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Roch MACKOWICZ

Breeding biology of the River Warbler *Locustella fluviatilis* (WOLF, 1810) in north -eastern Poland

[With Plates III—IX and 39 text-figs]

Biologia lęgowa strumieniówki *Locustella fluviatilis* (WOLF, 1810) w północno-wschodniej Polsce

Abstract. The data presented on the biology of the River Warbler were collected in north -eastern Poland in 1970—1980. The male does not differ from the female either in plumage or in size; the sex of the birds marked was determined on the basis of their behaviour. The breeding territories analysed, 290 in number, lay in wet alderwoods *Alnetea glutinosae* and forests *Querco-Fagetea*. Males arrive a few days before females, on the average about 20 May and occupy small territories. Courtship and warning songs, subsong and 9 other calls and voices are described. Forty-two nests, consisting of 4 layers, were found. The River Warbler has one brood a year, which in the case of its destruction may be repeated 3 times. The female lays 3—6 eggs (on the average 4.92). They are incubated by the male and female, whose various behaviours on the nest are described. The incubation period lasts 14—15 days. Young stay in the nest for 12—14 days. They are fed by both adult birds; butterflies, dipterans and arachnids prevail in their diet. Both parental birds attend to the young in the nest (disposal of faeces, brooding, protection against sunshine and rain). The breeding success in the nests studied is rated at 2.79 chicks per pair. The biology of the River Warbler is compared with the data presented for other species of the genus *Locustella* in literature.

CONTENTS

I. INTRODUCTION

The River Warbler *Locustella fluviatilis* (WOLF 1810) belongs to the birds which have been arousing fairly keen interest of ornithologists for nearly 100 years. This is so because of the secret ways of living of this species, inhabiting environments that impede observation, the resultant unreliability of the estimations of its occurrence in faunistic studies and lastly its poorly known breeding biology (NIETHAMMER 1937; SOKOŁOWSKI 1958; MAKATSCH 1976). Danger threatening the habitats occupied by River Warblers from anthropogenic changes as well as some fluctuations in the size of the area colonized in Europe complete the list of reasons for interest in this species.

The range of the River Warbler, as a Palearctic species, extends between the July isotherms of 17 and 23°C in Europe and Asia (VOOUS 1962). In Europe it reaches as far west as the Hamburg region (RUTHKE 1957; EGGERS 1972), from where its boundary runs north-east to the coast of the Baltic (KÜHNERT 1958; PUCHSTEIN 1959; SAGER 1959; AXT 1969; SCHLENKER 1969, 1971; BUSCHE & BERNDT 1971; HERKENRATH 1973) and east along the sea coast, embracing the Mecklenburg Lake District (KUHK 1939; GREMPE in KLAFS & STÜBS 1979), the Odra valley (DITTBERNER & DITTBERNER in RUTSCHKE 1983), West Pomerania (GÓRSKI 1982b; BEDNORZ 1983) and the area of its continuous distribution in the Mazurian Lake District (TISCHLER 1941; TOMIAŁOJĆ 1963, 1972, in press; MACKOWICZ 1977). Next the range boundary turns north and extends along the eastern coast of the Baltic through the Baltic countries of the Soviet Union (DEMENTEV et al. 1954; KUMARI 1954; IVANAUSKAS 1959) to the south-eastern part of Finland (MERIKALLIO 1958; ERIKSSON 1969; HAARTMAN 1969) and north of Leningrad to Lake Onega. Thence it runs east along the 61st parallel of latitude to Tyumen' and Tobol'sk and up to the middle section of the River Irtysh, where the range of the River Warbler ends in Asia. In similar biotopes further to the east it is replaced by the biggest species of the genus *Locustella*, the Taiga Grasshopper Warbler *Locustella fasciolata* (NEUFELDT & NECHAEV 1977, 1978; HARRISON 1982). The southern boundary describes a curve from the Irtysh across the middle course of the Ural River and the lower course of the Volga and traversing the Crimean Peninsula reaches the Black Sea at the estuaries of the Dnieper and the Dniester (KOVSHAR in DOLGUSHIN et al. 1972). In the Balkan Peninsula the occurrence of the River Warbler has its boundary in Bulgaria (SCHUBERT & SCHUBERT 1982; MICHEV & VATEV 1983) and the main breeding sites are grouped in two breeding areas on the Danube and Tisa up to the Bakony Forest and Sopron (GILBERT 1934; HORVÁTH 1963; HORVÁTH & HÜTTLER 1966). The range includes the oldest known breeding sites near Vienna (HECKEL 1853; FOURNES 1877, 1886; FOURNES 1930) and its south-western boundary runs along the Danube (KLOSE 1980) and its tributaries in the forefield of the Alps to the Inn (BEZZEL 1955; REICHHOLF 1966, 1971, 1973), Iser (BEZZEL 1955; KASPAREK 1975; STURM, ZINTL 1977) and up to the mouth of the Lech (HEISER 1972), where it turns north. The western boundary

of the range of the River Warbler undergoes fairly great changes. Starting from the mouth of the Lech, it encloses an area on the Main near Bamberg, colonized by small numbers of pairs not long ago (WILM 1973; BOSCH & LAUBENDER 1978), to withdraw next nearly up to Pardubice in Czechoslovakia (HUDEC et al. 1983) and the middle course of the Elbe (PODHORSKY & VAŇA 1964). It turns west again, crossing Thuringia in the Gera region (HOENE in v. KNORRE et al. 1986) and forming an arch through Lower Saxony in the vicinity of Brunswick (SCHIERMANN 1924; SCHLEGEL 1925; BERNDT & TAUTENHAHN 1960; FRANTZEN & LAMPE 1975). The last section of the western boundary extends through Drömling (DANCKER 1959; BERNDT & RAHNE 1975) west of the Elbe, embrances the population inhabiting the Lewitz valley in the G. D. R. to the east of the Elbe and forms an arch which reaches Hamburg (KASPAREK 1975).

In the range described, extending west-east over 4500 km and meridionally up to 2000 km in its widest place and about 4.5 million sq. km. in area, the River Warbler occurs very irregularly. This is above all conditioned by the presence of fairly specific, suitable habitats and in the western part of Central Europe, as in the peripheries of all ranges, the numbers of these birds are subject to rather strong periodical fluctuations, which reflect the population relations of the species. In general, most sites of River Warblers recorded are grouped in the hydrophilous habitats, such as riparian thickets on the Danube and its tributaries, the lower course of the Odra, Vistula, Lyna, Volga, Kama and Ural (DYRCZ 1964; KASPAREK 1975; GÓRSKI 1982b; LUNIAK 1971; TOMIAŁOJĆ 1963; ZATSEPINA 1978; KOVSHAR in DOLGUSHIN et al. 1972; USPENSKIY 1981), in lake districts (GREMPE in KLAFS & STÜBS 1977; TISCHLER 1941; TOMIAŁOJĆ 1972), compleves of ponds (PIKULSKI 1980 and others) and marshes (KUMARI 1954; DYRCZ et al. 1972, 1984 and others). And so there are places in this vast area where River Warblers are missing or occur only sporadically. This is above all true of sandr areas, cultivated fields and rather dry forest habitats. However, the places from which the River Warbler is absent are not definitively distinguished, because, as ERIKSSON (1969) and KASPEREK (1975) proved, the rise in the detectability of the sites of this species is positively correlated with the intensity of investigation and the number of orithologists taking part in field studies. On the other hand, some of the sites detected belong to migrating River Warblers and the observations are those of singing male non-breeders. This explains the periodical appearance of this species outside its range, reported from Belgium (CUYPERS 1963; LIPPENS & WILLE 1972), the Netherlands (KIST et al. 1970; LIPPENS & WILLE 1972), Denmark (LØPPETHIN 1967) and Sweden (FORSHILL 1959, 1981; FREDGA & PERSSON 1961; BJÄRVALL 1964; RODEBRAND 1977).

There are only several approximate estimates concerning the size of River Warblers' populations: their number for Mecklenburgia is estimated at less than 100 pairs (GREMPE in KLAFS & STUBS 1977) and for the Schwedt region on the lower Odra at 30 singing males DITTBERNER & DITTBERNER in RUTSCHKE 1983), whereas in neighbouring Thuringia scarcely a few pairs have been observ-

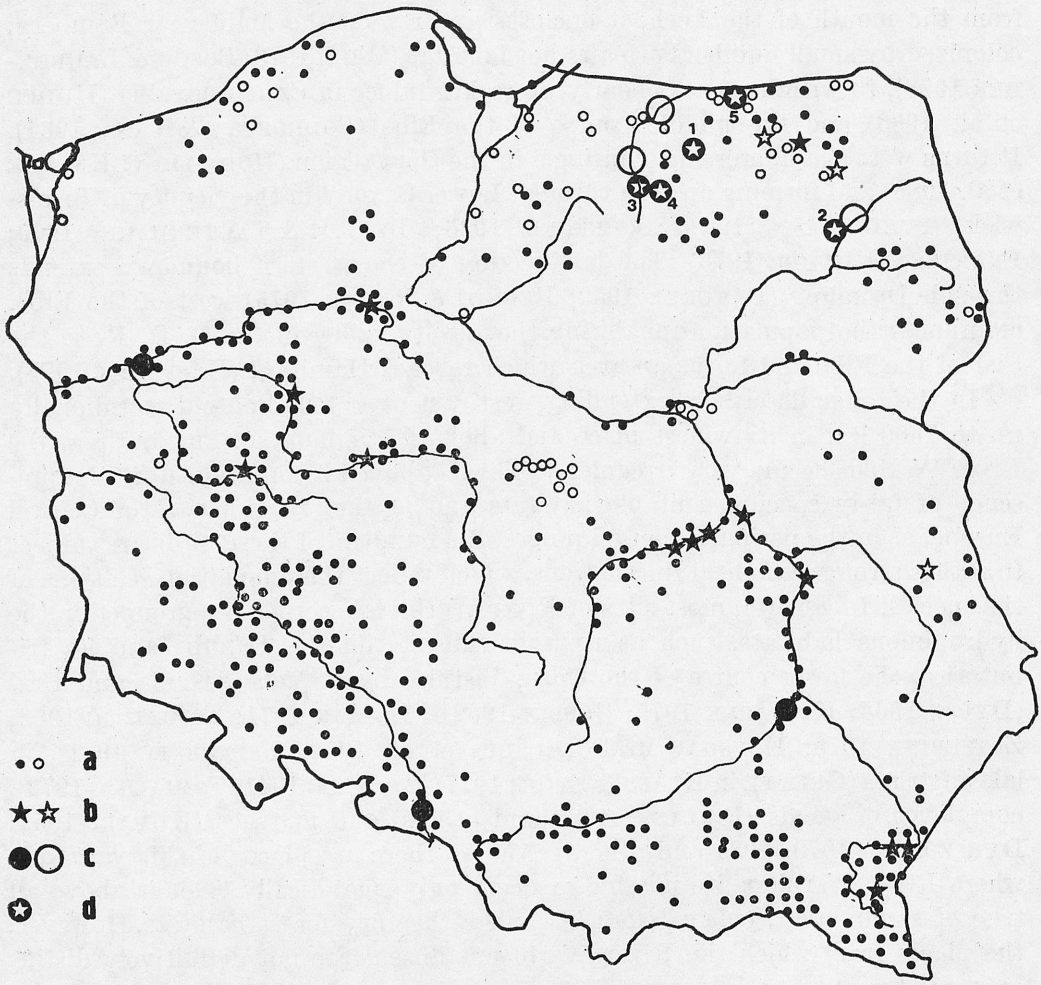

Fig. 1. Distribution of the River Warbler *Locustella fluviatilis* in Poland acc. to the present state of knowledge. Filled signs — materials so far unpublished (Bednorz et al. in prep., Bocheński et al. in prep., Chmielewski et al. in prep. a, b, c,. Dyrcz et al. in prep., Kuzniak in press., Mielczarek et al. in prep., and also information by letter (M. Kosowicz, J. Krogulec, T. Krotoski, P. Kunysz, H. Kurek, A. Mikusek, T. Mizera, J. Przybysz, E. Ranoszeak, K. Zyskowski, C. Żechowski). Open signs — data from literature (Dyrcz et al. 1973, 1984; Górski 1970, 1974; Górski & Górska 1974; Karczewski 1953; Karczewski et al. 1964; Kłosowski et al. 1978; Lewartowski & Wołk 1983; Markowski & Wojciechowski 1984; Luniak et al. 1964; Nitecki 1967; Nowysz & Wesołowski 1972; Domaszewicz & Lewartowski 1973; Harmata 1972; Jabłoński 1964; Okulewicz 1971; Strawiński 1963; Tomiałojć 1963; Tomiałojć et al. 1984; Wesołowski 1975; Wołk E. 1968; Wołk K. 1967). Explanation of signs: a — 1—10 males (pairs), b — 10—20, c — over 20, d — populations investigated by the author (1 — forests near Łężany, 2 — Biebrza bogs, 3 — Łyna valley, 4 — Pisa valley, 5 — "Kałeckie Błota" Reserve),

ed to nest sporadically (HOENE in v. KNORRE et al. 1986). In the south the highest density of the Bavarian population (200 males) was found on the lower Inn in 1973, now it has decreased to a tenth of that population (REICHHOLF 1973, 1985).

In Poland the largest populations are grouped in the north-eastern part of the country — chiefly in the Mazurian Lake District (TISCHLER 1941; TOMIAŁOJĆ 1972, in press) and in the basin of the Biebrza and Narew (DYRCZ et al. 1972, 1984). The most closely examined occurrence of the River Warbler in fairly large physiographic units is dealt with in papers on the results of studies made in the Carpathian Mts. (BOCHEŃSKI et al., in prep.), Silesia (DYRCZ et al., in prep.), the Polish Trough and Obra River (KUŹNIAK, in press) and the Noteć River Valley (BEDNORZ, WINIECKI in litt.). In the Carpathians the River Warbler was found in ca 25% of the area examined, its density being up to 10 pairs per 100 km² mostly along rivers and streams up to an altitude of 600 m (CAIS 1965; GŁOWACIŃSKI 1969). In Silesia it was found in ca 40% of the area investigated till 1986. In the Polish Trough and on the Obra River KUŹNIAK (in press) noted the occurrence of 61 breeding pairs, in one case 14 pairs in an area of 100 km². In the north of the country, in Western Pomerania, River Warblers occur on all pretty large littoral lakes (WOŁK 1967; GÓRSKI 1970, 1976) and on the rivers that open into the sea (GÓRSKI 1982b) and its density reaches 3.1 pairs per 10 ha there. Relatively little is known of the forest populations of the River Warbler in Poland (GŁOWACIŃSKI 1975a, b; LEWARTOWSKI & WOŁK 1983; TOMIAŁOJĆ et al. 1984) and for this reason it is difficult to determine to what extent the number above of 50 pairs in the forests of the Łężany region in Mazuria is exceptional. It is also hard to estimate the numbers of River Warblers in Central Poland, where in the agricultural landscape there are few biotopes which suit this species (JABŁOŃSKI 1964; LUNIAK et al. 1964, MARKOWSKI & WOJCIECHOWSKI 1984; LUNIAK 1983) except for the the valleys of the Vistula (LUNIAK 1971; PRZYBYSZ, pers. comm.) and Warta (SOKOŁOWSKI 1958; CZARNECKI 1975; NAWROCKI et al. 1982).

River Warblers are endangered in Europe owing to anthropopressure, above all, by the destruction of their habitats caused by soil amelioration work, bringing waste land into cultivation in the agricultural landscape, river engineering and draining marshes. And so it has become a potentially imperilled species (ZIMMDAHL 1985).

The River Warbler belongs to the European species, few in number, whose nesting biology is little known. This is so not only because of its secret ways of living but also on account of its not transparent biotope, dispersion of pairs and nests hard to find. The studies of its biology conducted so far have always been fragmentary, based on a small number of facts gathered most frequently at single nests. Although this gathering of facts on its biology was started soon after the description of the species (GLOGER 1833; HECKEL 1853; WODZICKI 1853; ARLT 1871; SCHAUER 1873; FOURNES 1877, 1886; HOMEYER 1885; LINDNER 1897), it was not before the second half of the twentieth century that ob-

servation was carried out directly at the nest (PUCHSTEIN 1959; HORVÁTH 1963; MIERA 1970; HEISER 1972; LUDOROWSKI 1978; DITTBERNER & DITTBERNER 1985, 1986, 1987). Unfortunately, too scanty observational material often led to wrong interpretations of bird behaviour (HORVÁTH 1963; LUDOROWSKI 1978).

For these reasons I resolved to study the nesting biology of River Warblers within the range of the natural occurrence of its fairly large groupings in north-eastern Poland in the manner I had applied before in my work on the Woodlark (MACKOWICZ 1970). In the process of study however the number of issues grew and they did not permit a full recapitulation of the results. The difficulties come across in field work caused that it took as long as 11 years (1870—1980). In my trouble and pains I was supported by my family and friends at home and abroad to whose kindness I owe the material collected.

I should like therefore to extend my thanks to all of them here, above all, to my wife, who shared the hardships of observation and raised my spirits at the moments of despondency. I am also grateful to my children — Maria, Tomasz and Joanna — and to Zbigniew BOCHEŃSKI for many a nest found by them and help with observation for all those years. I am indebted to Mr T. BANASIAK, Mr F. ULCZYCKI, Mr L. NIEPOKOJCZYCKI, who helped me for 3 breeding seasons and to Mr G. DERDOWSKI for help during 2 seasons; Mr W. KUTRITZ, Mr A. JARKOWSKI, Mr J. ŁOWCZAK, Mr J. ŻÓŁTOWSKI, Mr B. CHOJNOWSKI, Mr J. WALIŃSKI, Mr Z. KARCZEWSKI (†) and Mr A. SZWAGRZAK also joined me periodically in my field work. Mr W. STUŻYŃSKI contributed particularly much to the progress of my study, to his aptitude I owe most of the nests found. I thank Prof. Zygmunt BOCHEŃSKI for gathering the data about the nests of the Asiatic species of the genus *Locustella* from the Soviet collections and his continual supplying of missing bibliographic items.

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II. STUDY AREA AND METHOD

A field study of the biology and ecology of the River Warbler was carried out in several places of north-eastern Poland: in the valleys of the rivers Łyna near Olsztyn, Pisa in the region of the village of Patryki and Biebrza near the village of Budy, and in deciduous woods of the Reszel forest-range (Mrągowo District). Apart from these areas, every year suitable biotopes were inspected in the environs of Olsztyn, within a radius of 20 km. River valleys were searched for places in which males were singing. On the Łyna and Pisa they were clumps old alder stands or willow shrubs (mainly *Salix cinerea*), overgrowing the marshy banks rivers, old river beds and neglected drainage ditches. On the other hand, on the Biebrza the whole terrain of osieries and alderwoods in the fens between the River Kosódka and the village of Budy and the flooded alder pole-wood surrounding the road north of Budy were systematically examined.

A complex of forests grows in extremely rich habitats on brown soils in the Reszel forest-range near the village of Łężany. The rich edaphon is also reflected in the structure of the stands of trees. In the study area there are stands of beech which are situated farthest to the north-east in its range (forest reserve "Bukowy") and a comparatively large proportion of areas of oak-hornbeam forests. An exceptionally numerous population of River Warblers occurred in rich forest habitats, weedy forest clearings, gallery alderwoods along streams amidst the meadows as well as in seepage spring areas and morasses arising there owing to their headward erosion. There were 30—60 breeding pairs of this species in an area of 7.5—12 km² in which investigation was conducted for many years.

This field study included the observation of bird behaviour using 15 × 50 fieldglasses, the record of observations and the plotting of the sites of singing males, nests, etc. on the map. Whenever possible, the birds were caught in mist nets. Catching was done at dusk and at daybreak, since it was only then that they could not see the net; all attempts at catching them after sunrise and before sunset (in full daylight) were void. When scared away, the birds hardly ever took wing and the only effective method was to shoo them off so as to make them run away on foot. This is why most of them were caught in two bottom shelves of the nets. River Warblers' taped songs were several time used successfully as a lure. The birds caught were measured and marked individually according to the code with metal and coloured plastic rings (8 colours). The sites of singing were not only put down in a notebook but also marked with coloured ribbon in the terrain, which method made it easier to find the nest at a later time in the breeding season. In view of night singing observation was started just after midnight and ended late in the morning (10.00).

Birds were observed mainly from a hide situated 1.30—2.50 m away from the nest. All details of bird behaviour, such as movements connected with building the nest, turns of body, egg turning, preening, settling down in the nest, feeding, yawning, etc. were noted down. The ritual and rhythm of reliefs on the nest in the incubation period and after the hatch of chicks, the composition of

Table I

Period, results and place of studies of the biology of the River Warbler *Locustella fluviatilis* carried out in 1970—1980

Year	Field study carried out for				Results						Place of study
	days	hours	including continuous observation at the nest		Number of		No. of nests furnished with recorder	No. of days of automatic recording at nest	No. of birds ringed		
			days	hours	territorial males	nest found			breeding	of which females	
1970	27	163	14	115	4	2	—	—	—	—	Łyna valley
1971	9	31	—	—	3	—	—	—	—	—	Łyna valley and Olsztyn district
	9	95	—	—	16	1	—	—	—	—	Biebrza bogs
1972	15	154	—	—	20	—	—	—	—	—	Biebrza bogs

1973	18	74	—	—	3	—	—	—	—	—	Olsztyn district, Łyna and Pisa valleys
	1	15	—	—	4	—	—	—	—	—	Biebrza bogs
	14	151	—	—	14	1	1	1	—	—	Forests near Łężany
1974	3	10	—	—	3	—	—	—	—	—	Pisa valley
	47	310	4	18	25	11	3	29	—	—	Forests near Łężany
1975	3	10	—	—	4	—	—	—	—	—	Pisa valley
	19	118	—	—	22	1	1	8	—	—	Forests near Łężany
1976	57	548	30	261	53	14	6	63	33	10	Forests near Łężany
1977	3	6	—	—	1	1	—	—	—	—	Olsztyn — Kortowo
	73	556	31	232	28	5	1	17	23	2	Forests near Łężany
1978	56	478	24	180	32	5	—	—	18	1	Forests near Łężany
1979	6	64	—	—	12	1	—	—	5	1	Forests near Łężany
1980	3	30	—	—	9	—	—	—	2	—	Forests near Łężany
Total	363	2813	103	806	253	42	12	118	81	14	

food brought to the nest, the frequency of feeding, removal of faeces and in general care of progeny were also recorded. At the same time more than 700 black-and-white and colour photographs were taken of more significant events at the nests. An original automatic recorder was installed at more than ten nests. It consisted of a light barrier fixed on a stand, a photodiode and a relay system and recorded each arrival of the birds at the nest with the help of an actograph. This was a 24-hour drum thermograph modified for this purpose. The readings of the instrument were taken under a binocular microscope with an accuracy of 2 minutes. In the field the apparatus was energized from 6 V batteries, 14—68 kWh, replaced every day at the time of the exchange of the paper tape in the actograph. Unluckily, at first owing to the imperfect quality of the electronic system frequent breakdowns were caused by rainfall and disturbances by falling leaves and the like. The improvement of the contacts by the application of thyristors rendered the apparatus independent of whimsical weather conditions and increased its reliability in the last two years of the study. In order to verify the readings of the instrument observation was simultaneously carried out from a hide. The differences between the results obtained with the automatic recorder and the actual course of events at the nest did not exceed 10% of the number of feedings of the young.

The eggs and chicks were weighed using Pesola spring scales, 5 and 50 g (both with an accuracy of 0.05 g). Collar method was at first used to obtain food samples for determining its composition. Unfortunately, these attempts failed, for the feeding birds examine whether the chicks have swallowed all the morsels received and pull the unswallowed parts out even from the depth of their gullets. Neither were the experiments with older nestlings enclosed in a plastic fence, 50 cm high, placed round the nest to prevent their escape, successful, for, unable to swallow the food, they emptied it from their gullets by shaking their heads from side to side. And so to find the composition of the food brought to the nestlings we had to resort only to direct observations at the nest and to photographing the birds at feeding and next identifying the prey in enlargements or in negatives examined under a binocular microscope.

For convenience, the symbols used for pairs (and nests) combine their serial number in a given year and the last figure of the year; in the case of the repeated brood of the same pair the figure 1 is added before the figure of the year. For instance, pair No 23 having a repeated brood in 1976 is designated 23.1.6 or 2316 and pair No 1 in 1970 1.0 or 10. The pairs observed in 1980 were not numbered.

The field study was conducted altogether for 363 days (2813 hours) in 11 years, including 103 days or 806 hours of continuous observation from a hide and 118 days of recording by means of actographs at 12 nests. During that period the biology of 253 males or pairs was examined, 42 nests were found and 81 breeding birds, including 14 females, ringed (Table I). A breeding male was caught which 3 weeks earlier had been ringed when on passage on Lake Łuknajno (25 km away from the nest). The phytosociology of all the breeding territories

was worked out on the basis of a guide to plant communities of Poland by MATUSZKIEWICZ (1981). The data collected for 30 territories in the forest area flooded by beavers in the Kałeckie Błota and in 7 other parts of the Olsztyn Province after 1980 are included in the phytosociological description. Moreover, for a full appraisal of the criteria of nest site selection phytosociological records were also performed of plants surrounding 12 nests; as regards the other nests, only the number of characteristic plants of their surroundings was noted. Most of the nests found were collected and several of them analysed for material and construction. Statistical computations were made chiefly using a Canon F-73P calculator and ZX Spectrum computer.

III. SEXUAL DIMORPHISM AND BIOMETRY

During the study of the biology of the River Warbler an attempt was made to find such external features of this bird as would permit the discrimination between the sexes.

Some differences were found in plumage coloration, especially in the colour intensity of strokes on the upper part of the breast and on the throat: in some individuals the strokes were blurred, hardly perceptible against the grey throat, whereas in others the plumage on the throat was almost whitish and the grey strokes stood out against the background. The marking of birds with coloured rings showed that this coloration feature exemplified individual variation and not sexual dimorphism, for there were pairs in which the male had light contrastive plumage and others in which this sort of coloration was found in the female. No other colour differences between males and females were observed. Seeming colour differences appeared between the brooding bird and the relieving one in the rain, when the rainwater caused a temporary darkening of the feathers.

Unlike coloration the behaviour of the birds at the nest facilitated the distinction of the male from the female. The female behaved at ease and quietly, when incubating she sat deeper in the nest and with her feathers fluffed. On the other hand, the male behaved as if he were strange to the place, looked about him anxiously, was readily alarmed by unknown sounds and sooner left the nest. In addition, the male more often uttered voices on and off the nest. When seized in hand, he made violent movements to wrench himself free, whereas in the same situation the female lay quietly in the hand, waiting to be set free.

In addition to those differences in behaviour, the appearance of the cloaca permits the determination of sex in a bird captured, for in the breeding season the male's cloacal opening protrudes 3—4 mm beyond the surface of the belly, has a characteristic fold transverse to the body axis and is hollowed on the distal side (Fig. 2). The cloacal papilla is surrounded on sides by 7 pairs of feathers, growing in length distad. In the female the cloacal region is more flattened, protruding hardly 1—2 mm and surrounded by 5 pairs of short feathers. Its opening has the shape of the letter "C", which bulges distally (in the male the opening approximates to a transverse slit). An attempt was made

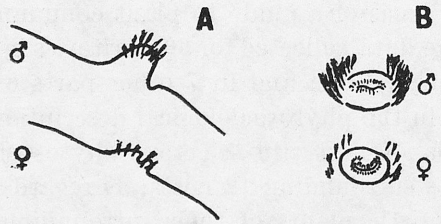

Fig. 2. The shape of the cloacal opening in the male and female River Warbler *Locustella fluviatilis*. A — side view, B — caudal view

to determine the sex of 11-day-old nestlings. Unfortunately, too scanty material made in impossible to verify the expedience of this method for all River Warblers.

In the breeding season also the brood patches are well seen in females. They are large and violet-red in colour, whereas in males they are paler, flesh-coloured and narrower.

Many authors identified females correctly on the basis of their quiet behaviour, even without marking the birds (ARLT 1871; HORVÁTH 1963; PUCHSTEIN 1959; HEISER 1972; DITTBERNER & DITTBERNER 1985). The protrusion of the cloaca in the male is a diagnostic character in many species of the *Passeriformes* (WILLIAMSON 1960; BUB 1969; GLUTZ, BAUER 1985). A difference in the coloration of the throast of partners in the same pair has already been observed by PUCHSTEIN (1959) and MIERA (1970), but basing themselves on the behaviour of the birds, they arrived at varying conclusions, for the former maintains that the female is darker and the latter that she is lighter. It should however be kept in mind that those authors were describing one pair each. Hence, in the light of the present results, the apparent discrepancy of the descriptions given by PUCHSTEIN (1959) and MIERA (1970) is fully explicable. DITTBERNER & DITTBERNER (1985) did not find brood patches in male River Warblers caught on the Odra.

All the River Warblers captured were measured. The measurements included the lengths of the folded wing, tail, tarsus, bill (from the base of feathers and from the distal edge of the nostril) and the distance between the ends of the rectrices and the ends of the undertail coverts. The birds were also weighed. The results obtained for 70 breeding birds are presented in Table II. The measurements of River Warblers quoted by other authors (DEMENTEV et al. 1954; WILLIAMSON 1960; KASPAREK 1980; HUDEC et al. (1983) are also included. Unfortunately, only KASPAREK (1980) gives the origin of the birds measured. The other authors provide no information whether the measurements were taken on living breeding birds or on museum specimens. Some discrepancies may result, as KASPAREK (1980) pointed out, from the measuring of museum specimens. The differences in the method of measuring were probably responsible for some discordance in the lengths of bill and tarsus of the Mazurian birds (from Łężany region) and the Danubian ones (KASPAREK 1980).

It may be assumed on the basis of the results collected that the length of

Table II

A comparison of measurements taken on 70 breeding River Warblers *Locdstella fluviatilis* from the forests near Łężany with those given by other authors

Body part measured	Sex (M—male, F—female)	No of birds measured					Range of measurements					Mean measurement ± standard deviation				
		Own results	Dementev et al. (1954)	Williamson (1960)	Kasparek (1980)	Hudec et al. (1983)	Own results	Dementev et al. (1954)	Williamson (1960)	Kasparek (1980)	Hudec et al. (1983)	Own results	Dementev et al. (1954)	Williamson (1960)	Kasparek (1980)	Hudec et al. (1983)
Folded wing	M	43	44	47	24	21	72—84	69.5—79.0	67—78	74—81	69.5—79	77.13±3.17	73.7	73.64±2.66	77.04±1.49*	75.7
	F	4	4	—	—	3	73.6—77	71.0—74.0	71—77	—	69—77	75.40±1.45	72.0		—	72
Tail	M	53	—	45	28	19	50—63	55—65	52—64	—	55—65	56.83±2.88	—	57.58±2.84	—	55—65
	F	9	—		—	3	46—62		55—61	—	55—65	54.88±4.42	—		—	55—65
Difference between the length of retrices and that of under-tail coverts	M	50	—	—	—	—	7—25	—	10—15	—	—	12.33±3.90	—	—	—	—
	F	9	—	—	—	—	8.6—18	—		—	—	11.78±2.76	—	—	—	—
Tarsus	M	22	—	34	53	4	21—25.2	—	20—24	19—24.6	24—25	23.41±1.00	—	21.91±1.06	21.64±0.87	24.5
	F	2	—		—	2	22.8—22.9	—		—	20	22.85	—		—	20
Bill from start of featheting	M	23	—	46	14	16	10.5—14	14—16	14.5—17	15—19	11—14	11.91±0.87	—	15.26±0.51	9.58±0.34	12.4
	F	2	—		—	2	10.5—13			—	12—13	11.75	—		—	12.5
Bill from nostrils to tip of bill	M	20	—	—	48	—	7.2—9.6	—	—	7.3—9.7	—	8.38±0.61	—	—	8.29±0.54	—
	F	1	—	—	—	—	9.4	—	—	—	—	9.4	—	—	—	—
Body weight in the evening	M	33	—	—	—	—	17.5—22.5	16.7—19.5	—	18.5—23	17.7—22.5	19.49±1.06	—	—	—	20.2
	F	5	—	—	—	—	18.5—20.5	—	—	—		19.60±1.02	—	—	—	
Body weight in the morning	M	31	—	—	55	—	16.5—21.5	—	—	17—21		18.43±1.09	—	—	19.18±1.22	
	F	3	—	—	—	—	19—20.5	—	—	—		19.7±0.8	—	—	—	

* Calculated on the basis of author's results.

Table III

Division of the territories of River Warbles *Locustella fluviatilis* studied in north-eastern Poland according to phytosociological units and plant societies prevailing in them

Dominant plant society in herb layer	D — dominant, C/D — codominant*, % — percentage of territories	Class: *Alnetea glutinosae*										Class: *Querco-Fagetea*												Total of the territories with: D-dominance of given plants in herb layer C/D-codominance of given plants	% of territories with D or C/D
					Ribo nigri-Alnetum							*Circaeo-Alnetum*					*Tilio-Carpinetum*								
		Salicetum pentandro-cinereae	*Betulo-Salicetum repentis*	*Sphagno-squarrosi — Alnetum*	Clearnings, wood plantations, clumps of tree amidst meadows	Forest edge	Young woods	Open high forest	Water-body edge	Total of *Ribo nigri-Alnetum*	Total of the class *Alnetea glutinosae*	Gallery woods on stream banks, forest edge	Plantations and young woods to 15 years	Open high forest	Wooded seepage spring grounds	Total of *Circaeo-Alnetum*	Clearning	Wood plantations (to 10 years)	Young and pole woods	Open high forest and forest edge	Total of *Tilio-Carpinetum*	*Melico-Fagetum*	Total of the class *Querco -Fagetea*		
Nettle *Urtica dioica*	D	5	—	—	5	9	3	6	—	23	28	34	5	5	5	49	4	—	—	3	7	—	56	84	50.9
	C/D	13	—	2	3	5	—	4	2	14	29	3	5	4	3	15	9	6	3	4	22	—	37	66	26.4
	%	12	—	1	6	9	2	7	1	25	38	25	7	6	5	43	8	4	2	5	19	—	62	100	
Grasses *Gramineae* and sedges *Cyperaceae*	D	16	5	—	5	—	2	—	—	7	28	1	—	—	—	1	3	7	2	—	12	—	13	41	24.9
	C/D	12	—	1	—	3	—	5	—	8	21	1	—	1	1	3	13	23	12	2	50	3	56	77	30.8
	%	24	4	1	4	3	2	4	—	13	42	1	—	1	1	3	14	25	12	2	53	2	58	100	
Raspberry *Rubus idaeus*	C/D	—	—	—	2	2	—	3	—	7	7	1	—	2	—	3	11	22	13	—	46	3	52	59	23.6
	%	—	—	—	3	4	—	5	—	12	12	2	—	3	—	5	19	37	22	—	78	5	88	100	
Dropwort *Filipendula ulmaria* or forest bulrush *Scirpus silvaticus*	D	—	—	—	—	—	—	2	—	2	2	—	—	—	1	1	2	—	—	—	2	—	3	5	3.0
	C/D	1	—	—	2	—	—	4	—	6	7	—	—	—	1	1	—	—	—	—	—	—	1	8	3.2
	%	8	—	—	15	—	—	46	—	61	69	—	—	—	16	16	15	—	—	—	15	—	31	100	
Other plants	D	1	—	—	1	—	—	2	—	3	4	—	9	—	—	9	2	15	2	3	22	—	31	35	21.2
	C/D	2	—	1	1	—	—	4	2	7	10	1	5	3	1	10	9	7	2	2	20	—	30	40	16.0
	%	4	—	1	3	—	—	8	3	14	19	1	19	4	1	25	15	29	5	7	56	—	81	100	
Total of territories with dominance of	one plant	22	5	—	11	9	5	10	—	35	62	35	14	5	6	60	11	22	4	6	43	—	103	165	100
	two plants (:2)	28	—	4	8	10	—	20	4	42	74	6	10	10	6	32	42	58	30	8	138	6	176	250	100
	total	36	5	2	15	14	5	20	2	56	99	38	19	10	9	76	32	51	19	10	112	3	191	290	
% of all territories of the association in particular habitats		x	x	x	27	25	9	36	3	x	x	50	25	13	12	x	28	46	17	9	x	x	x		
% of all territories of the class in particular associations		36	5	2						57	x					40					59	1	x		
% of the total of territories in particular classes											34.1												65.9		

* If a terriory enclosed two phytoassociations and it was not known in which of them the nest was built — each of the two plant species was encounted as codominant.

folded wing in male River Warblers in Europe averages 75.18 mm (n = 179, range 69.5—84.0 mm) and in females 73.24 mm (n = 11, range 69—77). The widest range of measurements was found in the population of Łężany (12 mm in males). The mean length of tail is 57.53 (n = 145, range 50—65 mm) in males and 56.49 (n = 12, range 46—65 mm) in females. The population of Łężany shows the greatest differention, 13 mm in males and 16 mm in females. Except for WILLIAMSON (1960) nobody measured the length of the part of the rectrices projecting beyond the undertail coverts; it is on the average 12.33 mm (n = 50, range 7—25 mm) in males and 11.78 mm (n = 9, range 8.6—18 mm) in females. The length of tarsus averages 22.17 mm (n = 113, range 20—25.2 mm) in males and 21.4 mm (n = 4, range 20—22.9 mm) in females. Seeing that the measurements of the bill length taken from the base of feathers differ significantly, which is so probably owing to differences in the definitions of the measuring place, the results in the table are left not generalized. This is not the case as regards the length measured from the distal margin of the nostrils. The measurements obtained for the Mazurian and Danubian birds are almost identical—the cumulative mean is 8.32 mm (n = 68, range 7.2—9.7 mm) in males. The only measurement taken on a female from Łężany, 9.4 mm, is exceptionally high.

The foregoing biometric measurements do not permit the finding of a significant difference in size which would make up sexual dimorphism, because of the small number of females examined. The means and ranges of measurements given above support the suppositions of earlier authors (HARTERT 1910; NAUMANN 1905) that females are somewhat smaller than males.

The birds at Łężany were caught and, consequently, weighed at twilight and very early in the morning, thanks to which some differences in weight were revealed. In the evening the weight of the males averaged 19.49 ± 1.06 (n = 33, range 17.5—22.5 g) and after the night 18.43 ± 1.09 (n = 31, range 16.5—21.5 g). The night loss in weight was 1.06 g and so equal to the value of one standard deviation.

Scarcely 10 females were weighed at Łężany. Two of them were in the course of egg-laying: one, before laying her third egg (full clutch of 4 eggs), weighed 26 g and the other, before laying the fourth egg (full clutch of 5 eggs), 24 g. The remaining results indicate that the females were generally heavier than the males. This was connected with the time of catches, preceding the incubation period and so that of the setting and formation of egg yolks. For this reason the differences in weight between males and females are incomparable and the rise in weight of the females at dawn indicates the formation of eggs, layed early in the morning. The weight of birds fluctuates not only within a day-and-night period but also during the breeding season. Males, right after arrival, when they try to attract females by all-night singing are the lightest. Two individuals weighed 16.5 g each. The incubation period is marked by an increase in weight, whereas in the feeding season the birds lose weight. E. g., male No 197 weighed 19.5 g on 29 May and 18.5 g on 1 July, when the fledgelings

had left the nest. In females this loss is still greater — e. g. female No 306 weighed 18.5 on 3 June, in the incubation period, and only 16.5 g a month later, on 6 July.

In European literature the weight of breeding River Warblers measured on captured or killed individuals is quoted casually and often without comments. Only KASPAREK (1980) carried out a series of measurements, including exclusively 55 males caught. He calculated the mean weight at 08.00 at 19.18 g (n = 55). This result is to a certain extent similar to the data from Łężany. The weights of migrating birds are smaller than those of the birds during the breeding season. In Ethiopia they average 16.6 g, in Kenia 16.3 g and in the winter quarters in Zambia rise on the average to 17.1 g (DOWSETT 1972). The mean weight of the wintering birds is 16.8 g still in January (BACKHURST & PEARSON 1976).

IV. BREEDING BIOTOPES

The areas of the regular occurrence of the River Warbler lie in the north-eastern part of Poland; here, therefore, wherever the type of vegetation provides suitable conditions, its nesting may be expected. Such places are waterside thickets, weedy clearings and glades with tree sprouts in rich habitats of deciduous forests, tall herb communities at the edges and in open parts of swamp alderwoods and oak-hornbeam forests, and the edges of willow brakes, meadows and fens.

The foregoing habitats are not always connected with the close vicinity of waters, this connection being sometimes secondary in nature, for although it is just in places adjacent to eutrophic waters that the plant communities satisfying the ecological demands of the River Warbler develop, forest clearings, often situated far from any bodies of water, may also be overgrown by similar plant communities. The phytosociological classification of all the habitats occupied by River Warblers, from the proto-valley of the Vistula to the Biebrza river in the east and the Borecka Forest in the north, was one of the purposes of this investigation. As a result, 290 breeding territories have been described. They all belong to only two phytosociological classes out of the forty-one distinguished in Poland (Table III). These are swamp alderwoods *Alnetea glutinosae* BR.-BL. et R. TX. 1943 and eutrophic deciduous forests of Europe *Querco-Fagetea* BR.-BL. et VLEIG. 1937. Within the range of these two classes the River Warbler nests only in 7 associations:

1) *Salicetum pentandro-cinereae* (ALMQ. 1929) PASS. 1961
2) *Betulo-Salicetum repentis* OBERD. 1964
3) *Sphagno-squarrosi-Alnetum* SOL.-GÓRN. 1975 Ms.
4) *Ribo nigri-Alnetum* SOL. GÓRN. 1975. Ms.
5) *Circaeo Alnetum* OBERD. 1953
6) *Tilio-Carpinetum* TRACZ. 1962
7) *Melico-Fagetum* LOHM. sp. SEIBERT 1954.

The brushwood communities of the circle *Salici-Franguletum* MALC. 1929, including the associations *Salicetum pentandro-cinereae* and *Betulo-Salicetum repentis*, occupied by River Warblers, form 41% of all the territories of these birds in the class *Alnetea glutinosae*. They are above all osieries of the broad-leaved willow association *Salicetum pentandro-cinereae* (36%) growing in the fens of the rivers Biebrza, Pisa and Łyna and swampy meadows amidst the forests of the Mrągowo and Srokowo forest-ranges. Hence, in many stands sedges and grasses dominate in the herb layer. The centres of these territories are however grown over by *Salix cinerea* surrounded by a stretch of nettles. River Warblers were not found in low scrub of willows *Salix rosmarinifolia* of the association *Betulo-Salicetum repentis* outside the Biebrza valley.

Wet alderwoods with peatmoss of the association *Sphagno-squarrosi-Alnetum*, which would develop sufficiently luxuriant herbaceous vegetation to meet the demands of River Warblers, are rare among the alder swamps. Except for 2 males in a forest flooded by beavers in the Kałeckie Błota Reserve, no River Warblers were found in the stands of that association. Most of their territories occurring in the class *Alnetea glutinosae* (57%) were in the association *Ribo nigri-Alnetum* (Table III). The lush growth of the herb layer, characterizing the River Warbler's breeding territories, attains its proper density outside the forest. As a result, more than a half of the territories are situated in open places, such as clearings, sparsely timbered areas, brushwood clumps amidst meadows, forest plantations and edges of woods and waters. In young woods and open high forests River Warblers also nest only in places with fairly thick herbaceous vegetation. The nesting of River Warblers in the stands of the association *Ribo nigri-Alnetum* was observed in all the study areas of north-eastern Poland, from the bog forests of the Biebrza to the Iława Forest.

Nearly two-thirds (65.9%) of the River Warbler's territories lie in deciduous forests of the *Querco-Fagetea*. The alder-ash carr *Circaeo-Alnetum* resembles the associations discussed above in its specific tree composition rather than in the structure of the herb layer. Gallery alderwoods growing on the banks of streams flowing amidst forests and meadows are the commonest carr form (50% — Table III). They are usually surrounded by fields of nettles mixed up with other herb species and provide a great many permanent breeding grounds for River Warblers in the Reszel forest-range (Mrągowo District), abounding in forest meadows. Luxuriantly developing forest plantations, browsed by animals, come in second. Seepage spring grounds, which however are not common in the forests of the Mrągowo District, also make an attractive habitat for River Warblers. They are marshes formed by headward erosion, often up to 3 ares in area, quaggy and overgrown by nettles and wood bulrush *Scirpus silvaticus*, surrounded by alders. River Warblers do not abandon these places, even if they have lost their broods.

As many as 112 breeding territories (59% of those in the class *Querco-Fagetea* and above one third of the total examined) were situated in subcontinental forests of the association *Tilio-Carpinetum*. In rich habitats of these forests

River Warblers find suitable conditions in clearings, open high stands and plantations up to 10 years of age. Herds of deer, abundant in these rich stands, damage seedlings and offshoots of trees and in consequence cause their condensation. Three-quarters of the River Warbler's territories in the *Tilio-Carpinetum* were situated just in such areas.

Before generalizing the foregoing results obtained in this phytosociological evaluation of the River Warbler's breeding territories for north-eastern Poland, we must take into consideration two qualifications of the material, which may distort the quantitative proportions of the habitats comprised in it: 1 — the results illustrate the habitats lying outside the natural range of beech; in the Reszel forest-range there was only one territory in fertile beechwoods of the suballiance *Eu-Fagion* Oberd. 1957 em. R. Tx. 1960, and in the poorest association — *Melico-Fagetum* — of fertile lowland beechwoods at that; it was an 8—10-year-old glade left after a ruined forest plantation; 2 — the particular setting-off of territories in the subcontinental *Tilio-Carpinetum* forests. Their share in the formation of the structure of the forests is slight. Felling policy and the browsing of seedlings by game in the Reszel forest-range created exceptional breeding habitats for River Warblers and during many years' investigation of this condensed forest population the percentage of the *Tilio-Carpinetum* territories increased in the total of territories of the populations studied.

And so what elements of the habitat decide in favour of the choice of a future territory? As mentioned above, River Warblers occur exclusively in associations of forest vegetation. The presence of high plants — shrubs and trees — is one of the elements decisive of the choice of the territory. The height of the trees has no influence on the choice of the place, since these birds nest both in low scrub of willows and in spaces amidst a 25-metre-high forest. The plants protruding above the herb layer do not enhance the birds' feeling of safety but serve, chiefly at the beginning of the mating season, as song posts or as places to start from on a flight to distant feeding areas.

The size, density and structure of herbaceous vegetation are of decisive importance to the choice of the future nesting territory. The River Warbler chooses above all places where the herbs form a sufficiently large dense plots (at least 1 are). Their height changes during the breeding season. At the time when the territory is taken the height of the vegetation is around 30 cm (e. g. nettles, wood bulrush, dropwort). The River Warbler seems to have preference for this height even later in the summer at the repeated brood, when the plant species preferred in spring have already grown markedly. For instance, on 13 July pair No 506 built a nest, but not in a field of nettles and dropworts, 1.5 m high at that time; it was placed beside it, in the 40-centimetre-high common goutweed *Aegopodium podagraria* and dog's mercury *Mercurialis perennis*. Similarly, on 6 July pair No 2316 set up a nest in 40-centimetre-high wood bulrushes, although the first nest existed nearby in nettles. The closeness of the plant cover should be such as to permit the birds to hide but not to make their movements on the substratum more difficult. Measurements showed that these con-

ditions are satisfied by raspberry fields with 15 to 27 canes in 1 m², dropwort scrub with up to 40 stems in 1 m² and nettle fields with 16—91 green and dry stems in 1 m². Grasses and sedges have three times as numerous stalks and blades in 1 m², the species forming tufts being evidently preferred by the birds (Table IV).

At classification of the plant associations of River Warblers' territories special attention was given to the dominant species of the herb cover. The results are presented in Table III. The optimal plant, providing a suitable breeding habitat for the River Warbler, is undoubtedly the common nettle *Urtica dioica*. It occurs as a dominant plant in 50.9% of the territories and as a codominant one jointly in 77.3%. Except for marginal stands in willow scrub in peatbogs and the *Melico-Fagetum* plantations it is present in each association studied. The nettle goes also to the making of the plant associations screening the nests, even when it does not form a dominant community (Table IV), for nettles, as they grow, augment the leafless space above the ground (shedding their lower leaves) from 20 cm at the beginning of the season to 60 cm in the feeding season. At the same time the thickness of the leaved layer screening the nests from birds of prey increases from 20 to 80 cm. The vertical stalks, on the average 10 cm apart, allow the birds to move easily on the substratum. Long and decay-resistant cellulose fibres present in the stems of nettles cause that a layer of the previous year's intersecting dry stems forms the floor of the nettle field. Such a mat of undecomposed plants makes it possible for River Warblers to escape their terrestrial enemies by hiding in a maze of stems and to move about above the substratum to get food and reach the nest, which is usually placed on an elevation.

Among the plants prevailing in the breeding habitats a whole set of species belonging to sedges and grasses comes in second (55.7% of territories). They either encroach upon River Warbler's territories from the neighbouring meadows (24.0%) or are a transitional element during the period when the clearings, sparsely timbered areas, and forest plantations get infested with weeds (43.0%). Wood bulrush *Scirpus silvaticus*, reed canary grass *Phalaris arundinacea*, or tussock grass *Deschampsia caespitosa* are prominent species among them. They are characterized by growing in rufts and the River Warbler avoids grasses and sedges which form dense monospecific stands.

Raspberries form fairly large accumulations in the territories in clearings and plantations of wet alderwoods and oak-hornbeam forests. However, the outlines of this plant do not secure full shelter to River Warblers from birds of prey, while the grasses and other herbs growing between raspberry canes impede the birds moving about on the substratum. On the other hand, the mixing of raspberries with nettles or grasses in clearings, with dropworts in old alder stands and with wood bulrush in spring carrs enhances the functionality of the plant associations of the herb layer as the breeding habitat of the River Warbler.

The breeding habitats described are distinguishable by the following features:

Table IV

The density of herbaceous plants (per 1 m²) in the surroundings of 12 nests of River Warbler *Locustella fluviatilis* in deciduous forests near Łężany

Plants	No of plants per 1 m²												Total of plants	Mean density	Percentage occurrence of territories	Percentage of plant species
	Nest Nos															
	18	38	318	108	118	17	27	197	126	316	336	346				
Urtica dioica	22	86	75	52	62	91	67	6	43	5	12	16	537	44.8	100%	49.1%
Rubus idaeus	—	—	—	27	—	—	3	—	—	23	15	—	68	17.0	33%	6.2%
Phragmites communis	—	—	38	—	—	27	—	—	—	—	—	—	65	32.5	17%	5.9%
*Cyperaceae**	3	1	10	—	—	11	—	15	—	—	—	—	40	10.0	42%	3.6%
*Gramineae**	8	20	2	30	23	5	2	—	1	4	1	—	72	8.0	75%	6.6%
Filipendula ulmaria	39	—	—	—	—	—	—	38	—	—	—	—	77	38.5	17%	7.0%

Cirsium oleraceum and *Cirsium* sp.	8	6	—	2	4	6	—	—	—	—	2	—	28	4.7	50%	2.5%
Galium sp.	—	—	14	6	—	2	—	—	—	—	—	25	47	11.8	33%	4.3%
Equisetum sp.	—	5	1	—	—	1	1	—	5	9	2	—	24	3.4	58%	2.2%
Mercurialis perennis	—	—	—	—	—	—	—	—	5	6	—	—	11	5.5	17%	1.0%
Labiatae	1	—	—	—	—	—	—	4	3	—	—	—	8	2.7	25%	0.7%
Scrophulariaceae	1	1	—	12	9	—	—	—	—	—	—	—	23	5.8	33%	2.1%
Humulus lupulus	5	—	—	—	—	—	—	—	—	—	—	—	5	5	8%	0.5%
Impatiens noli tangere	2	—	—	—	—	—	—	—	—	—	—	24	26	13.0	17%	2.4%
Asarum europeum	18	—	—	—	—	—	—	—	—	—	—	—	18	18	8%	1.6%
Stellaria sp.	—	—	—	—	—	—	23	—	4	—	—	11	38	12.7	25%	3.8%
Other plants	—	1	2	—	—	—	—	—	—	—	3	—	6	2.0	25%	0.5%
Total	107	120	142	129	78	143	96	63	61	43	35	76	1093	91.1	34.3%	100%
Density per 1 dcm²	1.1	1.2	1.4	1.3	0.8	1.4	1.0	0.6	0.6	0.4	0.4	0.8	0.9			

* Numbers of grasses and sedges are estimated on the basis of the number of tussocks and where they did not form tussocks the number of stems divided by 10.

1) the herb layer is dense to the extent that it completely screens birds walking on the substratum from above,

2) the vegetation exceeds 30 cm in height and the stems of particular plants grow sparsely enough to permit free movements of birds in the ground layer,

3) the substratum is covered with a layer of decaying and dead stalks, which facilitate walking at various levels of the herb layer and hiding under them in a case of danger and

4) single shrubs or trees with subhorizontal branches, which may serve as song perches for males, grow towering above the surroundings.

The problem arises whether and, if so, to what extent the River Warbler's habitats in north-eastern Poland are specific, typical exclusively of this region and depart from the others in the breeding range of this species. Apart from the quantitative proportions of particular communities, which in this study may be charged with a sampling error, they do not as a rule depart qualitatively from the habitats described from all over Europe. And so the descriptions of habitats from the class *Alnetea glutinosae* given in earlier papers correspond to the association *Salicetum pentandro cinereae* (Gloger 1833; Schauer 1873; Pleske 1891 after Naumann 1905; Kollibay 1906; Pax 1925; Hagemann 1948; Schönfeld 1977; Franzisket 1979; Otto in Rutschke 1983; Dementev et al. 1954, Fedushin & Dolbik 1967; Dolgushin et al. 1972; Zatsepina 1978; Uspenskiy 1981; Hudec et al. 1983). The riverside willow scrub in floodplains and old river channels might be included in the association *Salicetum triandro-viminalis* Lohm. 1952 of the class *Salicetea purpureae* Moor 1958, not mentioned in the present paper (Gloger 1833; Wodzicki 1853; Graessner 1890; Borchert 1927; Berndt 1940; Hagemann 1948; Peitzmeier 1969; Hölzinger et al. 1970; Reichholf 1973; Kaiser & Zimmermann 1973; Bezzel 1955; Bezzel et al. 1980; Cais 1965; Klose 1980) and in the association of poplar--willow carrs, *Salici-Populetum* (R. Tx. 1931) Meijer Drees., 1936 (Gilbert 1934; Kertner 1980).

Many authors emphasize the occurrence of nettles (Hagemann 1948; Wilm 1973; Schönfeld 1977; Heinen 1981) or reeds (Gilbert 1934; Fredga & Persson 1961; Peitzmeier 1969; Herkenrath 1973; Franzisket 1979) in the herb layer of willow habitats. Most authors regard wet alderwoods as typical habitats of River Warblers (Wodzicki 1853; Hartert 1910; Pax 1925; Langewisch 1930; Kuhk 1939; Tischler 1941; Kaiser, Zimmermann 1973), but chiefly those situated in swamps and peatbogs and on the banks of rivers and streams.

The foregoing classification of plant associations forming River Warblers' habitats has been based on the descriptions given by the authors quoted above. To their descriptions some of them add also the associations in which they observed this species: bog forest (Robien 1927; Beckmann 1934), open interior of high alderwood (Gilbert 1934; Dielitzsch 1940; Berndt & Rahne 1975), alder swamps (Kaiser 1950), raspberry-reed alder swamps (Dancker 1959), proper reed alder swamps and nettle alder swamps (Kaiser & Zimmermann

1973) or define it briefly as bog alderwood (KLOSE 1980). These associations are not mentioned in MATUSZKIEWICZ'S (1981) classification.

Ash-alder carrs, which form a quarter of all the stands studied in north-eastern Poland, belong undoubtedly to the important habitats on great rivers of Europe: the Odra and its tributaries (PAX 1925), Elba (BERNDT 1940; DORNBUSCH, pers. comm.), Danube and its tributaries (HORVÁTH 1963; BEZZEL 1955; BEZZEL et al. 1980; REICHHOLF 1966, 1973; WÜST 1970; HÖLZINGER et al. 1970; FERIANC 1979; KLOSE 1980) and Vistula and Warta (WODZICKI 1853; SOKOŁOWSKI 1958; CZARNECKI 1975). The River Warbler occupies the gallery forms of those communities in Hungary (HORVÁTH 1963), Czechoslovakia (HUDEC et al. 1983), along the Volga (ZATSEPINA 1978), along the rivers of Byelorussia (FEDUSHIN & DOLBIK 1967) and on steppe streams and lakes (DEMENTEV et al. 1954). Out of the 13 sample plots in natural woods in the Białowieża Forest, ash-alder carrs *Circaeo-Alnetum* were also the only breeding area and chiefly at the edge of a forest with the undergrowth of nettles at that (TOMIAŁOJĆ et al. 1984; MATTHES & NEUBAUER 1976). Alderwoods growing on the shores of lakes often belong to ash-alder carrs, in which River Warblers nest in Europe (BEZZEL 1955; FREDGA & PERSSON 1961; PÄTZOLD & BANZ 1964; HERKENRATH 1973; WILM 1973; ZATSEPINA 1978; SALMEN 1982) and so also on the lakes Kortowskie, Legińskie, Łuknajno, Pogubie and Drużno in north-eastern Poland (TISCHLER 1914, 1941; KARCZEWSKI 1953; KARCZEWSKI et al. 1964).

As early as the mid-nineteenth century WODZICKI (1853) wrote about the nesting of River Warblers in deciduous forests and SCHAUER (1873) stated simply that they nested in largest numbers in clearings in beechwoods. There are no such statements in many later papers (HECKEL 1853; FOURNES 1877, 1886; KOLIBAY 1906; NAUMANN 1905; HANTZSCH 1902), although singing males were observed in town parks (PAX 1925; FOURNES 1930; DEMENTEV et al. 1954; WÜST 1970). However, it was not before the twentieth century that clearings in rich deciduous forests were more often mentioned as River Warblers' breeding area (SCHLEGEL 1925; DOBAY 1927, after SALMEN 1982; NIETHAMMER 1937; DIELITZSCH 1940; TISCHLER 1941; SOKOŁOWSKI 1958; KUMERLOEVE 1961; HUDEC et al. 1966, 1983; REICHHOLF 1966; ZATSEPINA 1978). REICHHOLF (1973) even refers the increase in size in the Danube population to the heavy thinning of the carrs. The phytocenoses of gardens and orchards which have run wild form certain variants of the conditions prevailing in the clearings and this is why the nesting of this species was also observed in them (CSATÓ 1885, after SALMEN 1982; FOURNES 1930; DEMENTEV et al. 1954; CAIS 1965). In the East-European and Asiatic parts of their range the River Warblers more often nest also in coniferous forests (PLESKE 1891 after NAUMANN 1909; DEMENTEV et al 1954; DOLGUSHIN et al. 1972; ZATSEPINA 1978) and in a steppe environment in marshes void of shrubby vegetation (DEMENTEV et al. 1954).

The biotopes in which the River Warbler settles in the eastern borderland of Europe depart to a certain extent from the Central European ones. ZATSEPINA

(1978) listed them for the populations occurring between the Rivers Kama and Volga. Shrubby thickets in wet meadows and carrs are occupied by 30.7% of the total of River Warblers each. Only 2.2% nest in forest clearings, as many as 7.5% in pole woods and old coniferous stands (spruce-fir forests) and 2.2% in mixed coniferous forests. And so in the east of its range the River Warbler enters also coniferous stands.

V. THE SPRING ARRIVALS AND TAKING-UP OF TERRITORIES

The River Warblers arrive in north-eastern Poland exceptionally late. They are the last of the genus *Locustella* to appear, 2—3 weeks after the arrival of the Grasshopper Warbler and Savi's Warbler. During the 11-year-long investigation we succeeded eight times in observing the time of arrivals. The first day of singing of a River Warbler in the Łężany forests fell on the average on 20 May, ranging from 15 to 25 May. The forest population came later than did the birds in river valleys and on lakes. For example, in 1978 River Warblers sang on the Kortówka near Olsztyn as early as 15 May, on Lake Kortowskie on 16 May and in the Łężany forest the first three males (that year I observed 30 pairs) did not sing before 18 May.

On arriving, the males take into possession the best habitats and demarcate their territories by singing. The first males occupy too large areas. They often change their song posts in them, but as other males flow in, they reduce these areas, without trying to fight, to the optimal places, which in the future become their territories. For instance, male No 18 flew about an area of ca 80 ares, which in the previous year had been occupied by 3 pairs. After a fortnight, when having coupled with a female he entered upon nest-building, his territory had shrunk to 20 ares. Similarly, another male, neighbouring upon his territory, No 48, occupied an alder carr by a forest stream, but at the same time he flew over and sang in a small forest bog at a distance of 60 m and 10 ares in area, connected to the occupied carr by a drainage ditch; after a week he abandoned the bog.

A week after the arrival most territories are already occupied, passage migrant River Warblers still moving through the region. The migrating males are easy to recognize, for they sing in marginal places of herb layer communities too small in area or of inappropriate density. They generally occupy spaces which lack one of the four elements specified in the description of breeding habitats, and often appear in the vicinity of roads and rather thinly overgrown river-banks and lake-shores, thinned willow scrub along unattended-to drainage ditches or in weedy clearings many hectares in area. These areas are occupied for a short time, sometimes only one day, exceptionally up to one week (male No 238). The determination of the status of such migratory River Warblers is extremely difficult, if the area is rarely inspected, at intervals of, say, several

days, for the interruption of singing may be interpreted as the beginning of breeding activities and may encourage the observer in a fruitless search for the nest.

The optimal breeding territories taken up first of all are chiefly grouped in ash-alder carrs, wet alderwood with black currant, scrub of willows in wet meadows and at the waterside. Clearings in oak-hornbeam forests come in second, when the stands of alderwoods are already occupied. The River Warbler nests in reforested clearings until the cover of young trees has become closed to the extent that it chokes the herb layer. This usually happens when the plantation reaches the age of 10 years. When the shoots of trees are nipped off by animals, this period is prolonged till the age of the wood is 15 years. In the first years the birds occupy the low-lying parts, where high ground water table favours the luxuriant growth of plants. Later on, they choose higher-situated places and eventually they nest in a hummocky terrain, at the top of the plantation, or at the edge of deforested areas.

Males come first. A lonely male announces the occupation of the territory chiefly by his nuptial songs. He sings in a thicket of shrubs and in trees dominating over the surroundings. Observations support the opinion that he not only prefers some tree species but also chooses such trees among them as suit him in the given landscape. Subhorizontal branches suitably thick (up. to 1 cm in diameter), of which the male could make use to climb from the ground to the crown of the tree are the main requirement. The willow *Salix cinerea* in wet meadows of north-eastern Poland is the most functional species in this respect. Thanks to their subhorizontally arranged branches, birches and alders play a similar role and serve River Warblers as song posts. The male often begins singing hidden in the herb layer. Next, excited, he goes up a chosen shrub, higher and higher. If he has not been frightened away, he reaches the upper branches of the crown, 1 m below the top. This distance depends however on the presence of suitable branches, for in a willow shrub he stops before reaching the end of the branches, while in old alders in the lower third of the crown. Hence, in an open marshy area the male sings at a height up to 2 m and in a stand of old alders even at a height of 15 m (in an alder with a trunk up to 50 cm in diameter). He nearly always chooses trees or shrubs at the edge of an open area. He most frequently sings with his head turned just towards the open area and not to the competing male neighbour.

That climbing-up during the song is characteristic of single males from dawn to twilight, for in the night they sing either hidden in the herb layer or sitting in a shrub up to a height of 60 cm above ground. The intensity of singing of a single male is extremely great. After a few days of fruitless singing, they start to sing also all through the night. The arrival of females in the first period gives them a new impulse to continue singing, but when incubation has begun, the male stops singing entirely.

Females appear in the forests of the Łężany region about 10 days after the first singing males. And so towards the end of May most territorial males

have their mates. This can be inferred not only from the fall in singing intensity but also from the reaction of both partners to the invaders; the male utters warning calls and the female accompanies him in a warning voice.

The breeding territories of pairs are small. However, in estimating their size we are faced by difficulties, for even in cases of the congestion of birds and the occurrence of several pairs in one wood plantation the adjacent territories do not touch each other. They are always separated by a strip of no man's-land, which the neighbouring birds do not enter. This is why the estimation of the size of territories consisted in the determination of the area covered by the dominant herb community in the centre of the occupied territory, enlarged by the grounds connecting the extremal song posts of the male of the given pair. The areas of 124 territories calculated in this way are presented in Table V. Their size is certainly overestimated, since the area defended by a male can be determined more exactly only with the help of a tape-recorder. The smallest territories of River Warblers occur in ash-alder carrs *Circaeo-Alnetum* on the banks of wood streams and in seepage spring marshes. One of them was scarcely 2 ares in area: a narrow strip of nettles under an alder canopy, on the bank of a stream amidst meadows. The territories in spring marshes were also small: e. g. a 9-are area of wood bulrush and nettle. One of the pairs (No 226) took up a small wooded clearing, 20×15 m in area, since under the canopy of surrounding trees there was a large field of nettles, in which the birds only foraged. On the other hand, the largest territories, about 80 ares in area, were situated in sodded clearings and forest plantations independently of the habitat. The size of territories of River Warblers from a forest population averaged 0.36 ha (Table V). In view of the existence of neutral zones, the density was however — even in optimal habitats — much lower than possible.

A maximum of 8.4 pairs nested in a 10 ha area (4 pairs in 4.77 ha) in *Ribo nigri-Alnetum*, 5.6 pairs in 10 ha (4 pairs in 7.19 ha) in clearings in *Tilio Carpinetum* and 11.8 pairs in 10 ha (3 pairs in 2.64 ha) in *Circaeo-Alnetum*. At these densities the breeding territories of River Warblers occupied scarcely from 29% of the area in *Tilio Carpinetum* to 42% in *Circaeo-Alnetum* and therefore even in optimum habitats they hold less than a half of the area.

There were at the most 52 breeding territories in the study area near Łężany of about 4 km², which makes a density of 1.33 pairs per 10 ha. It is a very great density, twice as great as that in the fens on the Biebrza River at Budy, where I found 16 territorial males in an area of 2.5 km² (density of 0.64 pairs per 10 ha).

Analysis of the times of arrival of River Warblers in particular regions of their range comes across difficulties, chiefly because of the scarcity of observational material. The tracing of isopiptezes is besides difficult, since the times of arrival differ considerably with years, these differences reaching 10 days in Mazuria (Tischler 1941) and 1 month near Smoleńsk (Dementev et al. 1954). On top of this all there are hardly several points in Europe where observations of arrivals were carried on for many years.

Generalizing the data from literature I may state that River Warblers fly

Table V

The size of breeding territories (in ha) of River Warbler *Locustella fluviatilis* observed in various types of forests

Phytosociological association and characteristics of plant formation of territories		No of territories measured	Range of sizes of territories	Mean size of territories	Standard deviation
Salicetum pentandro-cinereae		4	0.12—0.40	0.31	—
Ribo nigri-Alnetum	Clearnings, wood plantations, clumps of trees amidst meadows	3	0.40—0.83	0.58	—
	Forest edge	5	0.20—0.40	0.36	—
	Young woods	2	0.30—0.40	0.35	—
	Open high forest	2	0.40—0.52	0.46	—
	Water-body edge	1	— —	0.40	—
Circaeo-Alnetum	Gallery woods on stream banks, forest edge	12	0.02—0.40	0.27	0.12
	Plantation and young woods to 15 years	11	0.25—0.40	0.28	0.06
	Open high forest	4	0.16—0.50	0.32	0.14
	Wooded seepage spring grounds	5	0.09—0.40	0.26	0.14
Tilio-Carpinetum	Clearnings	15	0.20—0.48	0.33	0.10
	Wood plantation (to 10 years)	35	0.15—0.80	0.41	0.16
	Young and pole woods	12	0.20—0.40	0.34	0.08
	Open high forest and forest edge	7	0.30—0.80	0.50	0.16
	Forest edge	3	0.25—0.50	0.35	—
Melico-Fagetum		3	0.30—0.60	0.43	—
Total of territories and respective data		124	0.02—0.83	0.36	0.14

over the Mediterranean Sea in April (via Malta — SULTANA et al. 1975) and reach Lower Austria in the second half of this month (FOURNES 1886; LINDNER 1897; FOURNES 1930). Towards the end of April they appear as far as Podolia and in the Ukraine up to Kiev (DEMENTEV et al. 1954), Bohemia (HUDEC et al. 1983), Slovakia (FERIANC 1979) and Moldavia (USPENSKIY 1981). In some years they can even be seen in Silesia at that time (LUDOROWSKI 1978). At the beginning of May they appear regularly in Hungary (HORVÁTH 1963), in Silesia (ARLT 1871; LUDOROWSKI 1978) and in southern Poland (WODZICKI 1853); they occur in the south-eastern territory of the USSR up to the Shkalov region (DEMENTEV et al. 1954). However, in the greater part of Central Europe male River Warblers appear in the second decade of May; first they take up sites on the Danube and its tributaries (HOLT et al. 1960; REICHHOLF 1971), on the Neckar (GATTER 1970), in the Wittenberg region (SCHÖNFELD 1977), in the region of Leipzig (SCHLEGEL 1925; GRÖSSLER et al. 1972) and on the Elbe

(LINDNER 1897; BORCHERT 1927). As early as mid-May River Warblers arrive in the Brandenburg province (RUTSCHKE 1983), often reach the Mecklenburg region (GREMPE in KLAFS & STÜBS 1979), west of Brunswick (FRANTZEN & LAMPE 1975) and Drömling (BERNDT & RAHNE 1975; BERNDT & TAUTENHAHN 1960). In mid-May they also arrive in the Mazurian Lake District (TISCHLER 1941) — the average day of arrival calculated from the data for 35 years falls on 15 May (from 3 to 23 May). A comparison with the present results shows that the River Warbler penetrates particular biotopes irregularly and appears earlier in river valleys.

In the east in the second decade of May River Warblers spread all over Byelorussia up to Grodno, the Berezina valley (FEDUSHIN & DOLBIK 1967), environs of Leningrad, Yaroslavl' and, further in the east, to Kuybyshev and the southern Ural Mts. (DEMENTEV et al. 1954). In some years, in the last decade of May males appear in the northern part of Central Europe, from Mecklenburg to Bashkir in the Ural Mts. (GREMPE in KLAFS & STÜBS 1979; TISCHLER 1941; DEMENTEV et al. 1954) and at that time they regularly reach the northern range of their distribution, from Schleswig (LILLE et al. 1978), through Sweden (FORSHILL 1981), Finland (MERIKALLIO 1958) to the Kirov region in the USSR (ZATSEPINA 1978).

The density of River Warbler pairs in their breeding habitats, given in works of different authors, varies considerably. It was 0.5 pair in 10 ha in an irrigation area near Słupsk (GÓRSKI 1982a). In the nearby valley of the Grabowa river 0.9 pair nested in 10 ha in a mixed wood and 3.1 pairs in willow scrub (GÓRSKI 1981b). The greatest density reported by GÓRSKI (1976) from a 65-year-old wet alderwood by Lake Jamno came to 3.9 pairs in 10 ha. In a *Tilio-Carpinetum* plantation in the Niepołomice Forest 2.6 pairs occurred in 10 ha and only 0.1 pair in a stand of old trees at a polyclimax phase (GŁOWACIŃSKI 1975b). In the association *Circaeo-Alnetum* in the Białowieża Forest the density was 0.1—1.8 pairs in 10 ha, whereas in a 7—15-year-old alder plantation with a field of nettles it reached 5 pairs in 10 ha (TOMIAŁOJĆ et al. 1984; LEWARTOWSKI & WOŁK 1983). In the Borecka Forest K. ZYSKOWSKI (pers. comm.) came across 8—10 singing males in a 5-hectare wooded clearing (i. e. 16 males in 10 ha). The greatest density in the Biebrza Basin was noted in a patch of open and well-lighted alder and birch woods, up to 40 years old, with dense understorey in Brzeziny Ciszewskie, namely, 5 pairs in 10 ha (DYRCZ et al. 1984).

In the Mecklenburgian lakeland the density ranges from 1 to 2 pairs in 10 ha, 2.5 pairs in alderwoods and up to 3.8 pairs in scattered copses (GREMPE in KLAFS & STÜBS 1979). Estimates made along rivers are based on the numbers of males occurring in 1-kilometre sections of the river. J. KUREK (pers. comm.) counted 23 singing males in a 23-km section of the San river and M. KOSOWICZ (pers. comm.) 8 singing males in a 4-km section of the Wel river. REICHHOLF (1971) reports 2.1—2.8 males in 1-km sections of the lower course of the Inn river.

VI. SONGS AND CALLS

Out of the 12 different songs and calls distinguished, 8 (1—8) are produced only by adult birds, 2 (11 and 12) only by nestlings and 2 by both adults and nestlings. The River Warbler sings hidden in the herbaceous vegetation or perching on a branch of a shrub or tree singled out in the territory but never on the wing.

1. Courtship and territorial songs

The courtship song of males is characterized by sharp short and more fully ringing longer notes following each other rapidly. These alternating notes make an impression of a broken strophe, which may be taken down as a dze-dze-dze... In the night or on dew their voice carries 300 m in an open area and even 500 m in a hilly one. The undulation of the voice power is usually audible, it is due to transverse swings of the head of the singing bird. These swings are relatively quick and take less than 1 second (M_{63} = 1.2 swings per sec.). The posture of a singing male is characteristic, his head being raised and the lower mandible dropped low; the chin is also lowered and, seen from below, it looks as if swollen. The male breaks his song for short to evacuate his bowels and also, during a fairly long strophe, as if to swallow saliva. These breaks, however, often take less than 1 second.

The male usually begins singing as early as the day following his arrival. In the Łężany forests this does not happen before the 29th pentad, i. e. before 16 May. On the first day the intensity and length of strophes are still small (Fig. 3) but as other males take up their territories, singing can be heard nearly at any hour round the clock (Fig. 4).

The main singing period of the breeding population lasts till the 31st pentad

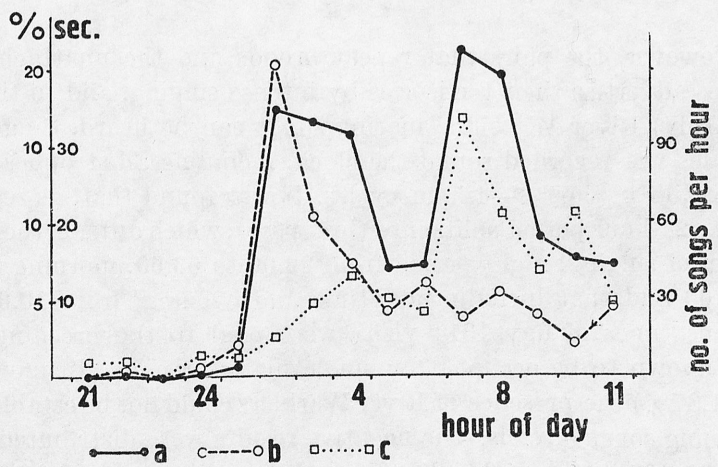

Fig. 3. The intensity (in %) — a, number of strophes (per hour) — b, and mean strophe length (in sec.) — c, of the songs of the unmated male River Warbler *Lucustella fluviatilis* in night hours and in the morning following his arrival

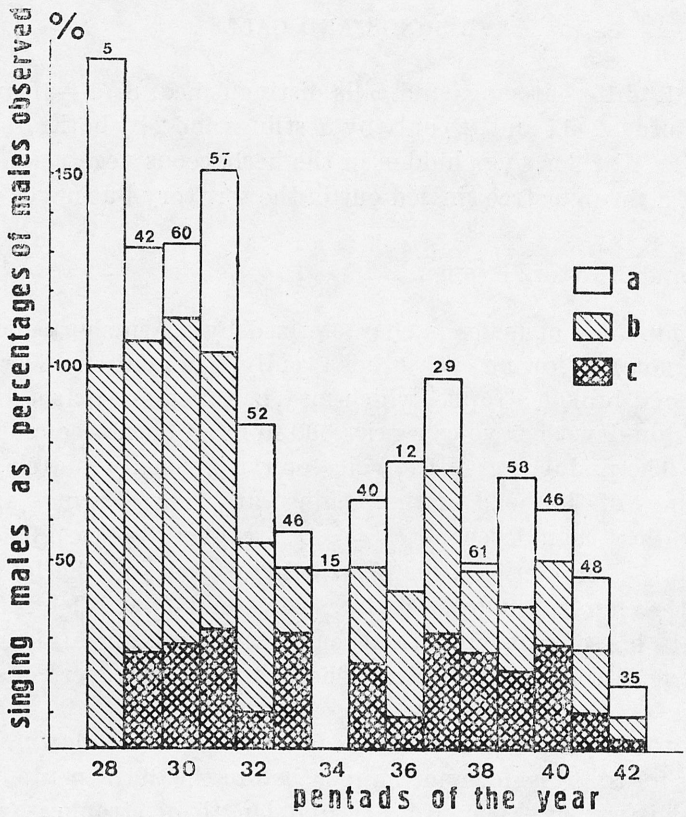

Fig. 4. The proportion of singing males of the River Warbler *Locustella fluviatilis* in the Łężany region in the breeding season (in successive pentads) at various time of day (a — 10.00—22.00, b — 03.00—10.00 and c — 22.00—03.00). The numbers of singing males are given above the blocks

(4 June). However, the pairs that repeat broods and the unattached and migrating males advertise their territories by intense singing, and so till the 42nd pentad (29 July) River Warblers' mating songs can be heard. Singing of more than ten males was recorded round the clock, including all strophes and breaks between them, or in their 3—4-hour cycles. It was found that, as regards River Warblers, the 24-hour period splits into three parts, which differ in their behaviour and the form of singing: night period from 22.00 to 03.00, morning period from 03.00 to 10.00 and that including daytime and evening, from 10.00 to 22.00.

At various times of day 1314 visits were paid to the breeding territories which were known to be occupied by single males or pairs. In more than half the cases (51.37%) the presence of River Warblers could not be established on the basis of warning songs or calls. The negative results were distributed as follows: as many as 45.2% in the night, 26.8% in the morning and 28.0% from 10.00 to 22.00. Figures 4 and 5 show that night singing occurs from the 29th to 42nd pentad and that the morning singing is the most frequent.

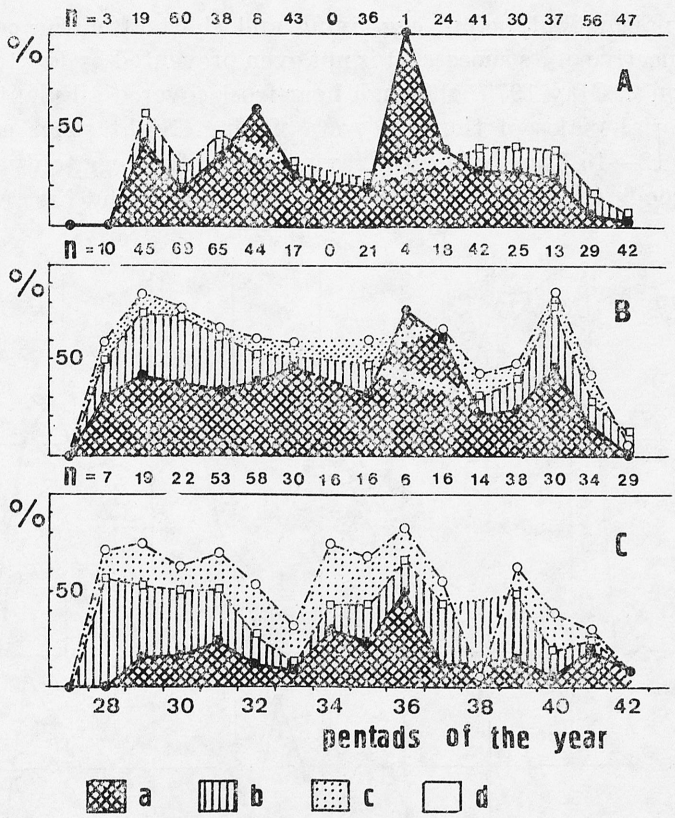

Fig. 5. Changes in singing intensity in male River Warblers *Locustella fluviatilis* in the Łężany region. A — in the night (22.00—03.00), B — in the morning (03.00—10.00) and C — in the daytime (10.00—22.00). The results of 1314 inspections (figures above graphs) of territorial males: a — intense continuous songs, b — short songs with long brakes, c — singing provoked by the presence of an observer, d — silent male

In respect of intensity the songs can be divided into long songs of very long strophes and short breaks, short songs of short strophes and long breaks and intermediate ones, which however may be caused by a long stay of the observer in the territory.

In 300 cases (22.83% of the total of inspections) the males met with were intensely singing long continuous strophes, 32.3% of them in the night-time, 47.0% in the morning and only 20.7% at the remaining times of day. Short songs of males were recorded 201 times (15.30%), 18.9% of them in the night-time, 44.8% in the morning and as many as 36.3% in the remaining part of day. In 99 cases (7.53%) the males were roused to sing by a long stay of the observer in their territory, e. g. searching for nests or capturing birds. Singing as response was heard mainly in daylight (3.0% by night, 32,3% in the morning and 64.6% in the remaining part of day).

Males sing by night at the peak of their sexual condition: before pair for-

mation, after pairing but before egg-laying and short after the completion of breeding, irrespective of its success. It is not even prevented by low temperatures, e. g. at 00.52 on 29 May 1975, although hoar-frost covered all plants in the valley, the territorial males of the area were singing. Night songs are most frequently heard 12—15 days before the laying of the first egg, only in two cases of repeated broods the males sang 3 and 5 days before the first egg was laid.

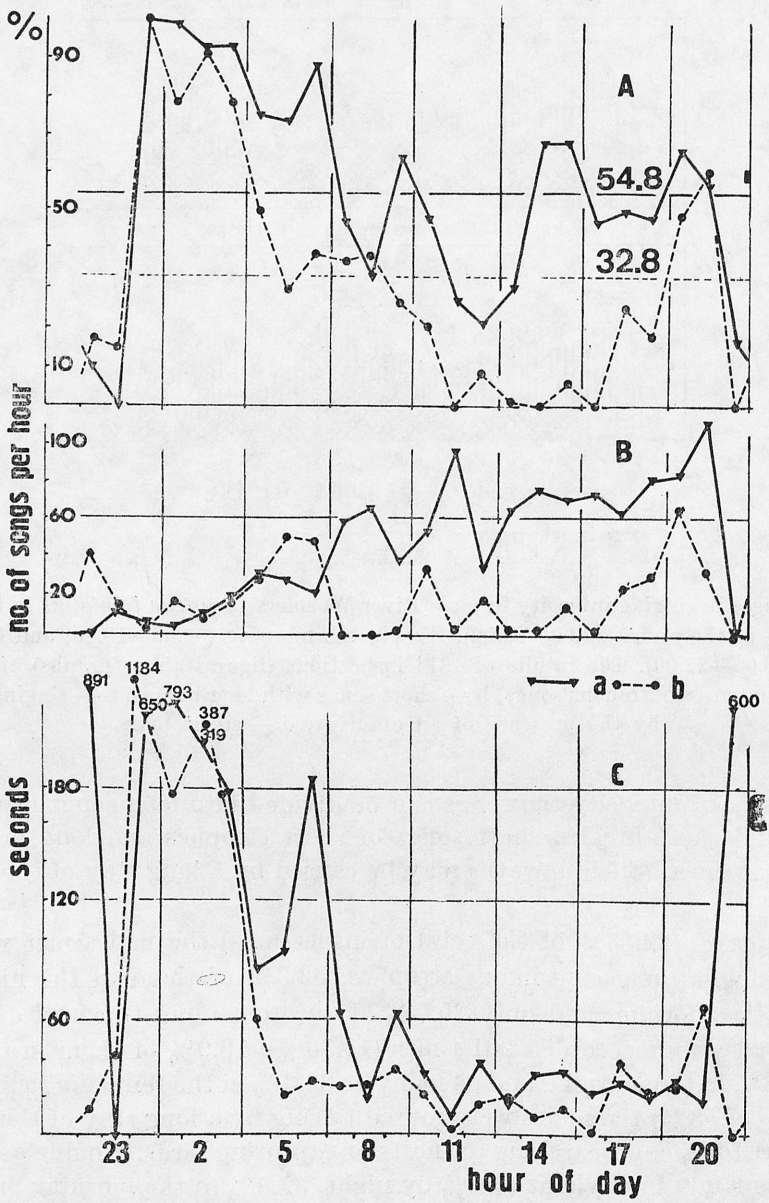

Fig. 6. Intensity of singing (in %) — A, numbers of strophes — B, and mean lengths of strophes (in sec.) — C in unmated (a) and mated (b) males in successive hours of day

A cycle of night singing lasts up to 3 days. In single male No 168 it however extended with breaks for a whole month, from 27 May to 23 June. At the beginning of the season the males who sing in the night-time maintain the intensity of singing also during the day, but towards the end of the season they confine themselves only to night singing.

River Warblers sing most intensely by night (Fig. 6A). A singular strophe may then take as long as 72 minutes and the song of a single male may occupy above 90% of the time till 03.00 (in a mated male till 02.00). At dawn the intensity decreases, the frequency of breaks rises and the strophes become shorter (Fig. 6C). In the daytime the single male sings more often (Fig. 6B), thus showing a greater intensity of singing than does a mated male, but then the strophes of his songs average less than 40 seconds. In the evening the frequency of singing increases but the strophes are not lengthened (particularly as regards single males, Fig. 6C).

The remaining males, single or mated, who do not sing in the night-time, begin to sing after 03.00 (summer time) in north-eastern Poland. Their daylight sensitivity threshold is lower than in Robins, Song Thrushes and Blackbirds. At that time the luminance measured was 3.8 Asb units. In the evening all the River Warblers having their territories in an area (including those singing by night) also cease to sing at the same time, about 22.10 with the clear sky. There follows a break and even playback of a call of uneasiness cannot induce the males to sing. At such moments they rather utter a call of fear. Towards the end of evening singing the light sensitivity threshold is lower than in the morning and comes scarcely to 1.5 Asb units. This is also manifested by the fact that River Warblers end their evening singing at the same time as or later than the species of the *Turdinae* do.

As in the case of night singing the singing of a River Warbler that does not wake up until at daybreak may also be vigorous in the morning and evening, but such intense singing ends two days before the laying of the first egg. On the other hand, singing of low intensity occurs at various times of day even on the first day of egg-laying and exceptionally on the day of the laying of the third egg. At the time of egg-laying the courtship songs come practically to an end. In the incubation and cheek-feeding periods they are replaced by warning songs.

Deviations from the above-described regularities appear in exceptional cases. E. g. in the first hours following the destruction of the brood, male No 10 sang 2—4-syllable strophes, which took less than 1 second. In the first hours they were rare, 7 hours later, at 09.00, the male sang as many as 245 strophes in an hour. This is the highest number of strophes recorded in the course of studies on the River Warbler. In the case of pair No 17, two days after the destruction of the brood, singing was reduced to 42 minutes, from 03.08 to 03.50, but the mean length of strophes was 6.5 seconds. The intensity of singing was 29.2% at that time and the frequency of strophes averaged 2.7 in a minute.

The repetition of syllables in the courtship songs of males may run at varied speed. It can be seen from a sonogram (Fig. 7) that this speed in quick songs

was about twice (1.9 times) as high as in ordinary songs. The period of such quick songs is short and occurs in still unmated males. It was observed only in the males that sang by night, even though they could be still heard in the morning. During the last night the male already sings slowly and only ends each strophe with a quick phrase, which takes 2—8 sec. to perform and sometimes connects it with the following slow part (e. g. in male No 75). It may be stated

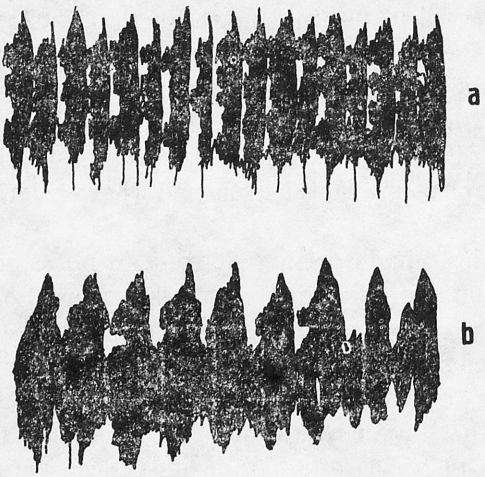

Fig. 7. A sonogram of the courtship song of male River Warbler *Locustella fluviatilis* No 75 in fast (a) and normal (b) tempi

in general that the quick song constitutes the culmination of the male's activities aiming at the attraction of a female. This is why such quick songs are, as a rule, heard only towards the end of May till the arrival of females.

2. Warning and threatening song

Having taken up a territory, the male, in particular, if he has got a mate, responds to disturbances and intrusions into his territory with a song, differing from the courtship song in volume, length and ending. It consists of similarly sounding but more sonorous syllables "dze-dze-dze..." (the volume of voice may be estimated to be at least twice as great); it is shorter and breaks suddenly with a stress on the last syllable. The strophes are not long (e. g. in male No 2306 they averaged 18.4 sec.) but the breaks are short and so the intensity of singing is great (in male No 2306 it comes to 88.5%). If the reason perists, e. g. another male or an observer stays in the proximity, the strophes become longer and the breaks remain short, taking several seconds. Next the voice loses its strength and the song changes slowly so that eventually it does not differ from the territorial song. Most frequently, however, especially when breeding is advanced, this behaviour ends after two or three songs of a few strophes each. The longest stimulated song did not exceed 5 minutes.

3. Subsong

From the late morning till sunset outside the periods of incubation and chick feeding the male's song can be heard which in its qualities is the reverse of the warning song; it is delivered in such a soft voice that it can be heard within a radius of scarcely 20 m and its strophes take 1—2 sec. to sing, while the breaks are much longer. It may occur parallel to courtship songs. At 16. 53 on 3 June male No 58 sang a subsong with an intensity of 20.8%, while the frequency of 1—2--second-long strophes (M_{23} = 1.2 sec.) was 10.5 per minute. The song of male No 10, after the destruction of his nest, may also be numbered in this category.

4. Calling voice

This is hardly a fragment of several syllables of the courtship song. It is uttered still more softly than is the subsong — in the thick of herbaceous vegetation it can be heard scarcely at a distance of 3 m. The birds use this voice to communicate with each other, when one of the mates approaches the nest to relieve the other or tries to make the other get off the nest, or, finally, before feeding the young to encourage them to open their bills. The male utters this voice more frequently, although there are individual differences in this respect in particular pairs (e. g., in pair No 67 the female used it more often than the male). The shortest form of this voice is a soft one-syllable "zhek" or "chik", produced by the female at intervals of 1.5 sec., when she feeds her 2-day-old nestlings.

5. Contact voice, "sneezing"

The birds produce it chiefly at mate relief on the nest in the incubation period. It is short, voiceless and rather resembles the sound of air escaping violently. For this reason I define it also as "sneezing". It is so gentle that it can be heard at a distance of 2 m only in windless weather. The details concerning the frequency of thid voice will be discussed in the section on incubation.

6. Call of uneasiness

This call is a one-syllable "beerr" or "peerr" uttered mainly by the male when he falteringly begins a song. He does not insert it before strophes when the intensity of singing is great but he often does it at the time of day when the singing intensity is low. At the beginning of a cycle he starts each strophe with this call. The male, forced by various disturbances in his territory to break intense singing, also uses a call of uneasiness at the beginning of each of the last strophes to confine himself exclusively to this call eventually. As his uneasiness grows, he repeats this call 2—3 times before beginning a strophe. Male No 10 produced it as many as 93 times an hour over a 3-hour period following the loss of his brood.

It is difficult to estimate the frequency of the call of uneasiness in the female, without seeing the birds. Never has a female been heard to utter this call at the nest. When a call of excitement was played back from a tape, female No 316 delivered a call of uneasiness, while the male was singing on. Females were often heard to utter a call of uneasiness once or twice in response to the call of warning.

7. Call of warning and anger

This call consists of a series of 4—6 rasping notes, which may be transcribed "gi-gyry-gyrit". The female most often delivers this call, when she has been alarmed by the encroachment of an observer upon the territory. And so in the female it is a counterpart of the male's warning song. However, the male, e. g., No 49, after playback of the warning song, also sang that song several times before giving a warning call. When an observer came on the to slope occupied by him, the male began to trill (call of excitement) and to an imitation of trilling he responded by coming up to a distance of 3 m and delivering whole series of 5—9-syllable warning calls.

8. Call of excitement and alarm

It consists of a series of smacks of irregular rhythm in accordance with the excitement of the bird; the more excited the bird is, the faster it utters them. The female smacks when she is upset by the presence of an observer from the beginning of incubation till the time when she leads the young after their departure from the nest. She never uses this call on the nest but out of it when alarmed by some changes in the surroundings. In the same situation the male oftener sings warningly but he manifests a higher degree of aggression by approaching the rival and smacking in his proximity. Male No 49, mentioned above, responded to playback of a recorded warning song by circling round the tape-recorder for 176 sec. and delivering, in addition to the warning call, smacks, 235 in number, their frequency being thus 80.1 a minute.

9. Voice of fear

The extremely frightened female or when she cannot draw an intruder away from the nest by luring and smacking, hisses in a voice resembling that of young starlings, "chshshshe", "tshshe" or "dzhzhe", with the vowel "e" scarcely articulated and soft hissing prevailing. An 11-day-old nestling also gave a voice of fear when a compression collar was being placed on its neck, but this voice was then hoarser, more modulated and shorter than the voice of adult birds.

10. Voice of pain

A voice of pain was heard when neck collars were being fixed in 10-day-old nestlings. It is a one-syllable voice, but if pain persists, it may be repeated se-

veral times. It sounds like "pssiy" or "psib". It is also a voice of pain of adult birds. Female No 67, captured several hours before laying the third egg, uttered a voice of pain, sounding like "tsiw" or "tsscew".

11. Food-begging call

This is a series of notes delivered at unequal intervals and sounding like "psee, psee, psee, pseeb". These voices are uttered starting from the very moment of hatching. On the first day they are so soft that with the microphone placed 50 cm above the nest they are hardly audible in the earphones but not recordable on a tape yet. They become louder from day to day and in the final period of their stay in the nest the chorus of begging nestlings is heard even at a distance of 5 m. In three one-week-old nestlings the frequency of syllables was 22.9—35.0 a minute. The rate of sounds increases with age the calls blend into a confused chorus, when the feeding time comes. In nest No 38, in which there was one chick it uttered 1.1—2.3 calls a second on the 7th day. This means that in 7 days the frequency increased elevenfold, from 11.7 to 130 notes a minute. From the 6th day onwards, in addition to such short notes of importunate begging for food, the nestlings utter also a protracted voice like "psseey". I do not distinguish it here as a separate kind of voice but I think that it expresses an aggressive behaviour.

12. Location call

The day before leaving the nest the young begin to give location calls, which sound like "weets" and enable the adults to find their young outside the nest to feed them. The oldest and best-developed nestling utters this call as if casually when, still in the nest, it is waiting for food, mainly in full daylight. Towards the evening the call becomes subdued to get louder again in the morning till the moment of nest departure. The age differences between the siblings cause that most frequently only one or two of them are heard simultaneously. Having left the nest and scattered amidst herbaceous vegetation, the fledgelings call by turns from different sides. These calls characteristically lack rhythm and in consequence each note comes unexpectedly. Although several hundred calls of a fledgeling were investigated, I failed to grasp the scheme of successive breaks. The call that follows a series of quick notes is usually utterd after a fairly long break. A fragment of the record of breaks between singular notes is as follows (the figures represent the intervals between particular calls in seconds): 3, 1, 6, 7, 3, 1, 5, 2, 2, 5, 4, 3, 1, 3, 1, 1, etc. A fledgeling delivers on the average 13 ± 4.75 location calls a minute ($N = 286$, range 8—22 calls a minute during a 22-minute period of observation). No doubt, this irregularity of rhythm makes it difficult for predators to discover a squealing fledgeling in the thick of vegetation.

I also heard a call of fright in nestlings and female but it is hard to describe it exactly for the scarcity of records.

Most descriptions of the River Warbler's singing are restricted to the courtship song. The transcriptions of its strophes given in literature are similar allowing for spelling differences between particular languages. Similarities between the song of the River Warbler and that of the Yellowhammer are often emphasized (HANTZSCH 1902; VOIGT 1933; NIETHAMMER 1937; BERNDT 1940; CUYPERS 1963; AXT 1969; ECK 1973). Although FOURNES (1930), PUCHSTEIN (1959), HEISER (1972) and LUDOROWSKI (1978) do not mention the warning song, their descriptions imply that it is this song that they mean in them. HEISER (1972) thinks that the warning song is a substitute action in a conflicting situation, while FOURNES (1930) and LUDOROWSKI (1978) treat it as indicative of the situation of the nest. BOSCH and LAUBENDER (1978), having probably heard a warning song produced at the nest, put forward the statement that the male sings throughout the nesting period, till the departure of the young from the nest. This opinion became the reason for some false conclusions concerning breeding based on observations of singing males. Some authors (PUCHSTEIN 1959; PODHORSKÝ & VÁŇA 1964) quote the lengths of particular strophes and breaks in singing, which correspond with the present observations.

A number of authors (HECKEL 1853; HANTZSCH 1902; NAUMANN 1905) associate night singing with warm moonlight nights. However, the present study shows that these factors are not decisive as regards night songs. WARNKE (1944) writes that between 6 and 13 June he observed night singing lasting from 22.00 to 02.30 with a 45-minute break at midnight at the outset of the nights of the midnight sun. In Belgium CUYPERS (1963) heard a male singing from 21.30 to 02.30, but he did not notice any breaks at midnight. These observations made on single males agree in respect of night singing pattern with the results of the present work.

VOIGT (1933), according to whom the River Warbler is a dusk singer, gives 15 minutes as the maximum length of a strophe. Likewise, PODHORSKÝ and VÁŇA (1964) write that the longest song takes 8 minutes. It is only the authors who heard night singing themselves that quote considerably higher figures (WARNKE 1944; CUYPERS 1963; ECK 1973). Some authors could not believe that a bird was able to sing on one breath for many minutes; WARNKE (1944) asserted simply that the observer's ear does not distinguish short breaks during which the singing bird breathes.

CUYPERS (1963) gives the transcription of the subsong without any details concerning its interpretation.

The call of uneasiness is presented as indistinct murmuring (SCHAUER 1873) and transcribed as "tr, tr" (VOIGT 1933), soft "pr, pr" (HANTZSCH 1902), "drrr", "knirr" (FRIDRICH 1922) and "trl, trl" (LUDOROWSKI 1978). SCHAUER (1873) and HANTZSCH (1902) write that this call precedes a song and VOIGT (1933) compares it to Chiffchaff's call. The calling voice of the female is a "tzack, chack" (FRIDRICH 1922), "dzhik, dzhik" (PODHORSKÝ & VÁŇA 1964), "zi, zi" (MIERA 1970) or "chk, chk" (LUDOROWSKI 1978). LUDOROWSKI heard a female uttering this call getting the young to leave the nest.

FOURNES (1930) named the call of excitement the call of fear and compared it to a single or double impatient mechanical smacking and FRIDRICH (1922) rendered it as "tot, tet, tet".

LUDOROWSKI (1978) writes about the call of warning as the call of alarm and rightly thinks that it is a counterpart of the male's warning song. He describes it as a sharp and shrill tetrasyllabic "tsitsitsitsi" and writes that the female utters this voice in the period of nest building and egg laying. It is in fact heard most frequently in this period. DITTBERNER and DITTBERNER (1987) name this call "the female's song", although it has nothing in common with singing.

As regards a break in singing in the incubation period, PUCHSTEIN (1959) writes that singing comes to an end the day before the first egg is laid, which agrees fully with the present observations. Moreover, HEISER (1972) found that males stop responding to playback of songs recorded on a tape at that time. REICHHOLF (1971) presented the course of singing throughout the breeding season and at different hours of the day. The graphs included in his paper show that the lowest intensity of singing falls between 14.00 and 16.00. According to the present data (Fig. 6A), this time is from 11.00 to 13.00. The difference may result from the summary treatment of the data by REICHHOLF (1971).

Finally, I should like to state that night singing in July is connected not only with repeated broods but, in view of partial moulting in the breeding area mentioned by KASPAREK (1981) and PEARSON, BACKHURST (1983), this intense though ephemeral singing may be associated with autumn sexual excitement.

Among the voices of the River Warbler recorded in Sweden (PALMER & BOSWALL 1973) there are some resembling those of the Great Tit, which I have never heard during my field studies of many years as yet. I think that this record refers to another species and not to the River Warbler. And so the sonagram presented by BERGMANN and HELB (1982) is incorrect.

In my previous work (MACKOWICZ 1977) I assumed that night is the best time for detecting breeding birds by the mapping census method. The present results show that to carry out a full census two counts should be made within a day-and-night period, in the night-time and at daybreak. The advantage of the morning song lies in the fact that in the morning males respond with singing to the presence of a human intruder, if he remains rather long in their territories, more often than they do in the night-time. And so to the end of June the highest numbers of birds are counted in early morning hours till 07.00 and in the daytime only a long stay in its territory makes it possible to detect a River Warbler.

VII. NEST

After forming pairs River Warblers stay constantly in the territories occupied by them. The male still sings vigorously while the female begins to build the nest. This activity has no as yet been observed by anybody. Nevertheless, some facts can be deduced from the behaviour of the birds and the structure of the nest.

The nest is nearly always situated near the place from which the male started to take up the territory and where more often than not he sings if he has not been scared away. The male's singing in the nest building period suggests that the nest is built chiefly by the female, though the male may take a partial share in this activity.

The situation of the nest in the biotope (Fig. 8) is determined by the occurrence of a suitable kind of herb layer. In such a community the nest is nearly always placed at the border, in the place where a relatively thick layer of litter

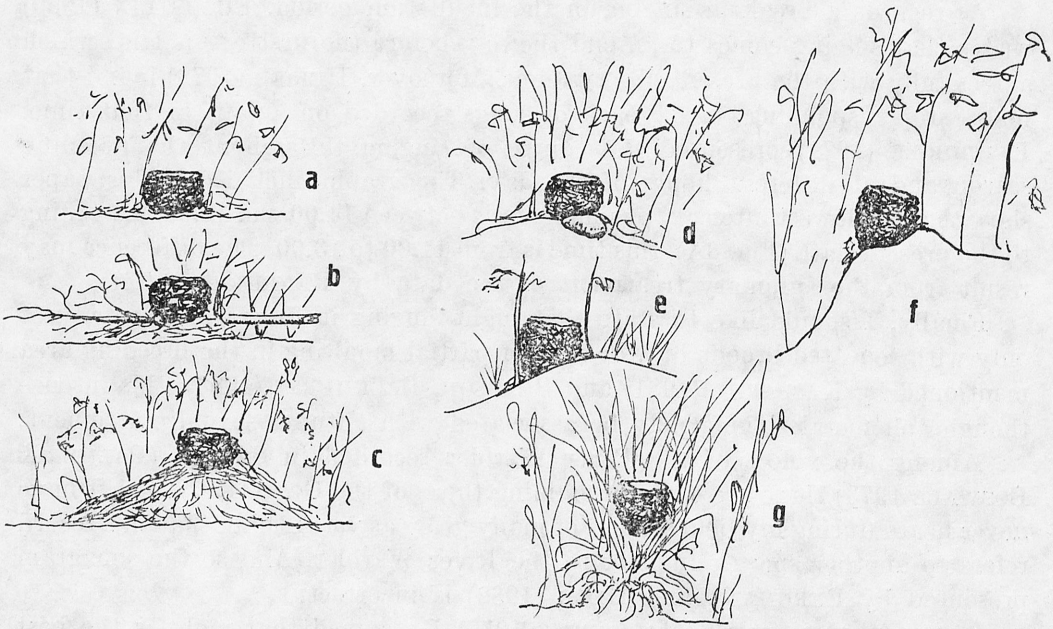

Fig. 8. The modes of the placement of nests of the River Warbler *Locustella fluviatilis*: situated in a flat place (a, b, c), on a stone (d), on an earth mound (e, f) and in a tussock (g)

of putrefying nettle stalks of the previous year, tree twigs, etc. covers the ground. For instance, the forest management type under which self-sown birches are cut down and left lying where they grew exceptionally favours colonization by River Warblers and provides suitable conditons for the placement of nests. Several nests in wood plantations were situated just next to the cut-down birches.

As has already been mentioned in the description of breeding habitats of River Warblers, these birds place their nests in 30—40-centimetre-high vegetation. This height is reached by nettles, dropworts and most grasses in north-eastern Poland at the end of May and the beginning of June. The proximity of trees or shrubs has no direct influence on the situation of the nest. None of the nests found was placed in a tree or at the foot of a tree or shrub. The ground relief influences the selection of the site more evidently. Small ground elevations above the layer of litter often serve as nest bases. And so River Warblers some-

times set up their nests in tussocks of last year's reed canary grass or forest bulrush (Fig. 8g), on small knolls (often), formed in connection with the preparation of soil for planting (Fig. 8f), on molehills or even on stones (Fig. 8d). In search of elevations some pairs built their nests even on anthills, which however they abandoned later.

Such ground elevations averaged 13.8±7.4 cm in height, the maximum height being 28 cm (Table IX). In a flat area without any elevations the birds place the nest, e. g., on a lying dead branch (Fig. 8b).

The nest structure consists of four layers (Fig. 9):

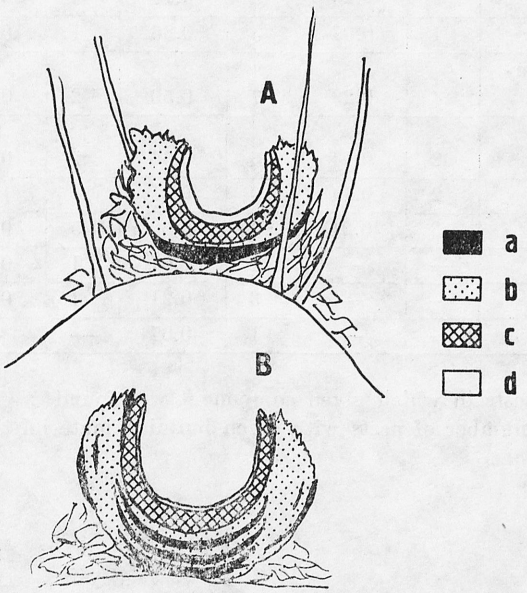

Fig. 9. A diagram showing the structure of the nest of the River Warbler *Locustella fluviatilis*: a — base, b — peripheral layer, c — nest body, d — internal layer (lining)

1) and underlay or layer isolating the nest from the soil, composed of last year's tree leaves, stalks of putrefied leaves, thicker stems of nettles or other perennials and rather thick fragments of sedges (e. g. forest bulrush) and grasses;

2) a peripheral layer, separating the nest from the plants among which it is built; it merges into the underlay at the bottom and is the most diversified layer as regards composition. The thickest fragments of grass and sedge are used in this layer;

3) the body of the nest, which is a fairly compact structure, emerges after the removal of the peripheral, circularly arranged grasses. It differs mainly in the presence of slantingly, nearly vertically interwoven grass stalks and blades. One or several (to 4) lenticular platforms lie on the bottom; they alternate with grass stalks which end in the side wall or at the top edge of the nest. In some nests the edge is furnished with a loose ring, which is missing in others at all;

Table VI

Plant and animal building materials found in 14 nest of River Warbler *Locustella fluviatilis* in the forests near Łężany, divided according to the nest layers in which they occurred

Material	Underlay		Peripheral layer		Body of nest		Lining	
	N	P	N	P	N	P	N	P
Tree leaves	14	1.00	6	0.43	—	—	—	—
Winged fruits	1	0.07	—	—	1	0.07	—	—
Leaf-stalks	4	0.29	2	0.14	2	0.14	1	0.07
Stems of nettles	1	0.07	5	0.36	1	0.07	—	—
Stalks of other perennials	4	0.29	7	0.50	2	0.14	—	—
Leaves of sedges (forest bulrush)	2	0.14	5	0.36	2	0.14	1	0.07
Grass stalks	2	0.14	10	0.71	14	1.00	14	1.00
Grass blades	3	0.21	7	0.50	5	0.36	5	0.36
Grass inflorescences	—	—	1	0.07	1	0.07	6	0.43
Rootlets and mosses	—	—	3	0.21	1	0.07	2	0.14
Animal hair	—	—	1	0.07	—	—	6	0.43

N — number of nests in which given component was found
P — ratio of the number of nests with given building material to the number of nests examined

Number (N), mean length in mm (M±SD) and total sum of lengths (L — in m) of dead frag

Building material	Underlay				Peripheral layer			
	N	M±SD	L	%	N	M±SD	L	%
Leaves of forest bulrush *Scirpus sylvaticus*	96	84.38±68	8.1	46	54	76.9±55	4.2	23
Blades of grasses *Gramineae*	73	85.3±61	6.2	35	114	68.4±46	7.8	49
Stalks of grasses and perennials	17	113.2±82	1.9	8	19	88.2±79	1.7	8
Leaves of trees	14			7	23			10
Leaf-stalks	9			4	24			10
Alder twig	—				1			0
Moss	1			0	—			
Total in layer	210			17.3	235			19.3
Aggregate length (in m)			16.2				13.7	

4) an inner layer, finer than the nest body, from which it is not always possible to discriminate it. Towards the inside it gradually passes into the cup lining, which consists of the most delicate stalks and blades of grasses used. In the lining of some nests there are animal (boar) hairs (Tables VI—VIII).

The form of the underlay and peripheral layer shows that they are an accumulation of material brought. The bird shapes the peripheral layer by turning round the axis of the future nest-cup and it uses its bill to weave the nes body and lining.

River Warblers build their nests as a rule of material available in the nearest neighbourhood. Hence, the nests built in meadows will differ in some details from those under the canopy of deciduous trees. In a nest placed in a tussock of forest bulrush, fragments of this plant occur in all the layers. Similarly, if millet grass and reed canary grass grow in the proximity of the nest, they are represented by fragments in the main body of the nest and by their panicles in the lining.

In order to prepare the place for the nest tree leaves of the previous year are gathered in it. In a grass tussock or on an elevation among nettles a layer of leaves is collected from the surroundings. In the closely analysed nests 47 leaves were woven into the structure of one found in a meadow and 180 leaves in another one at the edge of a wood (Tables VII and VIII). All of the 14 nests analysed contained tree leaves in the underlay and in 6 of them leaves went also to the making of the peripheral layer (Table VI). The numbers of leaves are connected with the specific composition of trees growing in the neighbourhood and with their rate of decaying. Since alders, hornbeams and willows grow in

Table VII

ments of plants used as building material in nest No 396 of River Warbler *Locustella fluviatilis*

Body of nest				Inner layer (lining)				Total in nest		
N	M±SD	L	%	N	M±SD	L	%	N	L	%
98	47.5±39	4.7	28	68	47.0±44	3.2	16	316	20.2	26.0
189	54.6±57	10.3	53	281	50.7±43	16.8	68	657	41.1	54.1
16	40.6±30	0.7	4	56	52.7±44	3.0	14	108	7.3	8.9
35			10	5			1	77		6.3
14			4	5			1	52		4.3
—				—				1		0.1
3			1	—				4		0.3
355			29.2	415			34.2	1215		100.0
		15.7				23.0			68.6	

the vicinity, their leaves occur in the structure of the nest. These leaves are strongly putrefied and this is why also their stalks can be found in the nest. On the other hand, leaves of beach and oak, more resistant to decomposition, are present in the underlay, although these trees do not grow in the proximity. Birch leaves often occur in the nests placed in forest plantations (Table VIII). The intense transport of these leaves to the nest site is indicated by the fact that their number in the underlay often by many times exceeds the number of leaves lying in the surroundings of the nest. Where the process of putrefaction is fast, the nests have fewer leaves in the underlay.

At the same time the birds begin to bring the material for the peripheral layer of the nest: thicker stems of nettles and other perennials, rotten parts of which lie in the vicinity of the nest, and whole stalks and blades of grasses and sedges.

Grasses are the main building material of the River Warbler's nest. Even in the environments in which grasses are scarce, the birds bring them from a longer distance. Grass stalks are more or less frequently met with in all the layers of the nests examined (Table VI). They are characteristic of the body and inner layer of the nest. The numbers of stalks and blades of grasses in particular layers can be analysed on two closely examined nests, No 26 and No 396. Their longest pieces occur in the peripheral layer (in No 26 — on the average 161.9 mm). Woven into the body of the nest, they break during this operation and so their length ranges here from 54.6 to 85.5 mm, similarly to the length of the leaves of forest bulrush (Tables VII and VIII). There is a bend in them every 4 cm ($M_{64} = 40.16 \pm 19.0$ mm). At a distance of 7.5 cm from the thicker end the stalk is bent at an angle of 180°, which may well be due to the fact that it was pushed in to the structure of the nest with the help of the bill. The total sum of the lengths of all stalks and blades of grasses and sedges was 67.217 m in nest No 26 and 68.425 m in No 396. The results are exceedingly similar despite the differences in building materials used. In nest No 26 (Table VIII) particular fractions were besides weighed, which made it possible to determine the differences in thickness, for dividing the aggregate length of elements by their weight we obtained the length of 2.68 m falling to 1 g of stalks and blades in the underlay, 9.35 m in the nest body and 26.13 m in the lining.

An analogic criterion was applied for tree leaves in different layers. A comparison of their numbers per gram shows that the leaves in the nest body are smaller and lighter (to 184 fragments per gram) than in the underlay (16.06 leaves per gram).

The inside of the nest cup is lined with the finest pieces of grass, namely, their inflorescences — panicles of *Milium effusum* or *Deschampsia caespitosa*. These panicles are however void of most ramifications, usually 1—3 peduncles are left. Half the nests examined contained animal hairs in the lining. There were exclusively hairs of the boar *Sus scrofa*, 4—8 in number in a nest.

Nest dimensions are given in Table IX. Only some of these nests were measu-

Table VIII

Number (N), mean length in mm (M±SD), total sum of lengths in or (L), weight at 10% humidity (G) and thickness index (L:G) of plant fragments used as building material in nest No 26 of River Warbler *Locustella fluviatilis*

Nest building material	Underlay						Peripheral layer						Body of nest						Inner layer (lining)						Total		
	N	M±SD	L	G	Thickness index	%	N	M±SD	L	G	Thickness index	%	N	M±SD	L	G	Thickness index	%	N	M±SD	L	G	Thickness index	%	N	L	%
Stems of nettles	18	29.3±33	4.1			10	15	58.5±33	0.9			9	—	—	2.3			—	—	—	1.0			—	33	8.3	2.9
Stems of other plants	65	54.5±36				36	—	—				—	34	67.7±60				10	25	41.0±28				6	124		10.9
Stalks and blades of grasses	7	62.9		2.1	2.7	4	28	161.9±87		5.9	1.7	16	226	72.6±53		2.0	9.4	64	370	85.5±63		1.3	26.1	85	631		55.3
Stalks and blades of other plants	29	38.2±19	1.5			16	39	123.4±54	9.3			23	—	—	16.4			—	—	—	31.7			—	68	58.9	6.0
Tree leaves	57	—	—	3.55	16	32	73	—	—	1.75	41.7	42	46	—	—	0.25	184	13	4	—	—	0.0	—	1	180	—	15.8
Leaf stalks	2	—	—	—	—	1	2	—	—	—	—	1	24	—	—	—	—	7	2	—	—	—	—	1	30	—	2.6
Birch twigs	2	—	—	—	—	1	1	—	—	—	—	—	1	—	—	—	—	0	—	—	—	—	—	—	4	—	0.4
Grass inflorescences	—	—	—	—	—	—	10	—	—	—	—	6	6	—	—	—	—	2	25	—	—	—	—	6	41	—	3.6
Rootlets	—	—	—	—	—	—	4	—	—	—	—	2	14	—	—	—	—	4	1	—	—	—	—	0	19	—	1.7
Moss	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	1	—	—	—	—	—	—	5	—	0.4
Boar hair	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	1	5	—	0.4
Remains of indet. plants	—	—	—	2.1	—	—	—	—	—	0.35	—	—	—	—	—	0.2	—	—	—	—	—	0.1	—	—	—	—	—
Total in layer	180	—	5.6	7.75	—	15.8	172	—	10.2	8.0	—	15.1	356	—	18.7	2.45	—	31.2	432	—	32.7	1.4		37.9	1140	67.2	100.0

red in the incubation period, the remaining ones after they had been left by the young.

The highest situated nest had its upper edge 28.0 cm above the ground and 15 out of the 39 nests examined lay directly on the substratum. A comparison of the mean measurements from the fresh nests measured in the incubation period with those left by youngs, presented in Table IX, shows that the differences are for the most part small, the longer inner diameter being longer and the height of the nest and its distance from the ground smaller as regards the means from used nests, which is only natural, since the young had stayed in them.

In the dead soil covering and among the stalks of grass tussocks only one or two ways lead to the nest. Nests accessible form many sides are rare (only 2 in 42 nests examined). Dry stems lying about often form a kind of foot bridge leading to the nest. These ways may approach from any quarter but the southern approach is the most frequent and the north-eastern one the rarest (Fig. 10).

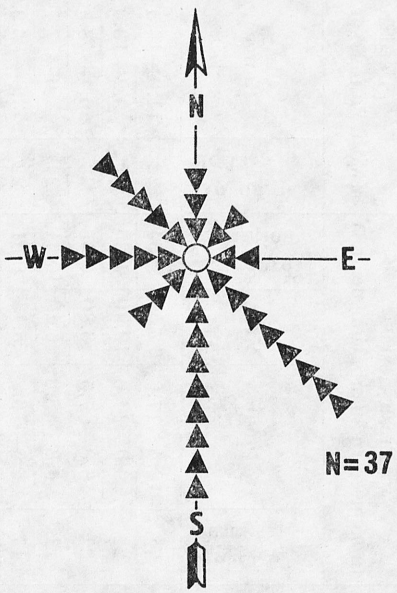

Fig. 10. Approaches to the nest of the River Warbler *Locustella fluviatilis* with regard to the points of the compass (N = 37 nests)

Nest building takes usually several days. In two cases of repeated broods there was a 7-day interval between the destruction of the nest and the laying of the first egg in a new one. The nest for the repeated brood of pair No 38 was built in the shortest time, within one day only (on June 14 the nest was destroyed and no later than June 16 in the morning the first egg was in the new nest).

Writing about the structure of the nest of the River Warbler, HARTERT (1910) mentions its three layers — external, internal and lining. Among the nest materials the authors name grasses and dry leaves of willows (FOURNES

Table IX

Dimensions of nests (in cm) of River Warblers *Locustella fluviatilis* and their situation in relation to the ground in north-eastern Poland

Dimension	Fresh nests (measured in incubation period)				Used nests (with youngs or abandoned)				All nest measured			
	No of nests	Range	Mean	Standard deviation	No of nests	Range	Mean	Standard deviation	No of nests	Range	Mean	Standard deviation
Longer outer diameter of nest	21	10.4—17.0	13.47	1.54	22	11.0—18.5	13.73	1.78	43	10.4—18.5	13.60	1.65
Shorter outer diameter of nest	21	9.0—14.0	10.90	1.35	22	9.2—13.0	11.30	1.06	43	9.0—14.0	11.10	1.21
Longer inner diameter of nest	21	6.0— 7.5	6.80	0.46	23	6.4— 8.5	7.07	0.59	44	6.0— 8.5	6.94	0.54
Shorter inner diameter of nest	21	4.8— 6.8	6.10	0.51	24	4.6— 7.1	5.93	0.66	45	4.6— 7.1	6.01	0.60
Depth of nest-cup	17	4.5— 6.2	5.11	0.51	22	3.8— 5.9	4.92	0.56	39	3.8— 6.2	5.00	0.54
Hight of nest	17	6.5—12.0	8.84	1.53	19	6.2—10.0	8.06	1.32	36	6.2—12.0	8.43	1.46
Distance of nest bottom from the ground	9	0.0—23.0	5.28	7.84	18	0.0— 4.5	0.64	1.19	27	0.0—23.0	2.19	5.00
Hight of ground hillock	10	7.0—28.0	16.40	7.93	12	5.0—27.0	11.63	6.47	22	5.0—28.0	13.80	7.40

1877, 1886; LINDNER 1897; NAUMANN 1905), leaves of alder and poplar (FOURNES 1930; NIETHAMMER 1937; PUCHSTEIN 1959) and those of beech and oak (LUDOROWSKI 1978; BOSCH & LAUBENDER 1978). DITTBERNER and DITTBERNER (1985) found 180 components of a nest, of which 50 thick stalks make up the external layer, 77 willow leaves the middle layer and 40 fine grass stalks the lining. In 2 other nests the same authors (DITTBERNER & DITTBERNER 1987) found 240 and 250 plant elements. It is interesting in so far that these figures for the nests analysed in the present study are 1140 and 1215 (Tables VII and VIII) and so 4—5 times as many. The lining of nests with animal hair is mentioned only by several authors (HARTERT 1910; REY 1912; NIETHAMMER 1937; DOLGUSHIN et al. 1972). The outer dimensions are rather variable, but the depth of the nest-cup is often given too small, which indicates that the measurements were taken after the departure of the young. The other dimensions lie within the range of those obtained for the population of north-eastern Poland. The situation of the nest on or just above the ground is described by most authors and only FOURNES (1886) observed two nests placed exceptionally at a height of 1 m. Most authors also write about the way leading to the nest from one side only (FOURNES 1930; HOFFMANN 1941; DITTBERNER & DITTBERNER 1985), comparing it to a foot-bridge of the Coot (TISCHLER 1941; BOSCH & LAUBENDER 1978).

VIII. EGGS AND INCUBATION

A. Size, colour and number of eggs in a clutch

The ready nest usually remains empty for several days. Only in the case of repeated broods, e. g. in pair No 38, the first egg was laid on the day following the completion of nest-building. Eggs are laid early in the morning, before 07.00. Females lay them towards the end of the night spent by them on the nes at daily intervals. Having laid an egg, the female generally stayed on the nest for some time.

In north-eastern Poland first eggs are laid between the 29th and the 34th pentad, i. e. from May 21 to June 19. Most females however lay them between May 31 and June 9. The modal date is June 7 (Fig. 11). Later dates of laying concern rather repeated or even second broods. In the population studied the latest date of the laying of the first egg was July 19.

The size of clutches of the River Warblers from north-eastern Poland averages 4.92 eggs per nest (modal = 5), ranging from 3 to 6 eggs (Table X). The size of clutches decreases in the period of egg-laying from 5 in the clutches from May and June to 4 in those from July (Fig. 11).

A total of 127 eggs of the River Warbler were measured. The mean dimensions of eggs of the population from north-eastern Poland were $19.67 \pm 0.80 \times 14.95 \pm \pm 0.46$ mm with N = 127 and a range of 17.7—22.15 × 13.6—16.05 mm.

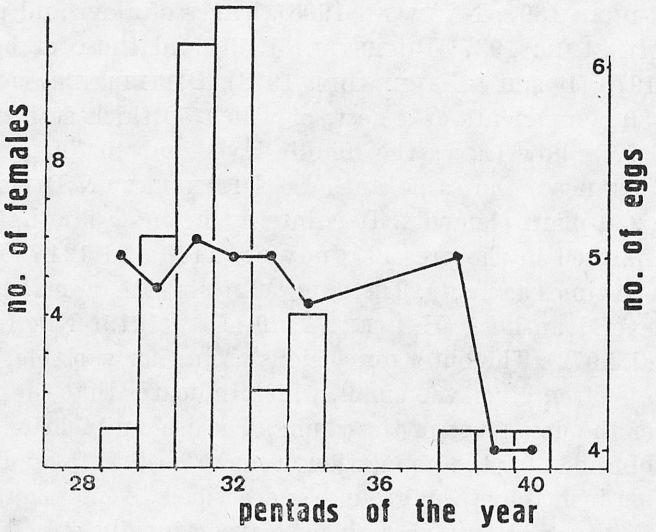

Fig. 11. Numbers of female River Warblers *Locustella fluviatilis* proceeding to egg laying in consecutive pentads (blocks) and the mean number of eggs in the clutch (solid line)

Table X

Frequency of various clutch sizes in River Warblers *Locustella fluviatilis* in north-eastern Poland

Number of eggs in nests	3	4	5	6	Total
Number of nests	1	4	29	3	37
Percentage	3%	11%	78%	8%	100%

The mean weight of the newly laid eggs is 2.54±0.36 g and it falls in the incubation period to 2.05±0.23 g (Fig. 12). The greatest fall in weight occurred in the heaviest egg, weighing 3.15 g and was 1.15 g, i. e. 36.5% of the original weight; in another egg, weighing 3.05 g it was 0.75 g or 31.1% whereas an addle egg lost hardly 13.1% (0.40 g, from 3.05 to 2.65 g). In the incubation period the egg loses on the average 0.49 g or 19.4% of its original weight (Fig. 12).

The eggs of the River Warbler are oval in shape. They are mostly white without gloss and finely spotted. Maculation is most frequently distributed evenly all over the surface, in about a quarter of the eggs examined it was intenser at the broad end. This density however usually does not form that wreath so distinct in some clutches of the Grasshopper Warbler, Savi's Warbler or Wood Lark. I found a well-seen wreath of spots only in one 5-egg clutch among all 127 eggs analysed. As a rule, two types of spots can be distinguished in each egg — deeper grey spots and superficial ones from red-brown in colour, through shades of pink-red to dark violet. Colour variation among particular clutches is fairly marked. Apart from the fact that the last eggs of a clutch are often paler, there are differences in the intensity of saturation of colours between clutches. Therefore, one may come across eggs in warm, dark-pink, greyish, dimmed colours

It was also observed that the intensely pink-red new-laid eggs became pale and greyish towards the end of the incubation period, before hatching. Unfortunately I failed to find what those changes consisted in. Generally, the more intensely pink eggs were the new-laid ones.

The dimensions of eggs quoted by various writers are mainly based on museum collections and are a generalization of the results obtained by other authors in various regions of the range of this species. HARTERT (1910) gives dimensions obtained from the greatest series of 100 eggs. They certainly included also eggs collected by him in north-eastern Poland. The mean dimensions from this collection are 20.01 × 15.12 mm. And so the Mazurian population has smaller eggs than are the eggs of HARTERT'S European set and 32 eggs measured by MAKATSCH (1976). Nevertheless, the extreme dimensions given by those authors lie within the range of those obtained for the population of north-eastern Poland.

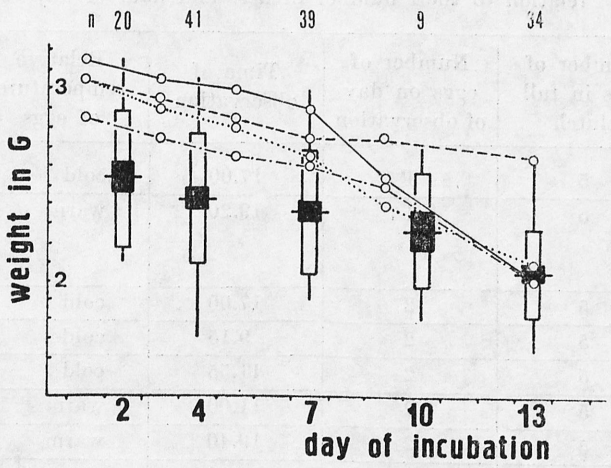

Fig. 12. Changes in the egg weight of the River Warbler *Locustella fluviatilis* during the incubation period. Vertical lines — range of variation, horizontal lines — arithmetic means, open blocks — SD, solid blocks — standard error of mean. The curves, besides, represent the all in weight of 4 eggs in one clutch

The matter of clutch-size in River Warblers dealt with by many authors presents itself similarly. LINDNER (1897) writes that most clutches consist of 4—5 and rarely 6 eggs. HARTERT (1910) adds that 3 eggs should be regarded as an incomplete clutch and NIETHAMMER (1937) accepts his opinion. The numbers of eggs in clutches given by DEMENTEV et al. (1954) differ from those stated by the foregoing European authors. According to him, the clutch contains usually 5—6 and sometimes 7 eggs. It may well be that the further to the east, the larger is the number of eggs in the clutch, although the other Soviet authors do not confirm this supposition, and MIERA (1970) observed near Leningrad even a nest with 3 eggs. The mean clutch-size from 18 nests from Czechoslovakia is 4.40 eggs (HUDEC et al. 1983) and so slightly lower than that for Poland.

Eggs of River Warblers were rarely weighed in Europe. The most exact data come from Czechoslovakia (HUDEC et al. 1983) but they suggest that they have been obtained from eggs advanced in the development of the embryo, weighed just before hatching.

B. Incubation

In River Warblers both males and females participate in egg incubation. After laying the fourth egg the female begins to incubate; single observations and finding of warm eggs in the nest show that no sooner has the female laid the first egg than she may spend the nights on the nest (Table XI).

Table XI

Temperature of eggs in nests of River Warblers *Locustella fluviatilis* in the Łężany area in relation to their number in nest and hour of day

Nest No	Number of eggs in full clutch	Number of eggs on day of observation	Time of observation	Relative temperature of eggs	Remarks
38	5	1	17.00	cold	
104	5	1	19.20	warm	Female scared away
26	5	2	17.00	cold	
104	5	2	9.15	cold	
226	5	2	11.55	cold	
38	5	2	11.00	warm	
2414	5	2	10.40	warm	
234	4	2	19.10	warmish	
306	5	3	17.00	cold	
234	4	3	8.45	warmish	
26	5	4	15.30	warm	
106	5	4	17.55	warm	
166	5	4	18.00	warm	
396	5	4	18.00	warm	

The incubating female has her breast thrust deep into the nest so that her head is of necessity upturned (the bill turned up even at an angle of 45°). The base of the bill often rests on the nest edge. Sitting down on the eggs, the female ruffles her feathers on the belly and stamps her feet. The characteristic ruffling of feathers, in which the whitish undetail-coverts often stick out beside the rectrices, and the deep thrusting of the breast into the nest are the features that permit us to distinguish the female from the male at first sight, for this last does not sit down so deep nor ruffles his feathers.

The warming of eggs during incubation demands that the bird shall stay in the same position for a fairly long time. And so the birds often fall asleep on the nest, such naps however do not last longer than 2 minutes. After awaking, the bird looks about attentively, especially when something is rustling in the surroundings of the nest or warning calls of other species can be heard.

As the nest is often placed in a clump of plants (e. g. that of sedges or nettles), River Warblers never fly direct to the nest, but come up to it on foot. The nest,

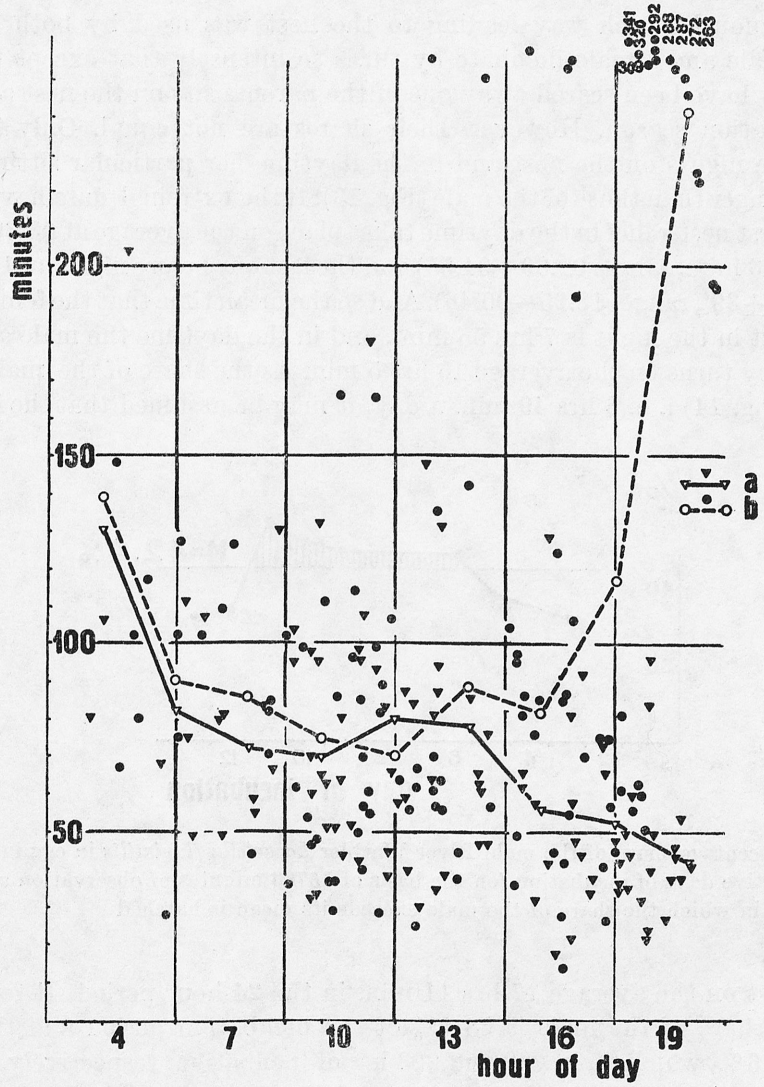

Fig. 13. Lengths of incubation periods in the male (a) and female (b) of the River Warbler *Locustella fluviatilis* started in consecutive hours of day. The curves connect the means in 120-minute periods from 35 days of direct observations of six nests

squeezed into a clump, can usually be reached by the birds from two sides and in some cases from one side only. Changes in the close surroundings of the nest, e. g. the cutting-away of the plants intercepting its view, made the birds change also their habit and they often used the strip cleared of plants as the main way to the nest. All the ways to the nest are used by both birds, although in the incubation period either of them shows a preference for one of the ways. The fact that the areas of activity of the male and female do not often coincide exactly in this period may be a general reason for such behaviour. During the period of chick feeding, when the birds were scouring the close vicinity of the nest strenuously, each way leading to the nest was used by both birds.

The male and female incubate by turns so intensely that except the whiles when they have been scared away one of the parents sits on the nest all through the incubation season. However, their shares are not equal. Only the female spends the nights on the nest and in the daytime her particular sittings on the nest are longer than those of the male (Fig. 13). If the extremal data have been left out, the first nest-relief in the daytime takes place on the average at 03.30 (n = 15, SD — ±46 min., range: 02.30—04.55) and the last one before night at 19.35 (n = 25, SD — ±39′, range: 18.25—20.46). And so the mean time that the female spends on the nest in the night is 7 hrs 55 min., and in the daytime the male and female incubate by turns on the average 16 hrs 5 min. As the share of the male average 42.4%, (Fig. 14) i. e. 6 hrs 49 min. a day, it may be assumed that the female sits

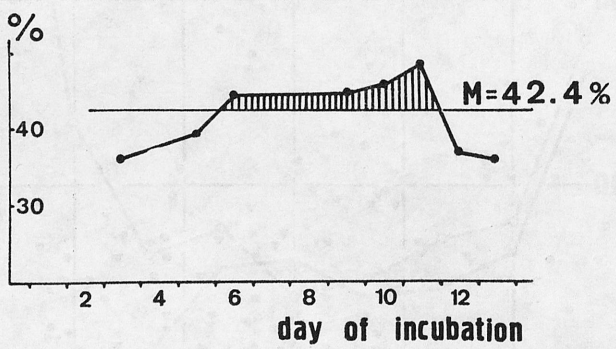

Fig. 14. Percentage share of the male River Warbler *Locustella fluviatilis* in egg incubation on the consecutive days of incubation (on the basis of 15766 minutes of observation at six nests). The period in which the share of the male exceeds its mean is hatched

on the nest on the average 17 hrs 11 min. in the 24-hour period. It follows that the total share of the male is 28.4% of the incubation period and that of the female 71.6%, which makes 89 and 223 hrs of incubation, respectively. Although in general incubation by the female prevails, three times daily the male sits on the eggs longer: following the first changeover after the female's night sitting, i. e. at 04.00, in the morning hours, i. e. at 10.00 and for the last time at 14.00 (Fig. 15). The male's share in incubation grows till the 11th day (Fig. 14)

to decrease later in connection with the release of his chick feeding instinct. This is manifested at some changeovers when the male arrives with food in the bill, which the female most frequently receives. However, this is not the feeding of the brooding female nor the manifestation of the male's desire to relax the tension evoked by the nearness of his partner, for he does not give all the food to her and sometimes even evades the begging female and when she comes off the nest at last, he endeavours to feed the chicks, of which there are none in the

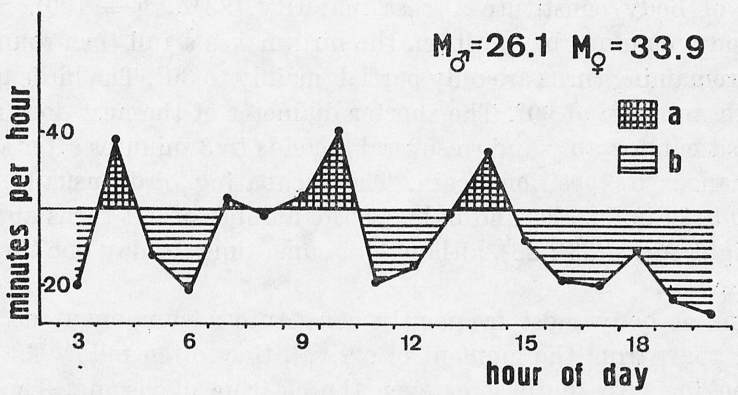

Fig. 15. Mean share of the male River Warbler *Lacustella fluviatilis* in egg incubation in minutes per successive hours of day. Periods of prevailing incubation by the male (a) or the female (b). Results of 31-day observation of incubation, during which the male incubated 6439 minutes (43.5%) and the female 8361 minutes (65.5%)

nest yet. While doing that, he sometimes utters calling voices, with which he usually induces the chicks to open their bills. It is not till then that he sits down on the nest, eating up the food left himself. The male and female change over on the nest on the average 6.7 times in 24 hours.

It would possibly seem that the time of a sitting on the nest is controlled by the arrival of the other partner in order to change over. However, it turns out that if the bird relief arrives too early, the incubating bird does not get off the nest. It happened that, after waiting over the incubating male for a few minutes, the female eventually gave up and went away. This occurred more frequently in wet and cool weather. When the male came with food, the female left the nest more readily, although there were only eggs in it. The comer is however able to get the incubating bird to rise from the nest with its restless behaviour and giving voices of discontent or by approaching from in front and pushing its bill and bent head under the neck or between the legs of the partner, or lastly, when coming from behind, by treading on it in the region of the wings or the tail.

In the course of the quiet warming of the eggs, the incubating birds present a number of behaviours, which are as follows:

1. Turns of body round the vertical axis of the nest

The vegetation that surrounds the nest not only causes its assymetric structure but also prevents the incubating birds from sitting whichever direction they please. The bird does not find enough room amidst the thick vegetation for its tail protruding beyond the edge of the nest. This is why, it usually takes adventage of the possibility to sit directed the same way it has got on to the nest or to perform a half-turn (through 180°) and to face the opposite way. Such turns of body constitute a vast majority (83%, n = 100). Sometimes, failing to find a comfortable position, the bird makes a full turn round the axis (360°). The remaining turns are only partial, mainly to 30°. The birds most rarely turn through an angle of 90°. The shorter diameter of the nest does not permit the bird to sit comfortably and so several seconds to 3 minutes after such a turn the bird changes its position again. The incubating birds usually turn both ways and so both in females and in males the number of left turns approximates to that of right turns (33 : 28), although at some times of day one the directions of turns prevails.

The turns of body most frequently constitute a component of a series of behaviours; apart from the moment of arrival, they often follow the turning of eggs, the looking into the nest or even the clearing of vermin. The frequency of turns is characteristic of particular specimens and therefore each pair examined pretty closely had its own rhythm, which differed highly significantly between pairs (test χ^2, $p < 0.001$). Females generally turn round more frequently (the frequency calculated from 506 turns noted in 247 hrs of observation was 2.31 turns per hr in females and 1.71 in males). Pair No 20 showed the highest difference in frequency in favour of the female, in whom it reached 282% of the male's frequency (Table XII). This however is not the rule, for in pair No 10 the male exceeded the female in frequency of turns by 140% (3.61 : 1.50), these differences being still higher on some days (Table XII). Similarly, the male turned more frequently in pair No 67 (1.32 : 1.08 — Table XII). The highest number of turns was noted in female No 20, who during one day (25 June 1970) made as many as 53 turns during 554 minutes of incubation (on the average 5.7 turns per hr), whereas on the same day the male turned about only 6 times in 421 minutes (0.9 turn per hr).

The turns decrease in number with the progress of incubation (Fig. 16A) and practically stop the moment the last chick hatches. The presence of eggs in the nest always stimulates impulsive turns of body even in the birds feeding their young. In the right-hand part of Fig. 16A it can be seen to what extent this impulse persists. The results of observation of pair No 38, which had 1 chick and addle eggs in the nest, are shown in this part. The body turns associated with egg turning occur also in birds feeding the young in the first minutes after the fledgelings have left the nest if at least one addle egg is in it (e. g. pair No 18).

In the day-and-night period the frequency of body turns undergoes greater fluctuations in females than in males (Fig. 17A). Males, having relieved females

Table XII

Frequency of turns of body and egg-turning and the number of egg-turnings falling to one body turn in males and females of 4 pairs of River Warblers *Locustella fluviatilis* on successive days of incubation

	Number of hours of observation of incubating bird								Number of turns of body per hour								Number of egg-turnings per hour								Number of egg-turnings falling to one body turn							
	Male				Female				Male				Female				Male				Female				Male				Female			
Nets / No / Day	20	106	67	38	20	106	67	38	20	106	67	38	20	106	67	38	20	106	67	38	20	106	67	38	20	106	67	38	20	106	67	38
3	5.0	—	1.42	—	8.57	—	3.58	—	0.4	—	2.1	—	5.5	—	1.4	—	3.2	—	0	—	5.6	—	0.6	—	8.0		0	—	1.0	—	0.4	—
4	—	—	2.13	—	—	—	2.75	—	—	—	2.3	—	—	—	1.1	—	—	—	0.5	—	—	—	1.1	—	—		0.2	—	—	—	1.0	—
5	7.02	—	0.45	—	9.23	—	1.6	—	0.9	—	4.4	—	5.7	—	0.6	—	3.7	—	6.7	—	4.8	—	5.6	—	4.3		1.5	—	0.8	—	9.0	—
6	7.85	1.08	1.57	4.2	7.33	1.97	1.93	5.02	1.4	1.8	4.5	3.1	4.9	1.5	0	1.2	4.5	5.5	7.0	4.5	5.3	2.5	2.6	4.6	3.2	3.0	1.6	1.5	1.1	1.7	∞	3.8
7	—	3.87	6.32	1.1	—	5.13	5.3	1.15	—	3.6	0.6	0.9	—	2.5	1.3	0	—	3.9	5.7	3.6	—	3.3	3.8	0.9	—	1.1	9.0	4.0	—	1.3	2.9	∞
8	—	3.93	6.48	1.43	—	3.68	8.27	2.65	—	5.1	1.4	1.4	—	3.3	1.5	1.7	—	3.1	6.3	1.4	—	6.5	4.7	4.2	—	0.6	4.6	1.0	—	2.0	3.3	2.2
9	—	—	5.47	2.85	—	—	2.6	3.07	—	—	1.6	2.1	—	—	0	2.9	—	—	5.3	1.4	—	—	1.9	3.3	—	—	3.2	0.7	—	—	∞	1.1
10	3.85	2.45	—	2.32	2.55	1.6	—	1.47	4.2	4.9	—	0.4	9.4	0	—	2.0	5.5	3.7	—	1.7	7.1	6.3	—	4.1	0.8	1.3	—	4.0	0.8	∞	—	2.0
11	1.65	3.65	3.27	1.53	2.52	5.53	1.8	1.98	5.5	2.7	1.2	1.3	1.6	1.3	1.1	2.5	1.8	3.6	5.2	0.7	1.6	4.5	4.4	2.5	0.3	1.3	4.3	0.5	1.0	3.6	4.0	1.0
12	0.83	4.43	4.73	3.17	2.17	3.9	5.87	5.15	3.6	3.8	1.1	2.2	3.2	1.3	0.5	1.6	4.8	3.2	5.7	4.1	6.5	5.4	4.9	5.6	1.3	0.8	3.0	1.9	2.0	4.2	9.7	÷3.6
13	0.1	0.97	6.75	5.02	1.7	1.43	8.10	6.9	10	3.1	0.4	1.4	4.7	1.4	1.5	1.6	0	2.1	1.9	3.0	6.5	9.1	2.7	4.9	0	0.7	4.3	2.1	1.4	6.5	0.9	3.1
14	1.68	3.43	—	4.53	2.17	7.52	—	4.02	3.0	2.3	—	0.9	6.5	0.5	—	1.2	1.2	3.8	—	2.9	0.5	1.5	—	2.2	0.4	1.6	—	3.3	0.1	2.8	—	1.8
	27.98	23.81	38.59	26.15	36.24	30.66	41.80	31.41	1.89	3.61	1.32	1.64	5.33	1.50	1.08	1.66	3.84	3.51	4.80	2.87	4.94	4.32	3.47	4.08	2.02	0.98	3.35	1.74	0.93	2.74	2.91	2.46
M_4	Total 116.53 h				Total 140.11 h				2.00				2.40				3.87				4.14				1.88				1.68			

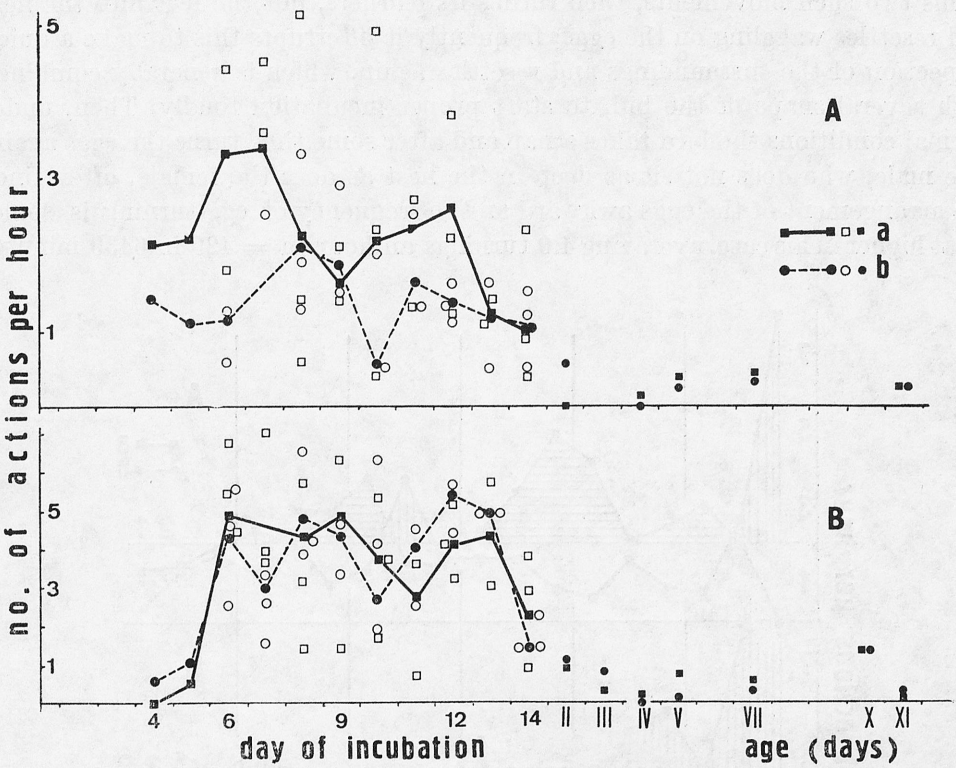

Fig. 16. The frequency of body turns (A) and egg turns (B) in male (a) and female (b) River Warblers *Locustella fluviatilis* in successive days of incubation. The results of observation of 3 pairs for 26 days: body turns, n = 326 for males and 364 for females. The results of observation of pair No 38 in the nest with 1 chick and addle eggs are given on the right hand side of the graphs

after their night-sitting on the nest, perform body turns most frequently during their first sitting period. Next in the daytime only about 13.00 and 17.00 they turn about more often than in other periods when, i. e. at 05.00, from 09.00 to 10.00 and from 14.00 to 16.00 females seemingly make up for males' inactivity. However, the body turns are not regularly spaced out during each sitting on the nest. Both the male and the female make the first turns immediately after starting incubation and so 68% of turns were observed in the first five minutes of sitting. Long periods of brooding are observed during which the birds do not turn about, followed by whiles in which turns occur at short intervals.

2. Egg turning

Having settled down on the nest, the incubating bird usually rises as early as the first minutes, moves back, leaning its tarsi against the edge of the nest. After a short inspection of the inside of the nest the bird swings its lower mandible backwards towards its body to change the position of the eggs. It often per-

forms two such movements, then ruffles its feathers, put the feet into the nest and resettles waggling on the eggs; frequently it interrupts this to make a quick inspection of the surroundings and resettles again, which is generally combined with several snaps of the bill, to start proper incubation finally. Then, under normal conditions the bird takes a nap and after some time turns the eggs again. The male, who does not sit as deep in the nest as does the female, often finds the arrangement of the eggs awkward and so frequency of egg-turning is somewhat higher in his case, averaging 4.0 turnings an hour (n = 429 in 6439 minutes

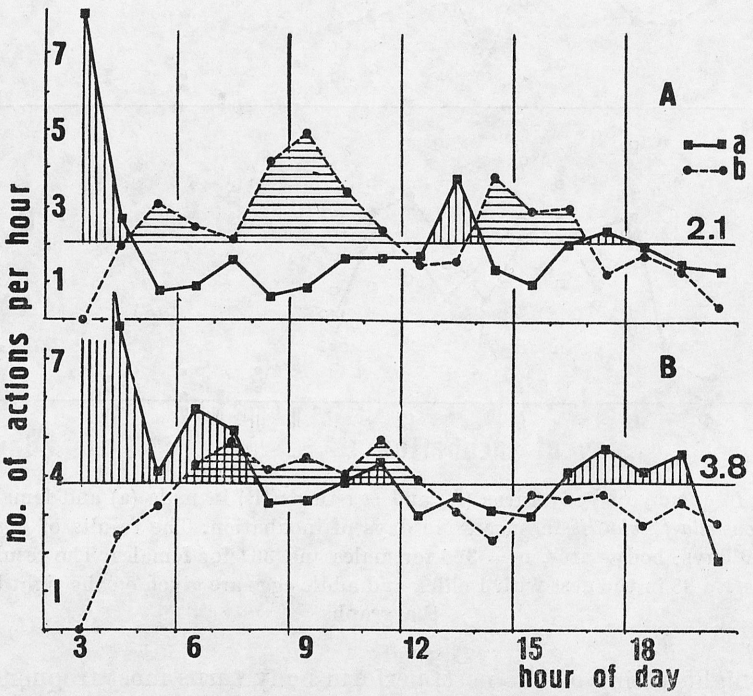

Fig. 17. Body turns (A) and egg turns (B) performed by the male (a) and female (b) River Warblers *Locustella fluviatilis* in consecutive hours of day. The results of observation of 5 nests for 31 days: body turns, n = 184 for males and 322 for females; egg turns, n = 429 for males and 510 for females

of observation), whereas it comes to 3.66 turnings an hour (n = 510 in 8361 minutes of observation) in the female. The frequency of egg-turning does not decrease as distinctly with the progress of incubation as does that of body rotation (Fig. 16B). After the hatching of the whole brood the action of egg-turning is replaced in the sitting bird by that of looking into the nest, which little differs in appearance from the former in the first three days. As mentioned above, in a nest containing one chick and addle eggs egg-turning was done despite the presence of the chick (Fig. 16B). The increase in the number of turnings on the 10th day was connected with the temporal absence of the only chick from the nest and the resumption of incubation of two addle eggs by the parents.

In the course of day the male turns the eggs more frequently at the outset of incubation, when he has relieved the female after her night sitting, up to 07.00 and towards the end of the day from 16.00 to 19.00. The female, who usually turns the eggs less frequently, shows a rise in this activity in the morning hours, between 06.00 and 12.00. (Fig. 17B).

As in the case of body turns the frequency of egg-turning is an individual feature and particular pairs show significant differences (chi-square test, $p < 0.001$). Pairs Nos 20 and 106, mentioned above, may serve as examples. Female No 20 overtopped her mate not only in respect of frequency of body turns but also in that of egg-turning, which is 4.94 turnings an hour ($n = 179$ in 2175 minutes of observation). On the other hand, female No 106 was in defiance of the rule less active as regards turns of body and yet, also despite the tendency prevailing in the population, was more active in egg-turning than the male and reached a higher mean than the average (4.32 — Table XII).

3. Keeping the brood safe

The vigilance of the incubating bird is manifested by its attentive observation of the surroundings of the nest. It responds in this way to each unfamiliar sound and to warning calls of Marsh Warblers, Garden Warblers and Blackbirds. Intense vigilance of the River Warbler is also elicited by the luring calls of the Red-backed Shrike, perching in the vicinity, and by various rustlings. The incubating bird reveals its anxiety and even alarm in three ways, according to the degree of stimulus. Ritualized watchfulness, usually following egg-turnings or short naps or occurring at the time of falling raindrops, manifests itself by a light rise of the head extended for 1 cm to the front. Having examined the surroundings with one eye and next the other, the bird feels reassured. The whole action takes scarcely about 2 seconds. The signs of a higher degree of alarm are an outstretch of the neck to a height of 2—3 cm and a longer inspection of the surroundings, with feathers ruffled on the head and sleek on the neck. Such a posture may be kept for 15 seconds and interrupted several times when the bird resumes its initial position. The highest degree of alarm, still allowing the bird to remain on the nest, is manifested by an extension of the neck for its whole length, while the feathers lie sleek all over the body and the head of the bird seems to be exceptionally small. The disquieted bird remains motionless for a pretty long time until the disturbance recurs or its cause becomes evident. At the sight of a bird of prey, e. g. a Hooded Crow, Jay or Red-backed Shrike, alighting not far away, it may keep still for some dozen seconds. Seen from the side, in posture it then resembles an alarmed Bittern. When the danger is fixed ot the enemy, e. g. a man, comes still nearer, the bird springs out of the nest to distract him by running zigzag in the lower layer of last year's stalks, without uttering any voices. Only rustlings are then heard, probably made by the rubbing of the vehemently stretched wings against the substratum. However, this distraction behaviour does not occur until the time immediately preceding

the hatching of the chicks and can be still observed as late as the 7th day of their life.

Attempts were made in this investigation to grasp all the moments of anxiety and vigilance. Some ritualized responses may have been overlooked by the observers working by turns. Nevertheless, all the alarms of second and higher degrees were registered. Their frequency per hour on successive days of incubation is presented for two pairs in Fig. 18. It shows that the female feels safer

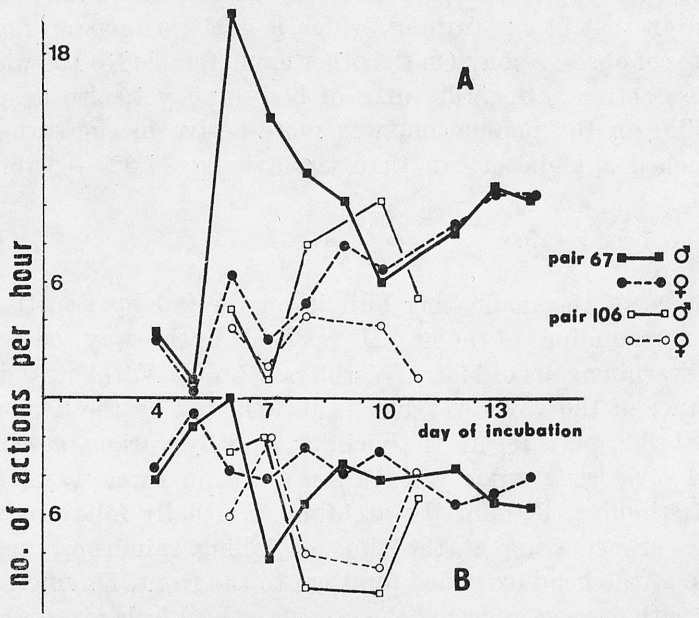

Fig. 18. The mean number of bouts of anxiety (A) and dozes (B) of River Warblers *Locustella fluviatilis* in successive days of incubation of two pairs: No 67 — thicker lines, No 106 — thinner lines, males — solid lines and females — broken lines. Means from 17 days of observation: watchfulness (n = 786) and dozes (n = 517)

on the nest than does the male. On the consecutive days of incubation the brooding birds do not become more used to their situation nor feel at rest but on the contrary they are more restless. Anyhow, in the course of day the male is at most rest when he has relieved the female after night, between 04.00 and 06.00 (Fig. 19A). As the temperature rises and the daylight brightens, he becomes increasingly restless till 13.00. After calming down about 15.00, he is uneasy to 17.00 and again at rest in the evening. The female shows an analogous daily pattern of the periods of restlessness only that her maximum watchfulness occurs an hour earlier, i. e. at 12.00 (Fig. 19A). The female is generally more at ease, with her mean of 3.48 alerts an hour (n = 485 in 8361 minutes of observation), while in the male this mean is 4.18 (n = 449 in 6439 minutes).

4. Sleep on the nest

Inactivity and motionlessness during incubation send the bird to sleep on the nest. However, although the bird's eyes are closed, its sleep is not deep, which is evidenced above all by its sensitivity to all uncommon and danger-foreboding sounds. Besides, the bird's head is kept in its normal position and not tucked under the coverts of the back and the wing, as it is during night sleep. Deep sleep with the bird's head turned backwards occurs only in the last minutes of the day, when the female starts her night rest on the nest. During 11 years' study there were only several observations of birds falling asleep in the daytime. Frequent slumbers on the nest during incubation take a short time even if there are no distinct reasons for awakening. In 95% of cases they did not exceed 2 minutes and the longest sleep bout lasted 5 minutes. As a result

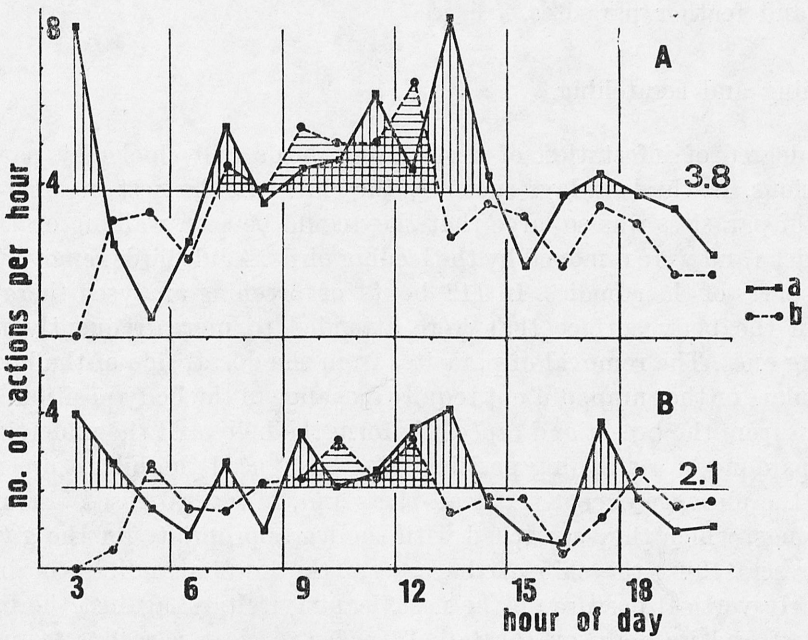

Fig. 19. Numbers of bouts of anxiety (A) and dozes (B) in the periods of incubating by males (a) and females (b) of the River Warbler *Locustella fluviatilis* in consecutive hours of day. Means from 31 days of observation of 5 nests: anxiety, n = 449 for males and 485 for females; dozes, n = 239 for males and 271 for females

these slumbers on the nest should rather be referred to as dozes. In addition to the bird's posture, they differ from deep sleep in that the boundary between wake and sleep is blurred. As the time passes, the bird, getting motionless, gradually narrows the eye slits, and the lower eyelid is drawn up until the eyes are closed completely. However, the bird often keeps the eyelids halfclosed as long as several tens of seconds, even turning its head towards the source of the sound without opening the eyes. The transition from the state of vigilance to sleep

usually takes a short time, the shorter the longer the birds sits on the nest at a stretch. On the other hand, the sleepy bird more often ends its naps with a short unquiet look at the surroundings to fall asleep again. This being so, it might seem paradoxical that the bird's frequent falling asleep induces an increased number of bouts of watching (Fig. 18B). In male No 67, except for the 5th day of incubation, when he was restless all the time he spent on the nest, the positive correlation of these two states is distinct. It is also supported by the fact that the male falls asleep on the nest more frequently (2.23 dozes an hour with n = 239 in 6439 minutes of observation) than does the female (1.49 dozes an hour with n = 271 in 8361 minutes). In the daytime the male falls asleep most frequently at noon, from 12.00 to 13.00, and short after 17.00. He also sleeps after the first changeover, following the female's night duty on the nest (Fig. 19B). In the female the daily pattern of slumber periods is more equalized. Sleep of the incubating birds may also be interrupted by bites of nest and feather parasites.

5. Preening and scratching

The degree of infestation of nests, adult birds and chicks by parasites is very various. In the last days spent by the chicks in the nest in some pairs the number of parasites was so large that they could be seen walking on the heads of the chicks and were removed by the feeding birds. Adult birds remove parasites from all parts of their bodies. In 112 bouts of preening analysed there were no places on the body surface that were attended to more frequently than the remaining ones. The removal of parasites from the dorsal side of the body, from the scapulars or the rump, did not require a change in the body position. Clearing of vermin from the breast and especially form the belly and the underside of the wings was done in a standing position. The birds used the bill to preen all the parts of the plumage except the head-parts and, in several cases, the underside of the wings, which they scratched with the leg appropriate for the given body side. For scratching the chin or the base of the lower mandible the bird took up a nearly vertical posture on the nest, leaning its tarsi against the back wall of the nest and its body on the tail. In order to clear parasites from the top and the posterior part of the head, the scratching leg reached the head avoiding the stretched wing from behind (behind the flight feathers).

In the period of incubation the frequency of preening and scratching is generally higher in the female (2.18 bouts an hour, with n = 304 in 8361 minutes of observation) than in the male (1.58 bouts an hour, with n = 170 in 6439 minutes) and increasing with the progress of incubation (Fig. 20). Intenser removal of parasites by the female is the consistent consequence of her longer stay on the nest. After the hatching of the young its frequency falls distinctly. Now the adult birds stay on the nest shorter and they spend more time getting food for the growing chicks, which does not permit them to busy themselves much in clearing their bodies of parasites.

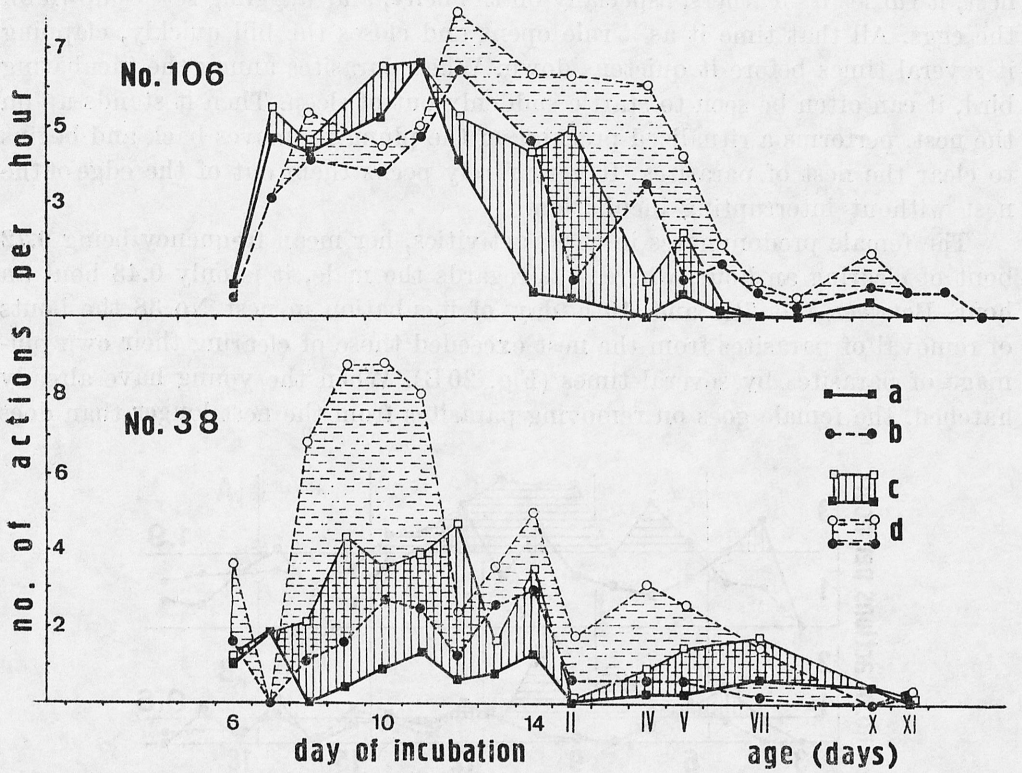

Fig. 20. The process of preening of male (a) and female (b) River Warblers *Locustella fluviatilis* and the pecking-up of parasites from the nest by males (c) and females (d) in successive days of incubation and the nesting period of chicks (age inscribed in italics) in broods of 4 chicks (No 106) and 1 chick (No 38). The curves connect the mean numbers of preenings of birds (n = 110 for males and 163 for females) and clearings of parasites from the nest (n = 71 for males and 106 for females)

In the course of day females preen on the nest most frequently between 06.00 and 14.00 and their activity curve resembles the curve of air temperature close to the ground, whereas as regards males, they preen more frequently towards the end of the first period of sitting on the nest (about 04.00), at 10.00 and at 12.00. And so, in general, a rise in the ambient temperature may activate nest parasites.

6. Pecking-up of nest parasites

Preening is a commonly known behaviour of incubating birds, but their activity aiming at finding parasites in the nest is more interesting; it is often confused with egg-turning, because the initial position of the bird is the same in both cases, namely, pecking up parasites, it stands in the nest with its tarsi lean ing against the nest edge and drawing its body high to the back, it bends its head down into the nest-cup, scrutinizes its inside at very close quarters, scarcely more than 10 mm, and pecks several (usually 3—5) times. Next, standing on the

nest, it ruffles its feathers, especially on the belly, and waggling settles down on the eggs. All that time it as a rule opens and closes the bill quickly, clapping it several times before it quietens down. When parasites annoy the incubating bird, it can often be seen to startle suddenly out of sleep. Then it stands up on the nest, performs a ritualized preening of the plumage, moves back and begins to clear the nest of parasites. It very rarely pecks them out of the edge of the nest without interrupting incubation.

The female predominates in these activities, her mean frequency being 0.72 bout of clearing an hour, whereas as regards the male, it is only 0.48 bout an hour. Between the 7th and 10th day of incubation in nest No 38 the bouts of removal of parasites from the nest exceeded those of clearing their own plumage of parasites by several times (Fig. 20B). When the young have already hatched, the female goes on removing parasites from the nest longer than does

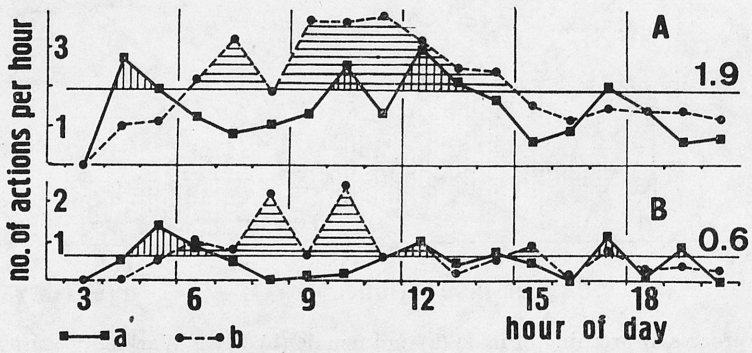

Fig. 21. Preening (A) and pecking-up of parasites from the nest (B) by males (a) and female (b) of the River Warbler *Locustella fluviatilis* in consecutive hours of day. The curves connect the means from 31 days of observation at 5 nests: preening, n = 170 for males and 304 for females; pecking up parasites, n = 51 for males and 101 for females

the male (Fig. 20A). Parasites are cleared from the nest at all times of day an increase in frequency being shown by the female between 08.00 and 10.00 (Fig. 21A). The small number of the bouts of clearing parasites from the nest by the male makes it impossible to establish his rhythm exactly. Nevertheless, his clearing the nest of parasites can be observed from time to time all day long (Fig. 21B).

7. Bill-clapping

The quick closing and opening of the bill is a very characteristic behaviour of the River Warbler on the nest. It is well known in all song birds. The movements of the mandibles are quick, several in a second. Their number is variable, more often than not conditioned by the preceding action. Attempts made to count the bill claps show that their number most frequently ranges from 3 to 8, but in some cases such a series may be repeated 2 to 4 times.

This behaviour mostly follows activities in which the bill is utilized, i. e. egg-turning, clearing parasites from the bird's body and the nest, catching insects and drinking dew or raindrops from plants. It is often observed also when the bird resettles on the nest or after moments of tension caused by a threat to the nest safety. After bouts of watchfulness it is a comfort behaviour. Hence a great concurrence of the frequencies of bill-clapping and resettling (Fig. 22 A). An increase is besides observed in the number of clappings in pairs Nos 106 and 67, parallel to the bouts of anxiety of male No 67 between the 5th and the 8th day and towards the end of incubation (Fig. 22 A). The shapes of the curves for pair No 106 are also similar but numbers of both bill-clappings and resett-

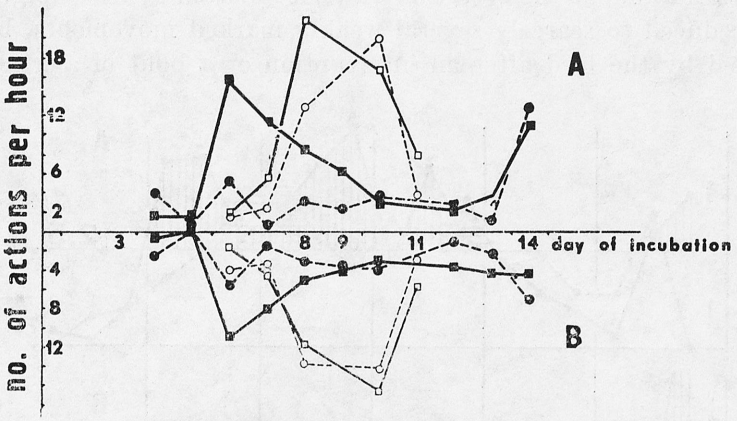

Fig. 22. The frequency of bill-clapping (A) and resettling on the nest (B) of River Warblers *Locustella fluviatilis* in successive days of incubation by 2 pairs (No 67 — thicker lines, No 106 — thinner lines, males — solid lines, females — broken lines). Means from 17 days of observation: bill-clapping, n = 237 for males and 185 for females; ressetling in the nest, n = 160 for males and 152 for females. Symbols as in Fig. 18

lings are considerably higher than that of bouts of anxiety. The greater frequency of clappings noted in the male than in the female to a certain extent confirms the fact this behaviour is a reaction to stresses. The frequency is, respectively, 2.96 clappings an hour (n = 318 in 6439 minutes of observation) and 2.12 clappings an hour (n = 296 in 8361 minutes of observation). Except for the last day of incubation this frequency is maintained at a similar level by the female and decreases in the male (Fig. 22 A). On the other hand, in the course of day it fluctuates from 09.00 to 17.00, showing similar maxima and minima, particularly in the male; in the female it decreases regularly from 14.00 till her night rest (Fig. 23 A). These activities were found to be least numerous in the male at 05.00 and from that moment to 10.00 the frequency of bill-clapping grew systematically. In the female the morning minimum is not so distinct. Nevertheless, she performs bill-clapping simultaneously with resettling on the nest.

8. Resettling on the nest

The contents of the nest, eggs at the time of incubation and chicks after hatching, make the sitting-down bird take some measures in order to protect them against destruction. And so it gets into the nest placing its feet on both sides of the eggs; bending its head forward, it ruffles its feathers both on the belly and on the back and starts to waggle quickly, lowering itself on to the eggs at the same time (which in German is termed "einkuscheln"). It has been mentioned above that the resettling of a bird is usually accompanied by its bill-clapping. Each time the bird stands up on the nest, e. g. to remove parasites, turn the eggs or turn round on the nest, this action is followed by resettling. Ritualized resettling, reduced to scarcely several weakly marked movements, begins each doze resumed by the bird after an interruption or a bout of alertness, during

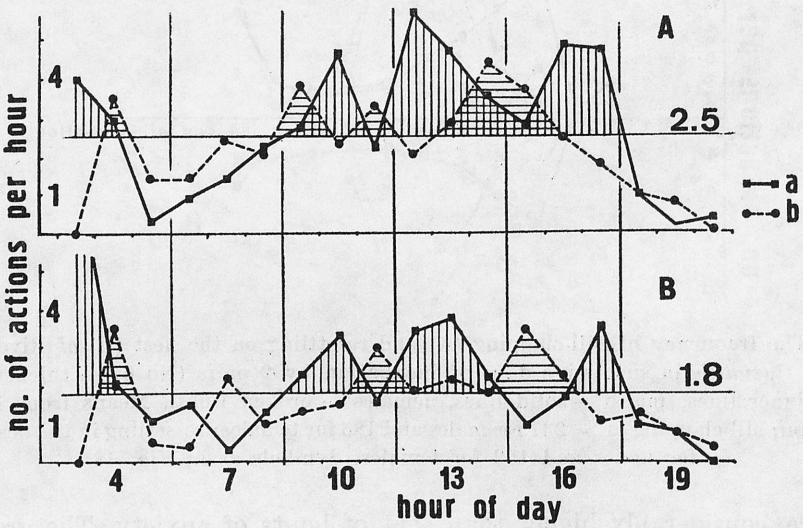

Fig. 23. Numbers of bill-clappings (A) and resettlings in the nest (B) of River Warblers *Locustella fluviatilis* during the incubation by males (a) and females (b) in successive hours of day. Means from 31 days of observation at 5 nests: bill-clapping, n = 318 for males and 296 for females; resettling in the nest, n = 220 for males and 225 for females

which it need not get up on the nest. A quantitative analysis of these activities (Fig. 22B) carried out on 2 nests shows similar changes in the frequency of resettling to those in bill-clapping. In female No 67 it keeps up at a similar level with a slight rise in the last three days of incubation and in the male of the same pair the great frequency on the 5th day (caused by his being often disturbed and unable to fall asleep) is followed by a decrease till the 9th day to a level which remains unchanged later up to the hatching of the young. In the male the frequency is higher and comes to 2.05 resettlings an hour (n = 220 in 6439 minutes of observation), whereas in the female it is 1.61 resettlings an hour (n = 225 in 8361 minutes). In the course of day the frequency behaves similarly

to that of bill-clapping, i. e. its minimum occurs in the morning, at 07.00 in the male and from 05.00 to 06.00 in the female. In the female it decreases continuously from 15.00. The male resettles most frequently after the first relief of the female following her night duty. The course of changes in the frequency of resettlings of the male during the day is exceedingly concurrent with the frequency at which the bird falls asleep (Fig. 23B and 19B).

9. Yawning

Among the activities which are not associated directly with the period of incubation and take place rather sporadically, yawinng is most regular. The incubating bird opens the mendibles very wide in a fraction of a second, without changing the position of its body. This may occur and in fact occurs most frequently just after its settling down or during a break between dozes or

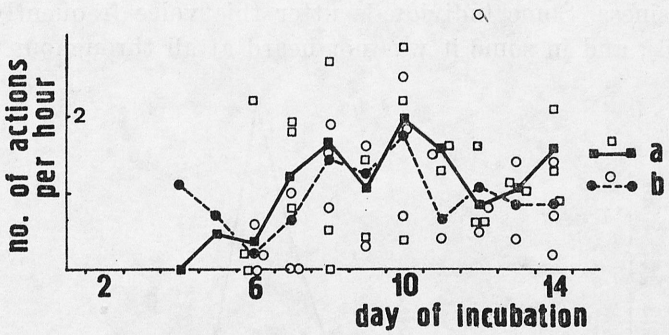

Fig. 24. The frequency of yawnings in male (a) and female (b) River Warblers *Locustella fluviatilis* in successive days of incubation. The curves connect the means of 3 nests from 26 days of observation of yawning (n = 209)

lastly, after egg-turning. The action is so short and unsignalled by any changes in the bird's behaviour that I failed to take a photograph of it.

The frequency of yawning is similar in both partners and increases slightly during the process of incubation especially in males (Fig. 24). It keeps at the same level in the period of chick brooding. However, individual birds show rather considerable differences in frequency, typical of each of them.

10. Feeding on the nest

The sitting bird as a rule feeds off the nest, when relieved by its mate. It can however be seen to eat a prey that has happened to be within the reach of its bill, no matter how much time has passed since it began incubating on the nest. The sight of an aphis moving about on a stalk releases an impulse in the sitting bird to snatch it. The bird reacts similarly to aphides, gnats and other small dipterans flying over the nest. It attacks them always keeping its sitting

position and only exceptionally stands up on the nest to eat an insect. The number of insects taken from the air is almost equal to that of insects caught on plants. Anyhow, this is not regular feeding but seems rather to be an automatic response to a visual stimulus. In the same way the brooding birds drink off raindrops hanging from plant stalks.

11. Uttering of sneezing-like sounds

The incubating birds in principle behave silently. Only sometimes the upset male utters a calling voice or call of uneasiness, when the female refuses to make room for him on the nest. And yet the sitting birds can produce a sound which is hardly audible at a distance of 2 m. Perhaps they utter it also off the nest. The sound is surd and rather resembles a vehement letting-out of air, lasting scarcely a fraction of a second and is similar to sneezing. The incubating bird utters it as if by the way and so without looking about for its mate nor at a moment of uneasiness. Some individuals utter this voice frequently, e. g. male No 67 (Fig. 25), and in some it was not heard at all throughout the period of

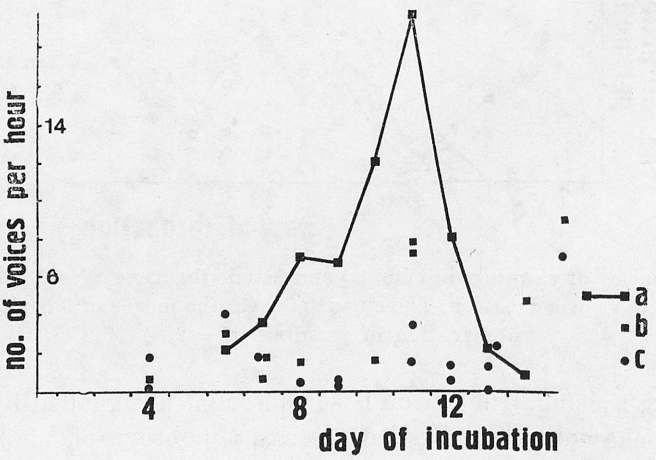

Fig. 25. The frequency of sneezing-like voices by incubating River Warblers *Locustella fluviatilis*; a — male No 67, b — other males, c — females

incubation. The male generally "sneezes" more often than does the female. "Sneezing" is more often heard in the hours of full day than early in the morning and in the evening. A sleeping bird "sneezes" sometimes as well. In some cases the voice is repeated several times at intervals of several seconds. Its frequency increases with process of incubation and it was also heard on the day of hatching. The frequency curve for male No 67 however shows the greatest activeness in this respect on the 10th day of incubation. The voice is uttered exceedingly rarely when the young remain in the nest.

* *
*

To sum up, particular types of behaviour rarely occurred separately. Body turns were usually followed by egg-turning and this by resettling and bill--clapping. Each slumber was interrupted by whiles of increased vigilance. When in this connection the bird rose on the nest, it next resettled for another doze. Each incident of insect catching, preening, clearing a parasite from the nest or egg-turning ended with bill-clapping. It was however hard to distinguish such groups of these activities as formed blocks of linked behaviours, because the bird modified them each time either by repetitions or by changes in order. For this reason each of them has been presented separately.

In the course of this investigation on the River Warbler a series of meteorological measurements were taken so as to elucidate the influence exerted by some weather constituents upon the process of incubation. Temperature was measured at the level of the nest, i. e. 5 cm above the ground and at a height of 1 m, the insolation of the ground surface was examined and the wind power and direction were recorded.

Air temperature and winds had no significant influence on the process of incubation. When at noon on hot days the sunshine reached a bird incubating on the nest, it panted for a few minutes. The strong wind only extended the while of vigilance on the nest and when it swept away and broke dry stalks all around, the bird showed third-degree alarm. The effect of precipitation was most distinct, for when it rained, the bird kept motionless, without turning its body and the eggs in a characteristic manner and without preening and resettling on the nest. The bouts of vigilance were also reduced to a minimum. After 15—30 minutes of rain the bird stood up on the nest and shook its feathers by moving the body from side to side in order to remove the raindrops from them. Sometimes it only clapped its bill. After the rain the bird usually drank off the raindrops hanging from the stalks of nettles. The rain also markedly delayed the evening changeover of the partners — up to 40 minutes above the average time. The influence of light is manifested mainly by the times of nest reliefs: the more cloudy the sky the later the first morning relief took place and the earlier the last evening one. This is more evident in the period of feeding of the young.

C. Hatching

As can be seen from Table XI, the incubation period begins after the laying of the fourth egg and ends with the hatching of the first young on the 14th day of incubation (in 6 nests) and on the 15th day in some nests with 5 eggs. Spending the nights on her incomplete clutch (Table XI), the female induces an increase in the interval between the hatching of the first and the last chick, which may reach 3 days. Hence it follows that the incubation period lasts

(counting from the laying of the fourth egg) (13) 14—15 (16) days. In nest No 38 the egg from which the only chick hatched was the first egg laid and it did not hatch before the lapse of 16 days.

The first chicks hatch mostly in early morning hours, the last ones at any time of day. Naturally, the chick hatches on its own. In most of the pairs observed the incubating birds, otherwise behaving in a routine manner, often look into the nest at this time. In the female the frequency of such inspections increases with the approach of hatching to four an hour, whereas in the male it decreases from day to day in the course of incubation, but on the day of hatching in pair No 38 the number of inspections was 7.1 an hour (Fig. 26). The

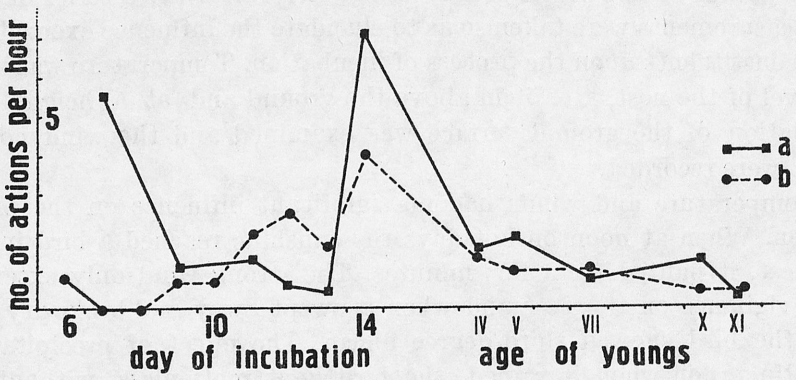

Fig. 26. The frequency of lookings into the nest by the male (solid line) and the female (broken line) of pair No 38 of River Warblers *Locustella fluviatilis*, incubating 5 eggs, of which only one chick hatched

egg-shells left by the young in the nest are removed chiefly by the female. Before pulling a shell out, she looks several times into the nest (seven times in 9 minutes preceding the removal in nest No 106), trying to take it by the edge in her bill. She swallows crumbling pieces before she finally succeeds in pulling out the whole half of the shell. The ways of the birds to remove 11 shell-halves were followed more closely; 10 of the halves were removed by the female and one by the male. The female always started disposing of the shells from the half with the broad end. In nest No 106 the female ate up the first shell-half in an extremely short time of 20 seconds, whereas 5 minutes later she ate up the second half, but with great difficulty; it took her 3 minutes. The eating of the top part of the narrow shell-half presents particular difficulties. The female is unable to gnaw it up with the bill edges, but she bites off the edges of the shell to swallow the uncrumbled top with great difficulty at the end. She does that on the nest, but when a fragment of the shell falls over its edge, she picks it up and eats off the nest. However, the female often seems to hesitate what to do with the shell she is holding in her bill. Female No 38 may serve as an example; having pulled the first shell out of the nest, she stood with it in her bill hesitating for 3 minutes and then moved off a few centimetres, ate up a quarter of the shell

and subsequently carried the rest away. She returned to the nest after 6 minutes, got the top part of the shell out of it and, as previously, began to eat it standing on the edge of the nest. Next she disposed of the part left uneaten. Out of the 11 shell-halves, 3 were eaten up by the female and 2, partly eaten, carried by her away. The remaining 6 halves were carried away, 5 by the female on foot and 1 by the male on the wing. After the hatching of the first chicks, the shells of the following eggs are only carried away from the nest.

On the day of egg hatching the behaviour of the adult birds undergoes a change. They as a rule stop turning about on the nest (sporadic turns may happen as long as the young are in the nest) and egg-turning is limited to the nests in which some addle eggs remain (e. g. nest No 38 in Fig. 16B). Preening is continued and even occurs more frequently when the birds stay in the nest, but as in the daytime they stay there less in favour of foraging, the total of preening bouts also decreases (Fig. 20). The other ways of behaving undergo certain modifications: the birds resettle waggling on the nest more delicately, with their parted feet leaned against the sides of the nest and the feathers ruffled even more than in the incubation period. A denuded area with a brood patch in it is well seen, especially in the female. Bill-clapping ceases with the ending of the feeding ritual and the aphides and mites caught, while flying by, by the birds sitting on the nest and eaten up by them hitherto, are now fed to the young. The sound of "sneezing" is still heard but rarely, for the male spends less time on the nest. While brooding the nestlings the birds yawn just as they did during the incubation period. On the other hand, rapid starts of the birds on the nest caused by the movements of the chicks tumbling under them are a new type of behaviour. The rhythm of taking turns in brooding the young is sped up by the combination of the actions of relieving one another on the nest and bringing food for the young.

The scientists differ in opinion as to the duration of incubation in the River Warbler. Puchstein (1959), Horváth (1963) and Horváth & Hüttler (1966) assert that incubation begins just after the laying of the 3rd egg. Ludorowski's (1978) results show that the birds may start incubating even from the 2nd and 4th egg and, according to Miera (1970) not before the 5th egg. In the jubilee edition of the classic work of Brehm (1928) is written that incubation begins after the laying of the 1st egg. In the light of my own study (Table XI) and observations published by other authors (Dementev et al. 1954; Puchstein 1959; Miera 1970; Ludorowski 1978) it may be assumed that the young hatch after 13 days of incubation, i. e. on the 14th day. It may be accepted as the rule that the birds begin incubation on the day of the laying of the 4th egg. The females probably spend nights on the nest as early as the 1st egg has been laid. Hence comes the false conclusion about earlier incubation and, on the other hand, this behaviour contributes to the stretching of the hatching process over 3 days in some nests.

It was not known for many years whether the male shares in incubation or

not (NIETHAMMER 1939; SOKOŁOWSKI 1958). HORVÁTH (1963) and HORVÁTH & HÜTTLER (1966) write on the basis of observations of River Warblers made at their nests that incubation is done only by females and, although PUCHSTEIN (1959) and MIERA (1970) have stated that males incubate as well, MAKATSCH (1976) doubts that. Observations carried out by LUDOROWSKI (1978) and BOSCH & LAUBENDER (1978) confirm the male's share in incubation. This notwithstanding, DITTBERNER & DITTBERNER (1985), basing themselves on the lack of brood patches in 40 males captured in the Odra valley, are still doubtful of the share of males in incubation. It may be believed that the present investigation settles this question definitively in favour of the male.

IX. NESTLINGS

A. Growth and development of nestlings

First day

Pale flesh-coloured chick with pale-slate areas of the temporal, ocular, humeral, spinal and alar feather tracts. Toes with claws, uropygial gland yellowish flesh-coloured, bill dorsally pale-grey, rictal flanges sulphur-yellow, 3 tongue spots — 2 black at the base of the tongue and one pale-grey at its tip. Beige-grey down, stuck together initially, present in the frontal, 2 ocular, humeral and nape tracts. The blue-grey eyeballs show through the eyelids.

An hour after the removal of the first shell the chick opens the bill begging for food. To the quakes of the nest and various sounds it reacts by opening the bill. During feeding it utters voices at a frequency of 22.9—35.0 per minute.

Third day

Body more intensely pink flesh-coloured and in shoulder region yellowish. Feather tracts darker, slate-violet. Down still present but more intensely brown. Bill pale grey-brown with brown tip, 1 mm long; rictal flanges intensely sulphur-yellow, hallux claw 2 mm long. Weight up to 7.2 g.

Fifth day

Top of head dark slate-coloured, including all the feather tracts of the head, not excepting the aural ones. Remaining pterylae — humeral, alar, nape and spinal — also slate-coloured. Incipient pin feathers appear — those on the breast whitish ventrally. Body pale flesh-coloured. Narrow horizontal concave eye slits appear in the eye areas. Chicks already blink but cannot see yet. Bill yellow horn-coloured, getting longer, upper mandible slightly hunched up.

Bill tip still dark. Pin feathers 2—4 mm long. Body weight up to 11.0 g. The chicks in the nest have their heads directed towards the middle. They already yawn, up to twice in 3 minutes.

Seventh day

Body flesh red in colour, which is particularly true of the back and breast muscles. Feathers are not, as yet, breaking from the pins, which are darker than the feather tracts, namely, dark slate, with light tips. The pin feathers of the breast tract are 4 mm long with 1 mm endings; the pins of remiges are 8 mm and their grey endings 2 mm in length, whereas the pins of rectrices are only 2 mm long. The bill, including the flange, is 13 mm long, the tarsometatarsus 19 mm and the hallux claw 3 mm. The weight ranges from 12.0 to 15.5 g (M = = 13.8±1.12 g). The area surrounding the ear opening has a flesh-pink border.

The chicks begin to see as early as the 6th day; in consequence, their arrangement in the nest changes, they turn towards the parental birds coming with food. Their closed eyes open during feeding. The chicks yawn and still react by opening their bills to the noise of the photo-apparaturs. They already preen and gape.

Ninth day

As early as the 8th day feathers begin to break from the pins. Now the emerging feathers on the nape, back and breast give a brown tinge to the chick and their belly is whitish. In most chicks the pins do not burst yet, the ones which do are dark slate in colour at the base, while the bursting end is whitish over a length of 5 mm. The throat of the chick darkens from sulphur-orange to orange--red.

The chicks assume an imbricate arrangement in the nest. They hear the coming parents 5 seconds before feeding. After being fed, the chick claps its bill up to 30 times in 21 seconds.

Tenth day

The chicks have pin feathers at the front of the head-crown, while on the nape and back the feather vanes have already broken through the sheaths. The first secondary remex is 22 mm long and at that time it is the longest feather of the wing, exceeding all the primaries and the remaining secondaries. The unfolding vane of this remex extends from 5 mm to half its length. Rectrices reaching 10 mm in length, with 2 mm vanes. The bill, including the gape flanges, is 14 mm long, the bill itself being 9 mm and the distance between its end and the nostrils 5.5 mm. Tarsometatarsus 24.0 mm long, hallux claw 6 mm. Weight from 16.00 to 18.3 g (M_5 = 17.5 g).

The chicks are very active, keep their eyes open all time, doze for a little

while after feeding and leap up towards the birds feeding them. In danger, but also without any visible reason, they may leave the nest. Before that the oldest nestlings utter location voices. In the nest they flutter the wings and stretch out leaning on their siblings. Outside the nest they run away by leaps in one run of 3—4 m.

Twelfth day

The area of violet-blue pin feathers on the forehead, cheeks and throat decreases between the 11th and 13th day, reaching the line connecting the back ends of the eyes on the 12th day and being reduced to the base of the bill only on the 13th day. The bill is elongated and the gape flanges distinctly narrower. The feathers have entirely emerged from the sheaths; as a result, the body back is brown with rusty-brown borders of the feathers and the coverts of the breast form darker zones on the flanks than the ventral part. On the belly the white feathers touch each other and so cover the ventral apterium. The strokes on the breast are produced by feathers with a darker dull-brown middle and lighter streaks on the sides. The tufts of natal down are still present and persist till the departure of the fledgelings from the nest — there are two tufts in the eye tract on either side of the head, two tufts in the humeral tract and three among the wing coverts — altogether 7 pairs.

From the 12th day onwards, unless the fledgelings have left the nest before, the oldest of them start uttering location voices. They are awake all the time, which they mostly spend preening. They void excrements beyond the edge of the nest, where the adult birds pick them up. The nestlings try their wings by fluttering them for a few seconds on the nest. They attempt to make the adult, standing over the nest, feed them by pecking at its bill. In the broods of five there is not enough room for all the young in the nest (at least one of them stands on its edge). They react to the overflying flies and to strange sounds, such as that of flash condensator. While they are being fed by the male and female from apposite sides they jump from edge to edge. They receive food standing. Starting from the 11th day, they sleep with the head turned backward and inserted under the coverts of the back.

B. Diet of young

During the incubation period River Warblers forage in their territories, not far from the nests, reaching their feeding-grounds on foot. As the nestlings grow their food demands increase and make the adult birds fly to more distant feeding-grounds. Similarly, in some ecotonic biotopes they may also forage in fairly distant areas and then they also fly to them. On the other hand, food is collected by walking birds from the surface of plants, from the underside of leaves chiefly of creeping plants but also where oblique or horizontal twigs

enable the birds to come up to their victims hidden high above the ground. Some victims are picked up from the ground or even caught in the air.

As has been mentioned above the food composition could not be determined with the collar method. And so attempts were made during observations of feeding to identify the victims being brought. Hardly a fraction of percent of the food brought by the parents to the nest was determined in this way: only 213 food components in 6950 feedings observed (3.06% — Table XIII). Only

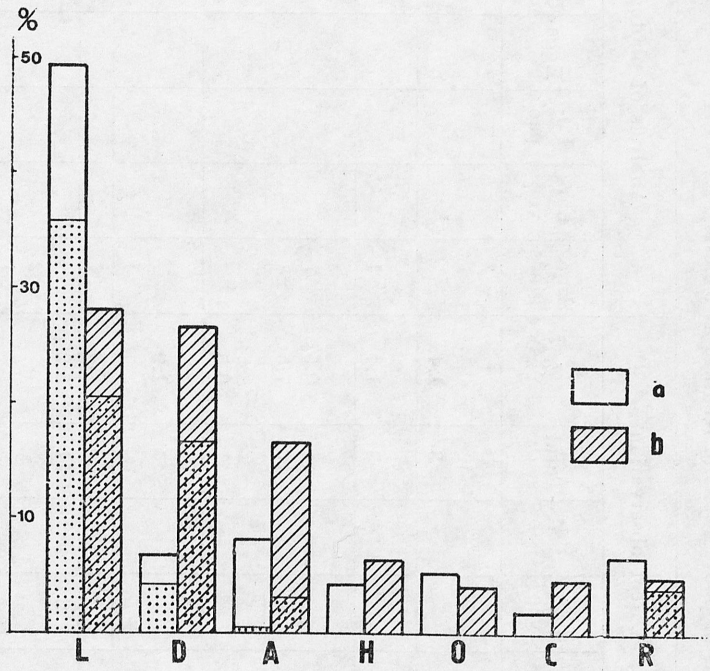

Fig. 27. Proportions of particular animal groups in the food of chicks of the River Warbler *Locustella fluviatilis*, determined by direct observations of feedings (a, N = 213 items) and by analysing the photographs of chick feedings (b, N = 223 items). L — *Lepidoptera* (stippled — caterpillars), D — *Diptera* (stippled — *Nematocera*), A — *Arachnida* (stippled — *Opiliones*), H — *Hymenoptera*, O — *Orthoptera*, C — *Coleoptera*, R — remaining insects (stippled — *Homo-* and *Heteroptera*)

big parts of victims sticking beyond the bill could however be identified by this method. The part of the portion that was kept in the gullet and inside the bill could not be determined. Another 223 victims were identified on the basis of 70 slides and photographs (Table XIII and Plate V). The results of direct determinations and those of analyses of the photographs are similar but the latter permitted the identification of smaller components (small arachnids at the first feedings and some dipterans — Fig. 27).

The River Warbler's diet consisted exclusively of animals and among these mainly of arthropods (98.4%). Molluscs (0.9%) and annelids (0.7%) constituted marginal food, bearing on proportion to their abundant occurrence in the habi-

Table XIII

Food of nestlings of River Warblers *Locustella fluviatilis* of the Łężany area, determined on the basis of direct observation and analysis of photographs of feedings at 9 nests

Food identified, arranged acc. to systematic units	Direct observation					Analysis of photographs						Total % in food examined
	Imagines	Larvae	Pupae	Total	%	Imagines	Larvae	Pupae	Eggs	Total	%	
Oligochaeta												
Lumbricidae				3	1.4							0.69
Gastropoda												
Limneidae (*Galba* sp.)				3	1.4	1				1	0.5	0.92
Arachnida												
Opilionidea (Palpatores)	1			1	0.5	7				7	3.1	
Araneida	16			16	7.5	28			2	30	13.5	12.38
Myriapoda												
Diplopoda	1			1	0.5							0.23
Insecta:												
Odonata (Anisoptera)	4			4	1.9							
(Zygoptera)						1				1	0.5	1.15
Ephemerida	5			5	2.3							1.15
Orthoptera	9	2		11	5.2							
(Tettigoniidae)						2				2	0.9	
(Gryllidae)						1				1	0.5	
(Acrididae)						5	1			6	2.7	4.59
Plecoptera	4			4	1.9	1				1	0.5	1.15
Homoptera (Cercopidae)						1	2			3	1.3	
Heteroptera						6				6	2.7	2.06

Coleoptera												
(Silphidae)							2			2	0.9	
(Elateridae)		3		3	1.4		3			3	1.3	
(Cantharidae)	1			1	0.5							
(Chrysomelidae:												
Agelastica alni)							2			2	0.9	
indet.							3			3	1.3	3.21
Trichoptera	1			1	0.5							0.23
Lepidoptera												
(Tortricidae)						7	1			8	3.6	
(Rhopalocea)	5			5	2.3							
(Nymphalidae)							4			4	1.8	
Metaheterocera	20	74	2	96	45.1							
(Geometridae)	1	2		3	1.4		2			2	0.9	
(Noctuidae)	1	1		2	0.9	6	9			15	6.7	
indet.						2	30	2		34	15.3	38.76
Diptera												
Nematocera												
indet.						4				4	1.8	
(Tipulidae)	1	1		2	0.9	22				22	9.9	
(Culicidae)	7			7	3.3	11				11	4.9	
Brachycera												
indet.	2			2	0.9	3				3	1.3	
(Tabanidae)	1			1	0.5	3				3	1.3	
(Syrphidae)	2			2	0.9	3				3	1.3	
indet.						10	3			13	5.8	16.74
Hymenoptera												
(Apidae:												
Bombus sp.)	1			1	0.5							
(Formicidae)	8			8	3.7	14				14	6.3	5.27
Insecta — indet.	1	30		31	14.6		17		2	19	8.5	11.47
Total	98	113	2	213	100.0	138	79	2	4	223	100.0	100.0

tat. There was also one myriapod, caught by accident, whereas 54 arachnids and their eggs suggest a certain preference for this kind of prey (12.4%). Butterflies, however, imagines and larvae, were no doubt the main food of River Warblers in respect of both number and weight (N = 169, that is, 38.76%). The butterflies taken were of medium size, chiefly moths of the families *Noctuidae Geometridae* and *Tortricidae*. They are not specially prepared before being fed to the young and, as a result, it happened several times that a butterfly put in the bill of a nestling glew out of its open gullet. The River Warbler's quick reflex allowed the adult bird to recapture it and continue feeding. How gentle must be the hold of the bill edges is evidenced by the fact that a butterfly flew out twice during a feeding before it had been swallowed by the nestling. While feeding a chick, another female recaptured a butterfly flying away after chasing it for a distance of 60 cm from the nest. Among the larvae, naked forms from the same families prevailed, 73% (N = 74) of them were green in colour. Dipterans, from small forms of the *Culicidae* to large specimens of *Tabanus* sp., came in second as regards number. This order was most frequently represented by tipulid imagines, since owing to their sluggishness, they made easy prey to the birds. They often suspended from the filled-up bill, because they had perhaps been caught on the way back to the nest. The *Orthoptera* were represented mostly by acridids, while coleopteran imagines, which abounded in the surroundings, did not constitute potential victims. The only specimen identified was a soft-winged *Cantharis* sp. Totals of 176 imagines (47.83%) and 192 larvae (52.17%) of insects were distinguished in the food brought to the nest. Egg deposits and pupae of butterflies were brought exceptionally.

C. Feeding of young

The instinct of feeding young awakens in the male as early as the 8th day of incubation. Therefore, on the day of hatching the male comes to the nest with food before the last egg-shells have been removed. Although the nestling, stimulated by the vibration of the nest and the calling voice of the male, begins to beg for food as early as the first hour of life, it rarely comes to feeding then, especially if the victims brought by the male are big. Unsuccessful feeding ended in the male eating up the food. In nest No 67 the male fed three larvae to the first hatched nestling after 6 abortive attempts and he tried to feed another one, still in the last shell, for 5 minutes and made about 30 attempts to put larvae in its bill. Feeding their young, River Warblers watch carefully to see if the food has been swallowed and the bill closed. This is why it is difficult to collect food from nestlings with the help of neck collars. The adult birds simply pull the unswallowed bits out of the bill of the nestling and put it in that of the next one or eat up themselves.

The share of both parents in feeding is various. The female's instinct of care of young, like that of the clutch in the incubation period, exceeds this instinct

in the male. And so the male, staying longer off the nest, is the main deliverer of food for the nestlings. On the first day his share in feeding was 61% and then it decreased systematically till the 10th day (52%) to rose again to 59% (on the 12th day). Towards the end of the nestlings' stay in the nest (from the 12th day onward) the intensity of feeding by the male lowers, for the frequency of his singing is again on the increase (Fig. 28).

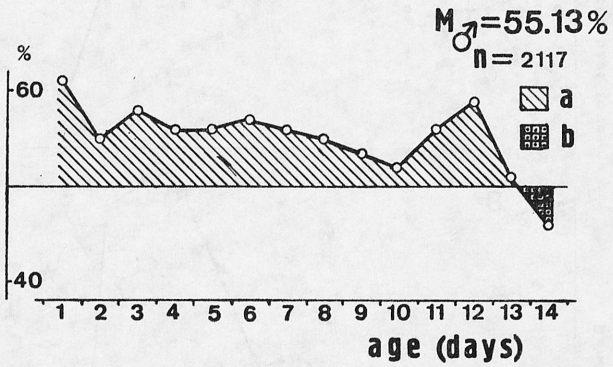

Fig. 28. Percentage share of the male in chick feeding in River Warblers *Locustella fluviatilis* in successive days of life of the chicks. The curve represents the mean from 2117 feedings observed at 6 nests: period of the prevailing number of feedings by the male — a, by the female — b

In the first days of feeding it happens that the female comes off the nest at the sight of the male approaching with food and waits for him to end feeding young; when the male has moved away, she resumes brooding them. This never happens the opposite way. The main rhythm of feedings by adult birds and their changeovers in brooding the nestlings resembles that during incubation. On its arrival the bird first feeds the nestlings, waits for their excretion, swallows the faeces and, having looked into the nest, sits down to brood the young. It stays on the nest till the arrival of the other partner.

During the first 24-hour period the nestlings receive food 6—45 times, which depends on their number in the nest. On the first day the mean is $0.77 \pm \pm 0.49$ feedings/hr/nestling (Fig. 29A). The number of feddings grows to the 11th day of life, reaching 2.60 ± 1.04 feedings/hr to fall in the last days of the stay of young in the nest below the level of their intensity on the 7th day (i. e. to 1.81 ± 0.75 feedings/hr). The largest number of feedings during 17 hours of continuous observation was noted at nest No 2416 with 5 nestlings; it came to 261 feedings (Fig. 29B).

The condition of the nestlings fed is determined not only by the number of feedings falling to one nestling but also among others by the size of items, which may be largely differentiated. In the first days they may be but 2—3 small spiders or gnats. In the following days the size of rations brought grows more quickly than does the size of the nestlings. The birds often arrive at the nest with such a large bundle of insects that some of them hang from the bill on both

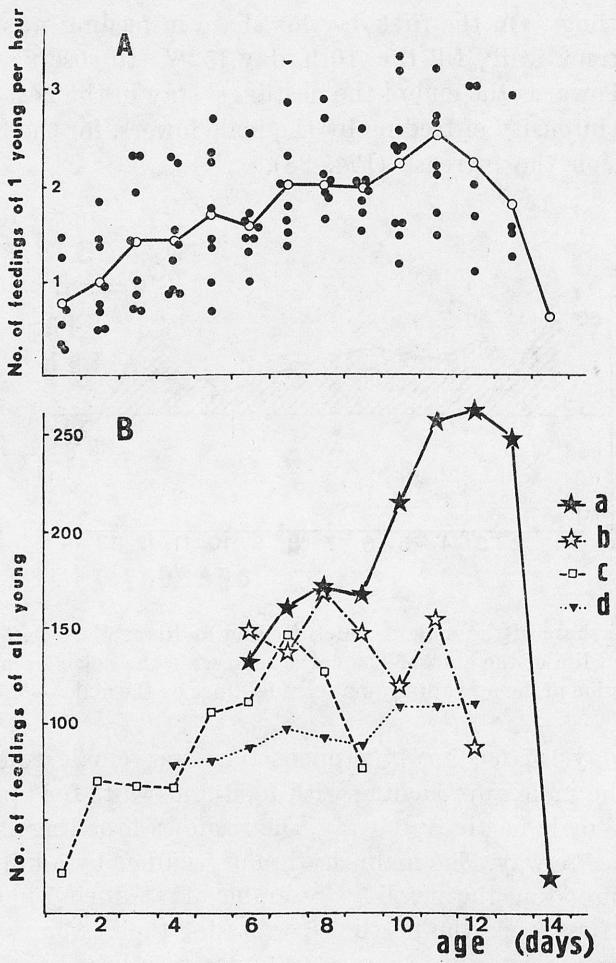

Fig. 29. The frequency of feedings falling to 1 chick of the River Warbler *Locustella fluviatili* (A) and the total sum of feedings (B) in nests with 5 (a, b), 4 (c), and 2 (d) chicks in successive days of their life. The curve A connects the means from 7274 feedings observed for 1022 hours at 11 nests and the dots show the dispersion of the means of particular pairs

its sides (Phot. 13). The coloured ringing of the mates made it possible to observe that in the period of the intensest feeding (after the 7th day) the same bird may return to the nest with food 2—2.5 times within a minute. It then brings single moths of the family *Noctuidae* or *Geometridae*, spiders, etc. gathered in the nearest neighbourhood of the nest.

Apart from the abundance of food in the environments inhabited by breeding pairs, the rhythm of feedings was to a great extent influenced by the fact whether the nest was exposed to the sunshine filtrated through the canopy of tree crowns or to the direct light shining through the herb layer surrounding the nest. This relationship can be read from the graphs divided into distinct groups (Fig. 30),

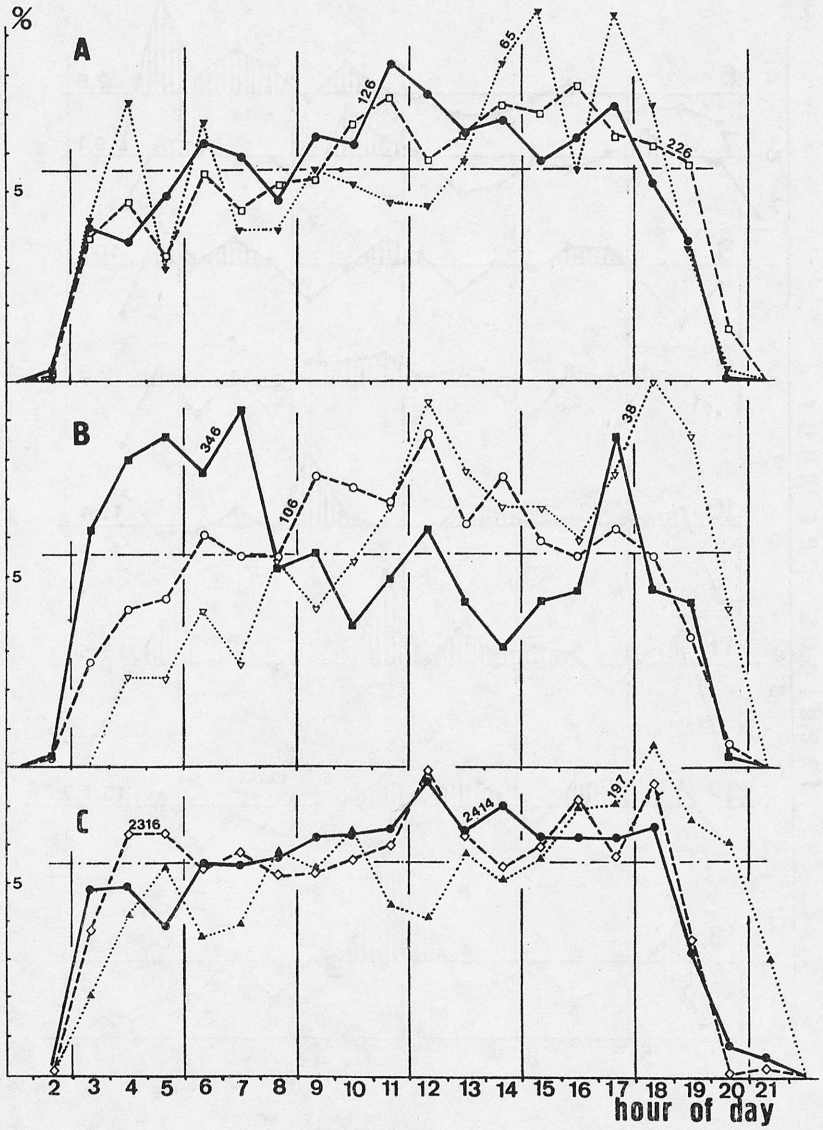

Fig. 30. The circadian rhythm of chick feedings in 9 nests of the River Warbler *Locustella fluviatilis*. The curves illustrate the average percentage of all feedings throughout the period of observation of nests situated: A — in wet alderwoods of the association *Ribo nigri-Alnetum* — No 126 with 2 chicks ($M_{962} = 5.14$), No 226 with 4 chicks up to 6th day and 3 later ($M_{582} = 5.29$) and No 65 with 4 chicks ($M_{695} = 7.81$), B — in alder-ash carrs *Circaeo-Alnetum*: full-grown wood — No 346 with 4 chicks ($M_{418} = 5.73$), in wooded areas on a stream in plantation — No 106 with 4 chicks ($M_{798} = 6.75$) and at the edge of marshes — No 38 with 1 chick ($M_{221} = 3.11$), C — at the edge of high forests: in *Tilio-Carpinetum* plantation — No 2414 with 5 chicks ($M_{872} = 8.07$), in wood bulrush in seepage spring brushwood *Circaeo-Alnetum* — No 2316 ($M_{1686} = 11.16$) and in dropworts at the NE edge of a wet alderwood and sedge meadow — No 197 with 4 chicks ($M_{735} = 5.56$)

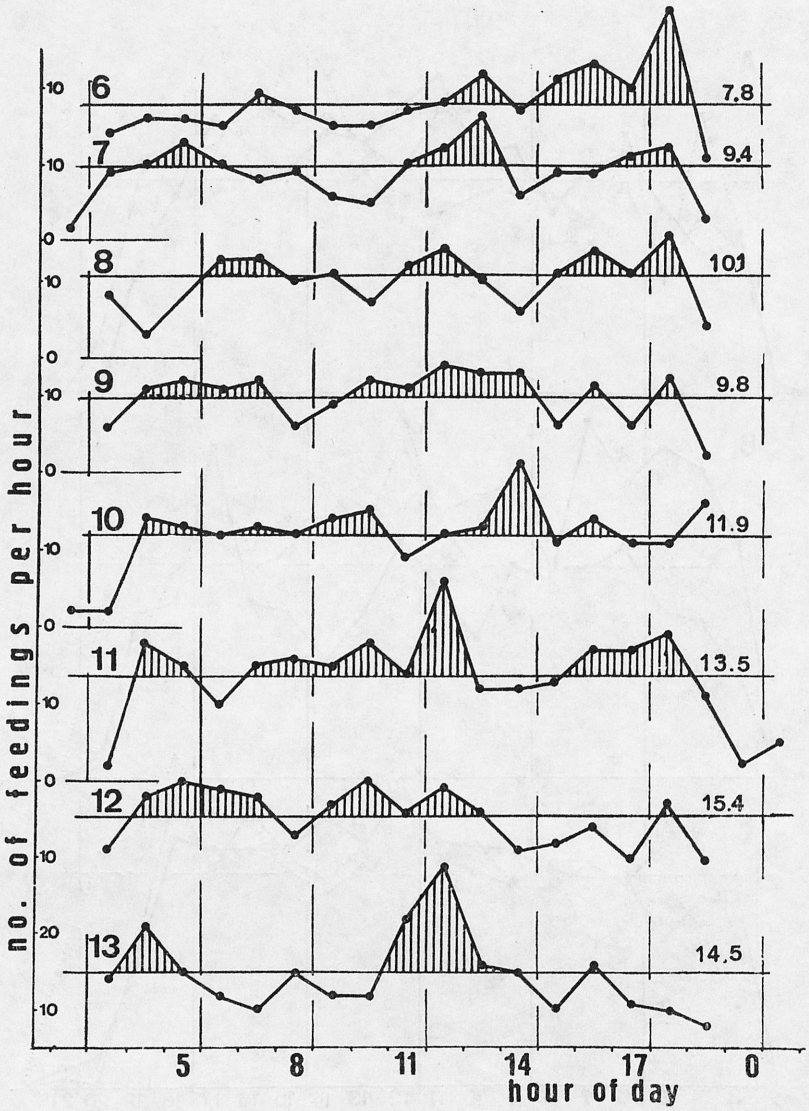

Fig. 31. Hourly number of feedings of 5 chicks of the River Warbler *Locustella fluviatilis* in nest No 2316 in the last eight days of their stay in the nest; successive day of life of chick marked on the left and mean daily number of feedings on the right. Periods of more intense feeding (above daily mean) are hatched

for the curve of daily feedings for the nests in forested areas has a different shape, with three peaks: in the morning, in the afternoon and in the evening. At the edge of a forest, where the rays of the setting sun and its afterglow reach the birds fedding young, the evening maxima last considerably longer (pairs Nos 38 and 197) than in the remaining nests. In the nests situated in open areas the evening maxima begin besides an hour later, i. e. at 18.00 (Nos 38, 197, 2316,

2414), whereas in the depth of a forest (Nos 65, 126, 346) or in a valley, beneath the western wall of a wood (No 106) at 17.00. In a nest at the edge of a clearing surrounded by a beechwood on the west side it occurs still earlier, as early as 16.00 (No 226, Fig. 30A). To what degree the curves of mean intensity of feedings reflect the actual rhythm of feedings each day can be investigated on the basis of Fig. 31, in which the curves from the 6th to the 13th day are presented for the most intensely feeding pair, No 2316. A fall in the number of feedings in the second half of the day becomes increasingly distinct in the last three days before the departure of the young.

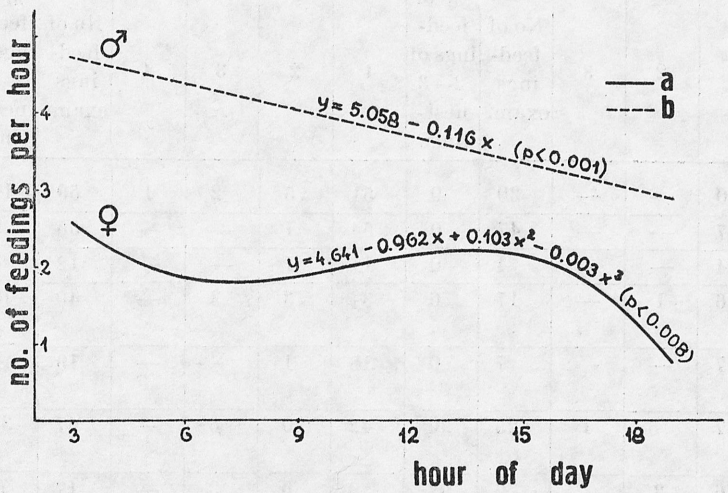

Fig. 32. Intensity of feeding of 4 chicks in nest No 106 of the River Warbler *Locustella fluviatilis* in particular hours of day; female — a, male — b. The curves represent means from 12 days of observation

The daily courses of feedings by the male and the female differ in intensity (Fig. 32), for the male feeds the young most vigorously at daybreak and next the frequency of feeding decreases gradually till the evening, whereas the frequency of feeding by the female is represented by curve 3° with two peaks: in the morning and in the afternoon.

It is besides difficult to estimate the amount of food brought to the nest, because the size of the portions changes in the course of a day according to the resources of the feeding ground and consequently also changes the number of nestlings that receive food at one feeding. The feeding of more nestlings at one visit to the nest usually occurs when they are older. In pair No 106 the male once distributed one portion among all the four nestlings in the nest. In the female of this pair feedings of more than one nestlings generally formed 7.3% and in the male as much as 19% of feedings (Table XIV).

In the first days the male and female take turns at feeding and brooding their young very regularly. This relationship loosens with time and in the last days simultaneous feeding by both parents may happen. In the first period of

Table XIV

Percentage distribution of feedings acc. to the number of nestlings out of the four in nest No 106, among which the female and male River Warblers *Locustella fluviatilis* divided the portions of food brought each time in the last 5 days of their stay in the nest

Day of life	Number of feedings										Remarks
	by female					by male					
	at which food was divided among the given number of nestlings										
	1	2	3	No of feedings exam.	% of feedings of 2—3 nestlings	1	2	3	4	No of feedings exam.	% of feedings of 2—4 nestlings	
8	30	—	—	30	0	51	5	2	1	59	14	
9	47	—	—	47	0	54	1	—	—	55	2	
10	4	—	—	4	0	11	1	—	—	12	8	
11	16	1	—	17	6	34	3	3	—	40	15	in the morning
11	7	—	—	7	0	18	1	—	—	19	5	in the evening
12	17	5	1	23	26	42	20	5	—	67	37	in the morning
12	6	3	—	9	33	8	6	3	—	17	53	in the evening
Total	127	9	1	137	7.3%	218	37	13	1	269	19.0%	
%	92.7	6.6	0.7	100		81.0	13.8	4.8	0.4	100		

life of young some of the brooding females rarely forage on their own and rather receive food from the male to feed the nestlings. In some pairs (Nos 38, 106, 67) the female sometimes tried to snatch a caterpillar from the bill of the male, who was just about to feed it to the young and eventually both parents fed parts of the torn-up victim to different nestlings. Such scenes of the snatching of food were particularly frequent at nests with one nestling (No 38).

D. Removal of faeces

Having fed the young either parent usually waits for their faeces to dispose of them. The intensity of disposal of the faeces during a day is the highest about noon. E. g. in pair No 106 this activity can be described with the equation $y = 0.975 \pm 0.507x^2 - 0.025x^2$ at $p < 0.005$ (Fig. 33). Their zeal in disposal of faeces is sometimes greater than in feeding. Being at the same time present

at the nest, the male and female occasionally snatched faeces from each other, tearing open the mucous sac, enclosing them.

The number of faecal sacs disposed of increases very fast till the 4th day, to keep at more or less similar level later up to the end of the stay of the young in the nest (Fig. 34). As in the case of feeding, their number is the highest on

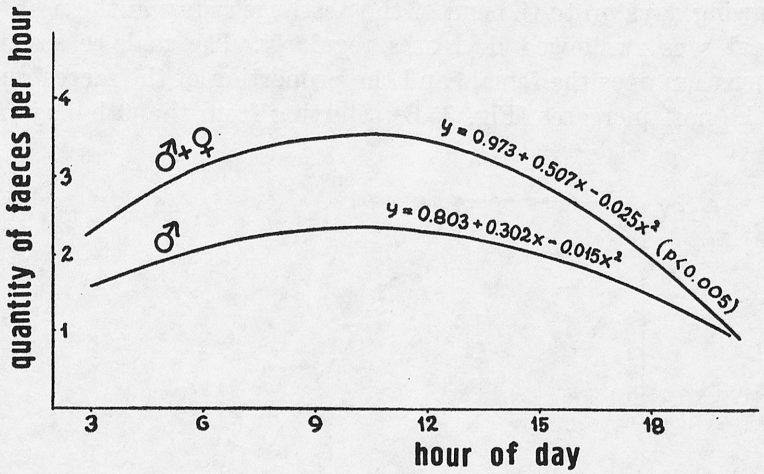

Fig. 33. The frequency of disposal of faeces of 4 chicks in nest No 106 of the River Warbler *Locustella fluviatilis* in particular hours of day by the parental pair and by the male alone. The curves represent means from 12 days of observation

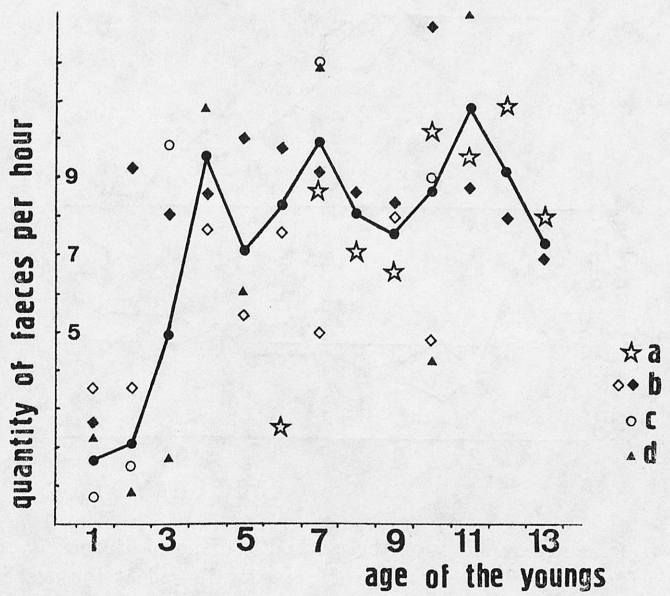

Fig. 34. The effect of the age of chicks of the River Warbler *Locustella fluviatilis* on the number of faecal sacs discharged. The solid line represents the weighted mean from 6 nests during 43-day observation of 860 faecal sacs discharged. Means from nests with 5 chicks — a, with 4 chicks — b, with 2 chicks — c and with 1 chick — d

the 11th day (1.08 faecal sacs/hr/nestling) and next it decreases till the departure of the nestlings. As the young age, the amount and consistence of faeces change and cause a change in the manner of their removal as well.

Till the 5th day each parent, having grasped a faecal sac, perks its head up and swallows the sac on the spot, before departing from the nest (Fig. 35A, B). In the following days up to the end of the nestlings's stay in the nest, the number of faecal sacs swallowed decreases regularly. The male ceases swallowing faeces sooner than does the female and the proportion of the faeces removed by him from the nest increases (Fig. 35B). Starting from the 9th day more than

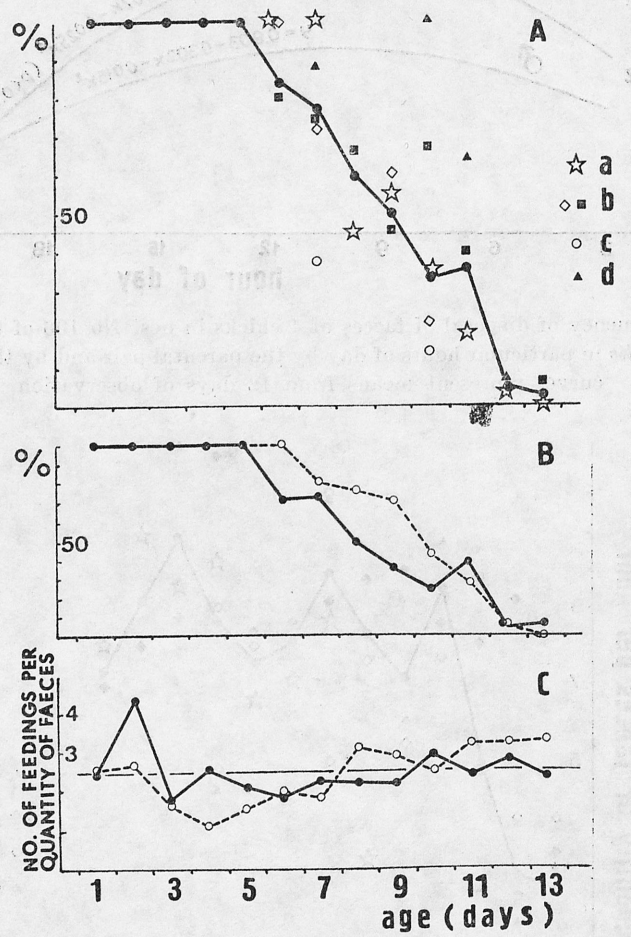

Fig. 35. The effect of the age of chicks on the method of disposal of faecal sacs by adult River Warbler *Locustella fluviatilis*. The percentage of faeces swallowed at the nest is given on the ordinates. A — mean from 6 nests in 43 days of observation, N = 860 faecal sacs disposed of; dispersion of means in marked for nests with 5 chicks — a, 4 chicks — b, 2 chicks — c and 1 chick — d. B — mean for male (solid line), mean for female (broken line); designation of coordinates as in A; C — number of feedings falling to 1 disposal of faeces by the male (solid line) and the female (broken line); the horizontal line represents the mean: 2.46 feeding to one disposal

half the faeces are carried away but swallowing may occur even on the last day. It is then visible what difficulty the birds have in swallowing big and hard parts of the faeces. The birds carry the faeces away walking along a constant route and drop them in special places, where they afterwards often take wing. Such a place was found 3.2 m away from nest No 94 and as many as 7 faecal sacs were within a radius of 30 cm in it.

One removal of faeces falls to 2.46 feedings (Fig. 35C). The male exceeds the female in faeces removal till the 5th day, then follows a period when the shares of both parents are equal and in the last three days of the stay of young in the nest the female disposes of faeces more frequently. The highly significant interrelationship between the number of feedings per day and the number of faecal sacs disposed of is confirmed by the data concerning nest No 106 ($y = 0.505+0.411x$ at $p < 0.001$ — Fig. 36).

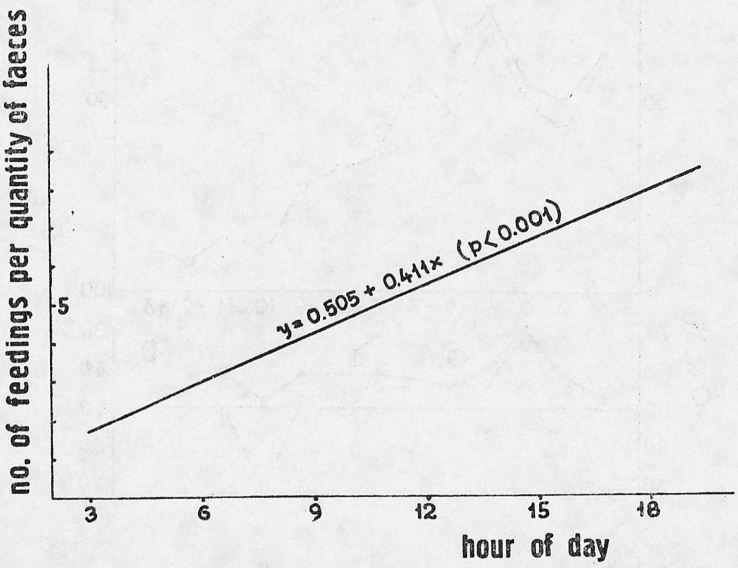

Fig. 36. The relationship between the daily intensity of feedings (x) and the discharging of faeces (y) in nest 106 with 4 chicks of the River Warbler *Locustella fluviatilis*. Straight line — mean calculated from 12 days of observation

E. Protection of young from harmful effects of weather

1. Protection from cool

New-hatched young have no satisfactory protective systems against the cooling of their bodies at the time of low temperatures in the night, in the early morning and in the evening. To be sure, they have tufts of down on the top of the head and on the back, but in the damp layer close to the ground, where the

temperature sometimes falls to 5°C at daybreak in June, their protection is not lasting. And so males and females continuously warm their young in the first days, just as they incubated the eggs previously, but assuming a different position, which has benn mentioned before in the description of hatching. The birds sit higher, especially when the young are bigger, they do not place their feet inside the nest-cup but on the opposite nest-edges, with their heels leaned on them. When the 10-day-old nestlings hardly find enough room for themselves in the nest, the female, before night brooding, leans her breast against a cone of nestlings, protruding high above the nest, and before covering the whole nest with her body, exerts a pressure for a few minutes until they resettle themselves.

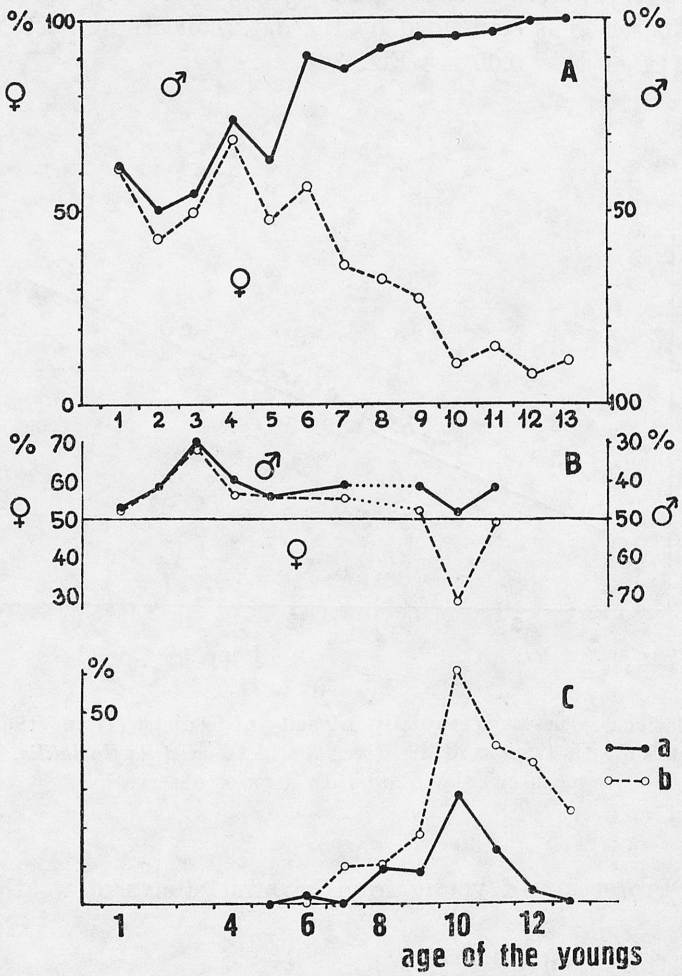

Fig. 37. The effect of the age of chicks on the duration of brooding by the male and female River Warblers *Locustella fluviatilis* in nests with 4 and 5 chicks (A) and with 1 chick (B) and the vigilance of the parental birds at nest No 106 (C). A — mean from 5 nests in 35 days of observation; B — sum for 1 nest in 8 days of observation; C — mean from 12 days of observation. Per cent of the total time of observation for A and B and per cent of the aggregate time of the stay of the birds at the nest for C are given on the ordinates

During the first four days brooding is carried on nearly round the clock, starting from the 5th day the male's share in brooding decreases rapidly and the time of brooding by the female is also shorter (Fig. 37 A). The time of brooding however depends on the abundance of food in the environment and on the food requirements of young. This opinion finds a confirmation in an observation of the process of brooding in the nest with one nestling (No 38). A single nestling has greater losses of energy, there being no siblings in the nest to keep it warm, but, as can be seen from Fig. 37 B the female and male brooded their young nearly uniformly till its departure from the nest. The adult birds, busying themselves less in gathering food, had an excess of time and spent it together at the nest: one of them brooded the young and the other stood beside (cf. Fig. 39 C).

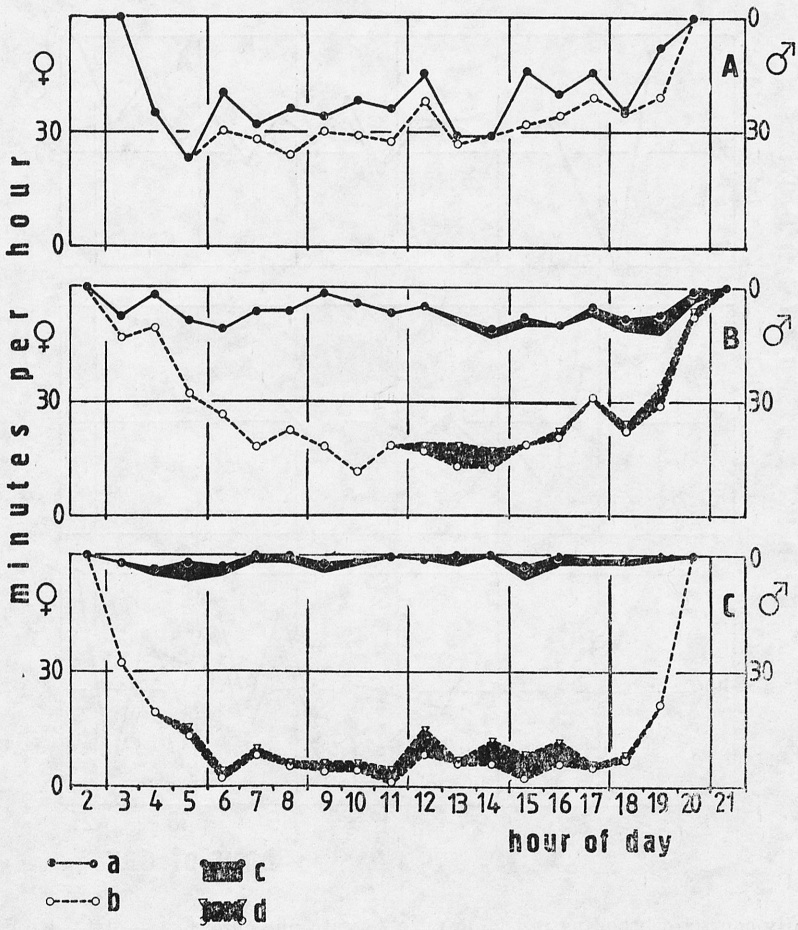

Fig. 38. The effect of the age of chicks of the River Warbler *Locustella fluviatilis* on the daily course of warming the chicks by the male (a) and female (b): A — 1st — 4th day, B — 5th—8th day and C — 9th—13th day. The time of vigilance at the nest without brooding of the male (c) and female (d). The curves are plotted by the means from 5 nests with 5 and 4 chicks obtained during 35-day observation

Such a scene has not been recorded from any nest with more than three nestlings. The fact that a female (No 38) had to wait to relieve the male, just brooding one nestling, proves that the generally smaller share of the male in brooding is connected with his greater involvement in feeding the young (Figs. 27A, C and 28). The development of the nestlings' own thermoregulation manifests itself also in the behaviour of the parents, who, starting from the 6th day of life of the nestlings, instead of brooding them in the daytime stand beside on the edge of the nest (Phot. 19) till the arrival of the other mate with food (Fig. 37C).

Till the 4th day the brooding birds leave the nestlings alone in the nest to 12 minutes an hour from 06.00 to 19.00 (Fig. 38A) but on the 8th day the young are already left partly uncared-for from 03.00 to 20.00. The nearer the noon the longer both parents remain off the nest (e. g. as long as 45 minutes at 13.00 —

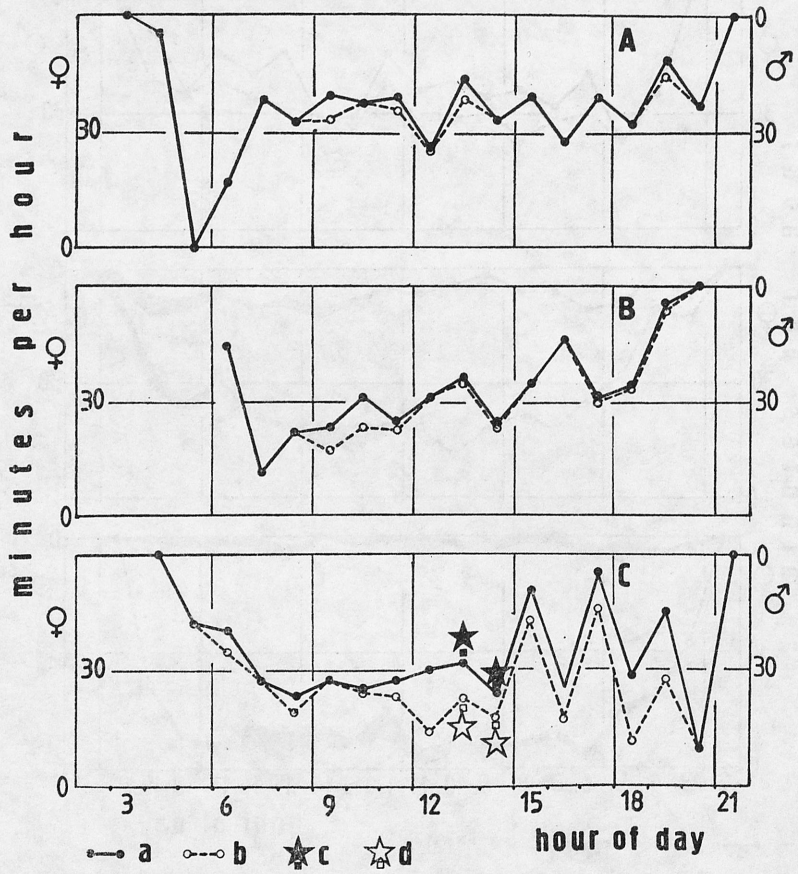

Fig. 39. Daily course of brooding in the nest No 38 with one chick: A — 1st—4th day, B — 5th—8th day, C — 9th—11th day of its life, a — by the male, b — by the female, c — the time of male standing by the brooding female, d — the time of female standing by the brooding male. The curves represent the mean time from 75 hours of observation during 8 days. The area between the curves for the male and the female represents the time when the adult bird were absent from the nest

Fig. 38B). In the last days brooding is done only throughout the night and scarcely a few minutes an hour in the daytime (Fig. 38 C). In the nest with one nestling the daily cycle of brooding, analogous to that in the nests with a larger number of young in the first four days (Fig. 38A and 39A, B), lasts longer, that is the male broods longer in the morning, when the female feeds after the night spent on the nest and later his share decreases till the evening. In the last days between 13.00 and 14.00 the parents were noted to be watching the nestling, which sat in the nest by itself (Fig. 39C).

2. Protection from overheating

The excess of heat in damp biotopes of luxuriant herbaceous vegetation inhabited by River Warblers is an exceptional occurrence. However, some cuts of plants connected with demands of observation or photographing caused that at some hours of the day the sunshine reached the nest directly, stimulating the young to pant. Then the parent does not sit on the nest but lifts itself somewhat over it and, stretching the wings a little, shelters the young from the sun. Older nestlings, left alone in the nest, pant more frequently, above all, those on top. Panting lasts from several seconds to 3 minutes. A change in the arrangement of the nestlings in the nest leads to the interruption of panting.

3. Protection from rain

When it starts raining, the parents, as in the incubation period, return to the nest within 3 minutes. The female is mainly the one who protects the young from rain. During a drizzle her posture resembles that taken by her to keep the nestlings warm, whereas during a downpour she stands distinctly higher over the nest and has her wings somewhat stretched as in protecting the young from the sun. On the average, every 20 minutes the bird shakes raindrops off its plumage. During the last days of the stay of the nestlings in nest No 2316 the parental care in the daytime was reduced exclusively to sheltering them from rain. If the rain drags on, the bigger nestlings may be left unattended, chiefly when the female leaves the nest to feed in the morning and in the evening.

F. Protection from enemies

In the case of River Warblers, building their nests on the ground, the protection of the brood against natural enemies is limited to a great extent. To the presence of Marsh Warblers, Blackcaps and even Blackbirds, nesting in the neighbourhood, the River Warbler sometimes reacts with warning calls and quite visibly defends the nearest surroundings of the nest. To birds dangerous to its brood, such as the Red-backed Shrike, Jay or Hooded Crow, it reacts by coming to a standstill and uttering no voice at all.

Lizards and frogs rustling in the litter round the nest evoke a reaction consisting in an impetuous departure from the nest or in extreme alarm. Mice and shrews excite a similar reaction. When a bigger animal (boar) or a man appears in the vicinity, the bird that sits on the nest with young keeps calm. The female may trill and the male may sing a warning song unless the enemy comes near the nest. If the man comes up to the nest, the bird makes efforts to lead him away. It springs out of the nest and runs on the ground in the entanglement of dry stalks, often sneaking under them as fast as a mouse. It circles in this way within a radius of 0.5 to 2 m from the nest, every now and then producing a sharp crack by rubbing its wings against dry stalks. In the highest excitement it utters a voice of fear (hiss) and flies at the "enemy", e. g. the hand seizing a nestling, and pecks at it. This reaction may occur as early as the last days preceding the hatching of nestlings and persists to the end of their stay in the nest. It was observed only in relation to man (an observer). Unluckily, we failed to of serve this reaction towards other enemies, although supposedly the birds behave similarly then.

G. Departure of young from the nest

The differentiation of nestlings in respect of age resulting from the fact that hatching may be stretched over three days causes that two days before their departure the oldest nestlings differ in behaviour from the remaining ones. They run out for a distance to 15 cm to meet the parents coming with food and next return to the nest. During long breaks between feedings in late morning hours they already utter location calls, peck at the bill of the feeding parent, sit and often stand highest in the nest and run across it treading on their siblings, if the bird with food is coming from a different side than expected. Their activeness is greatest in the morning hours. In the afternon they begin to quiet down so that they do not differ from the other nestlings in the evening. The direct cause of quieting down may be their sensation of satiety, since they have seized most food.

As has been observed, the departure from the nest always takes place on the nestlings' own initiative. Within 5 minutes after the departure of the most active fledgeling from the nest, the remaining ones join it (usually after two further feedings). In several cases a nestling, just after being fed, followed the parent, who was moving away. After the departure of young from the nest, at first the adult birds still come with food to the empty nest several times (for about 20 minutes). If there are addle eggs in the nest, the adult bird itself eats up the food, turns the eggs and starts incubating. The adult birds are only just learning the location call of the young. When the nestling ran out of nest No 38, avoiding measuring in the afternoon of its 10th day of life, its parents began to incubate two addle eggs, although at a distance of 1—3 m it puled its location calls for more than 3 hours. In this period the parents relieved each other 7 times,

just as they normally do while incubating, and gradually decreased the amount of food brought. The intervention of an observer saved the life of the wet and still puling chick, which the parents did not feed any more that evening. This chick left the nest on its own in the morning two days later. In the meantime it had not uttered a location call in the nest. If the fledgelings left the nest on their own initiative in the morning (06.40—09.45), the incubation of a single addle egg lasted, e. g. in nest No 18, only 5 minutes. If not scared away from the nest, the fledgelings leave it between the 11th and the 14th day of life (Table XV). The broods of a small number of chicks leave the nest sooner than do those of a larger number.

Table XV

Length of stay of young River Warblers *Locustella fluviatilis* in the nest relative to their number

Day of departure from nest	Number of nestlings in nest					No of nests	%
	1	2	4	5	6		
11		1				1	7
12	1	1				2	13
13			7	2	1	10	67
14				2		2	13
Total	1	2	7	4	1	15	100

Starting from the 11th day of life of the chicks, an intrusion of an observer or animal may evoke a strong impulse in all of them to leave the nest immediately. They at once scatter in various directions and move away from the nest for a distance not usually exceeding 10 m on the first day.

As late as 4 days after departure the nearly volant fledgelings were still seen being fed by the female off the nest. The males' singing and recoveries of adult River Warblers ringed earlier indicate that they stay in their territories as late as July. It cannot be established for the scarcity of material whether we are concerned here with repeated or second broods or the normal stay of the birds in their own territories. A month after the completion of breeding activities there are no traces of the presence of a breeding pair and its chicks. What is more, some ephemeral migrating males, who have not been seen in the study area before, begin to sing in the same territories.

The authors who investigated the biology of the River Warbler kept silent about the development of the plumage and behaviour of the chicks (PUCHSTEIN 1959; HORVÁTH & HÜTTLER 1966, LUDOROWSKI 1978; MIERA 1970; BOSCH & LAUBENDER 1978). Neither can any information about this subject be found in general works (NAUMANN 1905; HEINROTH & HEINROTH 1924—1931; NIETHAMMER 1937; DEMENTEV et al. 1954; SOKOŁOWSKI 1958). Some details, e. g.

about the colour of down, are given by FOURNES (1930) and HEISER (1972), who state that it is black. It is only recently that the development of young has been described on the basis of the data from two nests, supported with tables of growth and photographs (DITTBERNER & DITTBERNER 1987). In certain details their descriptions and the results presented in this work are complementary to one another.

Only a few authors write on the food of chicks. INOZEMTSEV (1963) gives the most detailed list of 65 victims collected in 16 samples. The most often mentioned items are caterpillars (PODHORSKY & VÁŇA 1964; HORVÁTH & HÜTTLER 1966; MIERA 1970; LUDOROWSKI 1978; DITTBERNER & DITTBERNER 1987; SCHÖNN & SCHÖNN 1987), besides, the first and the last authors cited emphasize that they were green in colour. As in the present study, some plecopterans, homopterans, hymenopterans, gastropods (INOZEMTSEV 1963) and spiders (INOZEMTSEV 1963; MIERA 1970; SCHÖNN & SCHÖNN 1987) were identified in the food of chicks. Dipterans were also found in large numbers (INOZEMTSEV 1963; DITTBERNER & DITTBERNER 1987). SCHÖNN and SCHÖNN (1987) saw also small moths brought to the nest, while orthopterans are mentioned only by HORVÁTH and HÜTTLER (1966).

The diet of adult birds differs from that of chicks in that in addition to caterpillars, butterflies, orthopterans and spiders they also eat small beetles (EWERSMANN 1866 in DEMENTEV et al. 1954; SCHAUER 1873; NAUMANN 1905; FRIDRICH 1922). F. and W. ZDOBNITSKY (1906 — after HUDEC et al. 1983) found small forms of the *Curculionidae* (*Polydrosus*, *Dorytomus* and *Phyllobius*) in 8 alimentary canals of River Warblers. In captivity a River Warbler, fed on larvae of meal beetles and ant cocoons, regurgitated undigested parts in the form of pellets (MOYAT 1906). During the present study we failed to observe this process either in adults or in young birds.

HORVÁTH & HÜTTLER (1966) think that feedings occur in 3—4 cycles of increased intensity daily, of 30—45 minutes each, when the young are fed every 3—4 minutes. On the other hand, MIERA (1970) writes that on the first day of life young are fed every 10 or 5 minutes, just when the parents relieve one another on the nest and on the 4 th day the feedings of four chicks took place every 3 minutes. DITTBERNER and DITTBERNER (1987) however give the most detail, namely, the number of feedings and removals of faeces, the way in which they are disposed of, how long the male brooded and how long the female; nearly all these data were gathered at one nest with 5 chicks. A comparison of their results with the results from nest No 2316, also with 5 chicks, shows their great concurrence. The biotopes of these two nests were similar. On the other hand, the description of the ethology of the male and female is striking. According to the DITTBERNERS (1987) and in opposition to the present observations, the "male" was the one who mainly brooded and came off the nest when the "female" was coming with food, to continue brooding the young later, whereas the "female" was the main food deliverer. The description of the birds' behaviours indicates that those authors misdetermined the sex of the adult birds in most

cases. It also shows that the hide was made too close to the nest and that the watching of "tamed" birds without hiding caused changes in the behaviour of the fairly skittish male. This is also true of some observations published by HORVÁTH and HÜTTLER (1966).

DITTBERNER and DITTBERNER (1986, 1987) followed the fate of River Warblers after hatching and arrived at the conclusion that they leave their breeding territories relatively early. The present results lead to a similar conclusion.

X. NUMBER OF BROODS AND BREEDING SUCCESS

The River Warblers as a rule raise only one brood a year. This however concerns scarcely 36% of pairs entering upon breeding. If their eggs or young have been destroyed, they resume breeding anew, often in the same territory. They do this when the eggs have been destroyed just after being laid but also when the eleven-day-old nestlings have perished in the nest. And so, as a result, the late broods observed even in mid-August may still be, despite repetitions the first broods. Threefold attempts at nesting were observed in as many as three pairs, whose fate was watched all the time and only in one of them the young left the nest without losses as late as August.

Out of the 42 nests observed, the young left only 15 by themselves. Three nests were abandoned before eggs had been laid in them and in three others the departure of the healthy chicks was advanced by an observer who came near to the nest. The remaining 21 nests were destroyed: broods that fell victims to birds (Red-backed Shrike, Hooded Crow and Jay — 10% of nests and 8.9% of eggs or chicks) mammals (rodents, fox and boar — 42% of nests and 33.9% of eggs or chicks) and man (mowing of nettles and meadows in the direct neighbourhood of nests and errors in the method used by the observers — 24% of nests and 22.3% of eggs or chicks) (Table XVI).

Out of the 184 eggs laid by 39 females, 106 hatched (57.6%). In 12 out of 37 nests 17 eggs were addle, mostly one egg a nest but in one nest 4 of 5 eggs were addle. Breeding success was recorded from barely 18 nests. A total of 27 young birds departed from them, i. e. 4 chicks per nest. And so the young that left the nests as fledgelings constituted only 39.1% of the 184 eggs laid. The breeding success and the reproductive rate of the species are therefore very low, 1.85 chicks leaving the nest per pair, i. e. 0.92 chick per bird entering upon the reproductive activities. These numbers are however modified by repeated attempts at nesting made by River Warblers, if their previous broods have been destroyed. Assuming cautiously, (as shown above) that a third of pairs having their first brood destroyed, raised 5 fledgelings each, then the reproductive rate should be increased from 1.85 to 2.79 chicks/nest or 1.39 chicks/bird entering upon breeding.

A few days following the fledgelings' departure from the nest, when they are

Table XVI

Extent of losses in the broods of River Warblers *Locustella fluviatilis* in deciduous forests near Łężany (data from 39 nests in which 184 eggs were laid)

Phases of breeding period		Losses	Addle eggs	Birds	Mammals			Man	Unknown cause	Total losses	Percentage losses	
					Rodents	Fox	Boar				in relation to total of destroyed eggs and nestlings	in relation to all eggs laid
Egg laying		nests	—	—	—	1	—	—	1	2	10	5.1
		eggs	—	—	—	2	—	—	2	4	3.6	2.2
Incubation	to 6th day	nests	—	—	—	1	3	2	1	7	33	17.9
		eggs	—	—	—	5	12	11	4	32	28.6	17.4
	to 7th—13th day	nests		1	1	—	—	2	1	5	24	12.8
		eggs	17*	5	5	—	—	10	5	42	37.5	22.8
Nestlings	to 9th day	nests		1	1	1	—	1	1	5	23	12.8
		nestlings		5	5	5	—	4	6	25	22.3	13.6
	after 10th day	nests		—	—	1	—	—	1	2	10	5.1
		nestlings		—	—	4	—	—	5	9	8.0	4.9
Total of destroyed nest			2	2	4	3	3	5	5	21	100	53.7
Total of destroyed eggs and nestings			17*	10	10	16	12	25	22	112	100	60.9
% destroyed nests			—	10	10	19	14	24	23	100		
% destroyed eggs and nestlings			15.2	8.9	8.9	14.3	10.7	22.3	19.7	100		

* These eggs (17) were found in 12 nests.

not, as yet, able to fly and the rainy weather commonly occurring in this country at that time lower the reproductive rate of River Warblers still more.

However, it should be taken into consideration what influence the activities of the investigator exerted on the calculate value of losses. In three cases the abandonment of the nest during incubation may be ascribed to the activities of an observer but, on the other hand, his permanent presence in the hide near the nest eliminated destructions caused e. g. by big animals like the fox or boar. In 6 nests which were under constant observation all the chicks fledged.

XI. THE BIOLOGY OF THE RIVER WARBLER AGAINST THE BACKGROUND OF THE GENUS *LOCUSTELLA*

The genus *Locustella* KAUP, 1829 comprises 6 or 7 species according to the opinion of a given systematist. These species inhabit the whole Palaearctic from the Atlantic to the Pacific Ocean. Three European species, the Grasshopper Warbler, River Warbler, and Savi's Warbler are replaced by Pallas's Grasshopper Warbler, Lanceolated Warbler and Gray's Grasshopper Warbler in the east and Middendorff's Grasshopper Warbler round the Sea of Okhotsk (HARRISON 1982). The species that have an extensive or discontinuous range created several subspecies.

The state of knowledge of the ecology and, above all, biology of nesting varies with particular species. I drew information about those species, naturally except the River Warbler, from the following items of literature:

Pallas's Grasshopper Warbler *L. certhiola* (PALLAS, 1811) — DEMENTEV et al. (1954), VOROBEV (1954), NAUMOV & KISLENKO (1965), PANOV (1973), ELTSUKOV (1977);

Middendorff's Grasshopper Warbler *L. ochotensis* (MIDDENDORFF, 1853) — DEMENTEV et al. (1954), GIZENKO (1955), KOBAYASHI, ISHIZAVA (1932 — 1940);

Gray's Grasshopper Warbler *L. fasciolata* (GRAY, 1860) — KOBAYASHI, ISHIZAVA (1932—1940), DEMENTEV et al. (1954), GIZENKO (1955), NEUFELDT & NECHAEV (1977, 1978), ELTSUKOV (1977);

Grasshopper Warbler *L. naevia* (BODDAERT, 1783) — WITHERBY et al. (1983), SHNITNIKOV (1949), BANNERMAN (1954), DEMENTEV et al. (1954) KOVSHAR (in DOLGUSHIN et al. 1972), MAKATSCH (1976,) LEISLER (1975, 1977), STUŻYŃSKI (1979);

Lanceolated Warbler *L. lanceolata* (TEMMINCK, 1840) — KOBAYASHI (1940), DEMENTEV et al. (1954), NAUMOV & KISLENKO (1965), KOVSHAR (in DOLGUSHIN et al. 1972), MAKATSCH (1976);

Savi's Warbler *L. luscinioides* (SAVI, 1824) — SCHIERMANN (1926),WITHERBY et al. (1983), SHNITNIKOV (1949), BANNERMAN (1954), DEMENTEV et al. (1954), MILDENBERGER (1958), LEISLER (1975, 1977), PIKULSKI (1980).

Descriptions, measurements and photographs of nests of *L. certhiola* (2 spe-

cimens), *L. ochotensis* (2), *L. luscinioides* (1) and *L. lanceolata* (1) derived from Dr V. V. LEONOVICH'S collection and the collection stored at the Zoological Museum in Moscow were also used here.

L. fasciolata (NEUFELDT & NECHAEV 1977, 1978) and *L. luscinioides* (PIKULSKI 1980) are best known in respect of their biology.

Nesting in thick herbaceous vegetation, often of tufty structure, is a common feature of all these species. They rather choose open habitats large in area, with single high stalks, shrubs or small trees, providing males with perches to sing courtship songs on. However, breeding pairs often occupy ecotone habitats. The adaptability of each of the species is often greater than the ecological differentiation of their characteristic habitats. All the species therefore inhabit meadows of high grass of sedges growing at the waterside — from seepage springs and streams amidst woods, through rivers, ponds and lakes, to ocean coasts. The choice of the site is however determined by the structure of the growth and not its hydrophilic nature, for they nest also far from water bodies, in mountain meadows of Asia (*L. certhiola* and *L. ochotensis*), in forest steppes of the Ural, Caucasus and Tien Shan Mts. (*L. naevia straminea*), in forest clearings (*L. fasciolata*, *L. fluviatilis* and *L. naevia*) or in thinned forests of Europe and Asia (*L. fluviatilis*, *L. cethiola*, *L. ochotensis*, *L. fasciolata* and *L. lanceolata*).

The body proportions and, in particular, the tapering wings and tail, adapted for long flights to winter quarters, hinder the members of the genus *Locustella* from flying freely in the thick of the vegetable environment. As a result, these birds chiefly walk on the soft vegetable litter and collect food from the surface of the litter and plants on foot. The River Warbler is the best walker of the European species and Savi's Warbler is the best at climbing vertical stems (LEISLER 1975, 1977).

Unmated males of all these species arrive 3—10 days before females and start singing in the territories which they are just taking up (NEUFELDT & NECHAEV 1978; MACKOWICZ 1977; PIKULSKI 1980). There are two types of singing: three Asiatic species — *L. certhiola*, *L. ochotensis* and *L. fasciolata* — sing short strophes repeated again and again, whereas the European species — *L. fluviatilis*, *L. luscinioides* and *L. naevia* and the Asiatic *L. lanceolata* — sing long monotonous songs. Males of all these species sing hidden in the herb layer or in shrubs and trees standing out above it. *L. certhiola* is an exception, its male sings also in display flight, just as does *Acrocephalus schoenobaenus* (KHAKHLOV 1937, after DEMENTEV et al. 1954). NAUMOV and KISLENKO (1965) write that such flights occur rarely. The members of the genus *Locustella* sing mainly at daybreak and in the evening twilight. *L. fluviatilis* (MACKOWICZ 1977), *L. fasciolata* (NEUFELDT & NECHAEV 1977), *L. naevia* (STUŻYŃSKI 1979). *L. laneolata* (IVANOV 1928 after DEMENTEV et al. 1954) and *L. ochotensis* (DEMENTEV et al. 1954) sing uninterruptedly also in some nights of the preincubational period. Under cover of the night *L. fasciolata* daringly takes up higher and more exposed song perches (NEUFELDT & NECHAEV 1977), which is also true of *L. certhiola* (DEMENTEV et al. 1954) whereas *L. fluviatilis* and *L. naevia* sing

then in lower shrubs, nearer to the ground. All the species of the genus *Locustella* perform horizontal transverse movements of the head while singing, causing undulation in the sound intensity. The same can be observed in the Asiatic species, which sing short strophes. These species also react in the same way to a danger: they stop singing abruptly and disappear, diving from the song perch into the herbaceous vegetation (TACZANOWSKI 1882, 1891; NEUFELDT & NECHAEV 1977; PIKULSKI 1980, and others). Out of the European species, the River Warbler sings the longest strophes (MACKOWICZ 1977), Savi's Warbler strophes of medium length (PIKULSKI 1980) and the Grasshopper Warbler the shortest ones (STUŻYŃSKI 1979). On the other hand, the mean length of songs of mated males was 24.0 sec. (n = 420) in the Grasshopper Warbler (STUŻYŃSKI 1979), 37.7 sec. (n = 811) in Savi's Warbler (PIKULSKI 1980) and 60.8 sec. (n = 168) in the River Warbler and they are roughly proportionate as 2 : 3 : 5. The songs of unmated males are on the average longer by a half.

The hydrophilism of the biotopes in most sites occupied by the species of the genus *Locustella* has given rise to a tendency towards building nests above the surface of the ground. This is above all true of the species, whose nests are placed just at the waterside — *L. luscinioides* and *L. certhiola*. They avail themselves of tussocks of sedges or high grasses and hillocks existing in the area to rest the nests on (SCHIERMANN 1924; PIKULSKI 1980; NAUMOV & KISLENKO 1965). As has been observed now, River Warblers, too, place their nests on small natural hillocks. Insular populations of *L. fasciolata* build the nests highest, from 25 to 180 cm above the ground, as reported by NEUFELDT and NECHAEV (1977, 1978). Some nests of *L. naevia*, *L. lanceolata*, *L. ochotensis* and *L. fluviatilis* and nearly all nests of the continental pairs of *L. fasciolata* are built directly on the ground (NEUFELDT & NECHAEV 1977; DEMENTEV et al. 1954). The Grasshopper Warbler stands out from them, for, as may be assumed, it sometimes makes a hollow in the ground.

The nests of the species of the genus *Locustella* are characterized by the following features:

1. the nest base is made up of dry tree leaves of the previous year (mainly those of willows, alders and birches — also in the Far East),
2. the nest body is built of stalks and blades of grasses and sedges of the previous year,
3. the inner layer and lining consist of fine end-pieces of grasses and inflorescences (panicles),
4. the elements of animal origin in the lining are limited to several hairs of the boar, roe or horse in *L. fluviatilis*, *L. naevia* and *L. fasciolata* and also contour feathers in *L. certhiola*, *L. ochotensis* and sporadically in *L. naevia*.

The birds collect material in the nearest neighbourhood of the nest. The outer layer of the nest is most differentiated. *L. luscinioides* builds it mainly of broad leaf-blades of reeds and *L. fasciolata* weaves also large pieces of stalks of perennials into this layer.

It might seem that the general size of nests is determined by the size of the

bird and that *L. fasciolata*, as the biggest, builds the largest nest and the smallest *L. lanceolata* has the smallest ones. However, an analysis of the dimensions of nests given in literature indicates some deviations from this rule, namely, the second biggest *L. fluviatilis* builds nests of relatively great outer and inner diameters but rather flat and shallow. The small *L. certhiola* has comparatively one of the largest nests. The nest of *L. ochotensis* from north-eastern Asia is the highest with the deepest nest-cup of all the species of *Locustella*, probably because of the severe climate of that area; only the nests of the continental from of *L. fasciolata* may be somewhat deeper.

Nests are built by males and females in the *L. naevia* (WITHERBY et al. 1938) and *L. luscinioides* (MILDENBERGER 1958; PIKULSKI 1980), only by female in *L. fasciolata* (NEUFELDT & NECHAEV 1977) and perhaps in *L. lanceolata*.

The size of clutches is as a rule 3—6 eggs in all species. The *L. naevia*, which lays 4—7 eggs (MAKATSCH 1976), is an exception. The male's share in incubation is known in *L. luscinioides* (PIKULSKI 1980), *L. naevia* (MAKATSCH 1976) and *L. fluviatilis*. My own results indicate that in the River Warbler his share is the greatest. NEUFELDT and NECHAEV (1977) claim that only the female incubates in *L. fasciolata*. However, the concurrence of many other details of biology and morphology and the methodological failures of various investigators permit us to put forward the hypothesis that both males and females incubate in the genus *Locustella*, only the percentage share of the male may be different in particular species.

Many authors assume a priori that incubation begins after the laying of the last egg. However, in Savi's Warbler hatching may take up to three days. The issue needs more precision, for it has appeared that in the River Warbler incubation as a rule begins on the day of the laying of the fourth egg and in some nests, no doubt, after the third egg has been laid. An analysis of PIKULSKI'S (1980) results inclines us to assume that also in Savi's Warbler incubation begins when the 3rd or 4th egg has been laid. If this correction has been introduced, it appears that in all the species of the genus *Locustella* incubation lasts 14—15 days, for this period is given for Gray's Grasshopper Warbler by NEUFELDT and NECHAEV (1977, 1978), for the Grasshopper Warbler by WITHERBY et al. (1938). I found such a period for the River Warbler and presumably it will be the same in Savi's Warbler.

As in the River Warbler, in Savi's Warbler the hatching of the first chicks falls in early morning hours (PIKULSKI 1980). In the latter species the male's share in disposal of the faeces is even greater than in the River Warbler (PIKULSKI 1980).

In all the species studied both the male and female participate in the feeding activities. In Gray's Grasshopper Warbler and Savi's Warbler the male feeds the young chiefly in the first five days of their life, for in Gray's Grasshopper Warbler only the female broods, whereas as regards Savi's Warbler little is known about the male's share in brooding (NEUFELDT & NECHAEV 1977; MILDENBERGER 1958; PIKULSKI 1980). It is however hard to decide on the basis of this

information as to the actual share of the male in feeding in these species until it becomes known to what extent the increased shyness of the male at the nest has been taken into account in the methods (MILDENBERGER watched the feeding of young at a distance of 1 m from the nest). The male brings a larger portion of food to the nest and distributes it among more nestlings than does the female (PIKULSKI 1980; NEUFELDT & NECHAEV 1977).

The diet of chicks is fairly well known only in River Warblers, Gray's Grasshopper Warblers and Savi's Warblers and in respect of its specific composition the results of studies agree very much with each other. It consists of groups of sluggish animals which feed, rest and move about in the ground layer of herbs and grasses. Small forms of slugs were found in the diet of the River Warbler and Gray's Grasshopper Warbler, arachnids in all the above-mentioned species. As regards insects, the preferred groups of food of all the species under study contain dipterans and among them *Tipulidae*, butterflies (above all *Microlepidoptera*) caterpillars — especially green in colour — of the *Noctuidae* and *Geometridae* (River Warbler and Grasshopper Warbler). Homo- and heteropterans go chiefly to the making of the diet of chicks of Gray's Grasshopper Warbler but also occur in the food of the Grasshopper Warbler and River Warbler. The number of caterpillars in the diet of chicks of Gray's Grasshopper Warbler is small in comparison with their frequency in the food of the European *Locustella*. In addition, a certain number of small beetles of the families *Chrysomelidae* and *Curculionidae* were also found in the food of adult birds in all these species.

Chicks of the genus *Locustella* leave their nests early, before they are able to fly, between the 12th and the 15th day of their life. In small species, e. g., in the Grasshopper Warbler this process may be shortened even to 10 days and in Savi's Warbler to 11 days (WITHERBY et al. 1938; PIKULSKI 1980; NEUFELDT & NECHAEV 1977).

All the pairs of the genus *Locustella* inhabiting Asia and the northern regions of Europe raise only one brood. On the other hand, some pairs of the Grasshopper Warbler and Savi's Warbler in Central Europe regularly proceed to raise the second brood (WITHERBY et al. 1938; PIKULSKI 1980).

On the basis of the foregoing comparisons of all these species in respect of their biology and, in particular, biotope, singing and nest building, in spite of differences in the completeness of data, the following conclusions can be drawn about the differences and similarities between them:

1) *L. luscinioides* differs most from the remaining species,

2) two pairs, *L. certhiola* and *L. ochotensis* as well as *L. naevia* and *L. lanceolata*, show most similarities, and

3) somewhat smaller similarities occur between *L. fluviatilis* and *L. fasciolata*.

It may be supposed that these relations are at least partly reflected in the morphology and plumage of these birds, for, e. g., VAURIE (1959) admits the possibility to recognize *L. ochotensis*, (with its subspecies *L. o. pleskei*) as subspecies of *L. certhiola*. Furthermore, WOLTERS (1980) distinguished five subgene-

ra in the genus *Locustella*. Their arrangement corresponds roughly with the above-mentioned conclusions drawn from their biology only that he placed *L. fluviatilis* and *L. fasciolata* in two separate unispecific subgenera.

Translated into English
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STRESZCZENIE

W latach 1970—1980 objęto badaniami 253 samotnych samców i par strumieniówek nad rzekami: Łyną, Pisą i Biebrzą oraz w lasach okolic Łężan (ryc. 1, tab. I). Pomiary biometryczne 70 ptaków wykazały dużą zbieżność z wynikami innych autorów (tab. II). Morfologicznie samce różnią się od samic kształtem kloaki (ryc. 2).

Samce wracają z zimowisk około 20 maja zajmując początkowo biotopy lęgowe nad rzekami i strumykami wśród podmokłych łąk, zarośla wierzbowe czy łęgi jesionowo-olchowe, a później zasiedlają lasy, najliczniej olsy porzeczkowe i zarastające poręby grądowe (tab. III). Zajmowane są miejsca o bujnej roślinności zielnej, szczególnie łany pokrzyw (tab. III i IV). Samice przylatują ok. 10 dni po przylocie pierwszych samców. Powierzchnie terytoriów lęgowych mają średnio 0,36 ha (tab. V) i na ogół nie stykają się ze sobą. Wyrazem zewnętrznym zajęcia terytorium jest śpiew godowy samców, który rozbrzmiewa od połowy maja do końca lipca (28—42 pentady). Samce śpiewają prawie przez całą dobę, początkowo mniej intensywnie (ryc. 3) potem, szczególnie nocą, śpiew jest intensywny, o bardzo krótkich przerwach (ryc. 4, 5, 6); samotne samce śpiewają intensywniej niż połączone w pary. W pierwszych dniach po przylocie samce mogą śpiewać zwrotki prawie 2-krotnie szybciej niż później (ryc. 7). Śpiew godowy kończy się na początku okresu inkubacji — od tej pory samiec tylko reaguje śpiewem ostrzegawczym na wtargnięcie w terytorium. Poza śpiewem opisano 10 dalszych głosów wydawanych przez strumieniówki.

Gniazdo jest zakładane zwykle na obrzeżu łanów roślinności zielnej o odpowiednim zagęszczeniu (głównie pokrzyw — tab. III, IV), gdzie warstwa butwiejących roślin, gałązek, ułatwia ptakom poruszanie się pieszo na różnej wysokości nad ziemią. Gniazdo znajduje się przeważnie na podwyższeniu, np. — kępie obumarłej turzycy, wzgórku ziemnym, kretowisku, czy w kępie traw itp. (ryc. 8). Gniazdo składa się z 4 warstw różniących się grubością i składem użytego materiału (ryc. 9 i tab. VI, VII, VIII). Do gniazda prowadzą na ogół 1 lub 2 dojścia, głównie od strony południowej i południowo-wschodniej (ryc. 10). Wymiary gniazd oraz ich zróżnicowanie przedstawia tab. IX.

Początek składania jaj przypada zwykle na pierwszą dekadę czerwca (ryc. 11). Liczba składanych jaj waha się od 3—6, a średnie zniesienie wynosi 4,92 jaj; najliczniejsze są lęgi 5-jajowe (tab. X). Ubarwienie jaj nie odbiega od stwierdzonego w Europie, średnie wymiary ($19{,}67 \pm 0{,}8 \times 14{,}95 \pm 0{,}46$ mm) jednak są nieco mniejsze od zebranych na zachodzie i południu Europy. Średni ciężar świeżych jaj wynosi $2{,}54 \pm 0{,}36$ grama i spada w ciągu wysiadywania o 0,49 grama, tj. 19,4% (ryc. 12).

W wysiadywaniu bierze udział zarówno samica jak i samiec, lecz udział samca jest mniejszy (ryc. 14) i ogranicza się do godzin dziennych (ryc. 14, 15). Długość zmian samca i samicy podczas wysiadywania zależy od pory dnia

(ryc. 13). Wysiadywanie rozpoczynają strumieniówki po złożeniu 4 jaja (tab. XI). Wśród wielu zachowań przy gnieździe zarejestrowano szereg czynności związanych bezpośrednio z ogrzewaniem jaj — obroty ciała i jaj (tab. XII, ryc. 16, 17), z reakcją na odgłosy i zmiany w otoczeniu — okresy zaniepokojenia i zapadania w drzemki (ryc. 18, 19), z usuwaniem pasożytów z upierzenia i gniazda (ryc. 20, 21), liczbę moszczeń w gnieździe i związanych z tym rytualnych kłapań dziobem (ryc. 22, 23), jak i niezależnych — ziewań (ryc. 24), wydawania głosu "kichania" (ryc. 25) i zaglądań do gniazda (ryc. 26). Obroty ciała, jaj, iskania siebie i gniazda oraz zaglądania do gniazda prześledzono również w okresie przebywania piskląt w gnieździe (ryc. 16, 20, 26). Pisklęta klują się w 14—15 dniu inkubacji, lecz w związku z rozpoczęciem wysiadywania niepełnego lęgu i nocowania w tym okresie samicy w większości gniazd klucie się piskląt rozciąga się do 3 dni.

Karmienie piskląt rozpoczyna się zaraz po wykluciu się pierwszego pisklęcia i jego częstotliwość wzrasta do 11 dnia, a największą liczbę — 261 karmień w ciągu dnia zarejestrowano w gnieździe z 5 pisklętami (ryc. 29). Średnia intensywność karmień w ciągu dnia jest uwarunkowana siedliskiem i warunkami świetlnymi przy gniazdach (ryc. 30). Wierzchołki krzywej ilustrującej intensywność karmień podlegają wahaniom w poszczególnych dniach życia piskląt (ryc. 31). Ogólnie samiec przynosi pokarm częściej od samicy (ryc. 28), a intensywność tej czynności spada w ciągu dnia (ryc. 32).

Na podstawie obserwacji karmiących ptaków i fotografowania strumieniówek przynoszących pokarm do gniazda oznaczono 436 ofiar (tab. XIII, ryc. 27). Przeważały wśród nich gąsienice i motyle, muchówki i pająki. Porcje pokarmu dostarczane przez samce są większe i stąd liczba obdzielanych nimi piskląt jest większa niż w przypadku samic (tab. XIV).

Liczbę wydalanych przez pisklęta odchodów przedstawia ryc. 34, a zmiany sposobu usuwania ich przez samca i samicę (połykanie i wynoszenie) w miarę wzrostu piskląt — ryc. 35. Liczby karmień przypadające na usuwanie odchodów wahają się w ciągu dnia jak i w okresie przebywania piskląt w gnieździe (ryc. 33, 35, 36).

Pisklęta są chronione przed przechłodzeniem i samica nocuje na gnieździe do końca ich pobytu w gnieździe. Do 4. dnia ogrzewa je również intensywnie w ciągu dnia. W ogrzewaniu bierze również udział samiec (ryc. 37). W miarę wzrostu piskląt spada intensywność ich ogrzewania (ryc. 37), przede wszystkim w środku dnia, między 6.00 a 17.00 (ryc. 38). Zmniejszający się w miarę wzrostu piskląt czas ich ogrzewania zależy nie tylko od wzrostu ich termoregulacji, lecz również od konieczności zdobywania pokarmu dla piskląt. Gdy w gnieździe znajduje się 1 pisklę, ogrzewanie praktycznie nie słabnie aż do końca jego pobytu w gnieździe (ryc. 37, 39).

W związku z dużymi stratami większość par powtarza lęgi. Straty spowodowane są przez człowieka, lisy, dziki, gryzonie i ptaki (tab. XVI). Ostateczny sukces lęgowy wynosi 2,79 piskląt na parę przystępującą do lęgów.

Biologia strumieniówki jest ogólnie podobna do opisywanej dla innych przedstawicieli rodzaju *Locustella*. Najwięcej jednak zbieżności ze strumieniówką, zwłaszcza w budowie gniazda, wykazuje świerszczak tajgowy *L. fasciolata*.

Redaktor pracy: prof. dr Z. Bocheński

Plate III

Some breeding biotopes of the River Warbler in NE Poland

Phot. 1. One of the best habitats — the wet alderwood with black currant *Ribo nigri-Alnetum*

Phot. 2. Another habitat frequently occupied by the River Warbler: *Tilio-Carpinetum* forests at streams

Phot. 3. The nettle field under an alder canopy is a typical nest territory

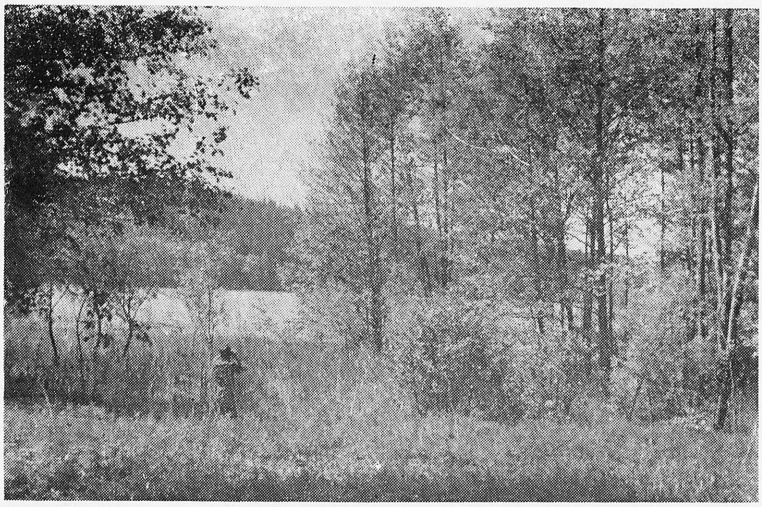

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Plate IV

Phot. 4. A male River Warbler singing in the night
Phot. 5. A nest of the River Warbler containing a full clutch of 5 eggs
Phot. 6. A River Warbler resettles on a nest — ruffled cover feathers on the belly can be seen

4

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Plate V

Phot. 7. An incubating River Warbler sleeps in its nest
Phot. 8. An incubating River Warbler in the posture of anxiety
Phot. 9. A River Warbler removing the egg shell just after the hatching of a young

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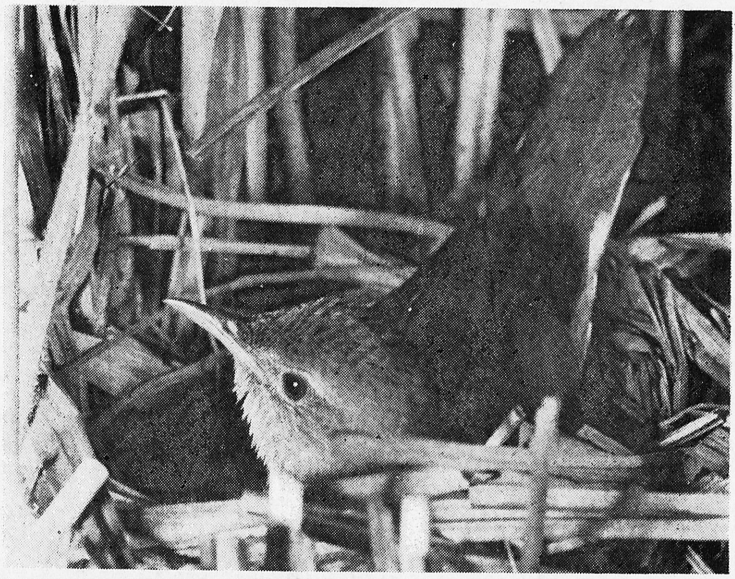

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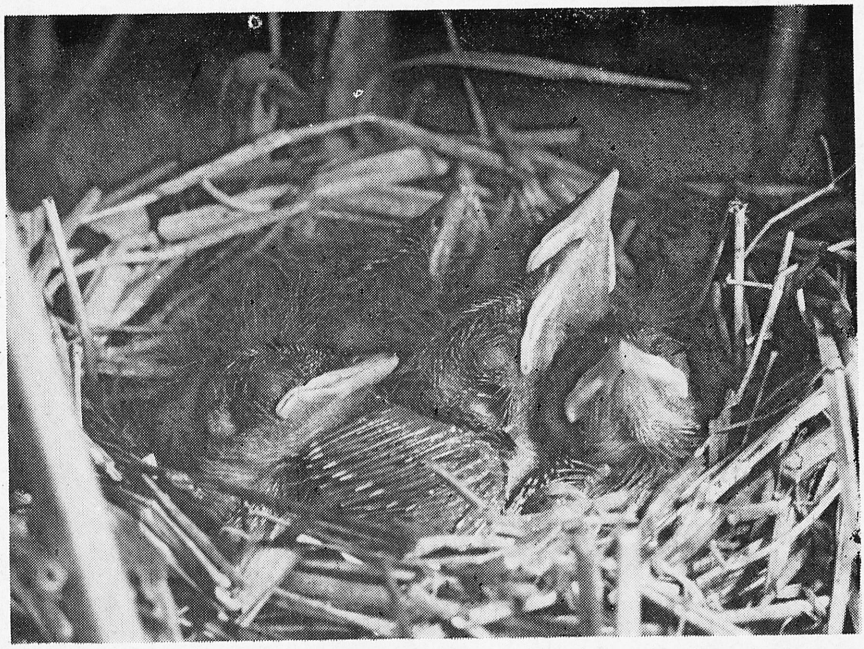
Plate VI

The various arrangements of River Warbler chicks in the nest:
Phot. 10. An example of "imbricate" arrangement
Phot. 11. Arrangement with heads directed towards the middle of the nest



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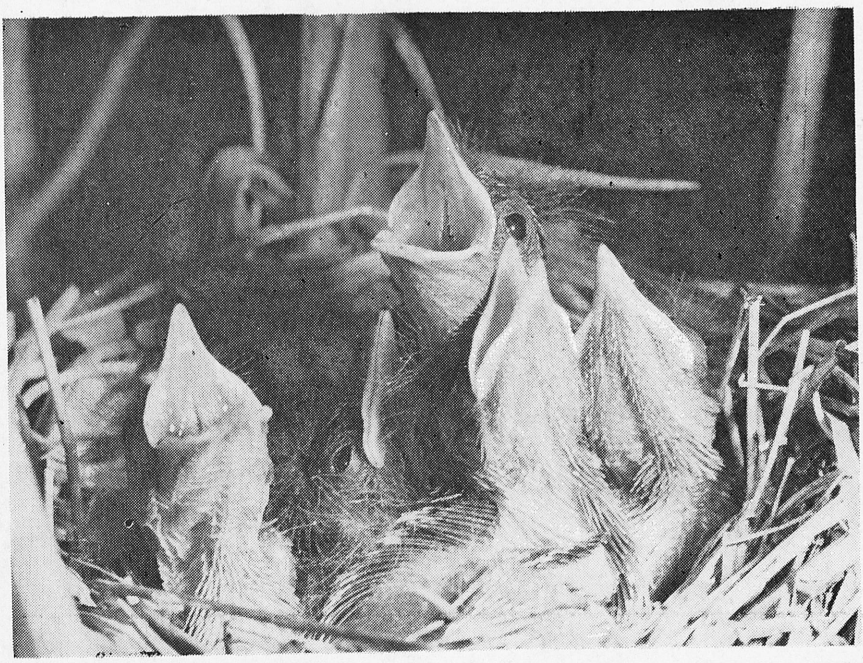

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Plate VII

Some examples of pictures used for the analysis of River Warbler chicks' food composition

Phot. 12. Feeding chicks with dipterans (including *Tabanus* sp.)

Phot. 13. Feeding chicks with dipterans (*Tabanus* sp., *Tipula* sp.) and orthopterans

Phot. 14. Feeding with nekad caterpillar

Phot. 15. The male feeds the chick with *Tipula* sp.

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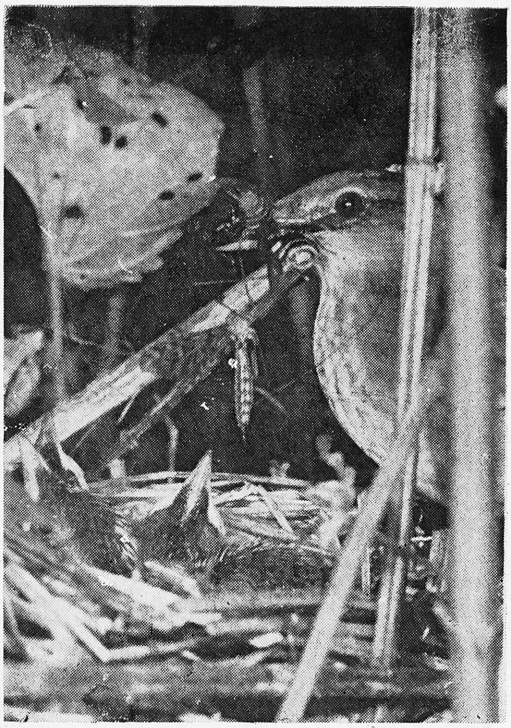

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Plate VIII

An untypical situation: the nest No 38 contained 1 chick and some addled eggs
Phot. 16. The male River Warbler, carrying food, makes the brooding female leave the nest
Phot. 17. The female interrupts brooding when the male has arrived with the food (a *Geometridae* moth)

16

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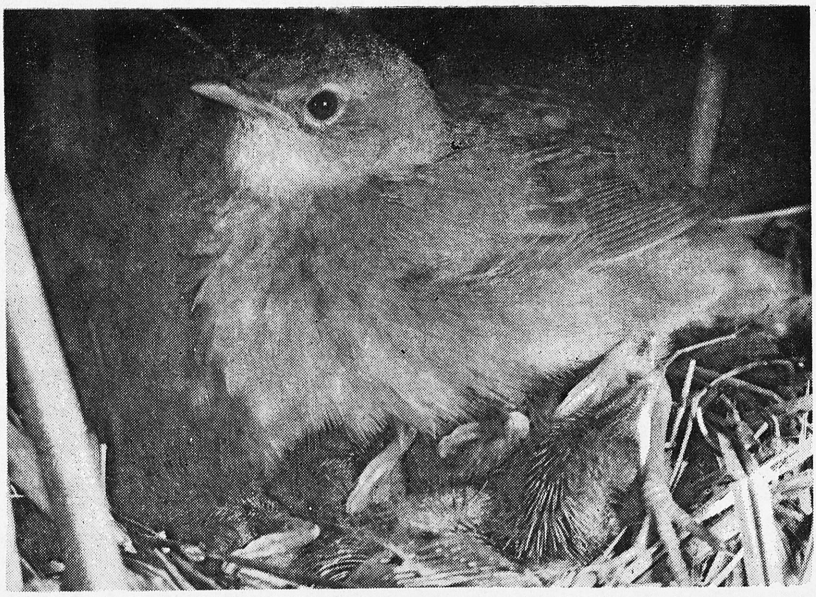
Plate IX

Phot. 18. An adult River Warbler broods its several-day-old chicks

Phot. 19. In the daytime, instead of brooding older chicks, a parent River Warbler often stands on the nest edge

Phot. 20. A parent River Warbler grasps its chick's faecal sack in order to dispose of it



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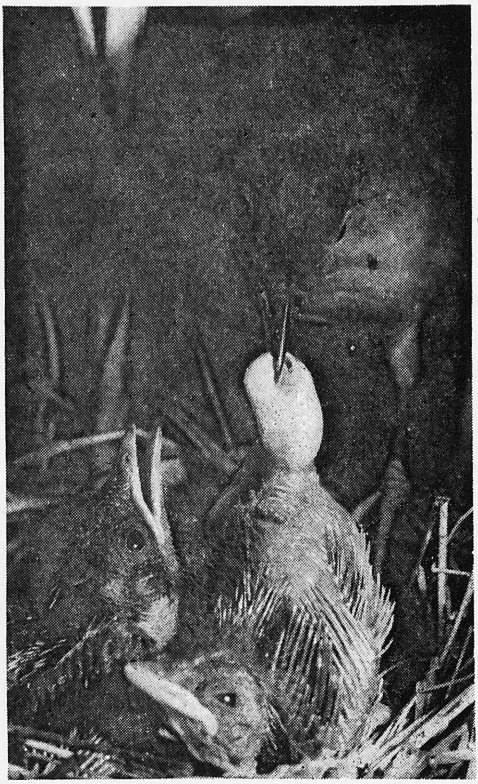

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