

Breeding ethology and ecology of the Reed Warbler, *Acrocephalus scirpaceus* (HERMANN, 1804) at Milicz, SW Poland

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Abstract. The settling pattern, territorial behaviour, pair formation, breeding site selection, nest building and breeding success of birds were studied in a population of individually marked Reed Warblers in 1980-1982 in the nature reserve "Stawy Milickie" (Milicz Fish Ponds), SW Poland. The intense territorial behaviour of males was limited to the period from the establishing of their territory to the arrival of a female. The nest site was selected by the female, which did not pay much attention to the original territory boundaries fixed by the male; 36% of nests of the first brood were located beyond the initial boundaries of the male territories. Several pairs often preferred the same part of the reedbed, and loose aggregations of nests were common. Nest losses were high (67%) and in 95% due to predators. As a result, the production of young was very low despite many repeated attempts at nesting. After the loss of the first nest, 76% of the females renested. Unsuccessful females were never observed in next years, whereas unsuccessful males returned.

Key words: *Acrocephalus scirpaceus*, breeding, ethology, ecology, SW Poland.

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I. INTRODUCTION

A population of individually marked Reed Warblers was studied in 1980-1982 in the nature reserve "Stawy Milickie" (Milicz Fish Ponds), SW Poland. Earlier studies on the same species in the same area (DYRCZ 1974, 1977, 1981; KRÓL 1984) provided many interesting data and posed new questions. The objective of this paper is to answer some of them by analysing detailed observations of the social behaviour of birds. Particular emphasis is put on territorial behaviour, seasonal and spatial patterns of area utilization, and breeding success of individual pairs.

II. STUDY AREA AND METHODS

Observations were carried out on the pond "Słoneczny" in the nature reserve "Stawy Milickie", ca. 5 km E of Milicz ($51^{\circ}33' \text{ N} - 17^{\circ}21' \text{ E}$), in a reedbed bordering on the southern dike. A detailed investigation was conducted on a 2-ha fragment of the reedbed, extending for 200 m and neighboring on the village in the east and on a young alder wood across the dike in the south-east. The dike was covered with luxuriant herbaceous plants (*Solanum dulcamara*, *Lysimachia vulgaris*, *Eupatorium cannabinum*, *Epilobium palustre*), trees (*Alnus glutinosa*, *Populus* sp.), and shrubs (*Salix* sp., *Rubus* sp.). Young alders and willow thickets invaded the reedbed in some places. The part of the reedbed under study was dominated by the common reed *Phragmites communis* with less abundant cattails *Typha angustifolia*, sedges *Carex* sp. water manna-grass *Glyceria aquatica*, and bulrush *Scirpus lacustris* (Fig. 1).

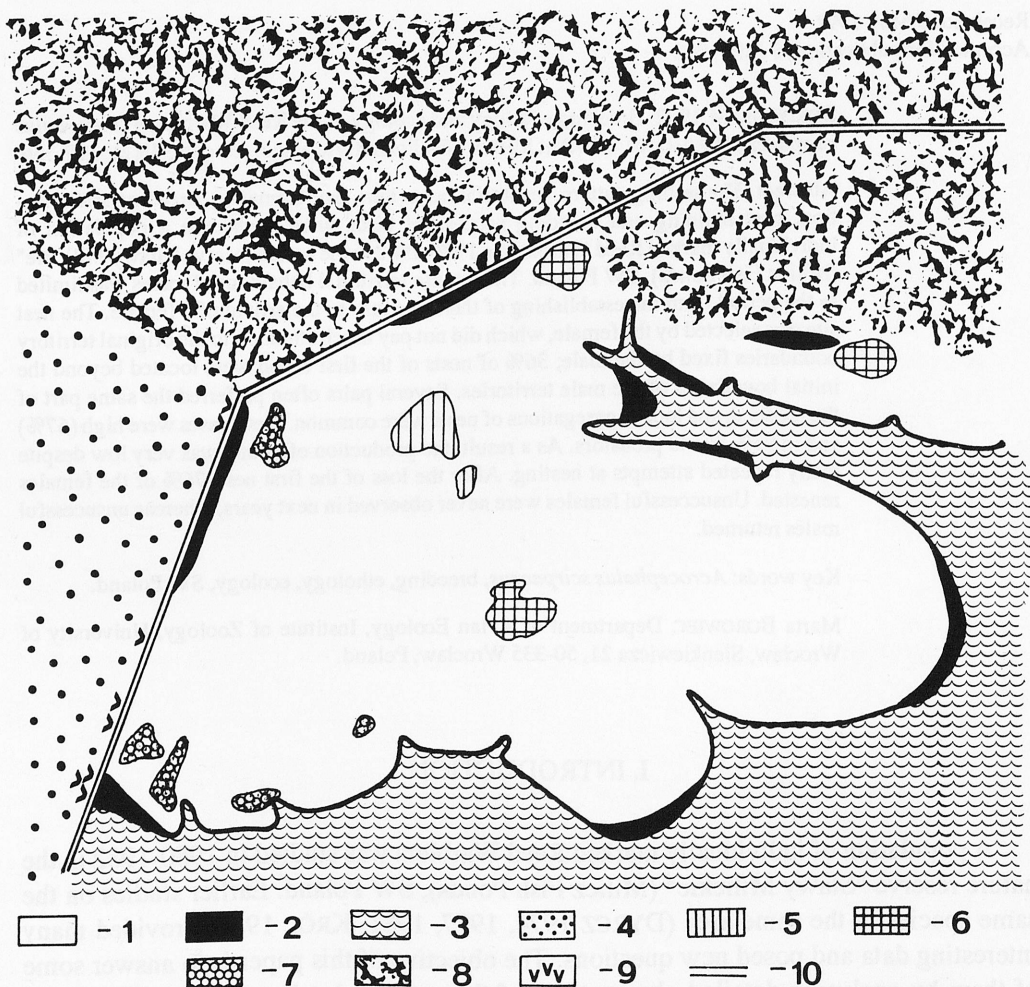


Fig. 1. Distribution of vegetation in the study area. 1 – reeds, 2 – cattails, 3 – water, 4 – meadow, 5 – sedges, 6 – bulrush, 7 – water manna grass, 8 – forest, 9 – trees on the dike, 10 – dike.

In a 2-ha part of the reedbed, adult Reed Warblers, including breeding and migrating individuals and visitors from other parts of the reedbed, were mist netted and marked with colour rings and a metallic ring from the beginning of May to the end of July. A total of 170 individuals were ringed over three years of study. Individually marked birds were observed at nests and from three observation towers located in the reedbed using 8x30 binoculars. A 20 m x 20 m grid of wooden sticks was laid down to locate the birds and map their song posts and directions of movements. The purpose of these detailed observations was to detect all individuals, to record the dates of their arrival, mating, nest building, egg laying, hatching, and fledging, and also to follow further fates of a breeding pair if the nest was lost. Searching for nests was continued throughout the breeding season so as to find all of them. Nest contents were checked every 1-3 days. A total of 186 nests were monitored. In addition, in July birds of all species living in the reedbed, including the Reed Warblers, were netted. These materials were used to analyze the movements of adult and young birds over the whole reedbed. Nestlings were marked only with metallic rings. A total of 116 nestlings were ringed. Territorial behaviour of males was analyzed in two ways: 1) the intensity of the response of males to conspecific songs was observed using a tape recorder and the distance they covered when following the tape recorder was noted, and 2) the type and intensity of the response of males to the presence of other individuals in the reedbed were noted on the basis of visual observations from the tower. The total number of days spent in the field was 270, and observations of the behaviour of birds were conducted for more than 780 hours.

III. SETTLING PATTERN OF MALES

The first individuals were noted in the first days of May every year. The earliest observation of a singing male was made on April 23 (L. TOMIAŁOJCZAK, personal comm.). In 1980-1982 the first singing males in the study area was recorded on May 9.

At least a part of the arriving males did not exhibit territorial behaviour from the very beginning. This was evidenced by a male, colour-ringed on 22 May 1980, which was not observed in his newly established territory till June 4.

The males settling latest of all were noted on July 7 in 1980, June 17 in 1981, and July 17 in 1982. The arriving males occupied territories in succession, and this process extended for 60, 40 and 70 days in consecutive study years. Presumably, this was due both to differences between the dates of arrival and to movements of the males from one territory to another. Fig. 2 shows seasonal changes in the number of male Reed Warblers. In 1981-1982, a fraction of nonbreeding individuals holding territories (4 and 5 males, respectively) were observed but after 5-9 days they left the study area without getting a mate. In addition to the residents, i.e. individuals without territories, defended them and were singing for a least one day, also individuals that established territories in the study area were observed or captured in nets. Some of them were likely to nest later outside the study plot, this being indirectly proved by the fact that they were recaptured in different parts of the reedbed

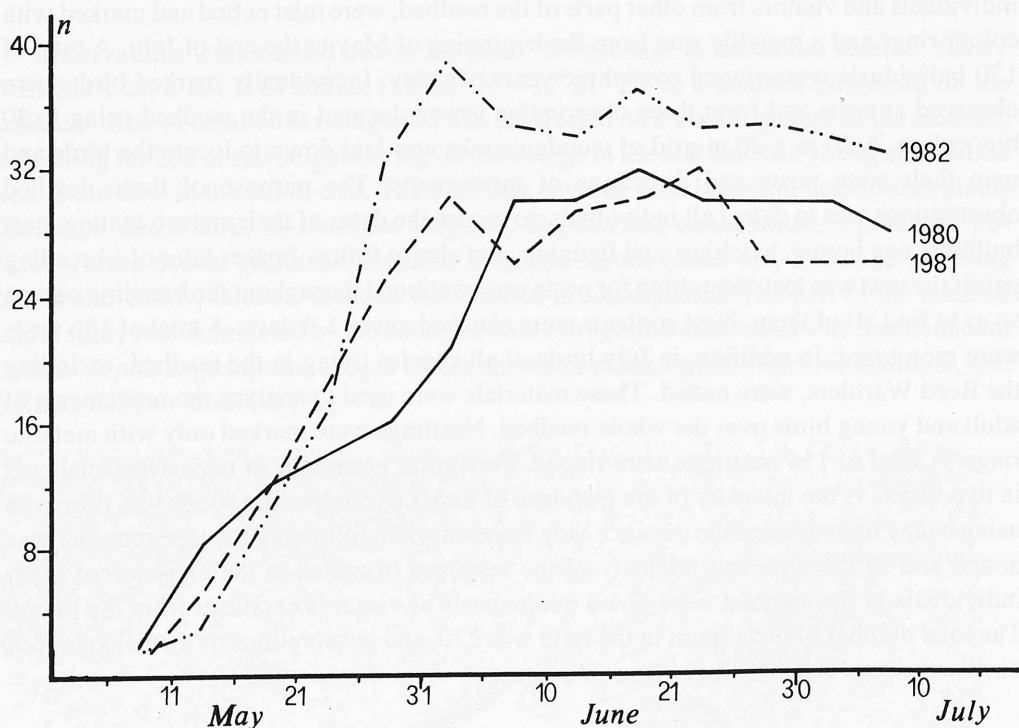


Fig. 2. Seasonal changes in numbers of male Reed Warblers in 1980-1982.

throughout the breeding period. In particular years the mean dates of settling in the study area were, as follows: May 29, 1980, May 24, 1981, and May 27, 1982.

IV. SETTLING PATTERN OF FEMALES

The presence of a female could be found for sure only after she selected a mate and established a bond with him. Earlier fates of the female, and especially the date of her arrival were obscure. Presumably immediately after arrival the females searched the reedbed and picked and chose males before taking one as a mate. This is suggested by the following observations:

- 1) a female was captured on 7 June 1980, but she was not recorded again in the territory of male M 26/80 till 16 June.
- 2) on 24 May 1981 a female without a brood patch was captured. Then she was recorded in the territory of male M 16/81 on 8 June. It should be noted that this male was first

recorded on 4 June. This was the only case when the female was observed in the study area earlier than her mate.

3) a female was captured on 29 May 1981 and recorded again in the territory of male M 3/81, while building the nest, on 11 June.

Females, like males, settled in breeding places in succession, but this period was less prolonged than in males and took 39 days in 1980, 43 days in 1981 and 34 days in 1982. In successive study years, the first females were recorded on 13 May in 1980, 13 May in 1981, and 16 May in 1982. Fig. 3 shows changes in the number of female Reed Warblers. In the study area the average settling dates in particular years were as follows: June 4, 1980, May 28, 1981, and June 4, 1982.

On the average, females settled 4-6 days later than males, but first females appeared in the study area long before the males reached peak numbers. As a result, the first females could choose only from 1-3 males. For example, in 1980, female F1, who chose male M1 and was observed for the first time in his territory on 13 May, had only two more males, M2 and M3, to choose from. In 1981, the first female had only one male at her disposal, and in 1982, the first female could choose out of three males, and she chose the male who arrived earliest. The last females settled on 20 June in 1980-1981 and on 17 June in 1982. Females, appearing at the peak time of arrivals, could always choose from several unpaired

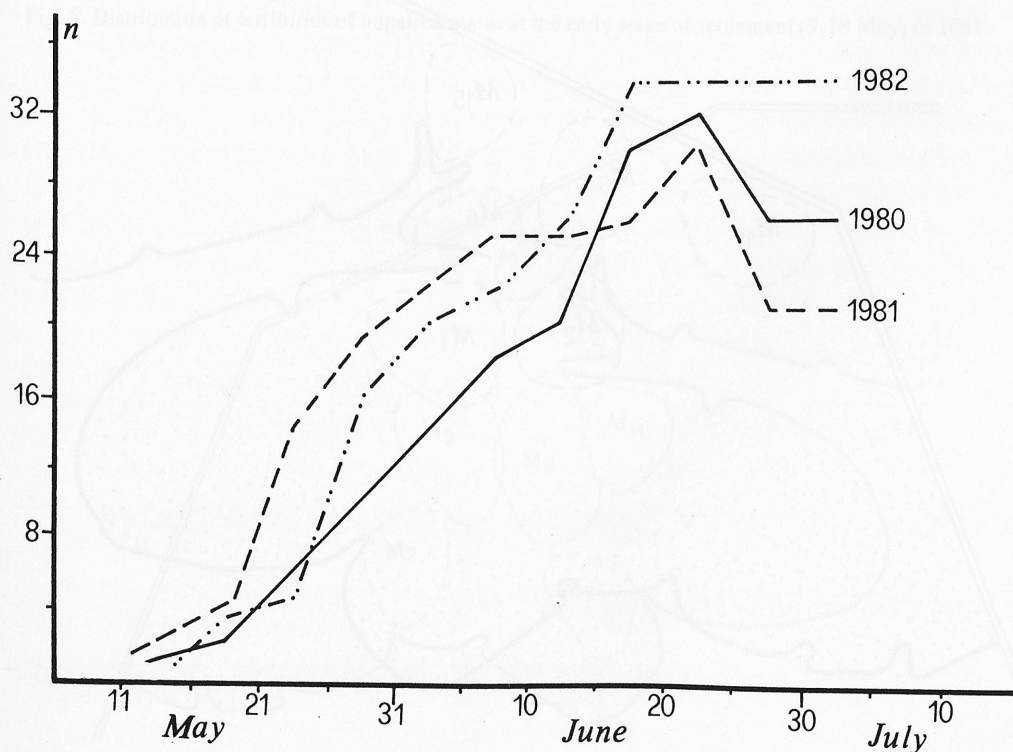


Fig. 3. Seasonal changes in numbers of female Reed Warblers in 1980-1982.

males. For example, on 27 May 1982 five new females were recorded, and 20 males were present on the plot that day, only seven of them paired and 13 without mates.

V. SELECTION OF BREEDING SITES AND ESTABLISHING THE BOUNDARIES OF BREEDING TERRITORIES

On arriving in the plot, the first males occupied territories in the central part of the reedbed. At first they searched relatively large areas ($1000-1400\text{ m}^2$), and then established their exact territories and song posts. Fig. 4. illustrates a clear tendency for males to aggregate early-spring territories in the central part of the reedbed and along the dike adjacent to the forest. Such a distribution of breeding territories was observed in 1980-1982, with some deviations caused by differences in the degree of reed destruction during winter (Figs 5-6). The first males established their territories in the best preserved parts of the reedbed.

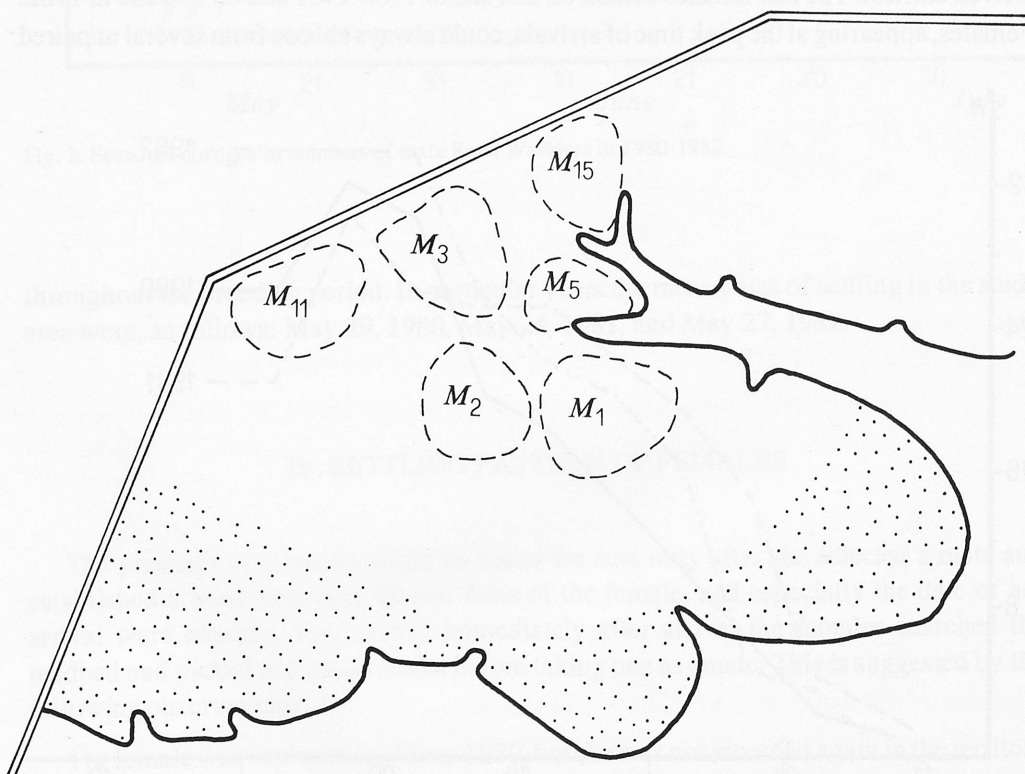


Fig. 4. Distribution of territories of unpaired males at the early stage of settlement (9-15 May) in 1980. Interrupted line – territory boundaries, M 4 – territory of male 4, dotted area – destroyed reed.

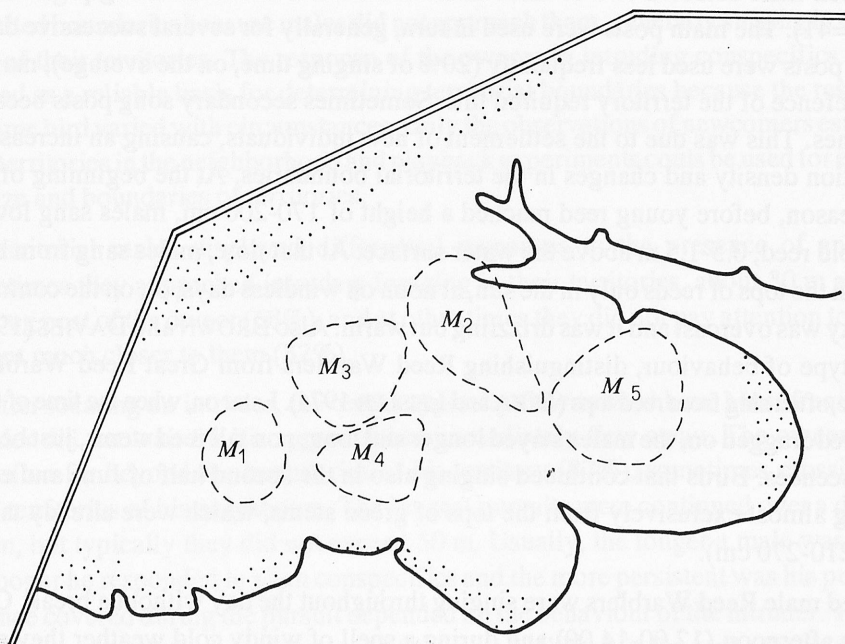


Fig. 5. Distribution of territories of unpaired males at the early stage of settlement (9-18 May) in 1981.

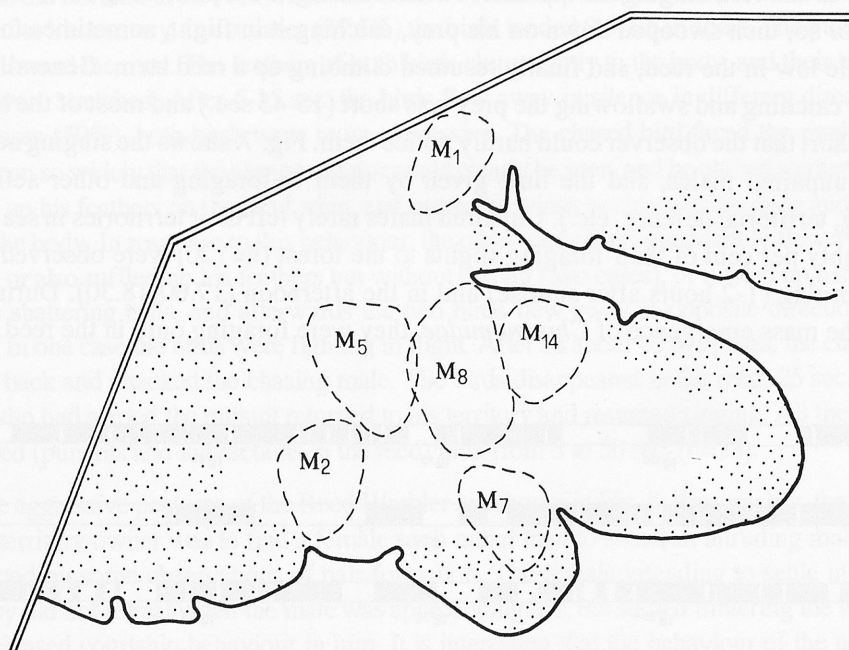


Fig. 6. Distribution of territories of unpaired males at the early stage of settlement (9-17 May) in 1982.

The male signalled the establishment of a territory by intense singing almost throughout the day. Each male selected two or three main and several additional song posts in his territory ($n=41$). The main posts were used in turn, generally for several successive days. Additional posts were used less frequently (20% of singing time, on the average), mainly when the defence of the territory required this. Sometimes secondary song posts became the main ones. This was due to the settlement of new individuals, causing an increase in the population density and changes in the territorial boundaries. At the beginning of the breeding season, before young reed reached a height of 170-200 cm, males sang low in clumps of old reed, 0.5-1.5 m above the water surface. At that time, males sang from high places, from the tops of reeds only in the sun, at noon on windless days, or, on the contrary, when the sky was overcast and it was drizzling but warm. Also BROWN and DAVIES (1949) noted this type of behaviour, distinguishing Reed Warblers from Great Reed Warblers, which more often sing from reed tops (JILKA and LEISLER 1974). Later on, when the time of their being unpaired dragged on, the males stayed longer and longer on tall reed stems, just below the inflorescences. Birds that continued singing also in the second half of June and early in July sang almost exclusively from the tops of green stems, which were already tall at that time (210-270 cm).

Unpaired male Reed Warblers were singing throughout the day without a break. Only in the early afternoon (12.00-14.00) and during a spell of windy cold weather they sang less loudly. When foraging in their territories, they hardly ever stopped singing. Every several minutes the singing bird slowly climbed up a reed stem, turning his head to the right and to the left, singing all the time. After reaching the top, he sang there a dozen seconds or so, then swooped down on his prey, catching it in flight, sometimes foraged for a while low in the reed, and finally resumed climbing up a reed stem. Generally, the break for catching and swallowing the prey was short (15-45 sec.) and most of the breaks were so short that the observer could hardly notice them. Fig. 7. shows the singing activity of three unpaired males, and the time given by them to foraging and other activities (preening, territorial defence, etc.). Unpaired males rarely left their territories in search of food. Eighty per cent of their foraging flights to the forest ($n=120$) were observed early in the morning (1-2 hours after sunrise) and in the afternoon (17.00-18.30). During the days of the mass emergence of *Chironomidae*, they were foraging only in the reed.

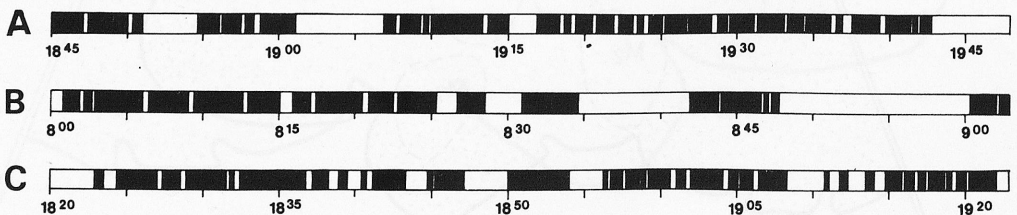


Fig. 7. Activity of singing in unpaired male Reed Warblers. Black area – singing, white area – foraging and other activities.

Territorial behaviour of settling males was observed on 38 males and observations of the settling behaviour lasted 184 hours. The territories of Reed Warblers had no clearly delimited boundaries because males did not approach them, generally singing in the central parts of their territories. The response of the owners to intruding conspecifics could not be used as a reliable basis for determining territorial boundaries because the responses of the same bird varied with circumstances. Only the observations of newcomers establishing their territories in the neighborhood and playback experiments could be used for estimating the size and boundaries of territories.

Territorial males displayed differential responses to the presence of an intruder. Sometimes they approached intruders foraging in their territories, about 30 m away from the song post of the owner (68%), and at other times they did not pay attention to intruders present much closer to them (32%).

After locating an intruder, the owner typically flew toward him. Most frequently, the intruder did not wait for his approach but immediately flew away. The owner followed him often far beyond the boundaries of his territory (87%), sometimes crossing two or three territories of his neighbours. The longest pursuits were continued over a distance of 200 m, but typically they did not exceed 50 m. Usually, the longer a male was unpaired, the sooner he responded to alien conspecifics and the more persistent was his pursuit. The distance covered during the pursuit depended on the behaviour of the intruder. The pursuit was continued until the intruder stopped fleeing and alighted in the reed. The pursuing male landed close to him. Out of 150 registered pursuits, 16 were ended sufficiently close to the observation tower to follow further developments. Only in one case (6.3%) after a 30-m pursuit the male did not land in the reed where the chased bird disappeared, but turned back in flight and returned to his territory. In six cases (37.5%) the birds landed 0.5-1.5 m apart. The pursued bird turned toward the rival. The feathers of both birds clung tightly to the body, and their heads and necks were stretched. After 5-15 sec. the birds flew away in silence in different directions. In eight cases (50%), both birds were more aggressive. The chased bird faced the rival with his beak open so widely that the orange interior could clearly be seen, and he uttered shattering calls, ruffled up his feathers on the head, chin, and rump, his wings being slightly open and drooped along the body. In response to this behaviour, the other bird either immediately flew away (two cases), or also ruffled up his feathers but without calling (two cases), or ruffled up his feathers, uttered shattering calls, and afterwards the two birds flew away in opposite directions (three cases). In one case the birds were fighting in flight. After an about 40 m pursuit, the chased bird turned back and attacked the chasing male. The birds disappeared in the reed. 25 sec. later the male who had started the pursuit returned to his territory and resumed singing. All the conflicts observed (pursuits and interactions in the reed) took from 5 to 50 sec. ($n=38$).

The aggressive postures of the Reed Warbler are shown in Fig. 8. Presumably, the intention of the territory owner was to find a female soon rather than to chase an intruding male. This is supported by some observations of pair formation. The female intending to settle in a male's territory did not retreat when the male was approaching her, but started fluttering the wings and thus released courtship behaviour in him. It is interesting that the behaviour of the newcomer released a suitable response of the territorial male, and not conversely. A retreat released the response of pursuit, the aggressive behaviour of the chased bird released the same type of

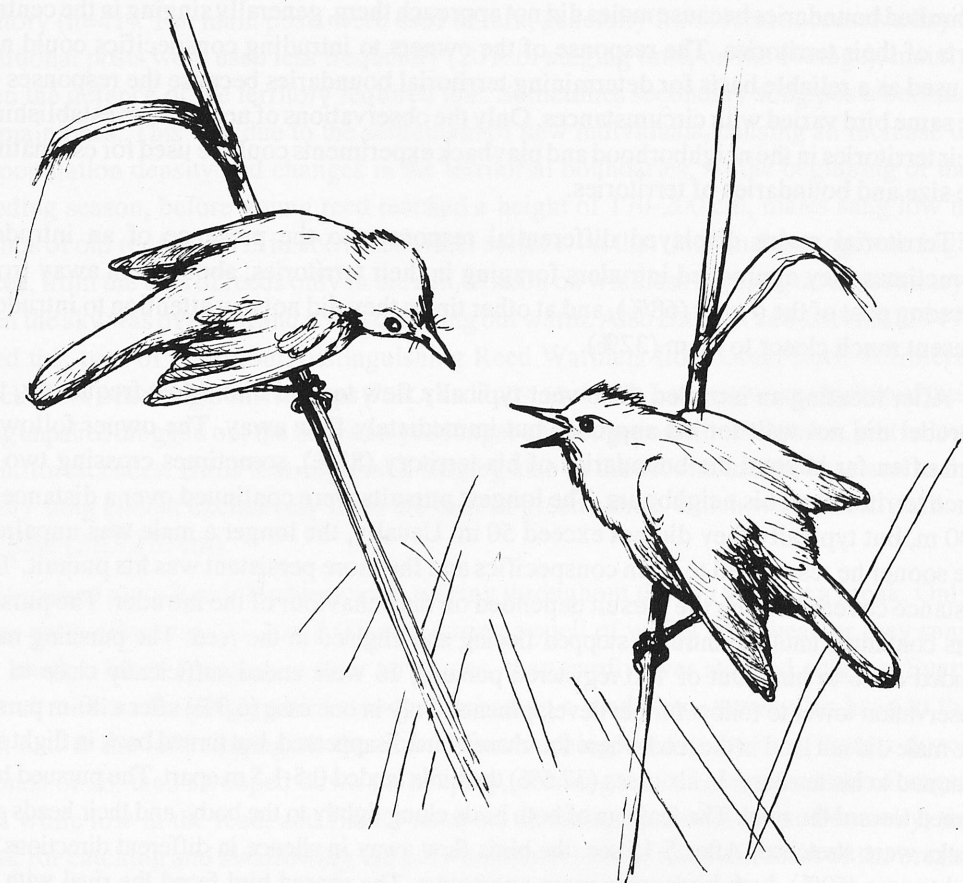


Fig. 8. Aggressive postures of Reed Warblers.

behaviour in the pursuing male, and wing fluttering by the female released a courtship display. It seems that the birds foraging in the reed and trespassing the territories of other males did not represent a threat to them because they did not compete for a female. Actual competitors were males that made attempts to settle near to or partly in the territory of another male and so their aims differed from those of females or foraging males. A quick response to any bird appearing in the territory is likely to increase the chance of getting a mate because the response of the alien individual provides information whether it is a trespassing male or a single female searching for a male.

Another type of conflicts was observed when new males arrived and the density of the breeding population increased. During the three-year study period no direct clashes between neighbouring males were noted and a stuffed Reed Warbler used in experiments designed to determine the territorial boundaries was not attacked. Play-back experiments with conspecific

songs in males' territories were performed 64 times (for 10 males in 1980, 20 males in 1981, and 34 in 1982). Every male behaved in the same way. The territory owner showed unrest and immediate response. He stopped singing for a while, surveyed the surroundings and listened, raising his feathers; then he flew toward the tape recorder. At a distance of 3-5 m from the recorder, he started to sing intensely, at a higher rate and louder than usual. Jumping from one reed stem to another, he was approaching the recorder in an attempt to see the rival. He followed the recorder when it was gradually shifted toward the boundary of his territory. It happened at the boundary that the neighbouring male also responded by approaching the tape recorder to a distance of several meters. It is interesting that the two neighbouring males attempted to find the alien bird by jumping from stem to stem and crossing the boundaries of their respective territories without paying attention to one another (5 observations), they were clearly searching for the common rival. More frequently, however, after approaching the territorial boundary, the male stopped responding and returned to his permanent song post (26 observations). Although the number of hours given to observation the behaviour of individual males and pairs was high, only on seven occasions the process of the setting of new-arrived individuals was successfully observed. In the other cases, a new spatial distribution, different from that observed on the preceding evening, had already been established when the observer returned to the plot. Since new individuals could not have come earlier than a few hours prior to the arrival of the observer, it may be assumed that the resident males soon accepted the presence of new individuals in the neighborhood, and no serious conflicts took place in such situations. In all the cases observed the establishing of a new male followed a similar pattern. The newcomer surveyed the area jumping from place to place and singing quietly. Very soon, however, after choosing a suitable area, he sang loudly. If his song post was located close to the boundary with the territories of one or two other males, or in the territory of another male, the owners approached in flight the new male, and alighted at a distance of 1-3 m from him. Then, the two males sang very intensely and loudly, facing one another. Their singing was becoming louder and louder and rapid as if the birds were duelling with songs. Their behaviour was quite the same as the response to conspecific play-back. This situation lasted from 5 to dozen minutes or so, and then the birds returned to their song posts, accepting the new neighbour, and often also the new boundaries of their territories. In no case did the resident male attack the newcomer and in no case did the newcomer leave the territory he had chosen under pressure from the males that had settled before.

VI. CHANGES IN THE SIZE AND LOCATION OF COURTSHIP TERRITORIES OF UNMATED MALES

Great seasonal variation has been found in the size, distribution, and boundaries of the territories of unmated males (Fig. 9). Most changes in the boundaries and size were due to the settlement of new individuals and the increasing population density (Fig. 10). In most cases (90 observations of stationary males) males remained in the same territory until they were mated. But in two cases (2.2%) the males changed their territories moving to another place. The direct causes of these changes are unexplained. No aggression was noted from other males or pairs.

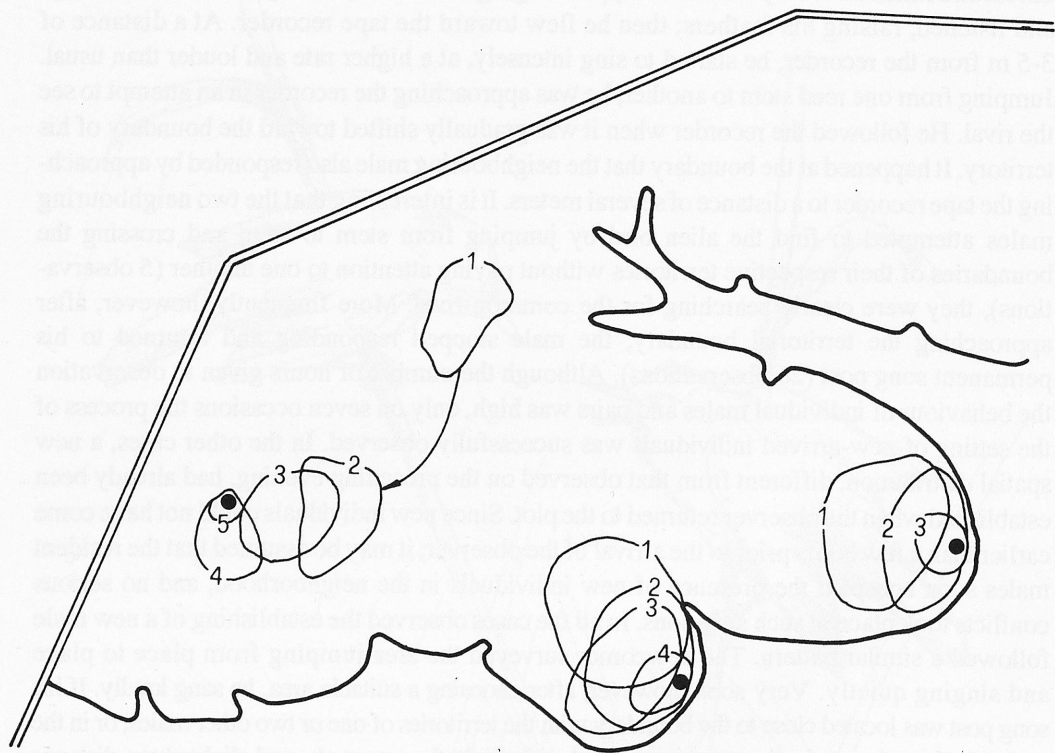


Fig. 9. Seasonal changes in the size and boundaries of territories of individual males, as illustrated for 1981. Figures denote successive territories of the same males, black dots – the nests.

Clear individual differences were recorded in the size of territories. Some males occupied territories of over 900 m^2 for a long time, whereas others held territories of about $300\text{--}400 \text{ m}^2$ even at a low population density. The mean territory size was about 400 m^2 (Table I), which is similar to the data of other authors (CATCHPOLE 1972; SPRINGER 1960). The first territories occupied at the beginning of the breeding season covered $800\text{--}900 \text{ m}^2$. With time, the mean size decreased to $200\text{--}300 \text{ m}^2$ (Table II). It should be noted that the territory size did not depend in a simple way on the size of the reedbed available and the number of settled individuals. The birds reached high densities on relatively small parts of the reedbed, whereas other parts also suitable for settlement remained empty to be occupied later. It is worth noting that the males arriving late (e.g. early in July, when most pairs raised successive broods, and a large area of the reedbed was available because of the decline of territorial behaviour in mated males) also occupied small territories, not exceeding $200\text{--}300 \text{ m}^2$ in area (Fig. 11).

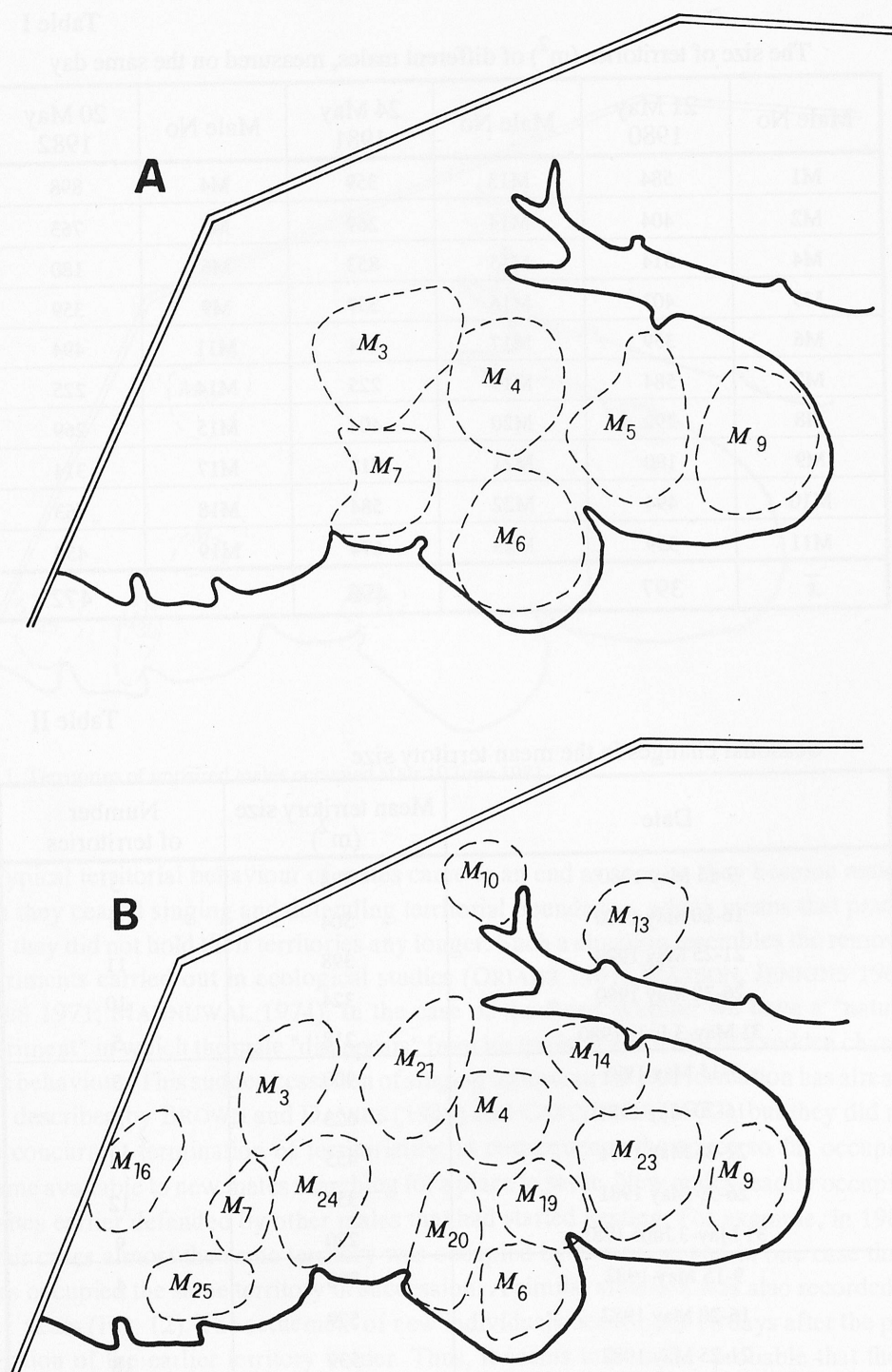


Fig. 10. Changes in territory sizes of the same males after arrival of new individuals. A – situation on 20 May 1981, B – the situation on 25 May, 1981.

Table I

The size of territories (m^2) of different males, measured on the same day

Male No	21 May 1980	Male No	24 May 1981	Male No	20 May 1982
M1	584	M13	359	M4	898
M2	404	M14	269	M5	763
M4	314	M15	853	M6	180
M5	403	M16	359	M9	359
M6	359	M17	484	M11	494
M7	584	M19	225	M14	225
M8	292	M20	404	M15	269
M9	180	M21	718	M17	314
M10	494	M22	584	M18	763
M11	359	M23	674	M19	450
\bar{x}	397		493		472

Table II

Seasonal changes in the mean territory size

Date	Mean territory size (m^2)	Number of territories
9-15 May 1980	788	5
16-20 May 1980	504	9
21-25 May 1980	398	11
26-30 May 1980	324	10
31 May-3 June 1980	218	5
9-15 May 1981	900	5
16-20 May 1981	623	8
21-25 May 1981	455	14
26-30 May 1981	358	12
31 May-3 June 1981	220	9
9-15 May 1982	898	4
16-20 May 1982	579	15
21-25 May 1982	539	18
26-30 May 1982	422	12
31 May-3 June 1982	292	7

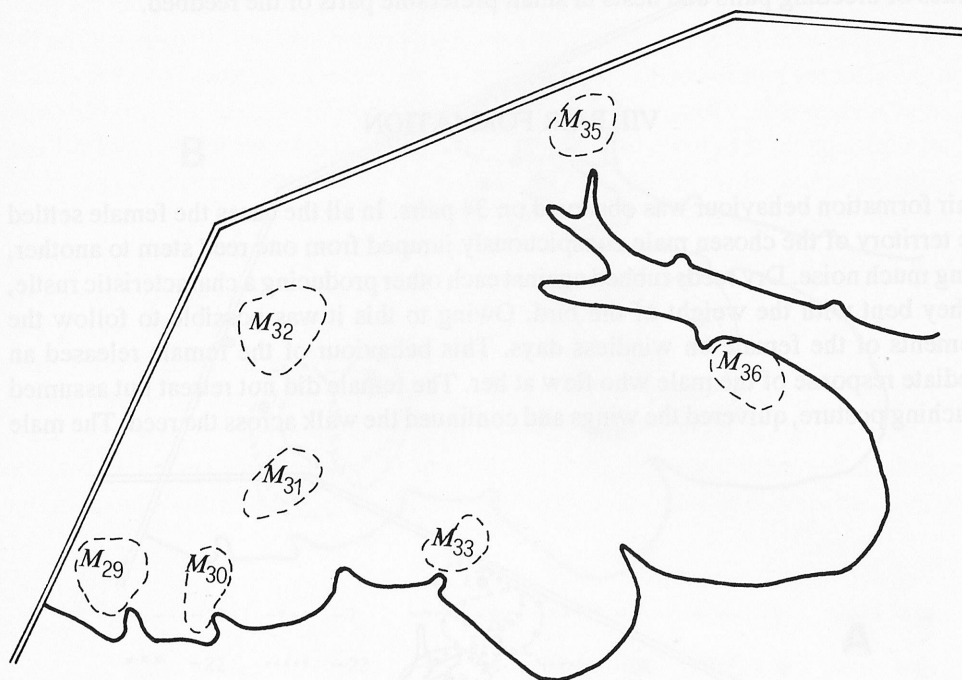


Fig. 11. Territories of unpaired males occupied after 10 June 1981.

Typical territorial behaviour of males came to an end as soon as they became mated. Then they ceased singing and defending territorial boundaries, which means that practically they did not hold their territories any longer. Such a situation resembles the removal experiments carried out in ecological studies (ORIAN 1961; WATSON, JENKINS 1968; KREBS 1971; MANNUWAL 1974). In the case of the Reed Warbler we have a "natural experiment" in which the male "disappears" from his territory as a result of a sudden change in his behaviour. This sudden cessation of singing following the pair formation has already been described by BROWN and DAVIES (1949) and CATCHPOLE (1972), but they did not note concurrent termination of territoriality; in consequence the space so far occupied became available to new males searching for a place to settle. New males readily occupied the sites earlier defended by other males that had started nesting. For example, in 1980, in four cases almost the same territory was occupied by two pairs, and in one case three males occupied the same territory in succession. A similar situation was also recorded in other years (Fig. 12). The settlement of new individuals occurred 2-10 days after the pair formation of the earlier territory holder. Thus, it seems to be little probable that these males formed a surplus population, and that the earlier presence of the rival was a serious obstacle to their establishing themselves. The selection of the same sites by different males certainly implies that they have similar habitat affinity and that these sites are very

attractive to them. Specific features of the behaviour connected with mating and the successive arrivals of different individuals to their breeding grounds account for high densities of breeding pairs and nests in small preferable parts of the reedbed.

VII. PAIR FORMATION

Pair formation behaviour was observed on 34 pairs. In all the cases the female settled in the territory of the chosen male conspicuously jumped from one reed stem to another, causing much noise. Dry reeds rubbed against each other producing a characteristic rustle, and they bent with the weight of the bird. Owing to this it was possible to follow the movements of the female on windless days. This behaviour of the female released an immediate response of the male who flew at her. The female did not retreat but assumed a crouching posture, quivered the wings and continued the walk across the reed. The male

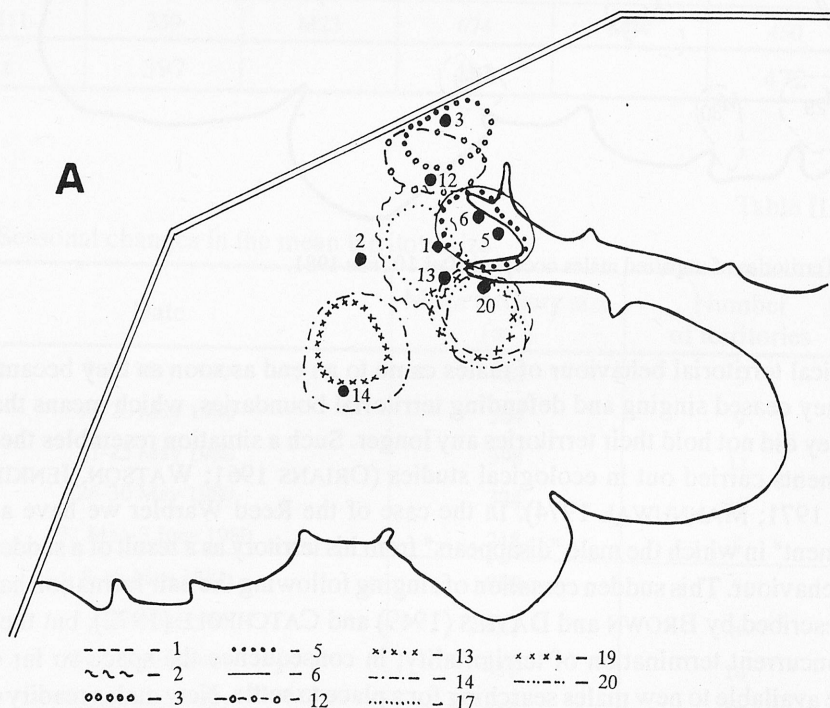
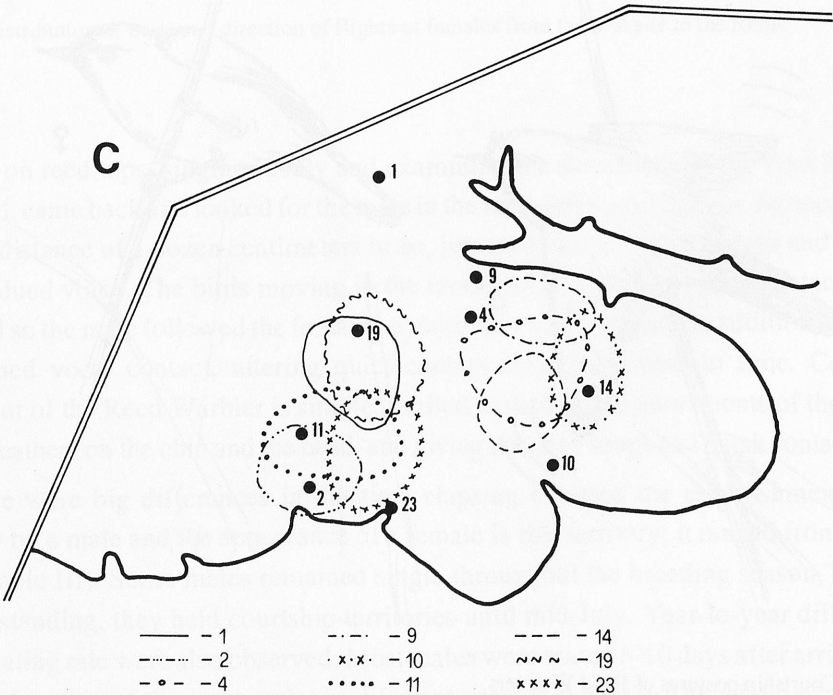
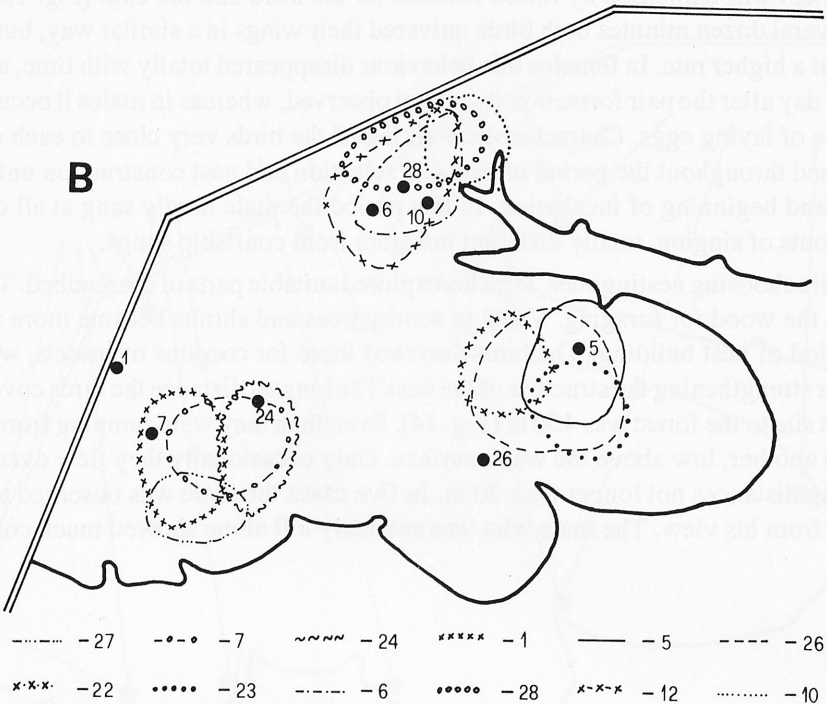


Fig. 12. Successive exchange of males with time and the location of nests. The graph illustrates the spatial overlapping of the territories held by males in different periods of the same season, and the fact that the nest may be located beyond territorial boundaries. A – periods of active territory defence by males in 1980: M 1 – 9-27 May, M 2 – 13-24 May, M 3 – 9-20 May, M 5 – 14-24 May, M 6 – 24 May-4 June, M 12 – 26 May-2 June, M 17 – 2 June-7 July, M 19 – 3 June-20 July, M 20 – 15 June-6 July; B – periods of an active territory defence by males in 1981: M 1 – 15-16 May, M 5 – 15-22 May, M 6 – 17-18 May, M 7 – 17-22 May, M 10 – 17-25 May, M 12 – 19 May-23 July, M 22 – 23 May-20 July, M 23 – 23 May-15 July, M 26 – 28-30 May, M 27 – 26-29 May, M 28 – 28 May-15 July; C – periods of an active territory defence by males in 1982: M 1 – 9-16 May, M 2 – 15-17 May, M 4 – 16-20 May, M 9 – 20-26 May, M 11 – 20-27 May, M 14 – 23-27 May, M 19 – 26 May-2 June, M 23 – 28 May-4 June.



accepted by the female followed her several dozen centimeters apart. His emotional excitement was expressed by raised feathers on the head and the chin (Fig. 13). For the first several dozen minutes both birds quivered their wings in a similar way, but the male did so at a higher rate. In females this behaviour disappeared totally with time, and on the second day after the pair formation it was not observed, whereas in males it occurred until the time of laying eggs. Characteristic walking of the birds very close to each other was continued throughout the period of nest site selection and nest construction until the egg laying and beginning of incubation. In this period the male hardly sang at all except for short bouts of singing, totally different in nature from courtship songs.

While choosing nesting sites, females explored suitable parts of the reedbed. They often flew to the wood for foraging. Visits to nearby trees and shrubs became more intense in the period of nest building. The birds searched there for cocoons of insects, which they used for strengthening the structure of the nest. The longest distance the birds covered from the nest site to the forest was 450 m (Fig. 14). Even then they were jumping from one reed stem to another, low above the water surface. Only occasionally they flew over the reed, covering distances not longer than 30 m. In five cases the male was observed to lose the female from his view. The male who was suddenly left alone showed much concern. He

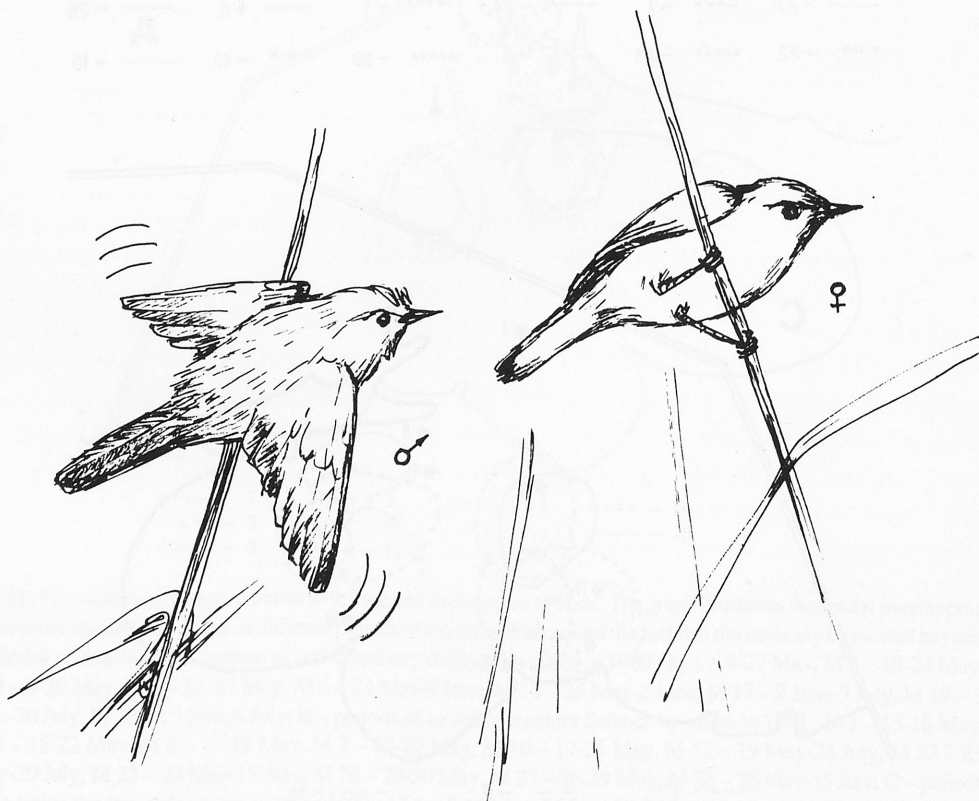


Fig. 13. Courtship postures of Reed Warblers.

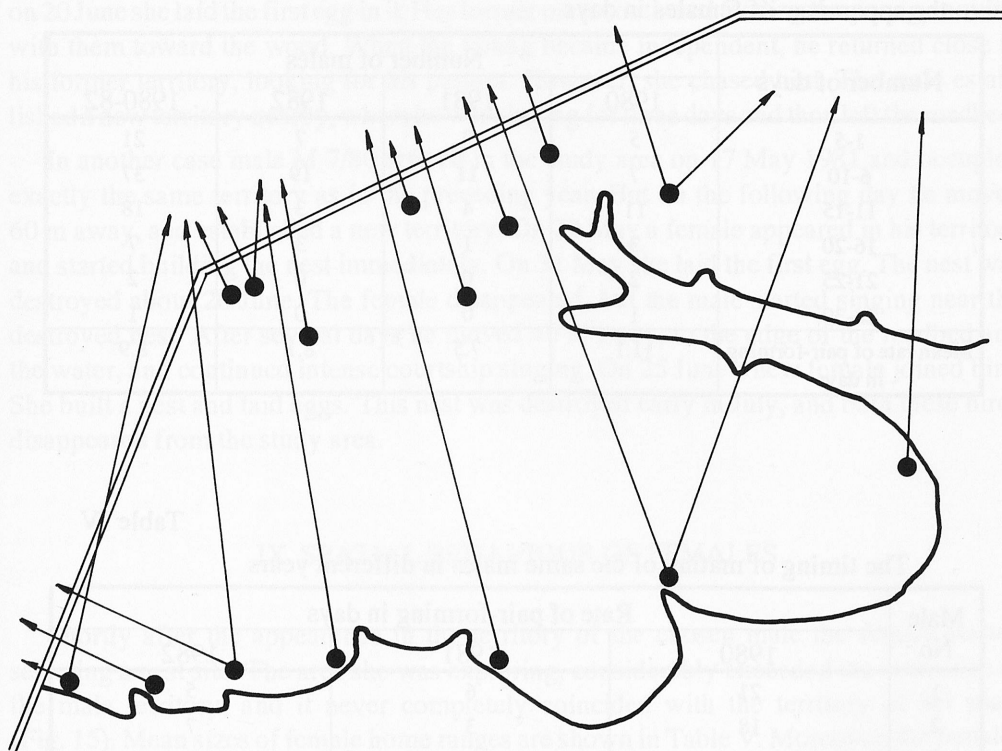


Fig. 14. Distribution of nests and direction of flights of females from the nest site to the forest.

perched on reed tops, singing loudly and examining the surroundings. He kept flying to the wood, came back and looked for the mate in the reed. After spotting her, he approached her at a distance of a dozen centimeters or so, intensely quivering the wings and singing in a subdued voice. The birds moving in the reed tried to maintain visual contact all the time and so the male followed the female no more than 0.5-1 m apart. In addition, the birds maintained vocal contact, uttering quiet contact calls from time to time. Courtship behaviour of the Reed Warbler is simple, limited to rhythmical movements of the wings, raising feathers on the chin and the head, and giving subdued songs and harsh contact calls.

There were big differences in the time elapsing between the establishment of the territory by a male and the appearance of a female in this territory; it ranged from 1 to 26 days (Table III). Some males remained single throughout the breeding season, but, this notwithstanding, they held courtship territories until mid-July. Year-to-year differences in the mating rate were also observed. Most males were mated 6-10 days after arrival. The timing of mating of the same males in different years is shown in Table IV.

Table III

The time elapsing between the establishment of the territory by male and the appearance of females in days

Number of days	Number of males			
	1980	1981	1982	1980-82
1-5	5	9	7	21
6-10	7	11	19	37
11-15	11	4	3	18
16-20	3	1	3	7
21-25	2	0	0	2
26-30	1	0	0	1
Mean rate of pair-forming in days	11.1	7.5	8.1	8.9

Table IV

The timing of mating of the same males in different years

Male No	Rate of pair-forming in days		
	1980	1981	1982
1	21	6	5
2	18	3	7
3	—	2	9
4	—	13	7
5	—	11	6
6	—	7	7

VIII. CHANGES OF THE PARTNER

In most cases ($n=79$, 96% of cases), Reed Warblers formed permanent pair bonds throughout the breeding season, and they raised successive broods (second or replacement) with the same partner. Over the three study years, only in three cases females disappeared after losing their nests (their mates remained, resumed courtship singing, but failed to acquire a new mate), and in two cases recorded the partners were changed for new ones before successive nesting attempts. In 1980, female F 1/80 successfully fledged the young on 12 June. Two fledglings left the nest, and at first were fed by both parents. The female often foraged in the territory of a single male that settled close to her nest on 1 June. She responded aggressively to his attempts to approach her. Very soon the birds became accustomed to each other, and on the third day she ceased feeding the fledglings and started searching the area overlapping the territory of the single neighbour. On approaching his

song post, she started flapping the wings rhythmically. The male immediately stopped singing and started to court the female. On 17 June the female began to build a nest, and on 20 June she laid the first egg in it. Her former mate continued feeding the young, moving with them toward the wood. When the young became independent, he returned close to his former territory, looking for his partner. However, she chased him. The male established a new territory nearby, where he was singing for three days and then left the reedbed.

In another case male M 7/80 arrived in the study area on 17 May 1981 and occupied exactly the same territory as in the preceding year. But on the following day he moved 60 m away, and established a new territory. On 22 May a female appeared in his territory and started building the nest immediately. On 31 May she laid the first egg. The nest was destroyed about 20 June. The female disappeared, but the male started singing near the destroyed nest. After several days he moved 40 m away, to the edge of the reedbed and the water, and continued intense courtship singing. On 25 June a new female joined him. She built a nest and laid eggs. This nest was destroyed early in July, and both these birds disappeared from the study area.

IX. SPATIAL BEHAVIOUR OF FEMALES

Shortly after the appearance in the territory of the chosen male the female started selecting a nest site. The area she was exploring, considerably exceeded the mean size of the male territory, and it never completely coincided with the territory of her mate (Fig. 15). Mean sizes of female home ranges are shown in Table V. Moreover, the females did not respect the territorial boundaries of other males and pairs, and they occupied the place they had chosen also if it was occupied by single territorial males or by breeding pairs of Reed Warblers. Single males singing from their permanent song posts were completely ignored, unless they stopped singing having seen the female and approached her. Only on four occasions conflicts were observed between a pair of birds searching for a nest site or building the nest and a single male holding a courtship territory totally or partly coinciding with the area searched by the female. At first, the single male immediately approached the searching female. She responded by raising feathers, uttering screeching calls, and sometimes snapping with her beak. On three occasions, her mate remained neutral

Table V

Mean size of female home ranges

Year	No of females	Mean size of home ranges (m ²)
1980	10	4530
1981	12	4234
1982	15	3936
Total	37	4233



Fig. 15. Territories of males before mating and home ranges of their mates during the period of nest site selection and nest building. Solid lines – boundaries of male territories, dotted area – female home range, solid circle – nest.

and once he, too, gave threatening calls. The single male immediately responded to this behaviour by returning to his song post, whereas the pair of birds resumed searching the reed. On repeated encounters, the single male either did not respond to the presence of the pair of birds, or he approached them but then quickly returned to his singing site.

Only once the behaviour of a female observed was different. Early in the May of 1982, a pair of Reed Warblers was observed on the second day after mating. The female F 15/82 just started to build the nest, but she was doing this very slowly. Most of the time she was foraging or preening and resting low in the reed. At noon a new male M 23/82 arrived and settled near the nest under construction. The mate of the female responded immediately with intense singing. The two males were singing loudly while perching face to face, in this way demonstrating their rights to that part of the reed. During this duel with songs the first male M 10/82 lost contact with his mate. He stopped singing immediately and began searching for her by flying over the part of the reedbed where the female was present most often. He did not find her there and three minutes later flew to the wood. When he was absent, the female appeared near the nest, followed very closely by male M 23/82. Both the birds had smooth, not raised feathers and did not quiver the wings, but the female did not exhibit

aggression, and she let the male follow her very closely. This situation was being continued when the absent male (M 10/82) returned four minutes later. On their encounter, the two males raised the feathers and were perching motionless and silently for about 15 min. Then male M 23/82 turned back and flew to his song post, and the pair of birds followed him. Further developments could not be observed because the birds disappeared low in the reed. They were silent during that time. A dozen seconds or so later male M 10/82 and his mate returned to their nest site and three minutes later the male M 23/82 resumed intense singing. No more conflicts between this male and the pair of birds were recorded.

After nest building and egg laying there were hardly any conflicts between the female and single males, because the female was either incubating or foraging in the wood or nearby shrubs, and then the male replaced her on the nest. In this situation there were almost no encounters and if there happened any, the conflicts followed the same pattern as in the period of nest building – the female displayed aggression to the approaching single male.

Only on one occasion the behaviour of a female was different. In 1980, a pair of birds was observed in the period of egg laying. Female F 7/80 just laid the first egg and was finishing building the nest. For this reason she often entered the territory of male M 4/80, who was single and was singing about 8 m from her nest. At that time her mate was foraging in the wood, so this was one of the rare occasions when he did not accompany the female, collecting nest material. Each time the female was close to the song post of male M 17/80, he stopped singing and flew towards her, to a distance of 1 m. The female did not display any aggressive response. After a 20-minute period of the absence of her mate (M 4/80), the female again entered the territory of M 17/80, and this time she was quivering her wings. At this signal, the male started courting her immediately. He followed her with his feathers raised and keeping a very short distance; he gave bouts of rapid but abated songs. Both birds were heading for toward the nest; the male moved to the top of the reed above the nest and started singing loudly but at a much higher rate than that of typical courtship singing. After 30 minutes of absence, M 4/80 came back and spotted the alien male at the nest. He approached him at a distance of 1.5 m, uttering a threatening call. Both birds were facing each other for several seconds, with their wings hanging down, and feathers raised on the heads and rumps. Then they both gave warning calls, and M 4/80 even snapped with his beak. About 13 seconds later, M 17/80 retreated toward his singing site, and M 4/80 returned to the nest. Throughout this incident the female was neutral, sitting on the nest.

Females not only entered the territories of single males but also ignored the aggression from neighbouring females building nests, incubating, or feeding nestlings, if they displayed it. For example, in 1980, two females were observed, who started building their nests 6 m apart almost at the same time. They finished these nests and laid eggs, although many disputes arose upon encounters of the two pairs. In 1981, a female was building the nest near four other nests. She was harassed and chased by two very aggressive neighbouring females each time they saw her. She managed, however, to complete the nest, lay the eggs, and fledge the young. During all the conflicts recorded, the males, if present, were neutral.

In all the other cases of concurrent or successive nest construction activities no aggression was noted between neighbouring females ($n=37$).

X. SELECTION OF NEST SITE AND FORMATION OF CLUSTERS OF NESTS

Nest sites were selected only by females. BROWN and DAVIES (1949) observed that they tended to build their nests in singing sites of males. That was not the case in the present study. Many nests were located beyond the boundaries of the territories originally established by males, in faraway unoccupied areas or even in the territories of alien individuals. In 76 situations analyzed in detail over 1980-1982, 27 nests of the first brood (36%) were located beyond the initial boundaries of the territories of males.

In all the study years the nests were clearly aggregated. The tendency to aggregation decreased with time (Fig. 16). It seems that most females tended to build nests in the same parts of the reedbed, and this was the direct reason for nest aggregations. Aggregations of nests were conspicuous not only when the concurrently occupied nests were mapped but also when all the nests built over the breeding season were analyzed (Fig. 17). This implies

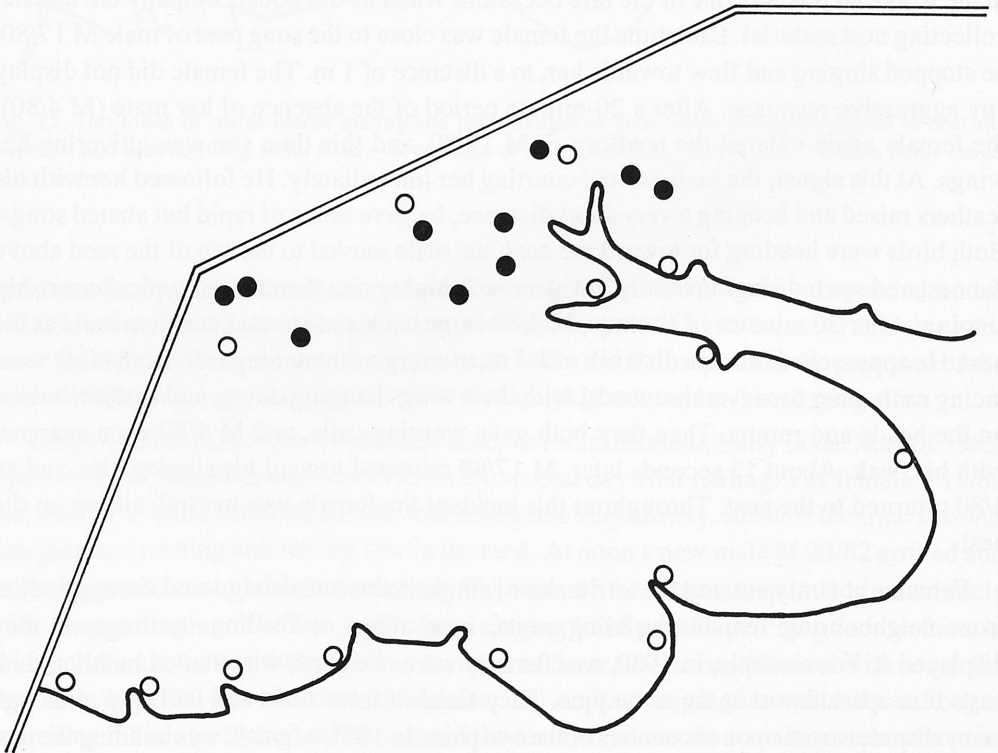


Fig. 16. Clustery distribution of nests built early in the breeding season and more dispersed distribution at the end of the season, as exemplified for 1981, solid cirklets – early nests, open cirklets – late nests.

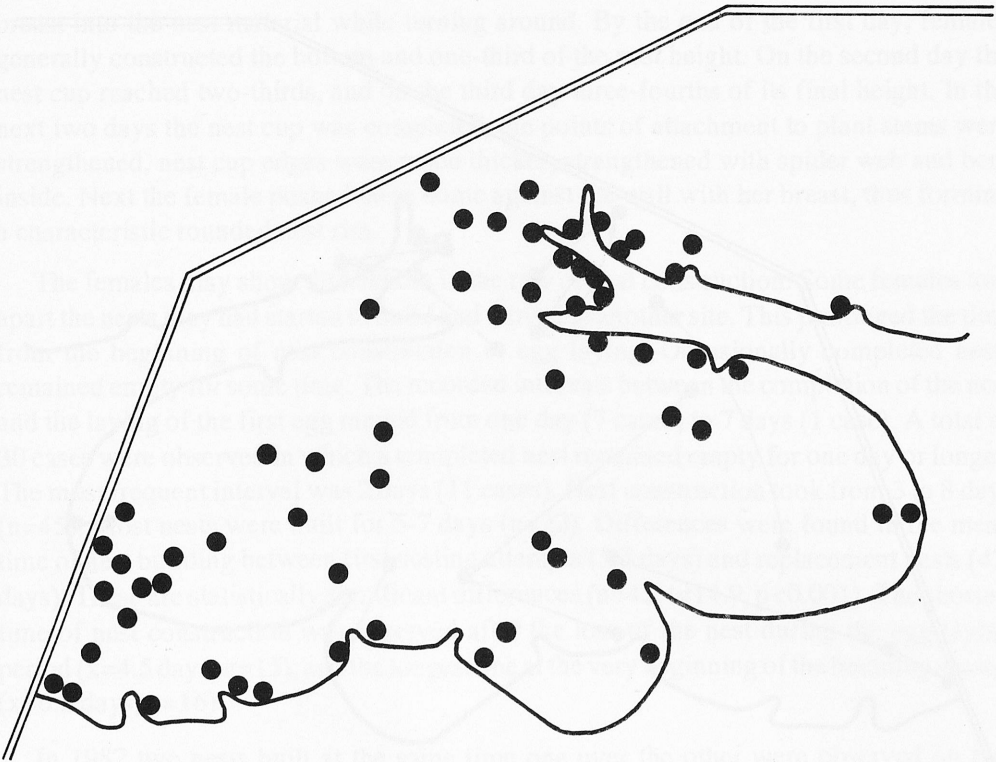


Fig. 17. Distribution of all nests constructed by Reed Warblers in 1981.

that many different females selected independently of each other the same part of the habitat, sometimes the same clump of reeds, although no occupied nests of Reed Warblers were present there. This provides evidence that habitat structure is more important than social stimulation to females searching for nest sites.

Each year, from 35 to 61% of the females that had lost their nests moved 45-200 m away for renesting ($N=88$), typically changing the "microhabitat" on this occasion (e.g. from central to marginal parts of the reedbed, bordering on open water, near the dam etc.), this being illustrated in Fig. 18. It cannot be excluded that few pairs or females that disappeared from the study area after the loss of the first nest renested elsewhere. That may have been so, especially when the nest was destroyed early in the breeding season and both parents disappeared. For second broods, after successfully raising the first brood, females built a new nest near the old one (on the average, 23 m away, $n=3$).

XI. BUILDING THE NEST

Nest-building behaviour was observed in 45 cases. The nests of the Reed Warbler were built only by females. Males were not active at nest building, but they accompanied

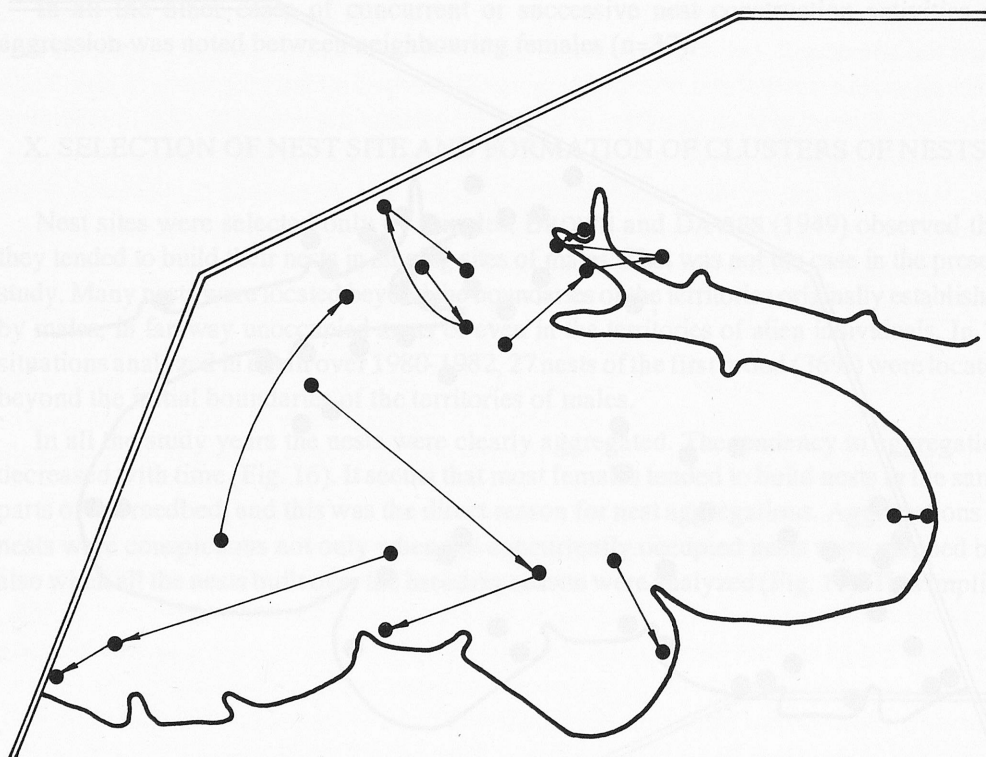


Fig. 18. Successive nests of the same females in 1981.

females in all their activities. Only on one occasion, a male holding a plant fibre in his beak was recorded. Most nest materials were gathered in the reed, whereas binding materials, joining various fragments of nest material together, such as cocoons of spiders and caterpillars, originated mainly from the adjacent wood and from the trees and shrubs growing on the dike. Getting nest materials must have been rather difficult as on several occasions females were observed stealing nest materials. Females also took nest materials from old nests. In 1980, for example, they took all but a few plant fibres from an abandoned nest with five eggs, and the eggs fell into water. Females readily used pieces of cotton threads scattered over the reed, and this facilitated the location of nests.

Nest-building was started with interlacing several long plant fibers around selected reed stems, from which the nest was to be suspended. Then females built the platform of the nest from fine plant material (down of cattail, moss), and the base of the nest. All these activities took from 3 to 5 hours. At this stage the nest was vulnerable to destruction by rain and wind, and typically females began the work early in the morning so that they could start the nest cup before dusk. The nest cup was built at a much slower rate. It was made of long plant fibres fastened around a reed stem in several layers, and the spaces between these fibres were filled with fine plant materials. The plant fibres were joined with caterpillar cocoons and spider webs. The female shaped the nest cup by pushing her

breast into the nest material while turning around. By the end of the first day, females generally constructed the bottom and one-third of the nest height. On the second day the nest cup reached two-thirds, and on the third day three-fourths of its final height. In the next two days the nest cup was completed, the points of attachment to plant stems were strengthened, nest cup edges were made thicker, strengthened with spider web and bent inside. Next the female pushed them home against the wall with her breast, thus forming a characteristic rounded nest rim.

The females may show differences in the rate of nest construction. Some females tore apart the nests they had started to build and moved to another site. This prolonged the time from the beginning of nest construction to egg laying. Occasionally completed nests remained empty for some time. The recorded intervals between the completion of the nest and the laying of the first egg ranged from one day (7 cases) to 7 days (1 case). A total of 30 cases were observed in which a completed nest remained empty for one day or longer. The most frequent interval was 2 days (11 cases). Nest construction took from 3 to 8 days ($n=45$). Most nests were built for 5-7 days ($n=22$). Differences were found in the mean time of nest building between first nesting attempts (5.8 days) and replacement nests (4.3 days). These are statistically significant differences ($n=45$, $t=14.9$, $p<0.001$). The shortest time of nest construction was observed after the loss of the nest during the egg laying period ($\bar{x}=4.5$ days, $n=15$), and the longest one at the very beginning of the breeding season ($\bar{x}=6.2$ days, $n=16$).

In 1982 two nests built at the same time one over the other were observed on two occasions. In the first case the nest was found at the initial stage of construction, and first beginnings of another nest were found above it (several plant fibers passed through reed stems and a little cattail down). The following day the upper nest disappeared, and the construction of the lower one proceeded at a normal rate. In the second case, the upper nest was more advanced (one-fourth of the cup). Two days later, the female tore that nest apart, re-using the materials for the lower one. A. KRÓL (pers. com.) found two almost completed nests located one over other; it is not known, however, if they belonged to the same female.

XII. DISMANTLING AND SHIFTING THE NEST

The females did not complete all the nests they were building. A large proportion of nests were torn apart, and the females re-used the building materials in a new nest (Tab. VI). Twice, almost completed nests (e.g. only without lining) were abandoned prior to egg laying, and the female built another nest in a different place. Most nests were moved at early stages of construction. This may have been caused by disturbances oppressing the female during nest construction and seems to represent an anti-predator response. Almost exclusively the first nests in the season were dismantled.

Table VI

Number of nests torn apart by females prior to egg laying

Year	Number of nests	Nests torn apart	
		N	%
1980	61	9	14.8
1981	57	7	12.3
1982	57	4	7.0
	175	20	11.4

XIII. NESTING TERRITORY

After building the nest, laying the eggs and starting incubation, the female spent most of the time on the nest. The male stayed in vicinity, and replaced the female on the nest from time to time, when she was foraging and preening. The time spent on the nest by males and females was not measured. The male replaced the female on the nest many times during the day, but for no more than 20 min. According to BROWN and DAVIES (1949), male Reed Warblers incubated only for 35% of the incubation time during the day. During incubation and brooding the birds are secretive and little aggressive. Both the male and the female are tolerant of other conspecifics near the nest (single singing males, foraging pairs of birds moving toward the forest). However, some observations suggest that a kind of nesting territory exists at that time. These are as follows: 1) over three years of the study only on one occasion the distance between two nests of different pairs was smaller than 10 m; 2) some females showed aggression toward other females building their nests in the vicinity (see Section: Spatial behaviour of females); and 3) males were typically singing quietly in the presence of other individuals. This singing could be heard from a distance of a dozen meters or so. But the same response of a male was recorded also in different situations and so it cannot be interpreted univocally in terms of territorial defense. This response was displayed within a distance of 10 m from the nest. But this distance varied depending on individual differences, stage of the nesting cycle (birds feeding the nestlings did not defend the nest surroundings at all) and also on weather conditions (when the audibility was reduced, e.g., on windy days, the birds responded only when the intruder came much nearer).

In 1980, a case of unusual aggression of a male toward the newly fledged young was observed when they approached his nest to a distance of 7 m. The male attempted to drive them away by bill-snapping and attacking from the air. The attacks were so violent that one of the fledglings lost its balance, fell down the reed stem and then hung by one foot from the stem 0.5 m lower. After a while it resumed the normal position. Attacks were repeated for about two minutes, then the male returned to his nest site. No more conflicts between the young and the neighbouring pair were recorded.

XIV. RESPONSE TO PREDATORS AND NEST DEFENCE

The intensity of active nest defence in Reed Warblers showed individual differences and depended on sex and the stage of the breeding cycle (Table VII). In this study the response of individual birds and pairs to an observer approaching the nest was noted in 83 nests. The observer represented a threat to adult birds and their nests, and they certainly regarded him as a predator. The response of birds involved quiet singing, disturbance calls, warning calls, sometimes combined with threatening postures, and, on one occasion, an actual attack, when one of the adults pecked at the hand of the observer ringing the nestlings.

During the period of nest construction the birds were very sensitive to disturbance. The presence of a potential enemy was signalled by a short song uttered by the male, and both birds gave disturbance calls, the intensity of which was increasing with the decreasing distance of the observer from the nest. At the same time the birds jumped from one reed stem to another, encircling the observer and the nest.

During incubation and while rearing the young no more than three days old, the parents were very secretive. The male signalled the danger with a short, quiet singing, which alerted the female. She opened her eyes, raised on the nest, and watched the sky and nest surroundings attentively. On discovering the presence of a man, she left the nest secretly, without calling. During his checking the contents of the nest, both birds stayed quietly in the vicinity, without giving any warning or threatening calls, sometimes uttering quiet attracting calls characteristic of pairs.

When the nestlings' age averaged four days, the behaviour of the parents changed. In the presence of an observer the male started singing loudly in a conspicuous place. Occasionally also the female was singing, but this was observed only three times over the three-year study period. KUSCHERT and EKELÖF (1981) have found that in some years more than 13% of females were singing.

Both parents uttered very frequent alarm calls and approached the observer to a close distance. In the period when the nestlings were covered with feathers (7 days old) the birds

Table VII

Type and number of reactions of the parent birds toward the observer visiting the nest

Type of reactions	Number of reactions			
	The stage of breeding cycle			
	incubation perios	young 1-3 days old	young 4-6 days old	young 7-10 days old
quiet call	44	53	0	0
short song	26	15	14	0
alarm call	0	2	56	69
attack	0	0	0	1

were more aggressive. They uttered alarm calls, assuming threatening postures and more frequently approached the observer to a close distance, sometimes snapping their bills.

Reed Warblers strongly respond to movement and noise. While standing motionless, an observer could easily observe the birds even without hiding himself, as the birds soon lost interest in a still man. Stuffed small predatory mammals (Mustelidae) presented to Reed Warblers did not elicit any defensive response, presumably, because they were motionless. On five occasions a stuffed weasel placed on the rim of a nest did not hinder the female to return to the nest only one minute later and to resume incubation.

Many times a group response to predators was observed. Not only the parents but also other individuals alarmed near the endangered nest (neighbouring pairs, single individuals nesting in other places but at the moment present nearby, single males holding courtship territories in the vicinity). Mobbing of such species as the fox, cat, Cuckoo, and Little Bittern was also observed. The appearance of a Marsh Harrier elicited singing in chorus and alarm.

XV. BREEDING SUCCESS OF INDIVIDUAL PAIRS

Nest losses in the population under study were very high (Table VIII) and in 95% due to predators. As a result, the production of the young was very low despite many repeated attempts at nesting. After the loss of the first nest, 76% of females ($n=74$) renested. The number of females not renesting and disappearing from the study area after the loss of the first nest varied from 20% in 1980 to 32% in 1981 ($n=18$). 16 females renested three times and 5 females four times a season. Although the females renested, each year only some of them raised one or more chicks throughout the season, and the others were totally unsuccessful. Females arriving earlier in the season (by the end of May) and starting breeding earlier, made more nesting attempts than the females starting later. The former had a little better chance of success: 65% of them raised at least one chick, as compared with 49% of the latter. The differences, however, are not statistically significant.

In 1980-1981 49% of the females raised at least one chick, as against 63% in 1982. The most successful female fledged 5 young over the breeding season. Also the number of females starting second broods after the first successful attempt was low. There were two such females in 1980, three in 1982, and none in 1981.

Table VIII

Nest losses in successive study years

Year	Number of occupied nests	Nest losses	
		N	%
1980	53	37	69.8
1981	52	41	78.8
1982	53	29	54.7
	158	107	67.7

Only few individuals were observed in the study area for several consecutive years. Their breeding success in different years is shown in Table IX. Unsuccessful females were never observed in following years, whereas unsuccessful males returned.

XVI. DISCUSSION

The described elements of the territorial and courtship behaviour of Reed Warblers cause that their territorial behaviour is not a mechanism which can ensure a uniform distribution of breeding pairs. These elements are: a) the decline of aggression towards conspecifics, b) the giving up of active defence of the territorial boundaries by birds after pair formation, c) keeping the female company by the male following at her heels during nest building when new males and females arrive successively, d) the choice of the nest

Table IX

Breeding success of individuals observed in consecutive years

Male No	Number of fledglings			Female No	Number of fledglings		
	Year				Year		
	1980	1981	1982		1980	1981	1982
1	0	0	5	1	2	0	—
2	0	0	3	2	1	2	1
3	4	2	0	3	2	1	—
4	5	0	—	4	3	1	3
5	0	3	—	5	4	1	3
6	—	3	4	6	0	—	—
7	—	0	0	7	0	—	—
8	—	4	1	8	0	—	—
9	—	0	1	9	0	—	—
10	—	1	4	10	0	—	—
				11	0	—	—
				12	0	—	—
				13	0	—	—
				14	—	3	1
				15	—	4	0
				16	—	3	—
				17	—	0	—
				18	—	0	—
				19	—	0	—
				20	—	0	—
				21	—	0	—
				22	—	0	—
				23	—	0	—

site beyond the boundaries of the original territory held by the male, and e) the removal of pairs after the loss of their nest to more distant places than the mean territory measurements. A tendency to semi-colonial breeding of Reed Warblers was described by many authors (HOWARD 1907-1914; BROWN, DAVIES 1949; RAITASUO 1958; CATCHPOLE 1972) and so this feature is not specific of the Milicz population. There are also data showing that nest losses are higher in places of higher densities of nests (CATCHPOLE 1972; BOROWIEC 1985). This is not consistent with the theory that one of the functions of territoriality is the dispersion of nests to reduce predation (LACK 1954; CROOK 1965). Many authors agree also that food is gathered mostly outside the nesting territory (HOWARD 1907-1914; LACK 1946; KRÓL 1984). Foraging outside the territory occurs in nobody's land and typically without conflicts. Only KRÓL (1984) observed that males had their exclusive foraging sites in oaks. The foregoing observations suggest that territories of the Reed Warbler are of no significance to its feeding behaviour. The fact that males hold their territories only until mating suggests that the territories serve their sexual purpose. Data on sexual selection and nest-site selection provide evidence that the size or shape of the territory held by males is less important to females than the quality of the male (older males acquire females sooner) and the location of the territory in the reedbed part selected by the female (BOROWIEC 1985). Males aggregate their territories in the places where aggregations of nests arise later, but the fact that some of these males remain single until the end of the breeding season suggests that the females choose the best of them.

Some specific features of the social and reproductive behaviour in the Reed Warbler can be regarded as the effect of the optimum adaptation of this cryptically coloured, small bird (body length – 12 cm) which colonizes a dense, little transparent reedbed habitat, which strongly limits visual and acoustic communication between individuals. It seems that living in the reedbed habitat has had most important evolutionary consequences to this species, and its behaviour is the result of a peculiar evolutionary compromise. The morphology of Reed Warbler is well adapted to the dense and tall vegetation of the reedbed (LEISLER 1972, 1975, 1980). Its colour harmonizes well with the ambient colours, making the bird cryptic in its natural habitat. Its habitat preferences slightly differ from those of the Great Reed Warbler and the Reed Bunting, the species with which it can occur in sympatry (LEISLER 1981). Also songs of the Reed Warbler are well adapted to the reed habitat, which ensures the optimum penetration of sounds (HEUWINKEL 1982). It seems therefore that also territorial behaviour may be considered to be the effect of the adaptation of the species to the reedbed habitat. The disappearance of territorial behaviour after pair formation and the escorting of the female may aim at guarding her so that she could not mate with other males. In this way the male can be sure that he is the father of the offspring he raises. The alternative solution such as maintaining the territory over the breeding season in this dense, little transparent habitat, where the density of birds is so high, would not provide the male with sufficient certitude. DAVIES (1985) observed that the number of copulations of female *Prunella modularis* with other males increased with the growing density of vegetation. Male Reed Warblers cannot maintain a fairly large territory coinciding with the area searched by females probably also for other reasons. As HEUWINKEL (1978)

pointed out, the audibility of the Reed Warbler's songs was sufficient to determine the size of its acoustic territory at about 700 m². The birds singing from reed tops are best heard, but most males sang from places low above the water surface. JILKA and LEISLER (1974) noticed a relationship between small territories and a tendency to the aggregation of singing males in small areas, on the one hand, and the heavy attenuation of songs by dense, tall reed, on the other. Moreover, dense reed even more strongly reduces visual contacts. A reduction in visual contacts may enhance the aggregation of males and increase their tolerance of the individuals not visible through dense vegetation. Among the European species of the genus *Acrocephalus*, Reed Warblers reach the highest densities during the breeding season, tolerate very small distances between individuals, and have a high threshold of excitability and aggression. The behaviour of the Reed Warbler is consistent with DAVIES and HUSTON's (1984) suggestion that territorial behaviour is less intense when the cost of defence of scarcely transparent vegetation is high.

After nest construction and egg laying, the male does not resume singing and territorial defence, but helps the female in incubation by replacing her on the nest; he also guards the female on the nest, warning her against the danger. Guarding the female on the nest and the mutual warning of the birds during their movements in the reed can increase the survival of the mates. Reed Warblers can survive, on the average 3.5 years, (WŁOSZCZYŃSKA 1981) and the maximum age recorded is 12 years (LONG 1975). The fact of reproducing many times in a season optimizes the production of such birds over their life span as compared with the birds having a single brood a year (STEARNS 1976). In this connection, the problem of the safety of adult birds becomes important, because their death constitutes a greater loss than the nest loss. Presumably, predation was an important factor determining the evolution of the Reed Warbler's behaviour. Many features of this species can be interpreted in terms of anti-predator adaptation. They include cryptic colour, secretive way of life through the avoidance of open spaces and flying over the reed for distances not longer than 30 m, tendency to singing from low places, strong alarm response to the presence of a Marsh Harrier, guarding of the female on the nest by her mate and warning her of the danger, frequent shifting of nest sites during nest construction if the female has been disturbed, building successive nests at a large distance from the place of the earlier unsuccessful nesting attempt, shortened period of incubation and nestling as compared with other species of the genus *Acrocephalus* (CATCHPOLE 1972), and small clutch size enabling frequent reneesting over the breeding season (DYRCZ 1981; OLSCHLEGEL 1981).

Reed Warblers are strictly monogamous. Although this species is frequently studied, only two probable cases of bigamy have been recorded (CATCHPOLE 1971). In recent years, some deviation from monogamy has been recorded in many typically monogamous species, including those of the genus *Acrocephalus* (DYRCZ 1977; LEISLER 1985). However, in Reed Warblers the evolution of monogamy is so advanced that the features which could enable the male to acquire a second female have been eliminated from his reproductive behaviour (they do not maintain territory and do not sing after mating). Presumably, also the close pursuing of the female during nest construction and egg laying and guarding the incubating female reduce the chance of the male to copulate with other females. So far, three conditions of monogamy have been recognized (WITTENBERGER

1976; WITTENBERGER and TILSON 1980): 1) monogamy must be more advantageous to the female than any other reproductive strategy, 2) the female must be able to recognize the status of the male and 3) the partners cannot leave one another. It seems that Reed Warblers satisfy the first two conditions, whereas the third condition can be violated in some cases. BROWN and DAVIES (1949) and SPRINGER (1960) observed that females abandoned their mates even after egg laying and mated with other males. Also some observations made in this study, such as those of a deep concern of the male when the female was out of view in the period of pair formation and attempts of the female to mate with another male during a long absence of her mate, suggest that females can abandon their mates and form new pair bonds. Strict monogamy in Reed Warblers may result from a heavy selection pressure on the part of the females. These mechanisms can function only when fidelity is an important factor conducive to the survival of parents or to their breeding success; owing to an early warning, the female can leave the nest secretly and thus increases the chance of avoiding predation not only for herself but also for the nest. Close pursuing of the female in the period of nest construction and guarding her during incubation may determine the value of the male as a partner in reproduction, and so be subject to natural selection. The data presented here indicate that females can choose from several males, and the presence of single territorial males by mid-July suggests that females are in short supply. In this situation, females could win the "struggle of sexes" by abandoning the males with inclinations to polygyny. The abandoned males might be again "only" monogamous, mating with another, perhaps worse female, or they might remain unpaired, taking the risk of losing the opportunity of breeding in that season. Removal experiments in which males would be removed at different stages of the breeding cycle could throw more light on this phenomenon and, perhaps, permit a new insight into the evolution of monogamy in birds.

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