Liczba zniesień	—	2	8	45	126	41	11	2	5.01	0.9	235
Percentage Procent wszystkich zniesień		0.8	3.4	19.1	53.6	17.4	4.7	0.8			
Number of clutches hatched Zniesień wyklutych	—	1	3	38	104	35	8	1			
No. of broods fledged Lęgów z młodymi lotnymi	—	1	3	36	101	30	5	1			
Number of hatched broods Liczba lęgów wyklutych	8	16	45	65	49	7	—	—	3.8	1.2	190
Percentage Procent wyklutych zniesień	4.2	8.4	23.7	34.2	25.8	3.7					
No. of broods fledged Liczba lęgów z młodymi lotnymi	5	15	44	59	47	7	—	—	3.07	1.1	177
Number of fledged broods Lęgi z młodymi lotnymi	18	28	70	45	16	—	—	—			
Percentage Procent lęgów z młodymi lotnymi	10.2	15.8	39.5	25.4	9.0						

Table 37. Reproductive success in relation to clutch size  
Tabela 37. Sukces reprodukcyjny w zależności od wielkości zniesienia

Clutch size Wielkość zniesienia	Number of clutches Liczba zniesień	Unhatched eggs Jaj nie wyklułych	Mean egg hatched Średnio jaj wyklułych	Young dead Młodych zmarłych	Mean fledged young Średnio młodych lotnych	SD	Actual production as a percentage of the number of eggs laid Produkcja zrealizowana jako % łącznej liczby zniesionych jaj
2	2	2	1.00	—	1.00	1.41	50.0
3	8	16	1.00	1	0.88	1.36	33.3
4	45	53	2.82	32	2.11	1.40	52.8
5	126	221	3.25	88	2.55	1.56	51.0
6 <sup>+++</sup>	19	41	3.84	16	3.00	1.70	50.0
6	41	100	3.56	46	2.44	1.82	40.7
6 <sup>++</sup>	22	59	3.32	30	1.95	1.81	32.6
7 <sup>+</sup>	11	51	2.36	10	1.45	2.02	20.8
8 <sup>+</sup>	2	12	2.00	1	1.50	2.12	18.8

\* Did not exist in period 1982–84 — Nie było w okresie 1982–84.

\*\* Period 1972–75 separately — Okres 1972–75 osobno.

\*\*\* Period 1982–84 separately — Okres 1982–84 osobno.

low in 1972–75 when it amounted to 32.6%, but in 1982–84 it increased up to 50%, that is, it was similar to the productivity of 4 or 5-egg clutches. The difference between the two study periods was significant ( $t = 2.76$ ,  $P < 0.01$ ) and easy to explain as a destructive effect of DDT on the reproduction of birds of prey. Older females, laying more eggs, had been exposed to DDT for a longer time than younger females. The former had accumulated more DDT in their bodies, thus suffered more losses from shell thinning, egg breakage, and low hatchability. The same was true of the clutches containing more than 6 eggs (Tab. 37).

Table 38 shows the production of young for different clutch sizes in successful nests. The proportion of fledglings increased with decreasing clutch size. In

Table 38. Rate of reproduction in relation to clutch size in broods successfully fledged  
Tabela 38. Reprodukcyjność w zależności od wielkości zniesienia w lęgach udanych

Clutch size Wielkość zniesienia	Number of clutches Liczba zniesień	Eggs unhatched % Jaj nie wyklułych %	Mean number of hatchlings per clutch (SD) Średnia liczba wyklułych młodych w zniesieniu (SD)	Mean number of fledglings per clutch (SD) Średnia liczba lotnych młodych w zniesieniu (SD)	Percent of eggs laid producing fledglings Procent lotnych młodych w stosunku do liczby zniesionych jaj
3	3	11.1	2.67 (0.6)	2.33 (1.2)	77.7
4	37	18.3	3.27 (0.8)	2.59 (1.0)	64.8
5	100	20.8	3.96 (1.0)	3.18 (1.0)	63.6
6	29	26.5	4.41 (1.3)	3.42 (1.1)	56.8
7	5	54.3	3.20 (1.8)	3.20 (1.8)	45.7

clutches of more than 6 eggs even the absolute number of fledglings was lower than in clutches of 6 eggs.

For all the clutches combined the number of young produced in the period 1972-75 represented 41.7% of the eggs laid. An average breeding pair reared 2.2 fledglings. In 1982-84, 50.7% of the eggs laid produced fledglings, and there were 2.5 young produced per breeding pair. The differences between the two study periods were mainly due to DDT. The production of young in successful nests was similar in the two study periods and amounted to 3.1 fledglings per pair.

## SURVIVAL OF YOUNG

In successful nests (Tab. 25), 80% of the hatched young survived until fledging. The oldest nestlings in the brood survived best (Tab. 39). Their mortality was merely 5.6%. In broods made up of 6 nestlings the youngest never survived.

Table 39. Survival of nestlings in relation to sequence of hatching  
Tabela 39. Przeżywalność młodych w zależności od kolejności ich wyklucia

	Sequence of hatching Kolejność wykluwania					
	1	2	3	4	5	6
Number of young hatched Liczba młodych wyklutych	36	36	35	27	14	4
Percent survived to fledging Procent młodych, które przeżyły do wylotu z gniazda	94.4	83.3	71.4	51.9	22.0	0.0

Table 40. Survival of young from clutches started early and late in the season

Early - started up to 25 April, late - started after 25 April

Tabela 40. Przeżywalność młodych ze zniesień wczesnych i późnych

wczesne - rozpoczęte przed 25 kwietnia, późne - rozpoczęte po 25 kwietnia

Period - Okres:	1972-75		1982-84		Total - Razem	
	early wczesne	late późne	early wczesne	late późne	early wczesne	late późne
Clutches started Zniesienia rozpoczęte						
Young hatched Młodych wyklutych	212	135	157	218	369	353
Young fledged Wyleciało młodych	158	95	122	169	280	264
Percent fledged = young survival Wyleciało młodych (%)	74.5	70.4	77.7	77.5	75.9	74.8

All differences insignificant (Chi-square test).

Wszystkie różnice są statystycznie nieistotne (test Chi-kwadrat).



No difference was found in the survival of the young between the early and late nests (Tab. 40). The mortality of the young in nests started in the first and in the second half of the season was about 25%. Thus, the significant differences in productivity between early and late nests were not due to differences in the mortality of the young.

#### NEST-SITE AND NATAL-SITE TENACITY

**Adult birds.** Several males with individual characteristic features returned to the same territories in successive years (one of them in four successive breeding seasons). This was also the case of one female. This nest site tenacity is also supported by the fact that the location of nesting territories and nest sites is similar or even identical from season to season in many cases.

**Young birds.** In the two study periods, all the young birds were ringed prior to fledging. If they showed a strong natal-site tenacity, it might be predicted that some of the 52 young ringed in 1972 would breed in the study area in 1974 and all of them in 1975.

In 1974, 1 male and 2 females were ringed among the breeding birds, and in 1975, 4 females. In 1982–84, the ringed breeding birds included 2 males and 4 females in 1982, 2 males and 6 females in 1983, and 1 male and 5 females in 1984. It is possible that the number of ringed males was underestimated, but the number of ringed females certainly was exact.

These data suggest that the natal-site tenacity in young birds is low, provided their mortality was not extremely high in the period between fledging and the beginning of reproduction.

#### FOOD

Over the two study periods, 1355 prey items were identified (Tab. 41). The material is divided into two groups:

- a) data from whole-day observations at nests from the hide,
- b) remains picked up from nests and feeding platforms, and data from observations of hunting marsh harriers.

Prey remains were collected from platforms, and observations were made since return of marsh harriers from their winter quarters. Pellets were not collected.

The material of the first group is of the greatest value. The observations were made for 85 days at different nests. They provide information on the food spectrum over the breeding season, and also show actual proportions of different items in the diet, which cannot be obtained by any other method since some prey (*e.g.* naked passerine nestlings and young of small mammals) are absent from the remains on the nest or in pellets.

Table 41. Food composition of marsh harriers in the breeding season in the Barycz valley  
 Tabela 41. Skład pokarmu błotniaków stawowych w okresie lęgowym w dolinie Baryczy

Prey Zdobycz	Prey recorded by nest observations from a hide Zdobycz stwierdzona podczas obserwacji gniazd z ukrycia		Prey recorded by field observations and nest and platform checking Zdobycz stwierdzona podczas obserwacji w terenie oraz kontroli gniazd i platform		Total Razem	
	Number Liczba	%	Number Liczba	%	Number Liczba	%
1	2	3	4	5	6	7
<i>Microtus arvalis</i>	156	19.1	39	7.1	195	14.4
<i>Microtus</i> sp.	14	1.7	3	0.5	17	1.3
<i>Arvicola terrestris</i>	12	1.5	19	3.5	31	2.3
<i>Lepus europaeus</i>	12		11	2.0	23	1.7
<i>Ondatra zibethicus</i>	10	1.2	10	1.8	20	1.5
<i>Murinae</i> unidentified	10		19	3.5	29	2.1
<i>Apodemus agrarius</i>	3	0.4	1	0.2	4	0.3
<i>Mus musculus</i>	3		—	—	3	0.2
<i>Rattus norvegicus</i>	3		2	0.4	5	0.4
<i>Talpa europaea</i>	3		9	1.6	12	0.9
<i>Clethrionomys glareolus</i>	1	0.1	—	—	1	0.1
<i>Sorex araneus</i>	1		10	1.8	11	0.8
<i>Crocidura</i> sp.	—	—	2	0.4	2	0.1
<i>Erinaceus europaeus</i>	—	—	1	0.2	1	0.1
<i>Sus scrofa</i> (carrion)	—	—	2	0.4	2	0.1
Total Mammals — Razem Ssaki	228	27.9	128	23.3	356	26.3
<i>Fulica atra</i>	74	9.1	94	17.1	168	12.4
<i>Alauda arvensis</i>	69	8.4	18	3.3	87	6.4
<i>Acrocephalus scirpaceus</i>	63	7.7	2	0.4	65	4.8
<i>Aythya ferina</i>	38	4.7	17	3.1	55	4.1
<i>Anatidae</i> unidentified	26	3.2	3	0.5	29	2.1
<i>Aythya fuligula</i>	21	2.6	10	1.8	31	2.3
<i>Podiceps cristatus</i>	19	2.3	23	4.2	42	3.1
<i>Sturnus vulgaris</i>	18	2.2	23		41	3.0
<i>Emberiza schoeniclus</i>	18		13	2.4	31	2.3
<i>Podiceps</i> sp.	15	1.8	14	2.6	29	2.1
<i>Acrocephalus arundinaceus</i>	7	0.9	1	0.2	8	0.6
<i>Rallus aquaticus</i>	6	0.7	6	1.1	12	0.9
<i>Perdix perdix</i>	6		3	0.5	9	0.7

1	2	3	4	5	6	7
<i>Passer montanus</i>	6	6.7	2	0.4	8	0.6
<i>Emberiza citrinella</i>	6		1	0.2	7	0.5
<i>Passer sp.</i>	5	0.6	2	0.4	7	
<i>Saxicola rubetra</i>	5		—	—	5	0.4
<i>Passer domesticus</i>	4	0.5	5	0.9	9	0.7
<i>Podiceps nigricollis</i>	2	0.2	6	1.1	8	0.6
<i>Podiceps ruficollis</i>	2		5	0.9	7	0.5
<i>Aythya nyroca</i>	2		1	0.2	3	0.2
<i>Larus ridibundus</i>	2		18	3.3	20	1.5
<i>Cuculus canorus</i>	2		3	0.5	5	0.4
<i>Gallinula chloropus</i>	2		1	0.2	3	0.2
<i>Turdus pilaris</i>	2		3	0.5	5	0.4
<i>Turdus merula</i>	2		2	0.4	4	0.3
<i>Turdus philomelos</i>	2		—	—	2	0.1
<i>Phylloscopus sp.</i>	2		—	—	2	0.1
<i>Vanellus vanellus</i>	1	0.1	3	0.5	4	0.3
<i>Sterna hirundo</i>	1		2	0.4	3	0.2
<i>Porzana parva</i>	1		1	0.2	2	0.1
<i>Carduelis carduelis</i>	1		1		2	
<i>Columba domestica</i>	—	—	1		1	
<i>Chlidonias niger</i>	1	0.1	—	—	1	
<i>Dendrocopos major</i>	1		—	—	1	
<i>Lanius collurio</i>	1		—	—	1	
<i>Coccothraustes coccothraustes</i>	1		—	—	1	
<i>Carduelis chloris</i>	1		—	—	1	
<i>Emberiza calandra</i>	1		—	—	1	
<i>Passeriformes unidentified</i>	53	6.5	20	3.6	73	5.4
<i>Anser anser</i>	—	—	19	3.5	19	1.4
<b>Total Birds — Razem Ptaki</b>	<b>489</b>	<b>59.9</b>	<b>323</b>	<b>58.8</b>	<b>812</b>	<b>59.9</b>
<i>Natrix natrix</i>	—	—	2	0.4	2	0.1
<i>Lacerta sp.</i>	—	—	1	0.2	1	0.1
<b>Total Reptiles — Razem Gady</b>	<b>—</b>	<b>—</b>	<b>3</b>	<b>0.5</b>	<b>3</b>	<b>0.2</b>
<i>Rana sp. (esculenta)</i>	18	2.2	12	2.2	30	2.2
<i>Rana sp. (temporaria/arvalis)</i>	1	0.1	10	1.8	11	0.8
<b>Total Amphibians — Razem Płazy</b>	<b>19</b>	<b>2.3</b>	<b>22</b>	<b>4.0</b>	<b>41</b>	<b>3.0</b>
<i>Cyprinus carpio</i>	81	9.9	61	11.1	142	10.5
<i>Abramis brama</i>	—	—	1	0.2	1	0.1
<b>Total Fishes — Razem Ryby</b>	<b>81</b>	<b>9.9</b>	<b>62</b>	<b>11.3</b>	<b>143</b>	<b>10.6</b>
Waterfowl's eggs Jaja ptaków wodnych	—	—	numerous liczne		numerous liczne	

The main food items of marsh harriers in the Barycz valley consisted of birds (60%), mammals (28%), fish (10%), and frogs (2%). *Passeriformes* accounted for 55% of the avian prey, and small mammals were dominated by rodents (82%). Fishes, with one exception, were represented by carps, mostly freshly dead, two-year-old individuals.

#### Diet of marsh harriers from their return in spring to the beginning of incubation (20 March–30 April)

In this period, the diet of marsh harriers can only qualitatively be characterized. This was the most difficult period to them in terms of prey abundance and availability. The remains of food on platforms and the prey caught by hunting individuals consisted mostly of starlings *Sturnus vulgaris*, frogs, fish, and eggs of waterfowl nesting early in the season. At that time, as in later periods, small mammals must have accounted for much of the diet, but their remains were scanty. Starlings were hunted on the land and also in the reedbed where they roosted at night. Each day marsh harriers attentively searched such roosting sites. Apparently many weak or dead starlings remained in them. This was also the mating period of frogs *Rana temporaria* and *Rana arvalis* and they aggregated in less dense reeds growing in shallow water.

The early April was the beginning of laying of coots and mallards. A little later also grebes, occurring in large numbers on the ponds, started laying. About mid-April, grey-lag geese hatched.

In this period, eggs of coots and mallards *Anas platyrhynchos* were important components of the diet. I cannot determine their percentage in the diet, but judging from the number of nests of these two species robbed by marsh harriers, it must have been significant. Eggs were eaten on the nest of the prey or near by. Only occasionally were they carried to platforms.

Grey-lag goslings probably did not represent a significant proportion of the marsh harrier diet, although in the first study period 132–154 pairs of this species nested on the ponds of complex Stawno, and in the second period about 180 pairs (author's own data). Goslings were well defended by their parents. Nevertheless, I observed a marsh harrier eating a gosling at the edge of the nest in the presence of an old goose brooding the remaining young.

#### Diet in the nesting period

The 62 prey items delivered to the incubating females by their mates consisted of small mammals, mostly common voles *Microtus arvalis* (63%), birds, mostly skylarks *Alauda arvensis* (29%), also frogs and fish (8%), but only on rainy days.

The food delivered to the small young did not differ from the food delivered to



the incubating females. Among small birds, many nestlings and fledglings were caught. Later on, harriers preyed upon chicks of larger water birds (coots, mallards, grebes) and young hares. As long as the food was delivered only by the male, the bulk of the diet consisted of terrestrial animals which were relatively small.

As the young grew older and the female started hunting, the number of prey from aquatic habitats increased. In the order of their decreasing proportion in the diet these were nestlings of grebes, ducks, coots and other *Rallidae*. Among mammals there were young muskrats *Ondatra zibethicus* and vole-rats *Arvicola terrestris*. Also the number of dead carps increased in the diet. Among small prey, nestlings of reed warbler were numerous.

The period when the young marsh harriers had highest food requirements was well correlated with the greatest abundance of food, especially in aquatic habitats. At that time the young of most water birds abundant on the ponds and representing the potential prey of marsh harriers, were already reared (WITKOWSKI 1967, DYCZ 1981, JANKOWSKI 1983).

#### Diet in the post-fledging period (15 August–30 September)

Sources of information concerning the diet in this period were scarce, based mainly on observations of hunting sites and estimates of potential prey in them.

In this period, not fully grown ducks, coots and grebes were rare. Young passerine birds were flying equally well as adults, and started migratory movements. In a word, the importance of aquatic habitats as the source of food for marsh harriers sharply declined, especially as compared with the preceding period. The remains on feeding platforms comprised fish, frogs, scarce coots, tufted ducks *Aythya fuligula*, and delayed black-headed gulls.

Many marsh harriers left the ponds and started nomadic movements. They hunted more often in farmland than on ponds. Harvest was just over, and small mammals, especially common voles, were then more available than any other prey on the ponds. But as soil fertility was low in the region of Stawno, no wonder that marsh harriers gave up hunting on crop fields very soon. They probably moved to the adjacent Oder valley, where crop fields were much more fertile and abounded in small rodents. For example, they were frequently observed between Trzebnica and Wrocław, where they certainly did not breed.

#### Differential food niches of males and females

A marked change in the food delivered to the young when the females started hunting suggested that the two sexes had different food niches. As the females delivered to the nest not only their own prey but also those passed by the male, it

was not possible to know which bird hunted a given prey when observing the nest from a hide in the reed. This problem was solved in two ways (see p. 232–233). Four nests were observed in different years to separate the prey hunted by each parent. The total material consisted of 441 prey items of which 252 were hunted by the male (Tab. 42) and 189 by the female (Tab. 43).

For all the nests the prey delivered by the male consisted mainly of animals from open land habitats (Tab. 44). They accounted for 70% of all prey items in two males (A and C). Only for one male (B) was this proportion below 50%; nevertheless land prey outweighed the prey from water habitats.

Table 42. Male's prey estimated in four pairs (A, B, C, D) of marsh harriers in the Barycz valley

L – prey from land habitats, W – from water habitats, N – from indetermined habitats

Tabela 42. Zdobycze samców z 4 różnych par (A, B, C, D) błotniaków stawowych w dolinie Baryczy

L – zdobycz pochodząca z siedlisk lądowych, W – siedlisk wodnych, N – siedlisk nie ustalonych

Prey Zdobycz	Habitat Siedlisko	Male – Samiec				Total Razem	Mean weight (g) Średnia masa (g)
		A	B	C	D		
<i>Microtus arvalis</i>	L	34	27	13	11	85	25
<i>Alauda arvensis</i>	L	18	9	4	4	35	30
<i>Passeriformes</i> unidentified	N	10	16	–	3	29	15
<i>Fulica atra</i> (pulli)	W	1	9	3	2	15	125
<i>Podiceps cristatus</i> (pulli)	W	3	5	1	1	10	100
<i>Lepus europaeus</i> (juv.)	L	6	2	–	–	8	200
<i>Microtus oeconomus/agrestis</i>	N	3	3	1	–	7	40
<i>Podiceps</i> sp. (pulli)	W	–	5	1	1	7	70
<i>Murinae</i> unidentified	L	–	5	1	–	6	20
<i>Anatidae</i> unidentified	W	–	5	1	–	6	60
<i>Aythya fuligula</i> (pulli)	W	3	2	–	–	5	60
<i>Sturnus vulgaris</i>	N	1	4	–	–	5	70
<i>Emberiza schoeniclus</i>	N	1	3	–	1	5	15
<i>Cyprinus carpio</i>	W	2	2	–	1	5	150
<i>Aythya ferina</i> (pulli)	W	–	4	–	–	4	60
<i>Perdix perdix</i> (pulli)	L	3	–	1	–	4	50
<i>Talpa europaea</i>	L	2	1	–	–	3	100
<i>Acrocephalus scirpaceus</i>	W	3	–	–	–	3	12
<i>Passer montanus</i>	L	3	–	–	–	3	25
<i>Rana</i> sp. (esculenta)	W	–	1	1	1	3	20
<i>Ondatra zibethicus</i> (juv.)	W	1	–	–	–	1	200
<i>Arvicola terrestris</i> (juv.)	W	1	–	–	–	1	70
<i>Mus musculus</i>	L	1	–	–	–	1	20
<i>Clethrionomys glareolus</i>	L	1	–	–	–	1	20
Total – Razem		97	103	27	25	252	46.8

Table 43. Female's prey estimated in four pairs (A, B, C, D) of marsh harriers in the Barycz valley  
L – prey from land habitats, W – from water habitats, N – from indetermined habitat

Tabela 43. Zdobytcze samic z czterech par (A, B, C, D) błotniaków stawowych w dolinie Baryczy  
L – zdobycz pochodząca z siedliska lądowego, W – z siedliska wodnego, N – z siedliska nie ustalonego

Prey Zdobycz	Habitat Siedlisko	Female – Samica				Total Razem	Mean weight (g) Średnia masa (g)
		A	B	C	D		
<i>Cyprinus carpio</i>	W	20	2	11	4	37	150
<i>Fulica atra</i> (pulli)	W	14	5	3	8	30	130
<i>Acrocephalus scirpaceus</i> (pulli)	W	11	4	3	3	21	12
<i>Rana sp. (esculenta)</i>	W	1	5	1	5	12	20
<i>Passeriformes</i> unidentified	N	5	2	2	2	11	15
<i>Aythya ferina</i> (pulli)	W	1	4	2	2	9	90
<i>Anatidae</i> unidentified	W	4	–	4	1	9	90
<i>Microtus arvalis</i>	L	2	3	2	1	8	25
<i>Podiceps sp.</i> (pulli)	W	4	3	1	–	8	120
<i>Arvicola terrestris</i>	W	5	–	1	1	7	80
<i>Aythya fuligula</i>	W	5	–	2	–	7	90
<i>Ondatra zibethicus</i> (juv.)	W	2	–	1	1	4	200
<i>Podiceps cristatus</i>	W	2	–	2	–	4	200
<i>Rallus aquaticus</i>	W	3	1	–	–	4	40
<i>Passer sp.</i>	L	2	–	1	1	4	25
<i>Cuculus canorus</i> (pulli)	N	2	–	1	–	3	60
<i>Alauda arvensis</i>	L	1	1	–	1	3	25
<i>Sturnus vulgaris</i>	N	–	1	1	–	2	70
<i>Acrocephalus arundinaceus</i>	W	2	–	–	–	2	25
<i>Emberiza schoeniclus</i>	N	1	1	–	–	2	15
<i>Podiceps ruficollis</i> (pullus)	W	–	1	–	–	1	200
<i>Larus ridibundus</i> (pullus)	W	1	–	–	–	1	300
Total – Razem		88	33	38	30	189	88.6

Not less than 70% of the prey caught by females represented aquatic animals. This provides evidence that male and female of marsh harriers of the Barycz valley had clearly separated food niches. Males typically hunted in meadows and crop fields, and females on ponds.

The prey hunted by females was twice as heavy as the prey hunted by males (Tabs 42 and 43).

The diet of marsh harriers did not include birds larger than fully grown moorhen *Gallinula chloropus* and mammals larger than a big rat. All prey items bigger than these two species and occurring in the diet of Barycz valley marsh harriers (Tabs 41–43) were young individuals, at the most half grown.

Table 44. Proportion of prey from different habitats in the diet of male and female marsh harriers in the Barycz valley

Tabela 44. Różnice siedliskowe pomiędzy ofiarami łowionymi przez samce i samice błotniaka stawowego w dolinie Baryczy

	Male's prey – Zdobycze samca					Female's prey – Zdobycze samicy				
	A	B	C	D	Total Razem	A	B	C	D	Total Razem
Prey from water habitats Ofiary pochodzące z siedlisk wodnych	14.4	32.0	25.9	24.0	23.8	85.2	75.8	81.6	83.3	82.5
Prey from land habitats Ofiary pochodzenia lądowego	70.1	42.7	70.4	60.0	57.9	5.7	12.1	7.9	10.0	7.9
Prey from unknown habitats Ofiary nie ustalonego pochodzenia	15.5	25.2	3.7	16.0	18.3	9.1	12.1	10.5	6.7	9.5
Total No. of prey – Liczba ofiar	97	103	27	25	252	88	33	38	30	189

Differences between the categories of prey caught by males and females are highly significant (Chi-square test,  $P < 0.0001$ ). In the case of males the prey from unknown habitats were added to the prey from water habitats and in the case of females they were added to the prey from land habitats.

Różnice pomiędzy kategoriami zdobyczy samców i samic są statystycznie wysoce istotne (Chi-kwadrat test,  $P < 0.0001$ ). Przy ich wliczaniu ofiary z nieznanego siedliska dodano do wodnych w przypadku samców, a do lądowych w przypadku samic.

## DISCUSSION

### ABUNDANCE

Many birds of prey became endangered in the second half of the 19th century (NEWTON 1979) mostly as a result of two kinds of human activity: large-scale changes in their natural habitats related to economic needs of man, and a deliberate, planned, and persistent persecution of all predatory vertebrates in an attempt to protect game and domestic animals. A classical example is Great Britain, where the marsh harrier was exterminated altogether at the end of the last century (UNDERHILL-DAY 1984). A similar fate, though not so drastic, happened to many west European and Scandinavian populations (CRAMP & SIMMONS 1980). Predators were also persecuted throughout Silesia, thus in the Barycz valley as well (KOLLIBAY 1906, PAX 1925).

During World War II, the persecution of marsh harriers was relaxed, and in many places their numbers slightly increased (GLUTZ *et al.* 1971, CRAMP & SIMMONS 1980, UNDERHILL-DAY 1984).

In 1958–70, populations of marsh harrier declined again in many parts of



Europe. At that time their egg shells thinned by 10–14% (ODSJO & SONDELL 1977, CONRAD 1978, UNDERHILL-DAY 1984). Cases of death in convulsion, indicative of poisoning, were described in the Netherlands (KOEMAN *et al.* 1969).

Fluctuations of the marsh harrier population in the Barycz valley went parallel to those in at least some parts of Europe (except, for example, in Sweden, where no decline was observed over the period of DDT use – ODSJO & SONDELL 1977).

#### OCCURRENCE

In the areas where marsh harriers are migratory birds, males return to their breeding sites about 10 days earlier than females (*e.g.* BENGTSOON 1967, GLUTZ *et al.* 1971). Data presented in Figure 2 show that this was the case only in the peak phase of the spring migration.

The dates of return depend on the latitude. The difference between the Barycz valley and the northernmost breeding areas of marsh harriers in Sweden (PERSSON 1975) was 10 days.

Marsh harriers of the Barycz valley left their breeding sites strikingly early, although some of them wintered already in the Mediterranean Basin (VOOUS 1960, CRAMP & SIMMONS 1980, author's own data).

This must have been an effect of rapidly deteriorating food conditions on the ponds. Young grebes, ducks and coots became too big to be the prey of marsh harriers, especially of the males, which are smaller than females, whereas common voles, an important component of the diet, could not occur in high densities on poor soils of this terrain (TRUSZKOWSKI 1982, PUCEK 1984).

#### DENSITY OF BREEDING PAIRS, TERRITORY, NEST LOCATION TERRITORIAL BEHAVIOUR

Most frequently the density of breeding pairs is calculated in relation to an administrative district. This is especially the true of German authors (LOOFT 1968, CREUTZ 1969, MISSBACH 1970, 1972). The area occupied by a breeding pair can then range from 9 to 41 km, depending on the district. These figures can be useful for faunistic purposes, but from the ecological point of view they are meaningless.

An ecologically useful density estimate can be expressed as the number of pairs in relation to the size of the habitat type in which nesting was recorded. When the density is calculated in this way (HILDEN & KALINAINEN 1966, KRETLOW in CREUTZ 1969), the area utilized by one pair is limited to 1–2.2 km.

The size of the hunting area is most difficult to find, especially when it is far from the nesting territory. Hence, it is difficult to estimate the home range of marsh harriers. This becomes possible when the males from the population under study are individually marked so that they can be identified at a distance. It is also possible in some peculiar situations, as in the study by THIOLLAY (1970), carried

out on an isolated plot of about 1800 ha in Camargue, France, where 7 or 8 breeding pairs of marsh harriers were recorded; thus, a mean home range size of a pair was 220 ha.

Home range of 5 pairs in Schleswig-Holstein, measured by the ODUM & KUENZLER (1955) method, ranged from 300 to 900 ha, depending on their location (BOCK 1978).

So far the only study of individually marked birds was carried out with *Circus approximans* in New Zealand (BAKER-GABB 1981). The mean nesting territory covered 31 ha (27 ha at Stawno), and the mean home range was 90 ha (160 ha at Stawno). Another method for estimating density showed that the density of marsh harriers in reedbeds of Neusiedlersee was 3.3–6.5 individuals per 100 ha (RIPFEL & SEZEMSKY 1983).

A relationship between densities of breeding marsh harriers and densities of their main prey, field vole, was shown by HAMMERSTROM (1979).

Sometimes marsh harriers can reach very high densities, as known from the literature (KONRADT 1966, BERG & STIEFEL 1968) and from the present study (for example on pond Nowy Świat Górny – Table 1). This can be explained by the fact that their hunting areas are separated from nesting territories. The size of nesting territories can be modified, depending on the presence of suitable hunting sites near by. Aggregations of marsh harriers can thus be considered as an adaptation for the best utilization of suitable nesting sites, the number of which is gradually declining, situated close to the areas abundant in food. SONDELL (1970) also indicates that aggregation facilitates group defence against predators.

In the Barycz valley, marsh harriers nested on ponds, in the reed, less often in *Typha angustifolia*, and occasionally in *Scirpus lacustris* or in shrubs of *Salix* sp. Similar nesting sites were selected over the study area. In heavily transformed habitats, marsh harriers nest in alfalfa or in winter crops (KIRCHNER 1961, SCHEMMELE 1974, BOCK 1978), or even in young pine cultures (GIRAUD-AUDINE & PINEAU 1974). In these new habitats, however, marsh harriers suffered the heaviest losses.

The descriptions and analyses of the so-called aerial dances of males (GLUTZ *et al.* 1971, CRAMP & SIMMONS 1980) suggest that they perform two functions: 1) they form a part of territorial behaviour (advertisement of territory occupancy), and 2) they are a part of mating behaviour. In my opinion, their basic, if not the only function is territorial advertisement.

#### POLYGAMY

The study of reproductive biology of monogamous birds has revealed that in some circumstances single individuals or even a large part of the population formed polygamous bonds. In *Falconiformes*, polygamy, and more precisely polygyny, was most frequent in the genus *Circus*. But also here, in some populations

polygamy was rare and in other populations the proportion of polygynous bonds exceeded even 30%. Populations of the first type are known from Finland (HILDEN & KALINAINEN 1966), Sweden (ODSJO & SONDELL 1977, ARVIDSSON 1980), Camargue, southern France (THIOLLAY 1970), and also from the Barycz valley (present paper). Frequent cases of polygyny were recorded from Netherland (SCHIPPER 1979) and Britain (UNDERHILL-DAY 1984). Polygyny was even more frequent in hen harriers *Circus cyaneus* from the Orkney Islands, where 75% of the females formed bonds of this type (BALFOUR & CADBURY 1979).

A question arises about the source of these differences. NEWTON (1979) and PICOZZI (1980) suggest that for hen harriers from the Orkneys they were due to an uneven sex ratio already in the nest (0.87 male : 1 female), reinforced by the fact that more one-year-old females than males could reproduce. As a result, the sex ratio of reproducing individuals was 1:2 in favour of females, and this biased sex ratio accounted for polygyny.

But the facts accumulated so far also provide evidence for another interpretation of polygyny in marsh harriers, based on TRIVERS (1972) hypothesis concerning an uneven parental investment: females producing highly energetic gametes should carefully select the male with his territory.

The most critical period in the breeding cycle for female marsh harriers is from laying until the young are about 10 days old. At that time females and the young totally depend on males for food. In all cases when females were forced to hunt in that period, the eggs were chilled and losses were very high. Such a situation could be frequent in territories of moderate or poor quality, thus polygyny should be rare in such areas.

Mates of males holding high-quality territories, quickly accumulate energy and start laying early. When another female appears later in the same territory, which can be accepted by the male, she can recognize the situation using different cues (e.g. the ability of the male to chase predators and alien males, safety in the territory, quantity and quality of the food delivered by the male, food supply in the territory), and she can stay in this territory as the second mate. The risk of such a female can be smaller than in a monogamous situation on a poorer territory.

The above arguments suggest that polygyny of marsh harriers is not necessarily related to a biased sex ratio. The quality of the male and of the territory may be of basic importance, as already suggested for *Passeriformes* (VERNER & WILLSON 1966, ORIANS 1969, DYRCZ 1977, PLESZCZYNSKA 1978, SEARCY 1979).

It is difficult to tell whether or not polygamy is a result of a local sex bias since data on sex ratio in the young generation of birds of prey are lacking. From Europe they are available only for the hen harrier on the Orkney Islands (PICOZZI 1980), peregrine falcon *Falco peregrinus* (HICKEY 1942), hobby *Falco subbuteo* (FIUCZYŃSKI 1978), sparrow hawk *Accipiter nisus* (NEWTON & MARQUISS 1979), and marsh harrier (SCHIPPER 1979, present paper). Data on harriers are not consistent. On the Orkneys there were more females than males, and polygyny was more



frequent than monogamy. In the Barycz valley males were more abundant than females and polygyny was rare. In the Netherlands, however, also males predominated but polygyny accounted for about 50% (SCHIPPER 1979). The last case contradicts the hypothesis of unbalanced sex ratio and seems to support the importance of the quality of the male and territory to the formation of polygynous bonds (see the description of food conditions, p. 229 and 286–287).

The basic criteria of the quality of a territory include available food supply and safety. As I have not data on safety, this issue cannot be discussed here. But the size of losses seems to suggest that safety conditions were similar for all the populations compared, except for the Dutch population (SCHIPPER 1979), where losses were very low (see Tab. 48).

Food conditions in a marsh harrier territory concern not only numbers (density) of prey but also their suitable size, quality, and availability in the breeding period. In monogamous populations (Finland – HILDEN & KALINAINEN 1966, Schleswig-Holstein – BOCK 1979, Barycz valley – present paper) the prey mainly consisted of small animals such as *Passeriformes* and *Micromammalia*.

In populations with a high proportion of polygyny, the diet consisted of larger prey. On the Orkneys it was dominated by rabbits (PICOZZI 1980), in Britain by young pheasant, partridges, rabbits (HOSKING 1943), and moorhens (COLLING & BROWN 1946). In the Netherlands, pheasants or partridges, depending on population, accounted for about 50% of the diet, and the proportion of *Passeriformes* was less than 15% (SCHIPPER 1973). Young rabbits and pheasants delivered to the nest averaged 250 g, whereas the mean weight of *Passeriformes* and *Micromammalia* was less than 50 g.

Territories abounding in large prey can be considered as optimal also for the formation of a polygynous system. The owner of such a territory could reduce his effort even to one-fifth to catch the same amount of food as the owner of an average territory. This situation could enhance polygyny in males holding optimal territories, whereas the excess of females could only extend the scale of this phenomenon.

Table 45. Comparison of fledging success of marsh harrier from nests with single and double mated males in the Barycz valley, Britain (UNDERHILL-DAY 1984) and Netherlands (SCHIPPER 1979)

Tabela 45. Porównanie sukcesu lęgowego samców błotniaka stawowego skojarzonych z jedną i dwiema samicami, pomiędzy doliną Baryczy, Brytanią (UNDERHILL-DAY 1984) i Holandią (SCHIPPER 1979)

	One female 1 samica	Two females 2 samice	Locality Miejsce
Mean young fledged per nest (female)	2.31	1.66	Barycz valley
Średnia liczba młodych lotnych na gniazdo (samicę)	2.15	2.53	Britain
	2.25	3.31	Netherlands
Mean young fledged per male	2.31	3.32	Barycz valley
Średnia liczba młodych lotnych na samca	2.15	5.06	Britain
	2.25	6.62	Netherlands



The next argument in favour of the hypothesis concerning the male and territory quality is breeding success, compared for mono- and polygamous birds in Table 45. The production of young per female in the Barycz valley, where polygynous nesting was rare, was much lower for polygynous than monogamous birds. In the Dutch and British populations it was higher for polygynous females. If it can be assumed that breeding success is a measure of territory quality, then this comparison indicates that polygynous males in the Barycz valley had territories of lower quality than polygynous males in Britain and the Netherlands, hence polygyny in the Barycz valley was rare.

#### NEST

A detailed description of nests and their construction is given by GLUTZ *et al.* (1971). According to WEIS (1923), males rarely bring nest material, which was not the case in the Barycz valley and in some other areas (COLLING & BROWN 1946, HÜBNER 1967).

NEWTON (1979) analyzed the role of the habit of bringing fresh green leafy sprays to completed nests. He rejected the suggestion that the greenery is a form of nest-sanitation or that it serves to maintain humidity. His alternative explanation is that the greenery is another form of advertisement serving to denote an occupied territory when the occupants are not around. Green sprays change colour quickly, so that the presence of green on the nest immediately signifies recent activity. This hypothesis does not seem to hold good in the case of the marsh harriers of the Barycz valley. Most often greenery was brought to the nest not in the first, but in the second half of the nesting cycle, after the young hatched. The presence of live, noisy young was a sufficient signal that the territory was occupied.

HILDEN & KALINAINEN (1966) and GLUTZ *et al.* (1971) argue that the new material added to the nest after hatching of the young is a form of nest-sanitation. JOHANNESSON (1975) disagrees and provides arguments that it consolidates the structure of the nest and enlarges it, and this protects the nest against destruction by increasingly active young. In my opinion the added material serves both these purposes. In addition, the enlargement of the nest surface as the young grow older can reduce aggression among the young when their parents deliver food. This can be especially important when the young can tear the prey without help of the mother. The sanitation function of the greenery is supported by the fact that large amounts of new material were added after heavy rains.

#### PERIOD OF LAYING

In the population studied, the earliest egg was laid on April 8, and this was the only case of the initiation of laying in the first 10-day period of April (Tab. 5). In

an area situated at the same latitude in the Netherlands, SCHIPPER (1979) recorded a similar timing of laying. The population of marsh harriers from Camargue, more than 1000 km to the south of the Barycz valley, started laying on April 4 (THIOLLAY 1970), and the Finnish population, living 1000 km to the north of the Barycz valley, started laying on April 25 (HILDEN & KALINAINEN 1966). I do not think that the length of the day was important in this case (KENDEIGH 1941). Probably temperature should reach a sufficiently high level to release laying (KENDEIGH 1963, SCHIPPER 1979). Marsh harriers started laying when in the period when they were potentially capable of laying, mean daily temperature exceeded 4°C and in following days did not drop more than by 28% (SCHIPPER 1979). This seems to apply also to the Barycz valley, as indicated by the comparison of mean daily temperatures with the timing of laying (see Fig. 4).

Half of the females in the population studied initiated laying by 30 April (Tab. 5). When the mean duration of all the other phases of the breeding cycle is summed, it can be seen that most young became independent by mid-August, and they left the breeding area immediately (Fig. 3). Most marsh harriers, both adult and young, did so by mid-September.

As compared with other breeding areas situated at the same latitude and even further north than the Barycz valley, this was a very early emigration; in the other regions marsh harriers stayed until mid-October or even until the end of October (TISCHLER 1941, HILDEN & KALINAINEN 1966, GLUTZ *et al.* 1971, CRAMP & SIMMONS 1980). This difference could have been due to rapidly declining food resources in the Barycz valley late in summer. The timing of laying was probably adjusted to this situation. Few females (3.3%) started laying after 15 May (Fig. 5). Females laying later would rear the young in the period of rapidly deteriorating food conditions.

#### CLUTCH SIZE

The mean clutch size of the Barycz valley population ranged from 4.7 to 5.4 eggs over seven years. If the clutch size depends on food conditions (LACK 1954, 1966), it can be inferred that food conditions did not change much over this period. A classical example illustrating the relationship between the clutch size and food conditions is rough-legged buzzard *Buteo lagopus* in Norway (HAGEN 1969), laying 4–7 eggs in the years most abundant in mice, and not laying at all in years of their low numbers. This is characteristic of species with a narrow food spectrum, such as buzzards, kestrels, and especially owls.

Marsh harriers of the Barycz valley population and other European populations have a very wide food spectrum (UTTENDORFER 1939 and 1952, HILDEN 1966, HILDEN & KALINAINEN 1966, GLUTZ *et al.* 1971, SCHIPPER 1973, BOCK 1978), thus year-to-year differences in their clutch size were small. Also BENGTON (1967) and BOCK (1979) found a very small range of clutch size variation (4.2–4.6 eggs),

although numbers of mice and common voles largely varied over the four-year study period of BENGTON'S study. SCHIPPER (1979) did not find any correlation between the clutch size and the abundance of the main prey.

A decrease in the mean clutch size within the season (Tab. 8) was recorded in many birds. The reasons accounting for this reduction are still not well understood (KLOMP 1970). SCHIPPER (1979) suggests that this must be the same factor as that responsible for the reduction of breeding success in clutches laid late in the season. The observed trends suggest that these must be factors related to the condition of the female rather than to her genetic make-up. The number of eggs laid in a clutch was related to the age and experience of females (COULSON 1963, JONES 1973, NEWTON 1976) or to their condition (ANDERSEN 1957), rather than to genetic factors (BENGTON 1967). Moreover, genetically programmed clutch size should not show any seasonal trend, unless it is conditioned in two ways, that is, females genetically coded to lay more eggs should also initiate laying earlier in the season.

A different result was obtained by HAVERSCHMIDT (1953), who collected materials in the Netherlands till the end of the 1960s. Clutches were smaller at the beginning of the season. They contained 3.36 eggs in April, 4.51 eggs in May, and 4.14 eggs in June. Later studies in that country (SCHIPPER 1979) revealed typical trend. It is possible that the results obtained by HAVERSCHMIDT were effected by the use of DDT (shell thinning and the resulting egg breakage).

In many cases replacement clutches were of the same size (3–6 eggs) as the lost clutches. But on the average, replacement clutches were reduced by 0.66 eggs. DEMENTIEV & GLADKOV (1951) and HILDEN & KALINAINEN (1966) recorded no more than 5 eggs in replacement clutches.

Birds laying more than two eggs in a clutch, including birds of prey, typically tend to lay larger clutches at higher latitudes. Factors accounting for this pattern were discussed by LACK (1954, 1968) and CODY (1966). In Europe, such a tendency was found for buzzard *Buteo buteo* and goshawk *Accipiter gentilis* (PICOZZI & WEIR 1974, HUHTALA & SULKAVA 1976). In *Falconiformes*, one case of a reverse trend is known. For unknown reasons peregrine falcon had smaller clutches in the boreal than in the temperate zone (HICKEY 1969), both in North America and in Europe.

No latitudinal trend exists in clutch sizes of different European populations of the marsh harrier (Tab. 46).

Shell thinning in the British population of sparrowhawk *Accipiter nisus* was noticed already in 1947 (NEWTON 1979), thus practically after two years of an intense application of DDT. It was noticeable at least until 1975 (no data from later years). It may thus be expected that in 1974 and 1975 many species of raptors, especially those living on insectivorous prey, were affected by egg breakage. If this was not taken into account when estimating clutch size of birds of prey in the period of DDT use, a large error could result (broken eggs could be overlooked). If the clutch size of the marsh harriers in the Barycz valley had been determined from only one visit to the nest in mid-incubation period, and not from



frequent visits during laying and marking eggs with numbers, the mean clutch size would have been underestimated by 20% (Tab. 47). This should be kept in mind when analyzing differences in clutch size of raptors.

Table 46. Mean clutch size in relation to latitude  
Tabela 46. Średnia wielkość zniesienia w zależności od szerokości geograficznej

Latitude Szerokość geograficzna	Number of clutches Liczba zniesień	Mean clutch size Średnia wielkość zniesienia	Reference Źródło informacji
63°N	73	4.66	HILDEN, KALINAINEN (1966)
62°N	28	4.32	ODSJO, SONDELL (1977)
56°N	43	5.07	BENGTSON (1967)
55°N	114	4.61	UNDERHILL-DAY (1984)
54°N	123	4.35	BOCK (1979)
	53	4.49	RICHTER, MEBS in GLUTZ <i>et al.</i> (1971)
53°N	71	5.21	SCHIPPER (1979)
	118	4.29	HAVERSCHMIDT in GLUTZ <i>et al.</i> (1971)
52°N	235	5.01	present paper
	120	4.60	CREUTZ (1968)
46°N	103	4.46	DOMBROWSKI in GLUTZ <i>et al.</i> (1971)
44°N	21	4.60	THIOLLAY (1970)

Table 47. Possible error in determination of clutch size in the DDT period, depending on the time of checking the clutch

Tabela 47. Możliwość błędu w ustalaniu wielkości zniesienia w okresie stosowania DDT w zależności od sposobu i czasu ustalania tego parametru

Year Rok	Number of clutches Liczba zniesień	Clutch size determined at laying period Wielkość zniesienia ustalona w okresie niesienia		Clutch size determined in mid-incubation period Wielkość zniesienia ustalona w połowie okresu wysiadywania		Number of eggs laid Liczba jaj zniesionych	Number of eggs broken Liczba jaj zgniecionych przez wysiadujące samice
		$\bar{x}$	SD	$\bar{x}$	SD		
1972	28	5.43	0.88	4.14	1.67	152	36
1973	28	4.68	1.06	3.71	1.65	131	27
1974	28	5.25	1.17	4.00	1.47	147	35
1975	33	5.24	1.00	4.67	1.16	173	19
Total Razem	117	5.15 <sup>+</sup>	1.06	4.15 <sup>+</sup>	1.51	603	117

\* STUDENT test — Test STUDENTA,  $t = 5.9$ ,  $P < 0.0001$ .



## EGG SIZE AND ITS IMPORTANCE

Birds evolved many mechanisms adjusting their reproductive effort to habitat conditions and to their own condition. They include clutch size (LACK 1954, KLOMP 1970), synchronous or asynchronous hatching (LACK 1954, RICKLEFS 1965), size and quality of eggs (SCHIFFERLI 1973), sex ratio in siblings (TRIVERS & WILLARD 1973, HOWE 1976, FIALA 1981). One of them is also differential egg size within a clutch (PARSONS 1970, HOWE 1976, RYDEN 1978, SLAGSVOLD *et al.* 1984). The existing evidence for 67 bird species suggested that differences in the size of eggs within a clutch are adaptive (SLAGSVOLD *et al.* 1984). This adaptation acts in combination with asynchronous hatching. The analysis was done for the species laying the biggest eggs as the last in the clutch.

Although large differences were observed in the size of eggs within clutches of marsh harriers in the Barycz valley, neither a decreasing nor an increasing trend was observed in the size of eggs laid in succession (Tab. 12). In most cases, the biggest (heaviest) eggs were laid in the middle. HOWE (1976) and FIALA (1981) have found that in the common grackle *Quiscalus quiscula* and the red-winged blackbird *Agelaius phoeniceus*, egg sizes increased in the sequence of laying. FIALA (1981) has also found that in four-egg clutches the last, biggest egg more frequently produced males than females. ANKNEY (1982) has found that in four-egg clutches of snow goose *Anser caerulescens* two first eggs were bigger and typically produced males.

In the present study a clear relationship was found between the relative weight of eggs within a clutch and the sex of the young hatched from them (see p. 263–264).

Few data exist on egg sizes in different marsh harrier populations. Hardly any can be used for comparison, as sample sizes are small or necessary statistical parameters (SD) are lacking.

On the average, the eggs of the marsh harriers in the Barycz valley were smaller than in the Netherlands (HELLEBREKERS in GLUTZ *et al.* 1971) and in most central European populations (JOURDAIN in WITHERBY *et al.* 1948). They were bigger, however, than in northern France and Belgium (VERHEYEN in GLUTZ *et al.* 1971). The existing data are not sufficient for analyzing the possible latitudinal or any other trends.

## INCUBATION

The participation of male marsh harriers in incubation is a controversial issue. Based on 19-hour observations at 5 nests, BENGTON (1967) found that, on the average, the female incubated for 90% of the time, whereas the male for only 10% with a range of 0–20%. According to BROWN & AMADON (1968), practically only the female incubates, and the male does this occasionally. HÜBNER (1967) observed a male incubating over two hours, but this happened in an unusual situation, when the female did not come back to the nest after being flushed by the

observer. Thus the male developed an incubation drive under stress conditions. I also observed a similar event. After building a hide in the morning I returned in the afternoon to start observations. The male was on the nest and the eggs were little warm. When the accompanying person left, the male returned to the nest and sat down on the eggs, and even moved them with the beak. Every several to a dozen or so minutes he flew away and came back shortly afterwards. After three hours of such behaviour, the male started pecking and eating one egg, then the second egg, and flew away. I left the hide and continued the observation from the dike until dusk. The female did not return, and the male was not around for a long time but returned after sunset. The following day I found all the eggs destroyed by a harrier. The male was still holding his territory and the female was absent.

In general, the observations of the behaviour of incubating females from the hides provided results consistent with those described by KONDRADT (1966). Only the breaks in incubation by the female were not so frequent in this study. During four full days of observation, the male did not replace the female at all. After an aerial food-pass, the male often landed on the nest when the female was eating, but he never incubated. If BENGTON (1967) took this behaviour for incubation, the frequencies of male's visits to the nest were the same in both studies, however this was not incubation but only staying on the nest. And under normal conditions I never observed a 4-hour break in incubation made by the female, as it was described by HÜBNER (1967).

Thus in the Barycz valley only females incubated. And if the male incubated, this happened only in critical situations such as symptoms of nest desertion by the female. However, if the female did not return to the nest on the same day, the male abandoned it too. Such cases provide a deeper insight into the role of the male in raising the young. In dangerous situations he took a greater risk than the female did.

In the literature there are some discrepancies concerning the duration of incubation: RUTHKE (in GLUTZ *et al.* 1971) – 30 days; KONRADT (1966) – 31 days; BOCK (1979) – 32–33 days; KATE & RICHMOND (in GLUTZ *et al.* 1971) – 35–36 days; BROWN & AMADON (1968) – 33–38 days. At least two explanations of these differences are likely: small sample size and arbitrary determination of the time of the initiation of incubation. It is generally believed that marsh harriers initiate incubation from the second egg. Using not very convincing criteria, BOCK (1979) concluded that a large proportion of females initiated incubation with the laying of the first egg, which is not far wrong. All the females observed in the Barycz valley initiated incubation with the laying of the first egg. Some of them incubated steadily from the very beginning, others with long and frequent breaks. With the laying of the second egg, however, almost all the females incubated properly. Thus the beginning of incubation is somewhat conventional, and the criterion should always be stated. The date of the laying of the first egg or one day later are the best criteria, and I used the latter.

## ACTIVITY OF THE YOUNG AND PARENTAL LABOUR DIVISION IN THE NESTING PERIOD

The behaviour of the young in the nest was described in detail by SACH (1967), so my description includes only the details complementing or modifying his description. In no case did marsh harriers remove the young from the nest in dangerous situations (KOENIG 1952), but I cannot exclude such a behaviour in the cases of the emergency nests mentioned already (see p. 241). I created many dangerous situations by frequent visits to the nests, and the only striking event was throwing one or two chicks beyond the nest by the flushed female. It is difficult to tell if this was an accident resulting from distress or an adaptive behaviour. If the nest were built in a tree or on a rock, the question would be groundless. But marsh harriers nest in the reed, and the base of the nest is a large heap of loose reeds and branches. The chicks thrown out landed in this loose material, and they were not visible at once. Thus in case of the attack of a true predator they had a greater chance of surviving than the other chicks, well visible in the nest. An experiment is needed to answer this question.

NEWTON (1979) writes that somewhat grown chicks of raptors call loudly when a predator is approaching the nest, by which they make their mother return if she is near by. I have not observed such a behaviour in young marsh harriers. When a man or a bittern approached the nest, the young silently fled from it and hid in the reed, or they went back to the opposite rim of the nest, adopting a frightening-defensive posture. They leaned their back against the reed, opened their bills, showing the throat, and shook their claws stretched forward. Perhaps the young of the birds nesting in trees respond in a different way than the birds nesting on the ground, and Newton did not consider this. Young marsh harriers were chipping when a male or a female appeared over the nest, or when other large birds appeared, or when they were very hungry. They uttered another call, more cricket-like chirping, when they were fighting for food, or when they were dying of hunger and cold, or were being killed by siblings, as observed in few cases of fratricide. They also uttered this call when attacking an alien young marsh harrier which incidentally landed on their nest.

The female tore the prey up and fed the young. GENTZ & HALLMAN (1957) described a case when the male fed the young. Although I observed a similar case, my impression was that the male had no proper feeding reflex. In both these cases the female disappeared. The male tore the prey up on the nest, and the young were sufficiently grown to pull the pieces out of his bill and claws, and to eat them. I am sure they would have died of hunger if the female had disappeared earlier, when they were very young.

In the literature there are inconsistent data on the age at which young marsh harriers start flying (KONRADT 1966 — 38–39 days; STEINFATT 1940 and BLANC & MANUEL 1956 — 42–44 days), but they were based on single observations disregarding the sex of the birds (see p. 251).



## GROWTH OF THE YOUNG

In the literature there are no data on the growth of nestlings of marsh harriers. The existing data on the development of young Montagu's harrier *Circus pygargus* (DOBBRICK 1917) and hen harrier (HAAS 1939, SCHARF & BALFOUR 1971, PICOZZI 1980) show that different species of harriers grow at a similar rate, and 2-4-day differences at some stages are related to differences in the body weight.

When young marsh harriers in the Barycz valley were 15 days old, the female joined the male in hunting for food. It was so because at about this age the hunting efficiency of the male became insufficient to meet the food requirements of a brood comprising 4 young plus the female, as it can be seen by comparing the requirements of the young (Tab. 17) with the mean prey size delivered by the male (Tab. 42) and his daily efficiency (see p. 253).

The mean weight of the males starting to fly equalled to 75% of the weight of the females. The same proportions were recorded for hen harrier (PICOZZI 1980). This difference in weight between the sexes developed at the age of 26 days. Since that age body weight was a good index of the sex.

## SEX RATIO IN YOUNG GENERATION

Sex ratio of the young marsh harriers in the Barycz valley was biased in favour of males. It should be noted that the sex ratio was determined not at hatching but prior to fledging. The sex of the nestlings which died earlier and of embryos in a large proportion of unhatched eggs was unknown. It cannot thus be concluded that the sex ratio at fledging corresponded to that programmed in eggs.

In almost all studies based on large series of individuals, the sex ratio at hatching was almost balanced (FOSTER & McSHERRY 1980), and deviations were typically in favour of females (KESSEL 1957, FIALA 1981a). In birds with asynchronous hatching, such as marsh harriers, the smaller-sex young (males in the marsh harrier) develop more rapidly than the larger-sex young (females), and selection can favour mothers producing the larger sex earlier, increasing in this way the synchronous fledging. An alternative strategy is also possible. As larger individuals tend to monopolize the food delivered by the parents, thereby delaying the development of smaller individuals, selection may favour an earlier production of the smaller sex (BURLEY 1980).

Since the males, which are the smaller sex in the marsh harrier, hatched from the heavier eggs in the clutch, and because typically small eggs were laid at the beginning and at the end of the laying sequence, neither strategy could develop. The size of eggs should either increase or decrease in the sequence of laying if any of these strategies were acting. The sequence with increasing egg weight (size)



would produce females first, whereas the decreasing sequence would produce males first. In the population studied, larger individuals did not monopolize the food. Smaller individuals equalized their chances by being brisker than larger individuals. Under typical conditions fratricide was not observed, either. Thus, selection did not have to favour any sex with respect to the time of hatching. However, the location of the males in the middle of the series of eggs laid shows that it was favoured (the eggs laid first, and especially those laid last, were more often lost – see Tab. 20). This is also indicated by the size (quality) of eggs, and as a result, the sex ratio was favourable to males. If this bias was adaptive or casual it is difficult to tell. Further studies are needed, based on large series, especially making it possible to determine the sex ratio at hatching, and to identify possible sex-related differences in death rate.

Also the sequence of egg sizes in a clutch (see Tab. 13) needs confirmation on larger series of nests, and in particular the phenomenon that relatively larger eggs produce males, which are the smaller sex. As has already been mentioned, ANKNEY (1982) found a relationship between the sequence of laying and the sex on a relatively small data, in snow goose but COOKE & HARMSSEN (1983) did not confirm this on a larger material.

A similar tendency as for snow goose was found for ringbilled gull *Larus delawarensis* in Canada: the first eggs in three-egg clutches produced mainly males, and the second eggs mainly females (RYDER 1983). Both these examples show a relationship between the sequence of egg laying in a clutch and the sex of the young hatched from them. So far no relationship has been found between the weight (size) and sex ratio (HOWE 1979, BANCROFT 1984).

Thus many facts indicate that the sex of an embryo depends on the position of eggs in the sequence of laying, but these trends are not consistent within the species, or even for neighbouring populations (CLUTTON-BROCK 1986). At the present state of knowledge it is difficult to tell if the relationships between the sex and the laying sequence, or between the sex and the relative weight of an egg, which would enable the female to manipulate the sex ratio, represent an adaptive strategy, or if these are artifacts (WEATHERHEAD 1985), resulting from some unknown processes.

Since no excess males were present in the breeding population of the marsh harrier in the Barycz valley, their death rate in the period between fledging and reproduction must have been higher than in females. The higher production of males could thus have been an adaptation compensating for their higher mortality. It is not so sure, however, in view of the fact that young marsh harriers show little tendency to breed in their natal sites (see p. 283 and GALUSHIN 1974).

#### POST-FLEDGING PERIOD

The period between the initiation of flights and the independence is not described at all in the literature, or its characteristics are misleading. Controversy

mainly results from ignoring the differences between males, which are lighter, and females, which are heavier, in developing certain skills, for example, flying, or from the lack of precise criteria for some events. For example, BROUVER 1934 (in GLUTZ *et al.* 1971) and SACH (1967) found that young marsh harriers became fully capable of flying on days 55–56. If the criterion of this activity is flight towards the parents and taking food from them in flight, than this period should be shortened by 7 days, at least for males (Fig. 8).

On the basis of literature data, CRAMP & SIMMONS (1980) characterize this period as follows: "Fledging period 35–40 days. Female remains with young further 15–25 days, but male usually leaves soon after young fledge". This last period is longer by 25 days for marsh harriers of the Barycz valley.

#### LOSSES AND PRODUCTION OF YOUNG

In the Barycz valley, the highest losses were caused by predators (39.6% of all the nests lost) and desertion (27.6%). The sizes and causes of nest losses were examined so far only in Britain (UNDERHILL-DAY 1984). They were mostly due to desertion (41.3%), and also to predators and collectors (25%). 24% of the losses were due to unknown factors. Although the proportions are reversed, the same factors accounted for major nest losses in the two regions compared. Among predators robbing nests of marsh harriers there are crows, foxes and different *Mustelidae* (BENGTSON 1967, BOCK 1979, UNDERHILL-DAY 1984). In the Barycz valley, crows were represented by about 50 breeding pairs and they did not rob marsh harrier nests. A special attention was paid to interactions between these two species for reasons described in the section of methods, and no signs of aggression were recorded. Not so rarely both these species nested on the same islet. Often marsh harriers perched on trees in close vicinity of incubating crows. Some mutually exchanged signals must have inhibited aggression. If this "treaty" was violated at any time, then both birds were attacking vigorously. I have never witnessed, however, a robbery of a marsh harrier nest by a crow or vice versa.

Also the bittern *Botaurus stellaris* is suspected of robbing marsh harrier nests (UNDERHILL-DAY 1984). Over 85 days of observations of marsh harrier nests I saw two visits of bitterns. One took place when the female was brooding very young nestlings, and the second occurred when the young were 18–23 days old and the female was not on the nest. In both these cases marsh harriers assumed a threatening posture, but the bittern even did not stop at the nest.

Wild boar is also known to destroy marsh harrier nests (CREUTZ 1968, THIOLLAY 1970, BOCK 1979), but in no other place were losses due to wild boars as high as in the Barycz valley.

Losses due to fratricide were very low in the Barycz valley (Tabs 25 and 33).

Thus it is not an obligatory phenomenon in marsh harriers (MEYBURG 1974, EDWARDS & COLLOPY 1983). This is probably the case in most populations of marsh harriers as few authors describe such cases, and only WEIS (1923) reports many cases from Denmark. The single cases of fratricide described on pages 278 and 279 seem to show that this is a kind of atavism displayed by few individuals when food is in short supply. A different matter was the killing of siblings with abnormal behaviour, for example, dying of hunger and cold (see p. 278–279).

Table 48 compares data on the breeding success and production of young in different European populations of the marsh harrier. The mean number of young raised by a successful pair was similar in most populations, being 3.0–3.5 young. GDR and British populations had a little lower mean values.

The proportion of unsuccessful nests can be calculated as the difference between the production of young per breeding pair and the production of young per successful pair (Tab. 48). Unsuccessful pairs accounted for 3–35% in different

Table 48. Fledging success of marsh harrier in Europe  
Tabela 48. Sukces lęgowy europejskich błotniaków stawowych

Country Kraj	Number of nests Liczba gniazd	Mean young fledged per nest Średnio lotnych młodych na gniazdo	Mean young fledged per successful nest Średnio młodych lotnych na gniazdo udane	Reference Źródło informacji
Sweden	30	?	3.3	PERSSON (1975)
Sweden	65	3.1	3.4	ODSJO, SONDELL (1977)
Sweden	182	3.24	3.5	ARVIDSSON (1980)
Sweden (Skane)	26	2.2	3.2	BENGTSON (1967)
Finland	51	2.3	3.0	HILDEN, KALINAINEN (1966)
Britain (1911–82)	383	2.2	2.9	UNDERHILL-DAY (1984)
Netherlands	14	?	3.2	HAVERSCHMIDT (1953)
Netherlands	99	3.3	3.4	SCHIPPER (1979)
FRG	123	1.9	2.8	BOCK (1979)
GDR	68	2.8	3.5	CREUTZ (1968)
GDR	36	2.6	3.3	MISSBACH (1970)
GDR	24	1.8	2.8	SCHMIDT, WEISS (1970)
Poland	235	2.3	3.1	present paper
Mean – Średnio		2.52	3.18	



populations. The mean value for Europe was 21<sup>0</sup>/<sub>0</sub>, and it was similar to that in the Barycz valley (19.5<sup>0</sup>/<sub>0</sub>) in the second study period. In the first study period in the Barycz valley, losses accounted for 30<sup>0</sup>/<sub>0</sub>. The lowest losses (3<sup>0</sup>/<sub>0</sub>) were recorded in the Netherlands (SCHIPPER 1979).

In the 1940s, DDT started to be widespread in the biosphere. The harmful effect of this insecticide, and especially of its metabolite, DDE, on calcium metabolism in birds was evidenced (PEAKALL 1970). The use of DDT caused shell thinning and egg breakage (RATCLIFFE 1967, 1970). The accumulation of DDT was faster in raptors feeding on birds than in those feeding on mammals (CONRAD 1977). The diet of marsh harriers in the Barycz valley was mixed (Tab. 40), but a mean content of DDT in their eggs of 12.7 ppm (Tab. 29) was comparable to that recorded for species feeding mostly on birds (NEWTON 1979).

It has been found that the DDT taken by the female was transferred into eggs, where its concentrations could be higher than in the body tissues (BOGAN & NEWTON 1977). The contamination of eggs and females affected breeding success directly (disturbed gas exchange and increased evaporation through thinned shell, poisoning of embryos, egg breakage), or indirectly through abnormal incubation, even lack of incubation, by contaminated females (PEAKALL & PEAKALL 1973).

Which of the above-mentioned symptoms of DDT contamination could be seen in the reproduction of marsh harriers in the Barycz valley?

In the first study period, when DDT was rather commonly used in Poland, 21<sup>0</sup>/<sub>0</sub> of the losses resulted from egg breakage (Tabs 23 and 26), all eggs being broken or a part of them, whereas the others did not hatch. In the second study period, when DDT was no more used, this sources of losses disappeared.

A similar effect of DDT was observed also in successful nests (Tab. 28).

In 1972-75, the nesting losses caused by DDT were so high that the general tendency to lower losses at the beginning than at the end of the season was reversed (Tabs 27 and 28). The possible mechanism of this reversal is described on page 272.

Despite high losses due to DDT in 1972-75, the mean production of fledglings by successful pairs was the same as in the period when DDT was not used. Thus, this group of birds did not account for the population decline in the years of DDT application. Thus, these were the birds, especially females, without breeding success. DDT could also reduce the survival of fledglings and the mean life span of adults.

When the production of young per breeding pair is compared for the two periods, the difference is small, amounting to only 0.3 young (Tab. 33). But when the causes of losses are compared, differences become significant, and univocally show that the population declined because some pairs could not produce off spring as a result of poisoning with DDT. High losses due to wild boars in the second period obliterated the numerical difference, but it should be noted that they were of local character, whereas the losses due to DDT were global.

A different method for estimating the effect of DDT and PCB on the



reproduction of marsh harriers was used in Sweden (ODSJO & SONDELL 1977). The level of insecticides in addled eggs was analyzed and correlated with the breeding success of the nest from which any given egg was taken. At higher levels of contamination, the success was lower. The production of young per breeding pair was higher by 0.68 young in the period when DDT was not used in Sweden (1919–49). However, the Swedish population of marsh harriers did not decline.

In the British population of marsh harriers, as in the Barycz valley population, no differences were found in the production of young per successful pair, although shell thinning reached 10<sup>0</sup>/<sub>0</sub> and numbers of birds drastically declined in 1961–75 (UNDERHILL-DAY 1984).

Attempts to determine the effect of DDT and its metabolites on the breeding success of marsh harriers were thus made in three populations. In the British population (UNDERHILL-DAY 1984) evidence was found for shell-thinning in the period of population decline. In Sweden, besides shell-thinning, a relationship between breeding success and the level of pesticides in eggs was found (ODSJO & SONDELL 1977). In the Polish population (present study) the size of losses caused by shell-thinning and unhatchability of eggs was estimated.

To sum up, it can be concluded that the decline of the marsh harrier population noted in many European countries in the period of DDT application did not go through a reduction of the breeding success of the individuals capable of reproducing, but through a higher death rate of adult individuals or a complete breeding failure.

Although the losses due to DDT were rather high in the first study period, the population was already in the phase of a slow increase. Thus the losses in the period of decline must have been even higher, unless the increase was due to immigration.

#### FOOD

The diet of marsh harriers from the Barycz valley during the breeding period can be compared with the diet of only a few populations in Europe. A little smaller sample of food than in this study was collected in Schleswig-Holstein (BOCK 1978). Relatively well known is the diet of different populations in the Netherlands (SCHIPPER 1973), though samples were small. The other data were based on samples sometimes not exceeding 200 prey items (Finland — HILDEN & KALINAINEN 1966; southern France — THIOLLAY 1970, SCHIPPER 1973; northern France — SCHIPPER 1973; Britain — HOSKING 1943).

On the basis of the above publications, two types of marsh harrier diet can be distinguished. One type mostly consisted of small animals such as *Passeriformes* and *Micromammalia*, and the other comprised young *Lagomorpha* and *Phasianidae* (see pp. 286 and 294).

Marsh harriers have a wide food spectrum. This means that they can hunt big and small animals, more or less mobile. The differences in the diet mentioned

above did not result from their preferences or specialization. Marsh harriers took least costly prey under given conditions. If a rabbit and a mouse could be taken at the same cost in terms of energy, they took the rabbit. The diet of the first kind, dominated by small animals, seems to be more primitive and natural. High densities of pheasants and rabbits are typical of man-managed areas. Nonetheless, the breeding success of marsh harriers was relatively high in such areas, and seemed to be limited by factors other than hunger. These areas were also suitable for the formation of polygynous bonds, as two or more females paired with one male had a higher breeding success than monogamous females (SCHIPPER 1979, UNDERHILL-DAY 1984).

It is known from the literature that females take bigger prey, on the average, than males do (GLUTZ *et al.* 1971, SCHIPPER 1973). PINOWSKI & RYSZKOWSKI (1961), who observed hunting marsh harriers, noted that the hunting areas of males and females were separate. Except for the Barycz valley, so far there is no information on differences in the species composition of the prey, indicating that the food niches of the male and female differ in the breeding period (Tabs 42, 43 and 44). In my opinion this phenomenon should not be limited to the Barycz valley, though differences in the scale can be expected. Lack of similar records may be a consequence of the methods used that do not permit separating the prey brought by the male from that brought by the female.

Such an acute partitioning of the niches in the Barycz valley could have been a result of high densities of marsh harriers nesting on the ponds. Territorial behaviour of males made it difficult to hunt on the ponds because of a permanent threat of conflicts with neighbouring males. Females were not so much affected by territorial behaviour during rearing the young.

In the literature there are no records of eggs in the diet of marsh harriers, or eggs of other species are thought to represent a very low percentage of the diet. This is a methodical artifact, as the diet is analyzed mainly from food remains. Eggs are brought to the nest only occasionally (KATE 1930). In pellets there are no remains of shells. The true proportion of eggs of different birds in the diet of marsh harriers can best be inferred from the losses of eggs in nests of the most common species sharing the ponds with marsh harriers. In 1980–82, a study of the coot was carried out on one of the biggest ponds in the Stawno complex, where five pairs of marsh harriers nested, on the average. Of 692 clutches of the coot, 301 were destroyed by predators, and at least 18% of these losses were due to marsh harriers (JANKOWSKI 1983 and pers. comm.) Marsh harriers accounted for heavy losses of eggs in *Charadriiformes* and *Anatidae* in the area of the Biebrza marshes, where in some places the prey developed an effective anti-predator behaviour (DYRCZ *et al.* 1981). Marsh harriers can even risk the loss of their lives when robbing nests of coots, as a result of group attack by coots (WITKOWSKI 1961).

Although the methods applied do not allow us to determine the proportion of eggs in the diet of marsh harriers, it should be emphasized that eggs are one of the most important component of the diet in April and early May, when other prey are not readily available in the Barycz valley.

## SUMMARY

1. Based on the literature data and on the author's own observations, an attempt was made to determine changes in the marsh harrier population since the end of 19th century. The results are as follows: from the end of the 19th century to 1925 the population comprised 15–20 pairs, between 1945 and 1950–25 pairs, then 13–15 pairs in 1958–65, 31.5 pairs on the average, in 1972–75, and 44 pairs in 1982–84.

2. The duration of different phases of the breeding cycle until migration was determined (Fig. 3). The mean duration of the breeding cycle (from initiation of laying to the complete disappearance of parental care) was 125 days. It was noted that marsh harriers left their breeding grounds very early in the season, and this was related to rapidly deteriorating food conditions.

3. The density of breeding pairs in the year of highest numbers was 1 pair/26.5 ha of the pond area. Such a high density was possible because the complex of ponds was surrounded by suitable hunting areas, providing sufficient amounts of food taken by male for the female rearing the young and for the young until the age of 10–15 days, and because the ponds abounded in food, though only over a relatively short period of rearing the young. A mean home range covered 160 ha. Location of nests only on the ponds with water and at the reed-open water interface was an anti-predator adaptation.

4. Using the present results and the literature data, a hypothesis explaining the formation of polygynous bonds by unbalanced sex ratio was criticized. A hypothesis of the quality of the male and the territory is proposed.

5. The initiation of laying and the rate of laying were correlated with high daily temperatures. The birds were potentially able to lay about 10 April; the median laying date was 27 April. Cases of laying after 15 May were rare, as the chances of rearing the young under the local food conditions were small.

6. Mean clutch size was 5.0 eggs, and it did not differ from the mean values in most European populations. It was a little higher in the first study period, when DDT was applied. This might have been a response to marked losses from egg breakage in this period. The mean clutch size declined as the season progressed (from 5.6 to 4.4 eggs). Replacement clutches were lower by 0.66 eggs than normal clutches.

7. There were differences in egg size within and between clutches. No significant differences were found in productivity between clutches containing big eggs and those containing small eggs. Some evidence exists that the relative weight of an egg in the clutch determined the sex of the young hatched from that egg.

8. The duration of incubation was determined for 143 eggs. It was 33 days for 69% of the eggs, and the range of variation for the other eggs was 30–36 days.

9. In the breeding season, adult birds were active for 16–17 hours. The period of most intense hunting was between 6:00 and 18:00 h. When the young were small and required less food, hunting activity declined during mid-day hours (Fig. 6 – A). Each parent caught 9 prey, on the average, during the day. The



timing of different activities in the young from hatching to fledging is shown in Table 14.

10. The highest increase in the length of flight feathers occurred between days 21 and 27 of age, and averaged 10 mm/24 h. The highest percentage increase in body weight was recorded at ages of 4 and 5 days (28 and 24<sup>0</sup>/<sub>0</sub>, respectively). The body weight of nestlings more than 25 days old practically did not increase. At this age, food was used for the development of feathers and the increasing activity of the young. The males weighed less than females. At the time of the initiation of flight, the mean weight of the males represented 75<sup>0</sup>/<sub>0</sub> of the weight of the females. Nevertheless, the daily food intake was almost the same in males and females. The males were feathered earlier and started flight earlier than the females. The daily food intake in the period of the highest requirements (between 25 and 35 days of age) was about 160 g/nestling.

11. Sex ratio in the period of the initiation of flight was 54.2<sup>0</sup>/<sub>0</sub> in favour of the males.

12. The young were dependent on the parents for food until the age of 85–90 days. They could catch little mobile prey already when 54 days old.

13. Two categories of losses were considered: natural losses (predation, desertion, etc.) and losses from DDT contamination (egg breakage, reduced hatchability). The results for the two study periods are compared. In the first period, DDT was applied, and in the second period, DDT had not been used for 7 years already. DDT accounted for egg breakage, and differences in losses between the two periods were highly significant. Losses due to predators were higher in the second period. Nonetheless, the population was increasing.

14. It is suggested that the decline of the population in the 1960s resulted from the lack of reproduction in a part of the population, and from an increased mortality caused by DDT. Moreover, marsh harriers were still persecuted by hunters in Poland.

15. Mortality of the young (24.7<sup>0</sup>/<sub>0</sub>) was highest in the first days of life. These losses were partly due to adverse weather conditions (rains, low temperatures), and also to a poor condition of some of the young hatched. Mortality from conflicts among siblings was very low.

16. Early clutches produced more fledglings than later clutches. Potential production was best realized in nests containing 4 or 5 eggs. In the two study periods, 3.1 fledglings were produced per successful pair. In the first study period, potential production (number of eggs laid) was realized in 41.7<sup>0</sup>/<sub>0</sub>, and in the second period it was higher by 9<sup>0</sup>/<sub>0</sub>. Reduction of losses from pesticides and legal protection of marsh harriers in Poland accounted for a noticeable increase of the population in the 1980s.

17. Food samples (1355 prey items) confirmed that marsh harriers have a broad food spectrum also in the Barycz valley. Birds accounted for 60<sup>0</sup>/<sub>0</sub> of the diet and small mammals for 28<sup>0</sup>/<sub>0</sub>. A clear separation of food niches was



documented for males and females over the period of raising the young. Females hunted on ponds, and males mostly in crop fields and meadows.

18. The elimination of DDT and human persecution, combined with the adaptation of the species to man-induced changes in habitat conditions create good prospects for the development of the marsh harrier population over its entire range.

#### ACKNOWLEDGEMENTS

I am grateful to Andrzej DYRCZ and Maciej GROMADZKI for critical comments on the first draft of the paper. I thank Andrzej PIKULSKI and Ewald RANOSZEK for their assistance in the field work, Aleksy B. ŁUKOWSKI for determining insecticide concentrations in eggs and calculating the index of shell thickness, and Wanda ZDUNEK for making the drawings.

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## STRESZCZENIE

[Biologia i ekologia błotniaka stawowego *Circus aeruginosus* w okresie rozrodu w dolinie Baryczy]

Badania prowadzono na stawach rybnych koło Milicza w dwóch okresach – w latach 1972-75 i 1982-84. W pierwszym okresie w Polsce stosowano jeszcze DDT i odstrzelivano niektóre gatunki ptaków drapieżnych, w tym błotniaki stawowe. Podstawowym celem prowadzonych wtedy badań było wykrycie czynników odpowiedzialnych za spadek liczebności błotniaka, który rozpoczął się w latach pięćdziesiątych. Przypuszczalnym sprawcą było DDT i jego metabolity, których oddziaływanie powodowało 1) cieniienie skorupy jajowej i w efekcie rozgniatanie jaj przez wysiadujące samice, 2) zamieranie zarodków na skutek nieprawidłowej wymiany gazowej przez cienką skorupę oraz na skutek licznych wad rozwojowych zarodków, spowodowanych zatruciem, 3) skrócenie długości życia osobników dorosłych i w efekcie mniejszą liczbę cykli reprodukcyjnych odbywanych przez samice w ciągu jej życia. W podjętych badaniach szczególną uwagę zwrócono na dwa pierwsze skutki oddziaływania DDT.

Badania powtórzono w latach 1982-84, tj. 7 lat po zaniechaniu stosowania DDT w Polsce i po objęciu wszystkich ptaków drapieżnych ochroną gatunkową. W okresie tym szczególną uwagę zwrócono na rozmiar i charakter strat łęgowych oraz inne czynniki wpływające na sukces łęgowy.

W obu okresach badań liczbę par łęgowych ustalono we wszystkich kompleksach stawowych w dolinie Baryczy (tab. 3). Badania szczegółowe prowadzono w największym kompleksie – Stawno (ryc. 1). Dla tego kompleksu przedstawiono liczebność błotniaka od końca XIX w. do połowy lat osiemdziesiątych obecnego stulecia. Wyróżniono pięć okresów, w tym dwa okresy spadku liczebności (do II

Wojny Światowej oraz w okresie intensywnego stosowania DDT, tj. w latach 1950–70) oraz trzy okresy wzrostu (okres wojny, lata siedemdziesiąte – charakteryzujące się wolnym wzrostem liczebności oraz lata osiemdziesiąte – o wzroście przyspieszonym). W kompleksie Stawno gniazdowało w różnych okresach 16–50 par (tab. 1 i 2).

Łotniak stawowy jest w dolinie Baryczy gatunkiem wędrownym. Najwcześniejszy pojaw stwierdzono 13 marca. Przebieg powrotu łotniaków z zimowisk przedstawia ryc. 2. Łotniaki przebywały w dolinie przez ok. 5 miesięcy. Poszczególne fazy cyklu życiowego łotniaka i czas ich trwania pokazano na ryc. 3. Łotniaki bardzo wczesnie opuszczały dolinę, co było prawdopodobnie wynikiem gwałtownego zmniejszania się zasobów pokarmowych, począwszy od sierpnia.

Zagęszczenie par obliczono w dwóch wariantach: 1) w stosunku do całkowitej powierzchni wszystkich stawów kompleksu, 2) w stosunku do powierzchni tylko tych stawów, na których łotniaki gniazdowały. W latach sześćdziesiątych zagęszczenie wyniosło odpowiednio 1 p./100 ha i 1 p./83 ha, w okresie 1972–75 – 1p./55 ha i 1 p./42 ha, a w okresie 1982–84 – 1p./40 ha i 1p./30 ha. Największe zagęszczenie na jednym ze stawów (tab. 1, staw Now Świat Górny) wyniosło 1p./7,5 ha.

Przeciętna powierzchnia terytorium gniazdowego, przy najwyższym zagęszczeniu w roku 1984, wyniosła niespełna 27 ha, a cała przestrzeń życiowa łotniaka (terytorium gniazdowe + terytorium łowieckie) wyniosła 160 ha. Terytoria łowieckie samców obejmowały pola i łąki. Łotniaki nigdy nie zakładały gniazd poza stawem, ani na stawie nienapuszczonym (por. tab. 1, staw Golica). Nie stwierdzono preferencji w lokalizacji gniazda ani w stosunku do wysp trzcinowych ani przybrzeżnych pasów szuwaru. Natomiast w okresie 1982–84 łotniaki budowały gniazda bliżej lustra wody niż w latach 1972–75 (tab. 4), co było reakcją na sposób penetrowania zarośli trzcinowych przez ciągle wzrastające liczebnie dziki.

Wydaje się, że tańce powietrzne wykonywane przez samce są rodzajem zachowania terytorialnego, nie są zaś elementem toków.

Niespełna 4<sup>0</sup>/<sub>0</sub> samic wchodziło w związki bigamiczne. Związki takie były niekorzystne zarówno dla samic skojarzonych z samcem jako jego pierwsze małżonki, jak i samic będących żonami drugimi. Produkcja młodych u tych pierwszych wyniosła 1,9, a u tych drugich – 1,4 młodego lotnego. U samic monogamicznych wyniosła ona 2,3 młodego. W okresie wysiadywania jaj i na początku okresu wychowu młodych samice bigamiczne ponosiły znacznie większe straty niż samice monogamiczne. Nie karmione dostatecznie przez samce musiały polować same, co zwiększało zarówno liczbę zaziębionych jaj, jak i śmiertelność młodych w pierwszych dniach życia. Rozważono dwie hipotezy wyjaśniające powstawanie poligynii u łotniaków – hipotezę niezrównoważonego stosunku płci oraz hipotezę jakości samca i terytorium. Na podstawie danych własnych i danych z piśmiennictwa (tab. 45) przyjęto hipotezę jakości samca i terytorium, która także wielokrotnie sprawdziła się w przypadku ptaków wróblowatych.

Gniazdo budowały samiec i samica. Po wykluciu młodych było ono często

strojone zielonymi gałązkami. Skrytykowano pogląd jakoby zachowanie takie miało sygnalizować zajęcie terytorium podczas chwilowej nieobecności właściciela. Rozbudowywanie gniazda w miarę dorastania młodych wynika nie tylko z potrzeby wzmocnienia jego konstrukcji wobec coraz aktywniejszych i cięższych piskląt, ale także z potrzeby zwiększenia przestrzeni życiowej piskląt, co osłabia ich wzajemną agresywność.

Przebieg rozpoczynania niesienia jaj w poszczególnych latach przedstawiono na rycinie 4. Samice zaczynały się nieść, gdy po osiągnięciu przez nie gotowości do niesienia średnia dobowa temperatura podnosiła się powyżej  $4^{\circ}\text{C}$  i utrzymywała się na tym poziomie przez kilka dni. Samice nie rozpoczynały się nieść przed 8 kwietnia (ryc. 5). Połowa samic badanej populacji rozpoczynała znoszenie jaj do 27 kwietnia (tab. 5). 94% jaj było składanych co drugi dzień (tab. 6). Zniesienia zawierały 2–8, średnio 5,0 jaj (tab. 7). W okresie 1972–75 średnie zniesienie było większe o 0,3 jaja od zniesienia w okresie 1982–84, co wynikało z braku w tym ostatnim okresie zniesień zawierających więcej niż 6 jaj. Średnia wielkość zniesienia wykazywała wyraźną zależność od terminu rozpoczynania znoszenia jaj w danym roku (tab. 5). Na początku sezonu średnie zniesienie było największe (5,6 jaja) i malało do 4,4 jaja w miarę jego upływu (tab. 8). Parametry jaj badanej populacji zestawiono w tabeli 9. Przeciętna różnica pomiędzy jajem najmniejszym i największym w tym samym zniesieniu wyniosła 9,4% masy jaja największego, zaś różnica największa 24%. Z jaj cięższych wykluwały się pisklęta cięższe i na odwrót, ale zależność ta nie była proporcjonalna – z jaj o mniejszej masie wykluwały się pisklęta proporcjonalnie cięższe niż z jaj o masie większej (tab. 10). Nie stwierdzono istotnych różnic ani w liczbie wyprodukowanych młodych, ani w ich śmiertelności (przynajmniej do wylotu z gniazda) pomiędzy zniesieniami składającymi się z jaj o masie małej, a zniesieniami składającymi się z jaj o masie dużej (tab. 11). W przeważającej liczbie przypadków jaja złożone jako pierwsze i jako ostatnie w zniesieniu były mniejsze od pozostałych. Zestaw stwierdzonych sekwencji znoszenia jaj przedstawiono w tabeli 12.

Pisklęta wykluwały się asynchronicznie, a czas wykluwania się całego lęgu zależny był od jego wielkości. Dla przeciętnego lęgu złożonego z 5 jaj średni czas wykluwania się piskląt wyniósł blisko 8 dni (tab. 13). Wysiadywanie jaj trwało 30–36 dni; 69% jaj wysiadywanych było przez 33 dni.

Aktywność młodych zależała od ich wieku. Różne rodzaje aktywności młodych i czas ich trwania u piskląt w różnym wieku zestawiono w tabeli 14.

Pisklęta zjadały w ciągu doby porcję pokarmu o masie wynoszącej  $1/4$ – $1/3$  masy ich ciała. W pierwszych 20 dniach życia porcja ta obracana była głównie na rozwój masy ciała piskląt, a później na rozwój upierzenia i wzrost aktywności młodych (tab. 17). Świeżo wyklułe pisklęta ważyły 22–32 g. Ich dzienne przyrosty, od wyklucia do wylotu z gniazda, z uwzględnieniem płci, zestawiono w tabeli 15. Pod koniec okresu gniazdowego samice były cięższe od samców przeciętnie o 190 g (masa samca osiągała 75% masy samicy). Samice nie pobierały więcej pokarmu niż samce, lecz rozwój ich był wolniejszy, a aktywność niższa w porównaniu z



samcami. Na rycinie 9 przedstawiono średni dobowy przyrost masy ciała młodych samców i samic błotniaków. Od 25 dnia życia masa ciała piskląt stawała się dobrym kryterium przy oznaczaniu płci. Rycina 10 ilustruje indywidualny dobowy przyrost masy ciała dwóch samców stanowiących pełny lęg.

Samce zaczynały latać w wieku 37–39 dni (ryc. 8), a samice pomiędzy 41–44 dniem życia. Źle karmione młode zaczynały latać później, nieraz dopiero po ukończeniu 50 dnia życia. Po 3–5 dniach od rozpoczęcia latania młode podlatywały ku zbliżającym się z pokarmem rodzicom, którzy jednakże odnosili jeszcze zdobycz do gniazda. Dopiero po dalszych 3 dniach następowało oddawanie ofiary w powietrzu, nie zawsze kończące się powodzeniem (ryc. 8). W wieku około 55 dni młode samce potrafiły samodzielnie upolować małą ruchliwą zdobycz; np. żabę. Młode były dokarmiane przez oboje lub przynajmniej przez jedno z rodziców do 80–90 dnia życia.

Aktywność łowiecką samca i samicy w okresie gniazdowym, mierzoną liczbą ofiar przyniesionych do gniazda w różnych porach dnia przedstawiono na rycinie 6. Samiec w ciągu całego dnia (16 godzin) potrafił złowić 20 ofiar, przeciętnie 12. Samica, gdy już nie musiała opiekować się potomstwem, łowiła przeciętnie 9,5 ofiary, które jednakże były większe od ofiar samców. Samce przynosiły tyle ofiar ile zdołały złowić, niezależnie od wielkości lęgu. Po włączeniu się samicy do zdobywania pokarmu niektóre samce zaprzestawały niemal zupełnie dostarczania zdobyczy do gniazda (ryc. 7).

Proporcje płci ustalono w 82 lęgach (tab. 18). W czterech z pięciu kategorii lęgów w przewadze były samce. Łącznie stosunek płci wynosił 54<sup>0</sup>/<sub>0</sub>, z korzyścią dla samców. Przeważały lęgi o mieszanym składzie płci (tab. 19), ale lęgi złożone z osobników jednej płci stanowiły 26<sup>0</sup>/<sub>0</sub>.

W zniesieniach złożonych z 5 jaj ujawnił się trend, w którym od pierwszego do czwartego jaja wzrastała liczba wyklutych samców, a malała liczba samic (tab. 20). Z jaj relatywnie cięższych wykluwały się na ogół samce, a z jaj lżejszych samice (tab. 21).

Straty oceniano osobno dla obu okresów badań. Wielkość strat poniesionych w wyniku kompletnej utraty lęgów zestawiono w tabeli 22, a ich przyczyny w tabeli 23. Podstawowe różnice pomiędzy okresem 1972–75, a 1982–84 polegały na tym, że w okresie pierwszym przeważały straty z powodu rozgniecenia jaj lub nie wykluca się piskląt, a w okresie drugim straty spowodowane przez drapieżniki (tab. 23), głównie przez dziki. Straty w lęgach nie udanych, w przeliczeniu na liczbę jaj i młodych, przedstawiono w tabeli 24. W okresie 1972–75 w gniazdach udanych dominowały straty z powodu rozgniecenia pojedynczych jaj. Równorzędną grupę stanowiły jaja niewyklute. Straty z tego powodu były także wysokie w okresie 1982–84, czego nie oczekiwano, w związku z zaprzestaniem stosowania DDT – prawdopodobnie w okresie tym na błotniaki oddziaływały inne trucizny. W gniazdach, w których wykluły się młode, straty w obu okresach były jednakowe. W konkluzji można stwierdzić, że podstawową cechą różniącą oba okresy badań była kategoria strat spowodowana rozgnieceniem jaj (tab. 26).



W okresie 1972–75 straty były największe na początku sezonu (tab. 27), co było znowu skutkiem oddziaływania DDT. Samice starsze, doświadczone, rozpoczynające wcześniej znoszenie jaj, były najsilniej zatrute kumulującym się w ich organizmach preparatem i one ponosiły największe straty z powodu rozgniatania i niewykluwalności jaj. W okresie 1982–84 rozkład strat był inny, a największe straty miały miejsce pod koniec sezonu (tab. 27). Straty całkowite w okresie 1972–75 również były wyższe w pierwszej połowie sezonu niż w drugiej, natomiast w okresie następnym było odwrotnie (tab. 28).

Zawartość DDT i jego metabolitów oraz Lindanu w jajach w okresie 1972–75 przedstawiono w tabeli 29. Przeciętna zawartość DDT w jajach błotniaków z doliny Baryczy można porównać do jego zawartości w jajach ptaków drapieżnych ptakożernych, u których dochodziło do największej kumulacji tego preparatu. Indeks grubości skorupy poddanych analizie jaj był o 23% niższy od jaj europejskich błotniaków przed stosowaniem DDT.

Stwierdzono istotną zależność wysokości strat od lokalizacji gniazda (tab. 30). W gniazdach założonych na wyspach trzcinowych straty były mniejsze niż w gniazdach założonych w przybrzeżnym pasie trzcin. Natomiast produkcja młodych w lęgach udanych była wyższa w gniazdach w przybrzeżnym pasie trzcin niż w gniazdach na wyspach (tab. 30).

Ciągłe opady deszczu zwiększały wysokość strat (tab. 31). Występowała wtedy większa śmiertelność młodych (z powodu chłodu i braku pokarmu) oraz więcej jaj było rozgniatanych przez samice, niecierpliwie wysiadujące podczas deszczu.

W obu okresach podobne były łączne straty spowodowane drapieżnictwem i porzucaniem gniazd (tab. 32). Typową kategorią strat dla okresu 1972–75 było rozgniatanie jaj, a dla okresu 1982–84 zatapianie gniazd, spowodowane tendencją błotniaków do budowania gniazd jak najbliższej lustra wody. Straty ogólne w odniesieniu do produkcji potencjalnej przedstawiono w tabeli 33.

Śmiertelność młodych (tab. 34) była najwyższa do 5 dnia życia. Od 25 dnia życia przypadki śmierci należały do wyjątkowych. Śmiertelność piskląt w okresie gniazdowym wyniosła 24,7%.

Ze zniesień rozpoczętych wcześniej wykluwało się więcej młodych i więcej ich wylatywało z gniazda niż ze zniesień późniejszych (tab. 35). Trend ten był jednakowy w obu okresach badań, pomimo różnego w obu okresach rozkładu strat.

Najefektywniejsze były zniesienia zawierające 4–6, a szczególnie 4 i 5 jaj (tab. 36). Z 80% tych ostatnich zniesień wyleciały młode. Produkcja potencjalna najlepiej (ponad 50%) realizowana była w gniazdach z 4 i 5 jajami (tab. 37). Produktywność zniesień złożonych z 6 jaj była niska (32,6%) w okresie 1972–75, a stosunkowo wysoka (50%) w okresie 1982–84. Różnice te znowu prawdopodobnie spowodowało DDT (starsze, znoszące więcej jaj samice były bardziej zatrute od samic młodszych, niosących mniej jaj). Produkcja potencjalna w lęgach udanych była realizowana tym lepiej im mniejsze było zniesienie (tab. 38). W lęgach zakończonych sukcesem (patrz tab. 25) 80% wykłutych młodych dożyło do wylotu

z gniazda. Najlepiej przeżywały młode wykłute jako pierwsze w lęgu, a z piskląt wykłutych jako szóste nie przeżyło żadne (tab. 39). Nie stwierdzono różnic w przeżywalności młodych w zależności od terminu rozpoczynania lęgu w sezonie (tab. 40), a zatem różnice w produktywności zniesień wcześniejszych i późniejszych powstawały wskutek strat innych niż śmiertelność młodych.

Przywiązanie ptaków dorosłych do miejsc gniazdowania jest prawdopodobnie znaczne, co stwierdzono na kilku indywidualnie rozpoznawalnych osobnikach, które z roku na rok gniazdowały w tych samych terytoriach. Natomiast ptaki młode odznaczały się niską filopatrycznością, gdyż zaledwie ok. 5<sup>0</sup>/<sub>0</sub> zaobrazkowych lotnych młodych gniazdowało w okolicy wyklućcia.

Pokarm badanej populacji błotniaków był zróżnicowany. 60<sup>0</sup>/<sub>0</sub> pokarmu stanowiły ptaki, 28<sup>0</sup>/<sub>0</sub> ssaki, 10<sup>0</sup>/<sub>0</sub> śnięte ryby i 2<sup>0</sup>/<sub>0</sub> żaby. Wśród ptaków 55<sup>0</sup>/<sub>0</sub> stanowiły *Passeriformes*, a w grupie ssaków dominowały (82<sup>0</sup>/<sub>0</sub>) gryzonie (tab. 41). Ofiary samców w przewadze pochodziły z siedlisk lądowych (tab. 42), natomiast ofiary samic głównie z siedlisk wodnych (tab. 43). Różnice siedliskowe w pochodzeniu ofiar samic i samców (tab. 44) były wysoce istotne, co upoważnia do stwierdzenia, że u badanej populacji wystąpił podział nisz pokarmowych. Samce łowiły przeważnie na polach i łąkach, a samice na stawach. Ofiary samic były przeciętnie dwukrotnie większe od ofiar samców (tab. 42 i 43).

Przypuszczalny mechanizm spadku liczebności błotniaków w dolinie Baryczy w latach 1950–70 był następujący. Część samic, zwłaszcza starszych, a więc bardziej doświadczonych, skumulowała w swoich organizmach znacznie więcej DDT niż samice młode i nie była już zdolna do rozrodu. Wszystkie zniesione przez te samice jaja ulegały bądź zgnieceniu podczas wysiadywania, bądź nie wykluwały się z nich młode, gdyż zarodki uległy zatruciu. To, jak również przyspieszona skutkami zatrucia śmiertelność ptaków dorosłych, powodująca zmniejszenie liczby cykli reprodukcyjnych, odpowiedzialne było najprawdopodobniej za spadek liczebności.