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Breeding ecology of great reed warbler *Acrocephalus arundinaceus* and reed warbler *Acrocephalus scirpaceus* at fish-ponds in SW Poland and lakes in NW Switzerland

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On oligotrophic lakes (OL) the microhabitats of two studied species were spatially more separated than on eutrophic fish-ponds (EFP), while the prey size and its composition differed more on EFP than OL (former study). The larger body size of great reed warbler in comparison to reed warbler influenced nest site, breeding losses, clutchsize and polygamous tendency. Nestlings' starvation was found more often in great reed warbler and on EFP only. Populations of the same species from two regions of study did not differ regarding timing of breeding season, nest' situation and brood losses (except in 1966 when great reed warbler brood losses amounted only to 8%); slight differences were found in clutch-size and number of pairs which started with second brood.

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Экология гнездового периода дроздовидной камышевки *Acrocephalus arundinaceus* и тростниковой камышевки *Acrocephalus scirpaceus* на рыбных прудах ЮВ Польши и озерах СВ Швейцарии.

Экологические ниши двух исследуемых видов были более изолированы простарнственно на олиготрофических озерах (OJ), чем на рыбных прудах (ESR) в то время, как величина и видовой состав кормовых объектов больше отличается у исселдованных видов на ESR, чем на OJ (результаты предыдущих исследований). Дискутируются экологические последствия бо́льшего размера тела дроздовидной камышевки по сравнению с тростниковой камышевкой. Эти различия влияли на положение гнезда, потери в выводках, величину кладки и частоту встречаемости полигамии. Гибель птенцов от голода чаще имела место у дроздовидной камышевки и только на ESR. Популиции одного и того же вида не отличались с разных районов исследований временем гнездования, положением гнезд и потерями в выводках (за исключением 1966 г., когда потери в выводках дроздовидной камышевки составили только 8%). Имелись незначительные различия в величине кладки и пропорции гнездовых пар, приступающих ко второй кладке.

INTRODUCTION

The populations of great reed warbler and reed warbler were studied during five breeding seasons (1970–1974) at the Milicz fish-ponds, Wrocław Voivodship, Poland and during two breeding seasons (1975–1976) on Lac de Neuchatel, Bielersee and Murtensee in North-West Switzerland. These two closely related, similar species inhabit nearly the same habitat, but they differ strongly in size. I investigated how this size differences might influence differences in breeding ecology between the species in the localities of sympatry. I studied both species in two widely-separated areas to find the intraspecific differences in breeding ecology between populations from different geographical localities. So far, in its biology and ecology, the reed warbler has been studied (Brown and Davies 1949, Impekoven 1962, Havlin 1971, Catchpole 1972, 1973 and 1974, Davies and Green 1976) little more than great reed warbler (Kluijver 1955, Haneda and Teranishi 1968a and b, Havlin 1971, Saitou 1976a and b), but many aspects of breeding ecology of both species need further study. The results of my observations on nestlings' growth, food and polygamy in the great reed warbler were published separately (Dyrcz 1974, 1977 and 1979).

STUDY LOCALITIES AND METHODS

Milicz fish-ponds. The study was carried on the group of ponds, located 5 km from Milicz (altitude 104 m). Some ponds were several hundred years old. The size of ponds ranged from 40 to 180 ha. The water depth was mostly 50–150 cm. The vegetation and animal life was rich. In some ponds, which were protected as wildfowl breeding grounds, extensive reed-beds were tolerated. Besides *Phragmites communis*, the emergent vegetation comprised patches of *Typha* sp., *Scirpus lacustris*, *Acorus calamus* and *Glyceria aquatica*. The dikes surrounding the ponds were vegetated with old trees (mainly oaks) and bushes (mainly willows). For intense research I chose a pond called "Słoneczny" (180 ha), around which the emergent vegetation covered 15.9 ha. At the south edge, the reed-beds formed a strip 1 km long and 40–160 m broad, and in the middle of the pond were several reed islets. Reed also formed narrow belts along the remaining dikes.

Swiss lakes. The main areas for great reed warbler in 1976 included: south-eastern shores of Lac de Neuchatel (nature reserves Fanel, Witzwil and Cudrefin) and fragments of its southern shores (Champittet near Yverdon and neighbourhood of Chevroux), StPetersinselweg on Bielersee and the eastern shore of Murtensee. The study area for reed warbler comprised only Fanel and Witzwil Reserves. Along the above mentioned lake shores, extensive reedbeds grew, in some localities reaching 200 m in breadth but mostly only 30–50 m. In contrast to the Milicz fish-ponds, a large proportion of reed-beds stood on dry grounds.

The total area of reed-beds on the study plots amounted to about 50 ha. Other emergent vegetation included *Typha* sp. and small areas of *Scirpus* sp.. The depth of water at the outer edges of reed-beds rarely exceeded 1 m. Except for parts of the shores, the vast area of the lakes showed an oligotrophic character. The lakes were situated at the altitude 429 m at the foot of Jura hills.

The study was done each year from mid-May to the end of July or to mid-August. The basic routine included attempt to find all nests on study areas and

Table 1. Breeding density of great reed warbler and reed warbler on Słoneczny fish-pond (n = total no. of nests or breeding pairs; d = no. of nests or breeding pairs per 10 ha)

	Size of studied area in ha	Year											
		1970		1971		1972		1973		1974		$\bar{x}$	
		n	d	n	d	n	d	n	d	n	d	n	d
Great reed warbler, no. of first broods	15.9	23	14.5	26	16.4	25	15.9	49	30.8	37	23.3	32	20.1
Reed warbler, no. of breeding pairs	1.85	23	124.0	24	130.0	40	216.0	–	–	–	–	29	156.8

Note: – = no observations

Table 2. Breeding density of great reed warbler (GRW) and reed warbler (RW) in Switzerland

Locality	Year	Species	No. of first brood nests	Area of reed-beds in ha	No. of nests per 10 ha
Fanel Reserve, Lac de Neuchatel	1975	GRW	8	ca 5.5	14.5
	1976	GRW	10	5.5	18.2
Witzwil Reserve, Lac de Neuchatel	1975	GRW	4	8.0	5.0
	1975	RW	37	11.2	33.0
Cudrefin Reserve, Lac de Neuchatel	1975	GRW	4	7.0	5.7
	1976	GRW	3	7.0	4.3
StPetersinselweg, Bielersee	1975	GRW	8	14.5	5.5
	1976	GRW	8	14.5	5.5
Champittet, Lac de Neuchatel	1976	GRW	16	ca 7.0	22.9
Total/average	1975+1976	GRW	61	69.0	8.8

Note: RW sample area comprised also reed-beds on dry ground.

follow their fate. The study area for great reed warbler in Milicz comprised Słoneczny pond and in some years also neighbouring ponds. I looked for the nests in the territories of singing males. For reed warbler the study area in 1970 comprised the whole Słoneczny pond, in 1971–1973 only its southern part, and in 1975 the Fanel and Witzwil Reserves. In 1974 and 1976 no observations of this species were made. As the breeding density of reed warbler in some localities was very high, the only possible method to try to find all the nests was searching through the reed-beds spot by spot. For both species the study area was searched several times during the breeding season to find the late nests. Together 444 nests of great reed warbler and 704 nests of reed warbler were found and checked. As polygyny is frequent in great reed warbler (Dyrcz 1977), I shall avoid the term "breeding pairs" (Table 1 and 2) and express density as the number of first brood nests per 10 ha of reed-beds. In both studied species the number of breeding birds was determined on the basis of nests found.

T — test has been used for analysis of the significance of differences.

BREEDING DENSITY

Great reed warbler. At Milicz during the first three years density was stable, and then in 1973 it doubled (Table 1). The reason might be local, for in April 1973 one of the nearly ponds was suddenly dried and the males which had started to sing there, soon left. Perhaps these birds accounted for the increase on Słoneczny. In the study area in Switzerland the local breeding densities differed greatly one from another (Table 2), perhaps because of food and foraging conditions differences between localities. In Witzwil, Cudrefin and StPetersinselweg Reserves low densities occured. In the last two localities, the breeding places were far from larger tree stands, which usually comprise important foraging grounds for great reed warblers (Dyrcz 1977). Breeding density was also low at the east shore of the Murtensee (not included to Table 2 as I have no exact data about reed-beds acreage there) in spite of luxuriant, deciduous wood bordering the reeds. But the reed stems there were too dispersed and too weak, to support the nests. Densities at Champittet were close to the highest values found on the very rich, eutrophic fish-ponds at Milicz. This part of Lac de Neuchatel represents a small bay which is separated from the open lake by narrow sand bar. The middle of the bay is not vegetated with reeds because of the rocky bottom, but elsewhere reed stems are large and make dense clumps good for great reed warbler nesting. Dense bushes and various trees were at hand. So probably both factors — food resources and reeds — were optimal there.

Reed warbler. It showed strong local differences in breeding density connected with the size of reed-bed area (Fig. 1). Also the density in this same place in different years can be very different (Table 1).

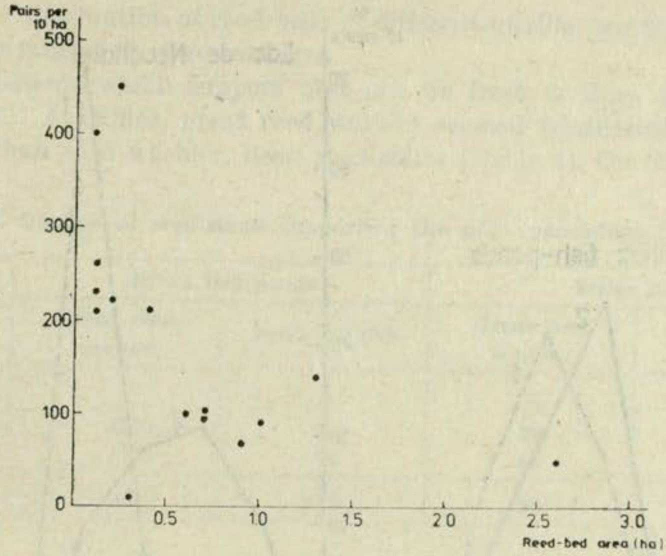


Fig. 1. Breeding density of reed warbler in relation to the size of reed-bed area.

BREEDING HABITAT

The main difference in breeding microhabitat between species, on lakes, was that the great reed warbler bred more often at the edges of reeds bordered with open lake, where the thick reed-stems usually predominated, and the reed warbler bred nearer the shore, not infrequently over dry ground (Table 3, Fig. 2 and 3). At Milicz it was not possible to show such clear microhabitat differences, but again in thin and dense reeds the reed warbler strongly predominated. In thick reeds, I more often found great reed warbler than reed warbler nests.

Table 3. Percent of nests situated in different habitats in Witzwil Reserve — Lac de Neuchatel (no. of nests in parentheses)

	Thick reeds standing in water	Isolated clumps of thick reeds standing in water	Thin, not dense reeds, standing in water	Thin, dense reed, standing in water	"Jungle" of reed-stems (fresh and dead) standing on bare ground	Clumps of reeds with admixture of *Carex* sp., soaked ground	"Jungle" of dead reed-stems
Great reed warbler	89 (31)	6 (2)	3 (1)	3 (1)	—	—	—
Reed warbler	6 (5)	—	—	51 (45)	25 (22)	16 (14)	2 (2)

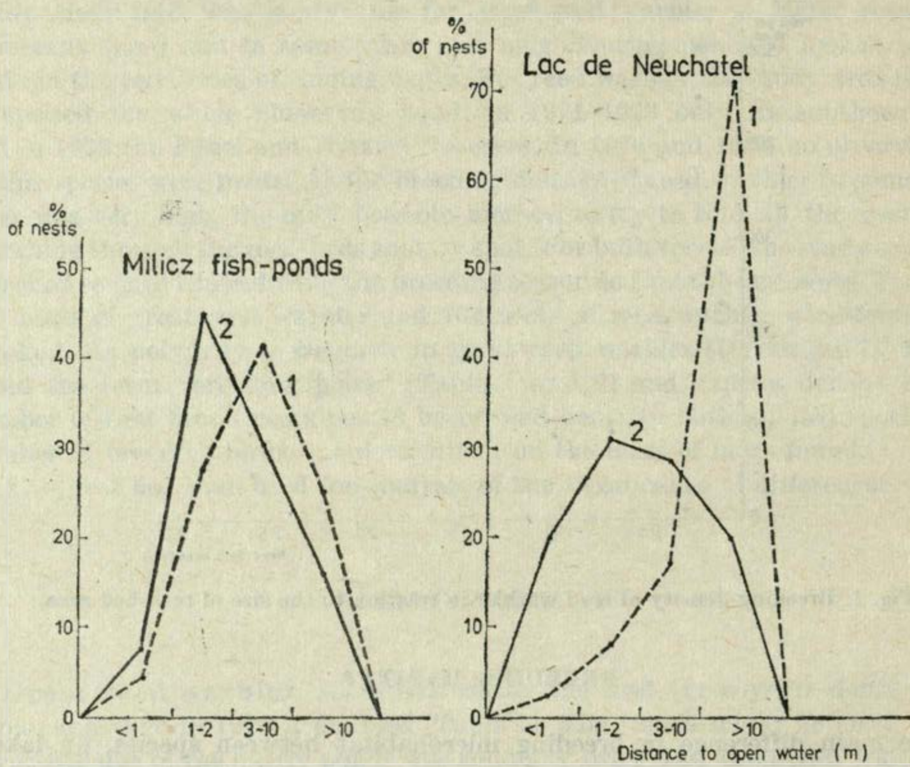


Fig. 2. Spatial distribution of nests in relation to the distance from open water 1 — reed warbler, 2 — great reed warbler.

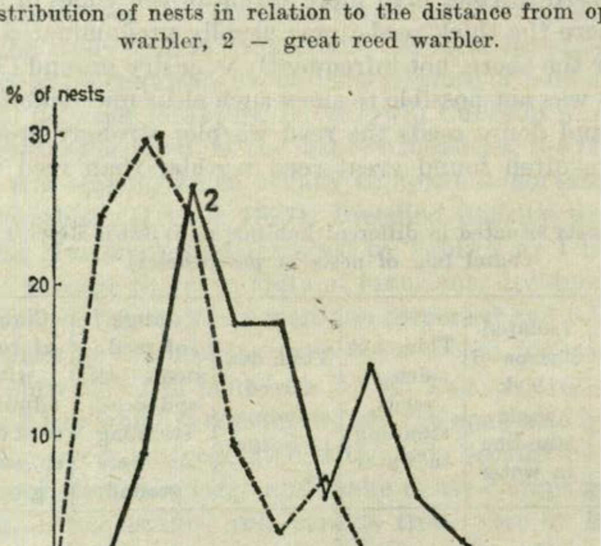


Fig. 3. Spatial distribution of nests in relation to water depth under the nest 1 — reed warbler, 2 — great reed warbler.

At Milicz the distribution of reed-beds of different quality was in a mosaic, and the same was true of the two warblers.

The reed-stems which support nest can be fresh or dead (from previous years growth). At Milicz, great reed warbler seemed (statistically NS) to use more often than reed warbler, dead reed-stems (Table 4). On the Swiss lakes,

Table 4. Quality of reed-stems supporting the nest (percentage frequency)

	Milicz fish-ponds		Swiss lakes	
	Great reed warbler	Reed warbler	Great reed warbler	Reed warbler
Dead	6	7	3	16
Dead + fresh	66	53	50	56
Fresh	27	39	46	27
No. of nests	125	247	95	73

however, the situation was reversed, with reed warbler more often in dead reed-stems ($P < 0.001$). This was because in Witzwil Reserve, when the main study was done, the reed warbler nested more in "inland" reed-beds, where the destruction of old reed-stems by waves did not occur. Also in the dense "jungle" of dead stems, only scarce new shots of reeds can find their way up. On the other hand, in Milicz fish-ponds the dead reed-stems are much more scarce, owing to more or less regular mowing off.

Regarding the selection of plant species for nesting (Table 5) both species showed a high predilection for reeds, a little less strong in the case of reed warbler in both study areas. Sometimes great reed warblers built nests under plant leaves – *ca* 6% of nests. But these nests experienced no less predation, so perhaps the roof offers protection against rain or sun. In Switzerland, in four nests the pieces of plastic were incorporated into nest construction.

Table 5. Percent of nests built on different kind of plants

Kind of plants	Milicz fish-ponds		Swiss Lakes	
	Great reed warbler	Reed warbler	Great reed warbler	Reed warbler
Phragmites communis	96	88	99	94
Typha sp.	3	7	—	—
Phragmites communis + *Typha* sp.	+	4	—	—
Salix sp.	+	1	—	1
Phragmites communis + *Solanum* sp.	1	—	1	3
Phragmites communis + *Salix* sp.	+	—	—	—
Phragmites communis + other plants	—	—	—	2

SPATIAL DISTRIBUTION OF NESTS

At Milicz the nests of both species had been built lower (Great reed warbler – $\bar{x} = 50.4$ cm, reed warbler – $\bar{x} = 66.9$ cm) than on Swiss lakes (Great reed warbler – 74.2 cm, reed warbler – 79.7 cm; $P < 0.001$; Table 6). It is unlikely

Table 6. Distribution of nest heights (%)

Species	Locality	Height (cm)															No. of nests
		10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	
Great reed warbler	Milicz fish-ponds (1970–1972)	1	6	16	20	20	15	12	6	4	1	–	–	–	–	–	138
	Swiss lakes (1975–1976)	–	–	2	11	11	14	19	15	12	11	3	–	2	–	–	93
Reed warbler	Milicz fish-ponds (1970–1972)	–	3	5	11	13	24	13	12	5	5	3	4	2	1	+	303
	Swiss lakes (1975)	–	–	1	5	12	9	13	22	14	7	9	5	–	3	–	77

Note: + – percent less than 1.

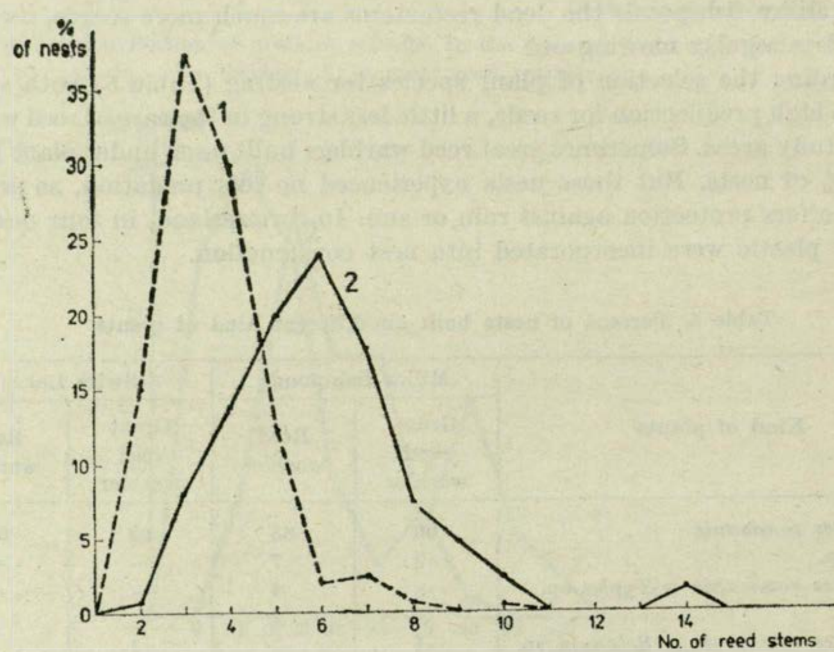


Fig. 4. Number of reed-stems which supported the nest 1 – reed warbler, $N = 247$, 2 – great reed warbler, $N = 125$.

that this was caused by any differences in reed-stem heights between study areas, and I suppose that the higher nesting on the lakes was caused by much stronger water level fluctuations. The nest of the great reed warbler was usually supported by a larger number of thicker reeds (Figs 4 and 5) that the reed warbler's nest.

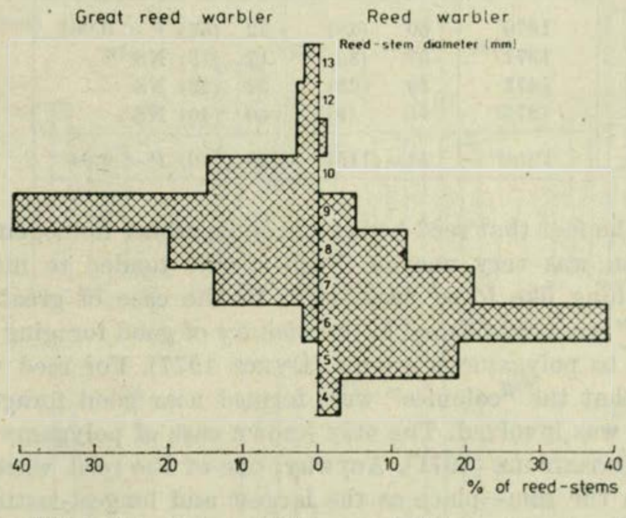


Fig. 5. Diameters of thickest reed-stem which supported the nest, great reed warbler $N = 59$, $\bar{x} = 8.9$ mm, reed warbler $N = 113$, $\bar{x} = 6.4$ mm, $P < 0.01$.

Seasonal variation in nest heights was found in all seasons for both species and in both study areas (Table 7). It is obvious that birds can breed higher, later in the breeding season when reed-stems have attained their full height. The studied birds took this opportunity probably because the losses from predation were lower among the nests situated higher, at least in the reed warbler (Table 8). Catchpole (1974) found similar seasonal variation of nesting heights in reed warbler.

Table 7. Average nest height (cm) in early and late spring

Year	Great reed warbler		Reed warbler	
	Early spring	Late spring	Early spring	Late spring
1970	49	59	61	93
1971	44	59	49	60
1972	35	58	61	69
1975	57	87	73	93
1976	69	77	—	—
Average	49	66	60	77
No. of nests	151	100	266	189

Table 8. Nest heights and percent of nests robbed by predator in reed warbler (no. of nests in parentheses)

Year	Nest height	
	up to 50 cm	80 cm and more
1970	60 (48)	32 (57) $P < 0.001$
1971	37 (35)	17 (18) NS
1972	39 (23)	32 (25) NS
1975	75 (9)	60 (40) NS
Total	51 (115)	39 (140) $P < 0.04$

In spite of the fact that reed-beds seem to be rather homogenous, horizontal nest distribution was very uneven. Both species tended to make clusters of nests — something like loose "colonies". In the case of great reed warbler, these "colonies" were established in the vicinity of good foraging sites and nests often belonged to polygamous groups (Dyrcz 1977). For reed warblers, I did not get proof that the "colonies" were formed near good foraging places, nor that polygamy was involved. The only known case of polygamy in this species was found by Catchpole (1971). Anyway, one of the reed warbler "colonies" was situated in the same place as the largest and longest-lasting "colony" of great reed warbler occured, bordering luxuriant bushes and trees suitable for foraging.

TIMING OF BREEDING

Great reed warbler. At Milicz the mean first-egg dates of the population differed little from year to year, the maximum difference being 6 days (Table 9). The earliest clutch started on 11 May 1973, the latest on 27 July 1972 (nestlings left the nest on 22 August). Most clutches started between 15 May and 18 June. On Swiss lakes, first-egg dates were similar. The start of breeding was connected

Table 9. Mean dates of the laying of the first egg

Locality	Year	Great reed warbler	Reed warbler	Difference in dates, in days
Milicz fish-ponds	1970	25 May	15 June	20
	1971	19 May	6 June	17
	1972	23 May	13 June	20
	1973	23 May	17 June	24
	1974	24 May	16 June	22
Swiss lakes	1975	21 May	12 June	21
	1976	24 May	—	—

with the rise of mean daytime temperature, usually above 10°C. Later in the season temperature seemed to have no influence on the laying dates. At Milicz heavy daily precipitation was usually connected with cold spells, which inhibited the starting of laying. Moderate precipitation connected with temperature rise seemed to stimulate nesting. In Figure 6 the beginning of breeding in the great

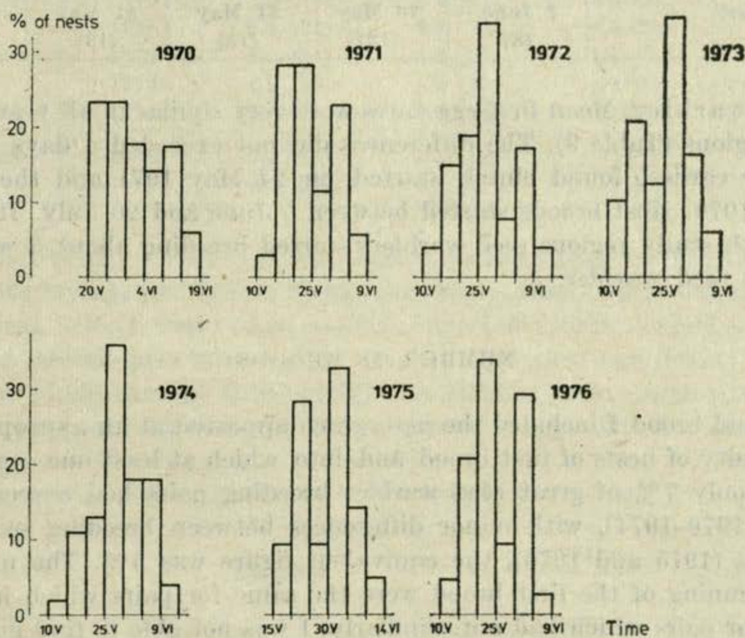


Fig. 6. The onset of laying (in 5-day periods) of the great reed warbler in the first part of the breeding season.

reed warbler is presented in generalized form (cumulation per 5-day period) to show the existence of two peaks in the start of nesting. Possibly two waves of birds arrived in spring. I was not able to detect such a bimodal distribution for reed warbles, except in 1970. Kluijver (1951) and Perrins and Moss (1974) have found in *Parus major* that the first time breeders start nesting a little later in the season than older birds, and the last authors found also that young birds have on average smaller clutches. So I made comparison of clutch sizes between early breeders and late breeders (except very late broods, additional broods and second broods) in the great reed warbler. At Milicz, the average clutch size for the first group was 5.15 ($n = 89$) and for the second group – 4.85 ($n = 62$, $P < 0.05$). On Swiss lakes the equivalent figures were 4.86 ($n = 35$) and 4.62 ($n = 29$, NS). In great reed warbler, the first-egg dates were also on average 6–9 days earlier in optimal habitat (reeds quality, food resources) than in suboptimal ones (Table 10).

Table 10. Mean dates of the laying of the first egg and the habitat quality (no. of selected broods in parentheses) in great reed warbler

Habitat quality	1970	1971	1972	1973	1974
Good habitat	27 May (8)	23 May (21)	22 May (25)	24 May (31)	27 May (35)
Poor habitat	2 June (8)	30 May (12)	31 May (13)	31 May (13)	3 June (9)

Reed warbler. Mean first-egg dates were very similar in all years of study in both regions (Table 9). The differences did not exceeded 4 days (except in 1971). The earliest found clutch started on 24 May 1971 and the latest on 1 August 1970. Most broods started between 5 June and 20 July. In all years and in both study regions reed warblers started breeding about 3 weeks later than great reed warbler.

NUMBER OF BROODS

As second brood I included the nest which appeared at an appropriate date in the vicinity of nests of first brood and into which at least one egg was laid. At Milicz only 7% of great reed warbler breeding pairs had a second brood (total for 1970–1974), with minor differences between breeding seasons. For Swiss lakes (1975 and 1976), the equivalent figure was 5%. The mean dates of the beginning of the first brood were the same for pairs which had second brood as for pairs which had not. Similarly, I was not able to find more second broods in optimal habitat than in suboptimal. Also, the rate of brood losses and number of additional broods seemed to have no influence on the number of second broods. E.g. on Swiss lakes in 1975, in spite of the fact, that breeding losses were very small and food conditions unusually favourable, only 6% of breeding pairs started second broods. The interval between the date the nestlings of the first brood left the nest and the date the first egg of second clutch was laid, varied from 6 to 23 days; on average 13 days. In reed warbler at Milicz (1972 and 1973) 11.5% of pairs started second brood and on Swiss lakes 8%. As in the great reed warbler, an early first brood did not increase the chance of second brood being attempted. The re-nesting interval was 4–14 days, on average 8 days.

CLUTCH-SIZE

Great reed warbler. In all years clutches laid at the end of the breeding season were smaller than these laid earlier, as there was a general seasonal decline (Table 11). In some years however, at the very beginning of the breeding

Table 11. Seasonal variation of great reed warbler mean clutch-size in different years (no. of clutches in parentheses)

Locality	Year	Dates			Whole breeding season
		11-31 May	1-20 June	21 June-27 July	
Milicz fish-ponds	1970	5.0 (9)	4.8 (11)	4.0 (3)	4.8 (23)
	1971	5.1 (31)	4.8 (5)	4.5 (8)	5.0 (44)
	1972	5.1 (34)	4.4 (21)	4.1 (7)	4.8 (62)
	1973	4.9 (35)	4.5 (13)	4.2 (5)	4.7 (53)
	1974	5.0 (34)	4.7 (24)	3.7 (6)	4.8 (64)
Swiss lakes	1975	4.7 (12)	4.3 (12)	—	4.5 (24)
	1976	4.8 (39)	4.6 (11)	4.0 (5)	4.7 (55)

season the average clutch-size was slighty smaller than during the period of most intens laying. In 1975 on Swiss lakes the seasonal variation of clutch size was atypical, being lowest in mid season, connected with prolonged cold and rain. The mean clutch-size was slightly (statistically not significant) smaller on Swiss lakes (4.65) than at Milicz (4.80). The smaller mean clutch-size in Switzerland was produced by a larger proportion of 4-eggs clutches and a smaller

Table 12. Percent of clutches of different size

Species	Locality	Clutch-size				No. of broods
		3	4	5	6	
Great reed warbler	Milicz fish-ponds (1970–1974)	2	25	63	10	251
	Swiss lakes (1975–1976)	4	30	63	3	79
Reed warbler	Milicz fish-ponds (1970–1973)	24	67	9	—	351
	Swiss lakes (1975)	35	59	6	—	51

proportion of 6-eggs clutches than at Milicz (Table 12). Out of the 27 six-eggs broods found at Milicz, 20 were situated in optimal habitat (in the vicinity of bushes and trees), 2 in suboptimal habitat and 3 in intermediate habitat.

Reed warbler. Mean clutch-size varied little from year to year (Table 13). It decreased during the season but in some years was again slightly lower at the very beginning of breeding season. Generally, the additional and second clutches were on average one egg smaller than firsts. The largest mean clutch-size was again found in 1971. The mean clutch-size at Milicz was 3.85 and on Swiss lakes 3.71. The difference is statistically not significant. Smaller mean

Table 13. Seasonal variation of reed warbler mean clutch-size in different years (no. of clutches in parentheses)

Locality	Year	Dates			Whole breeding season
		24 May-20 June	21 June-9 July	10 July-1 August	
Milicz fish-ponds	1970	4.2 (33)	3.6 (31)	3.4 (44)	3.7 (108)
	1971	4.3 (32)	3.9 (59)	3.6 (25)	4.0 (116)
	1972	4.0 (40)	3.9 (24)	3.5 (11)	3.9 (75)
	1973	4.2 (11)	3.7 (26)	3.3 (10)	3.7 (47)
Swiss lakes	1975	4.3 (20)	3.6 (14)	3.2 (8)	3.8 (42)

clutch-size in Switzerland was produced by smaller proportion of 5-eggs clutches (Table 12). In two nests more than 5 eggs were found (Dyrcz 1976). Probably two females laid in one nest. The mean clutch-size given by Catchpole (1974) from England is very close to found in this study.

BREEDING LOSSES

Great reed warbler

During six years of study, in both study areas, the total annual losses varied little, being limited to the range 43–50% of nests (Table 14). In 1976, however, on Swiss lakes the losses from predation (and total losses as well) amounted to only 7.6%. It is apparently the lowest figure recorded for any open-nesting Passerine species (e.g. Lack 1954, Nice 1957). It is based on a sample of 53 nests found over a 50 ha area of reeds and in places situated up to 45 km apart. For possible explanation, see "Discussion".

Table 14. Breeding losses in great reed warbler

	Milicz fish-ponds					Swiss lakes	
	1970	1971	1972	1973	1974	1975	1976
No. of nests	28	49	81	82	82	33	53
% of clutches lost during laying and incubation periods	14	10	17	21	15	33	2
% of broods lost during nestling period	25	33	26	22	23	9	4
% of broods lost in total	50	43	43	44	46	49	8

Note: Sometimes I failed to establish on phase the brood was destroyed. So % of total losses is not always sum of two above it sections.

Predation. I listed the brood as predated if between consecutive inspections the nest contens had disappeared. Additional indicators might be the deformation of the nest, crushed reeds, fragments of egg-shell left and remnants of nestlings or parent (two cases). Predation was the most important mortality factor (Table 15). I made no direct observation to find which predators were

Table 15. Cause of brood losses (%)

		Milicz fish-ponds					Swiss lakes	
		1970	1971	1972	1973	1974	1975	1976
Great reed warbler	No. of lost broods	14	21	35	36	38	16	4
	Predation	50	57	74	86	53	81	100
	Starvation	7	33	9	0	18	0	0
	Desertion	14	5	6	14	8	6	0
	Other reasons	22	5	11	0	11	6	0
Reed warbler	No. of lost broods	95	60	42	46	—	61	—
	Predation	63	48	64	87	—	75	—
	Starvation	11	5	2	4	—	0	—
	Desertion	6	10	7	2	—	8	—
	Strong wind	8	15	10	0	—	7	—
	Cuckoo	3	3	5	0	—	2	—

Note: Sometimes I was not able to decided what are the reason of brood loss, so the sum for a given year is not always exactly 100%.

responsible. Taking into consideration the comparatively inaccessibility of nests and some circumstantial evidence, I suppose that at Milicz the most important nests predators included *Ixobrychus minutus* and *Circus aeruginosus*. During his unpublished yet study on the feeding biology of *C. aeruginosus* on Milicz fish-ponds, J. Witkowski found that quite large part of prey items brought to the chicks were the nestlings or fledglings of great reed warbler or reed warbler. Especially on windy days, the proportion of these species as the food was high as the reeds bend down and it makes easier for a hovering harrier to reach nests or fledglings (J. Witkowski — pers. com.). Pinowski and Ryszkowski (1961) stated that small birds breeding in reeds and *Carex* sp. and especially of the genus *Acrocephalus*, made up the bulk of marsh harrier females prey.

In *ca* 5% of nests with nestlings I found *Diptera* larvae of the genus *Calliphora*. These larvae eroded mainly the outer parts of the belly and caused slight bleeding. But the average weight of nestlings in attacked by *Diptera* nests was not lower than in other nests, and nestlings successfully left the nests, so *Diptera* as a harmful factor seem to be unimportant. On Swiss lakes marsh harrier as a breeding bird is lacking but the predation rate here in 1975, was not much different than at Milicz. It did not seems unlikely that *Corvus c. corone* can reaches some great reed warbler nests. At Milicz the losses from predation was lower among the nests contained eggs than nests contained nestlings. The same was found in most studied Passerine species. On Swiss lakes however, the situation was opposite (Table 14).

In the area with strong human interference, predation rates were lower (Table 16). This area comprised a small part (*ca* 6 ha) of study area. It was most often penetrated by myself, as mist-nets were located there. It was also the only part of reed-beds which, at the one edge, bordered upon a small settlement. Predation was also markedly lower in places with high nesting density than low density (Table 17; see also Dyrcz 1977).

Table 16. Percent of nests destroyed by predators and locality (no. of nests in parentheses; only 1972 data)

Species	Area with stronger human interference	Rest of the study area
Great reed warbler	10 (10)	36 (70) $P < 0.01$
Reed warbler	21 (53)	39 (41) $P < 0.05$

Table 17. Percent of nests destroyed by predators in relation to breeding density (no. of nests in parentheses)

Species	Areas with very high breeding density	Areas with very low breeding density	Average for the whole study area
Great reed warbler (1971–1974)	16 (49)	50 (80) $P < 0.001$	32 (311)
Reed warbler	40 (121)	56 (32) $P < 0.01$	37 (520)

Starvation. In 1971 the detailed data on nestling weights were taken (see also Dyrcz 1974). I ascertained that nestlings which I found dead in the nest, suffered in previous days from weight decline or lack of increase. I think that it is enough evidence that the cause of death was starvation. Starvation occured during adverse weather and often in broods belonging to polygamists. It was greatest in 1971 and 1974 (Table 15), when cold and prolonged rain occurred in the period when many nests contained youngs. Days when dead nestlings were found coincided with the strongest temperature declines, connected with heavy rain (Fig. 7). During such weather, insects activity is low and they are more difficult to be find; at the same time the energy demands of nestlings increased owing to higher costs of keeping warm. Out of 18 broods in which starvation was found, in 11 the nestlings were 7–9 days old. Probably this is the age at which this birds become homoiothermic. No starvation at the age of 1–3 days was found. At this age nestling food demands are comparatively low and they are warmed by parents.

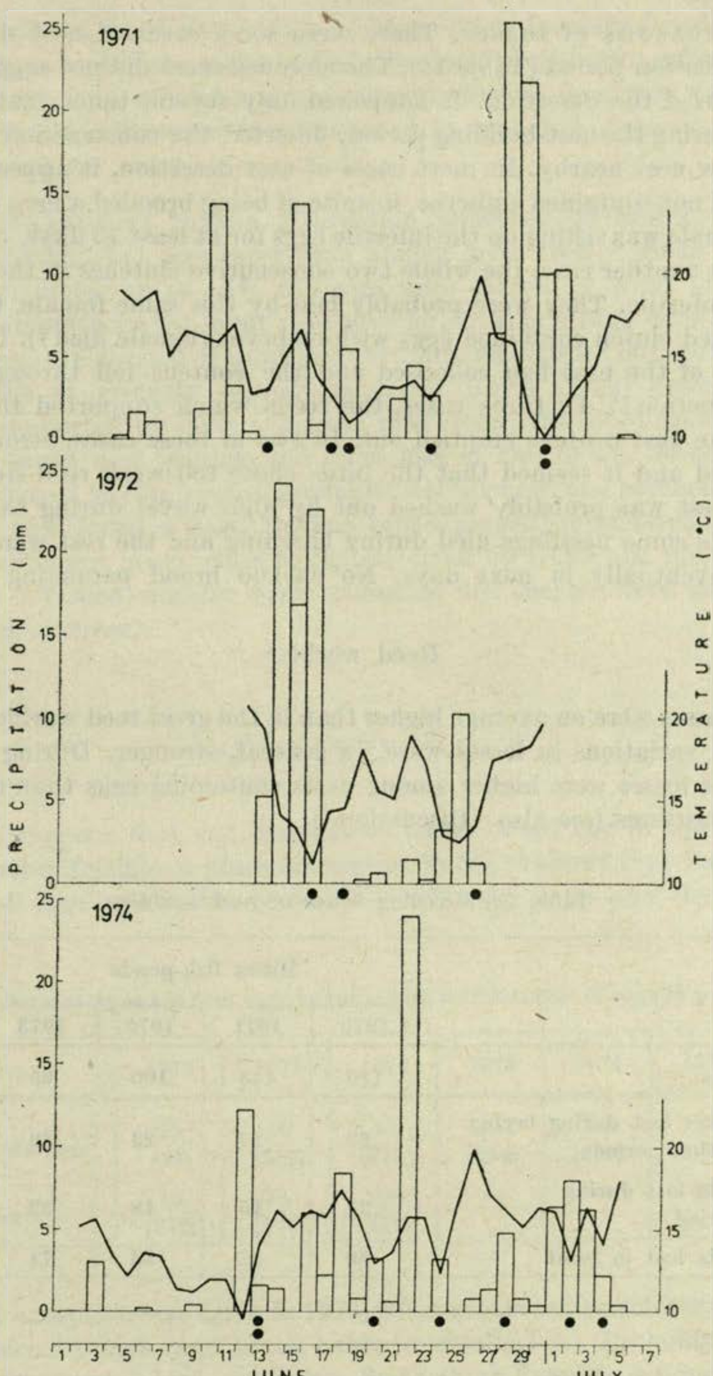


Fig. 7. Days in which nestlings' starvation occured (black spots) versus mean daytime air temperature and precipitation in mm (columns).

Other reasons of losses. There were some cases of nest desertion, all during incubation period (Table 15). The circumstances did not suggest that my activity caused the desertion. It happened only several times that the female disturbed during the nest-building period, deserted the construction and started to build new nest nearby. In most cases of nest desertion, it appeared that all the eggs did not contained embryos, in spite of being brooded a long time. In one case the female was sitting on the infertile eggs for at least 16 days, before I took the eggs. In another case, the whole two consecutive clutches in the same territory were infertile. They were probably laid by this same female. Only in two cases deserted clutch contained eggs with embryos (female died?). In four cases the bottom of the nest had collapsed and the contens fell through (defect in nest construction?). In three cases, the reeds which supported the nest bent over and the nest contens emptied out. In two of these cases, strong wind was not involved and it seemed that the birds chose too weak reed-stems. In two cases the nest was probably washed out by high waves during thunderstorm. In two nests some nestlings died during hatching and the rest were very weak and died eventually in next days. No cuckoo brood parasiting was found.

Reed warbler

Brood losses were on average higher than in the great reed warbler (Table 18) and annual variations in losses were, in general, stronger. During all seasons of study the losses were higher among nests containing eggs than among nests contained nestlings (see also "Discussion").

Table 18. Breeding losses in reed warbler

	Milicz fish-ponds				Swiss lakes
	1970	1971	1972	1973	1975
No. of nests	170	143	100	65	82
% of clutches lost during laying and incubation periods	29	27	22	39	39
% of broods lost during nestling period	23	15	18	32	17
% of broods lost in total	56	42	42	71	65

Note: see Table 14.

Predation. Brood losses owing to predation were greatest in 1972 and 1973 (Table 15), as in the great reed warbler. In contrast to this last species, reed warbler showed a predilection to build nests inside reed-beds. I tried to find all the nest only on small plots, while on larger areas I searched mainly on reed-bed edges where nests were easier to find. The reed warbler also suffered less nest predation in the areas of higher concentration than in localities with low nest density (Table 17). However this phenomenon was less pronounced than in great reed warbler.

Other reasons of losses. Starvation appeared at Milicz during cold and rainy weather, but was rarer than among great reed warblers (Table 15). On the other hand, up to 15% of losses were caused by wind which had no appreciable importance for great reed warbler. During strong wind, some nests broke into pieces, collapsed or leant and the contents emptied out. Some nestlings survived even in strongly leaned nests. As BOYD (1932) described, when a nest was supported by dead and fresh reed-stems, the rapid growth of living stems may cause nest leaning and even loss of the brood. Sometimes older nestlings managed to climb out of gradually leaning nest, and perched on its outer side, which now forms a base. Cuckoo brood parasitism affected 1.6 to 4.8% of losses in different years, close to figures given by GLUE and MORGAN (1972) for Britain. All reed warbler nests parasited by cuckoo were situated near dense bushes or trees.

HATCHABILITY OF EGGS

It often happens that one (sometimes more) intact egg in the clutch does not hatch and unfertility is often the reason. Table 19 shows that the percentage of unhatched eggs was rather constant in different years and similar in both

Table 19. Percent of unhatched eggs in successful clutches (no. of eggs in parentheses)

Species	1970	1971	1972	1973	1974	1975	1976
Great reed warbler	13 (99)	10 (229)	11 (271)	15 (294)	14 (329)	12 (97)	4 (244)
Reed warbler	10 (272)	14 (413)	10 (216)	—	—	16 (132)	—

species. The exception was again in 1976, when great reed warbler eggs hatchability was unusually high (and brood losses unusually low). Probably it was connected with the parent birds condition. So the high fledgling production in 1976 resulted mainly from low nest predation rates, but also from higher eggs hatchability.

PRODUCTION OF FLEDGLINGS

In great reed warbler the average production of fledglings per nest was rather constant during the first six years of study. Only in 1976 it was twice as large as normal (Table 20; see "Discussion"). Reed warbler showed on average about

Table 20. Average number of fledglings produced per brood

Species	1970	1971	1972	1973	1974	1975	1976
Great reed warbler	2.6	2.1	2.0	2.1	2.1	2.1	4.0
Reed warbler	1.3	1.7	1.7	0.9	—	1.1	—

half this production, owing to smaller clutches and higher brood losses. Regarding the production of fledglings per breeding pair, the differences between two species should be smaller as seconds broods appeared more often in reed warbler, which partially compensates for larger clutches and for smaller losses in the great reed warbler. For this last species however, it was biased by presence of polygamous groups. Long (1975) evaluated the yearly mortality of full grown reed warblers as high as 44% for adults and 76% for juveniles. Applying these figures to the studied populations, the yearly production of 1.5 fledglings per pair does not quite balance the yearly mortality. Using Czarnecki's (1975) data the deficit would be much larger. The number of great reed warbler fledglings produced per nest (Table 21) was strikingly higher (2.55) at high density

Table 21. Number of fledglings produced per nest in relation to breeding density (no. of nests in parentheses)

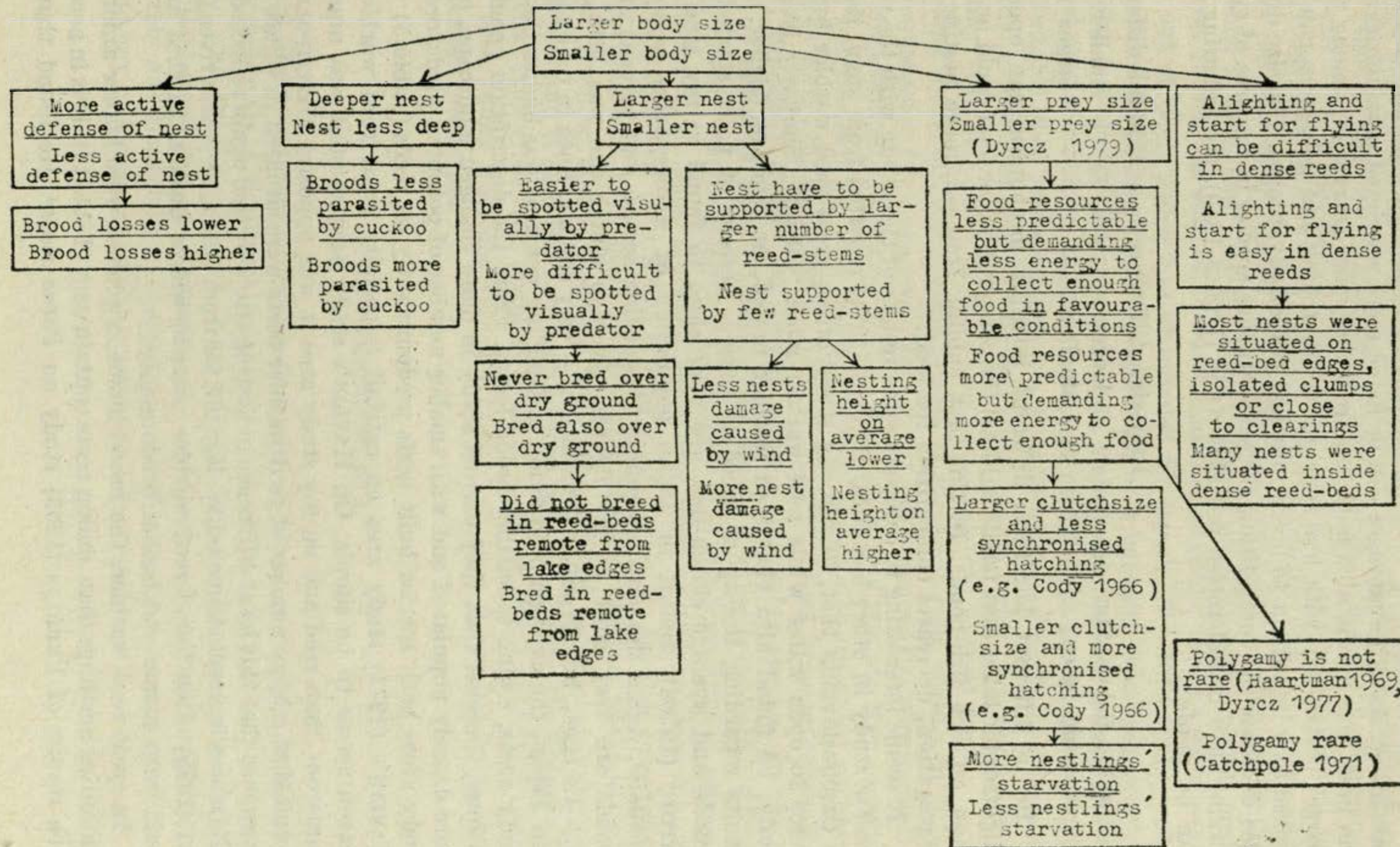
	Localities with very high breeding density	Localities with very low breeding density
Great reed warbler	2.6 (49)	1.3 (80)
Reed warbler	1.5 (121)	1.4 (32)

than for the same species breeding more scattered (1.29). The main reason is lower predation upon high density nests, as there was no essential difference in clutch-size.

DISCUSSION

In Table 22 possible consequences of body size difference between two study species were listed. Table 22 needs however some more comments. Larger body size gives some advantages and some disadvantages. Advantages are

Table 22. The ecological consequences of body size difference between two studied species (Great reed warbler — underlined; Reed warbler — not underlined



connected with smaller breeding losses from predation, wind and cuckoo brood-parasiting. As disadvantages can be listed more restricted possibilities to locate the nest, less predictable food resources and more starvation among nestlings. Larger clutch-size with less synchronised hatching and polygamy can be recognized as adaptations to level these last two disadvantages. The size differences also decrease the competition between studied species in the area of sympatry. Taking into consideration previous study (Dyrcz 1979), the following diagram can be made:

	Prey-size difference	Habitat difference
Eutrophic fish-ponds	larger	smaller
Oligotrophic lakes	smaller	larger

So in different localities, different isolating mechanism can operate. On oligotrophic lakes (less fertile habitat) the competition for food could be stronger than on rich fish-ponds. In this first habitat however, more nesting habitat segregation, decreases competition for food.

It seems interesting to compare some results of this study with the results of similar study in other localities. Havlin (1971) reported from small fish-ponds in Czechoslovakia that, like in my study areas, great reed warbler built nests closer to open water while reed warbler more "inland". Similarly like in this study, he found also that reed warbler nested, on average, higher. Also his results regarding timing of breeding season, percent of pairs started second broods and average clutch-size, are very close to found in my study areas. Saitou (1976a) studied in Japan population of *Acrocephalus arundinaceus orientalis*. Again the data for timing of breeding season and percent of second broods are very close to my figures. Average clutch-size was little smaller (4.1–4.6 eggs), but its seasonal variation — very similar. Both in Czechoslovakia and Japan, the average production of fledgling per nest was higher than in my study areas, owing to smaller brood losses. From the description given by the authors, it seems that they carried study in more changed landscape, probably more densely populated and with smaller number of potential predators. In my study areas both species built nests predominantly on reeds (Table 5) while in Havlin's (1971) study area on catstail (especially great reed warbler). The reason seems to be simple. On Havlin's study area catstail was much more numerous than reed and on my study area it was opposite. Catchpole (1974) found that a large number of reed warbler nests were situated in willow bushes. I suppose that this local difference in nesting-site selection again reflected mostly differences in vegetation quality. E.g. not far from Milicz, at Warta river Czarnecki (1975) often found reed warbler nests in willow bushes. In that area, the reeds were scarce and bushes predominated.

In great reed warbler, the brood losses in general were higher among nests containing nestlings than among nests contain eggs (Table 14). It is in accordance with results of Perrins (1963) study on *Parus major*. He found that noises by nestlings help predators to find occupied nests. In reed warbler losses among the nests contain eggs were higher (Table 18). I can not exclude the occurence in my populations of the same puzzling phenomenon which was described by Brown (1946) and Brown and Davies (1949); namely that the eggs were sometimes pushed out or eaten by the parents or other reed warblers. I did not observe such a behaviour, but my observations from hide, close to the nest, were scarce. In *Sturnus vulgaris* it was found that male can throw eggs or even nestlings out of nests which was abandoned by female (M. Gromadzki, pers. com.). Wyllie (1975) found that *Cuculus canorus* is not only brood parasite for reed warbler but also predates some broods, mainly incubated clutches. It was interpreted that the main reason for host-nest predation is to provide a continuity of suitable nests for cuckoo to use. Cuckoo predation might happen also in my study area making losses during incubation period higher. Anyway I found reed warbler nests parasited by cuckoo but no great reed warbler nests.

Regarding unusually low breeding losses in the great reed warbler in 1976, the only explanation I can suggest is that spring and summer 1976 were unusually dry in Switzerland, with no rain in the study area from the late May to early July. The water level in the lakes was low, but still suitable for great reed warbler, as reed-beds were still in water. During the drought, insect became unusually abundant; especially aphids but probably also many other species. In these condition no nestlings starved. But in this species the main mortality factor among the broods was predation, and I suppose that in the presence of superabundant insect food, some potential great reed warbler nest robbers turned mainly to this source of food which was so easily obtained. Another reason for low nest predation in 1976 might be the abundance of shallow water at the lake edges. Shallow water probably facilitates for the *Ixobrychus minutus* catching fishes and it paid less attention to nest robbing. During the drought I observed that even great reed warblers brought small fishes (two cases) to their nestlings. Also young warblers were not hungry, so they made less noise and did not attract predators.

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SUMMARY

1. The highest densities of great reed warbler were found in places of good foraging conditions (vicinity of luxuriant bushes and tree-stands), accompanied by proper quality reeds for breeding (thickness and density of reed-stems). Local very high density (up to 6 nests per 0.3 ha) was possible because of the existence of polygamy. On Milicz fish-ponds, the density during the first three years of study was stable, than doubled after the neighbouring pond was dried at the beginning of the breeding season. The breeding density of reed warbler was higher. Similarly like in first species, the spatial distribution of nests formed concentrations. The breeding density of the reed warbler was inversely related with the size of reed-bed.

2. The great reed warbler showed a strong inclination to breed at the edges of reed-beds, while the reed warbler had high breeding density also inside vast areas of reeds. This difference was especially pronounced on the study area at Lac de Neuchatel.

3. Most nests in both species were built on reed-stems exclusively. Nests in bushes comprised only 0.5% and 0.3% of nests.

4. Great reed warbler built nests on average lower than reed warbler. Both species nested higher in the reeds on Swiss lakes than on Milicz fish-ponds. It was probably connected with the larger water level fluctuations during the breeding season on lakes. In both species, nests built in the later part of breeding season were situated higher.

5. First-egg dates were similar at Milicz and Swiss lakes in both studied species. Reed warblers in both regions started about 3 weeks later. At Milicz in optimal habitat the first-egg dates for great reed warbler were on average 6–9 days earlier than in suboptimal one.

6. 7% of pairs of great reed warbler at Milicz and 5% on Swiss lakes attempted second brood (after successful completion of first brood). The respective figures for reed warbler were: 11.5% and 8%.

7. The breeding losses in great reed warbler in 1970 ranged from 43 to 50%, but in 1976 were only 8%. In reed warbler the brood losses ranged from 42 to 71% in different years. In first species the losses were higher at the nestling stage while in the second at the eggs stage. In both species the main brood mortality factor was predation. In great reed warbler predation rates were

lower in places with high breeding density than in places with low density. This same was found for reed warbler but less markedly so. Nestling starvation formed on different years from 0 to 33% of brood losses in great reed warbler and from 0 to 10% of losses in reed warblers. Starvation happened exclusively during spells of prolonged cold and rain. Up to 15% of reed warbler brood losses were caused by strong wind.

8. Production of great reed warbler fledglings per nest was 2.0–2.6 (in 1976 – 4.0); in reed warbler: 0.9–1.7.

9. The unusually high production of great reed warbler nestlings in 1976 (unusually dry and hot breeding season) resulted mainly from low predation rates (and slightly better hatchability of eggs) while the clutch-sizes and number of second broods did not differ from normal.

10. On Swiss lakes both species overlapped less regarding breeding microhabitats but more as regards nestlings' food (Dyrcz 1979). On Milicz fish-ponds it was reversed.

STRESZCZENIE

[Ekologia rozrodu trzciniaka *Acrocephalus arundinaceus* i trzcinniczka *Acrocephalus scirpaceus* na stawach w południowo-zachodniej Polsce i jeziorach w północno-zachodniej Szwajcarii.]

1. W latach 1970–1974 badania prowadzono na eutroficznych stawach rybnych koło Milicza, a w latach 1975–1976 na oligotroficznych jeziorach północno-zachodniej Szwajcarii. Łącznie znaleziono i kontrolowano 444 gniazda trzciniaka i 704 gniazda trzcinniczka.

2. Zagęszczenie populacji lęgowej trzciniaka było najwyższe w miejscach o najlepszych warunkach pokarmowych (sąsiedztwo bujnych zarośli i zadrzewień), które równocześnie obfitowały w trzciny o odpowiednim zwarciu i grubości łodyg. Lokalnie, wyjątkowo wysokie zagęszczenie gniazd (do 6 na 0,3 ha) było możliwe dzięki występowaniu poligamii. Zagęszczenia populacji lęgowej trzcinniczka były wyższe. Podobnie jak u trzciniaka, rozmieszczenie przestrzenne gniazd było bardzo nierównomierne. Miejscami tworzyły one luźne „kolonie".

3. Trzciniak wykazywał zdecydowaną tendencję do zakładania gniazd blisko brzegów łanów trzcin, trzcinniczek raczej w głębi. Te różnice szczególnie zaznaczyły się na Lac de Neuchatel. Badane populacje zdecydowanie preferowały trzciny jako miejsce zakładania gniazd.

4. Trzciniak zakładał gniazda przeciętnie niżej niż trzcinniczek. Średnia wysokość umieszczania gniazd przez oba gatunki była wyższa na jeziorach szwajcarskich niż na stawach milickich. Łączy się to z większymi wahaniami poziomu wody na jeziorach, w okresie lęgowym. U obu gatunków, gniazda późniejszych lęgów były na ogół wyżej umieszczone.

5. U obu gatunków terminy rozpoczynania lęgów na stawach milickich

i na jeziorach szwajcarskich były bardzo zbliżone. Trzcinniczek w obu rejonach rozpoczynał lęgi o około 3 tygodnie później.

6. 7% par trzciniaków na stawach milickich przystąpiło do drugiego lęgu, po szczęśliwym ukończeniu lęgu pierwszego. Na jeziorach szwajcarskich 5% par. Dla trzcinniczka odpowiednie liczby wynosiły: 11,5% i 8%.

7. Straty wśród lęgów trzciniaka w ciągu sześciu sezonów w obu miejscach badań wahały się od 43 do 50%. Natomiast w r. 1976 (jeziora) tylko 8%. U trzcinniczka: 42–71%. U pierwszego gatunku większość strat przypadała na okres przebywania piskląt w gnieździe (zwłaszcza na stawach), u drugiego na okres składania i wysiadywania jaj. Główną przyczyną strat u obu gatunków było drapieżnictwo. U obu gatunków (ale wyraźniej u trzciniaka) straty powodowane przez drapieżniki były niższe w miejscach o wysokim zagęszczeniu gniazd. Ginięcie piskląt z głodu i zimna w czasie załamań pogody obserwowano tylko na stawach. Do 15% strat lęgów trzcinniczka było spowodowanych przez silny wiatr. Pasożytnictwo kukułki stwierdzono tylko w lęgach trzcinniczka.

8. Średnia produkcja podlotów na gniazdo wynosiła u trzciniaka przez pierwsze sześć sezonów badań od 2 do 2,6, a w r. 1976 —4,0, u trzcinniczka zaś od 0,9 do 1,7.

9. Na oligotroficznych jeziorach Szwajcarii mikrosiedliska lęgowe badanych gatunków wykluczały się w większym stopniu, rozmiar i jakość zdobyczy w mniejszym stopniu (Dyrcz 1979). Na eutroficznych stawach Milicza mikrosiedliska lęgowe wykluczały się w mniejszym stopniu, a rozmiar i jakość zdobyczy w większym stopniu. Interpretuje się to jako działanie różnych mechanizmów ekologicznej izolacji, w różnych częściach sympatrycznego zasięgu badanych gatunków.

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