ECO-ETHOLOGICAL ASPECTS OF BREEDING IN THE MARSH WARBLER, *ACROCEPHALUS PALUSTRIS*

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The Marsh Warbler *Acrocephalus palustris* is a locally numerous species over much of its European breeding range. Adapted for exploiting dense herbaceous vegetation (of late development), it has a very brief breeding season and high local densities, which makes a population study most rewarding. Moreover, most nests built low in the vegetation are of relatively easy access ; provided that the habitat chosen is fairly open, the extravert temperament of many individuals allows one to gather accurate data on various aspects of the species's behaviour. Despite these attractive features, no extensive eco-ethological study had been undertaken so far. The only detailed research on its ecology is an investigation of the breeding success of a West German population (Schulze-Hagen, 1975), which remained unpublished.

In spring 1974, I started a detailed study of the breeding, territorial and vocal behaviour of 12 colour-ringed pairs of Marsh Warblers near Liège, in the Meuse valley of eastern Belgium. This sample was part of a breeding population of slightly over 60 pairs. In 1975, most of the 62 pairs present were colour-ringed and monitored, and in 1976 and 1977 the whole population (respectively of 35 and 48 pairs, excluding the extra females of bigamous males) was under control. This paper describes the eco-ethological aspects of the breeding cycle, stage by stage, and includes data on breeding success. The emphasis is on an annual comparison of the breeding patterns (such as the timing of territorial settlements and egg-laying, the distribution of nest-sites), as these were greatly influenced by the changing conditions of the habitat from year to year. On the other hand, daily watching of individually marked birds provided many data on the life-history of many pairs. The various aspects of the breeding behaviour will often be exemplified by descriptions of the behaviour of

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individual birds so as to demonstrate the large variety of individual temperaments. The latter point has been stressed in Dowsett-Lemaire (1979 a) in relation to mate fidelity : many pairs remain together until the fledging of their single brood, but not infrequently one of the partners (most often the male) deserts the breeding territory at an earlier stage. Some males attempt (a few successfully) to become bigamous. The variety of situations required that the subject be treated separately.

Other aspects of this population study published elsewhere (Dowsett-Lemaire, 1978, 1979 c, 1980) deal with the annual turnover of the breeding population and with the vocal and territorial behaviour of the species and will be referred to only briefly here.

1. — *STUDY AREA AND HABITAT*

The study area is situated in the north-eastern suburbs of Liège (alt. 110 m), and covered 5 ha of green spaces in 1974 and 1975. A third of the habitat was destroyed between 1975 and 1976.

The habitat consists of dry filled-in grounds on the edge of fields and a cemetery, where a dense herbaceous vegetation has developed in the last two decades. *Urtica dioica* is by far the dominant herbaceous species ; other common perennials are listed in Dowsett-Lemaire (1978). *Rubus* spp. are locally common. Small trees cover from 1/6 to 1/8 of the area and are dominated by *Salix caprea, Robinia pseudoacacia, Sambucus nigra, Betula alba* ; some large patches of *Polygonum cuspidatum* cover up to several ares ; a few *Sarothamnus scoparius* and *Acer pseudoplatanus* grow locally.

The breeding population of the Marsh Warbler is denser than that of any other species ; the other dominant breeding birds are mentioned in Dowsett-Lemaire (1978). Its sibling the Reed Warbler *Acrocephalus scirpaceus* is a very common spring migrant and has occasionally settled here, particularly in *Polygonum cuspidatum*. This brought about direct competition and aggression with territorial Marsh Warblers and even hybridisation (see Lemaire, 1977).

2. — *METHODS*

All adults mistnetted were marked individually with combinations of two or three rings (a numbered aluminium ring plus one or two coloured ones). A single aluminium ring was used for young birds which were marked as nestlings usually at the age of 5 to 7 days. Most males were caught very soon after their arrival ; playback of the species's song was systematically used to attract them into the net. The catching success for females was lower as most of them did not react much to playback. They were more often caught on their way to or from the nest at various stages of breeding. In 1974, a little less than half of the population was marked, and from 1975, from 94 to 98 % of the breeding males and 49 to 63 % of the breeding females were colour-ringed. A total of 383 nestlings were ringed.

All adults and fledglings caught were also weighed and measured. A few ringing sessions were organised at various stages of the cycle to examine variations in weight, fat and plumage conditions. The analysis of weight variations of breeding birds is published elsewhere (Dowsett-Lemaire & Collette, 1980). The retrappings of juveniles after fledging provided some information on the development of plumage related to age.

Observations were carried out daily from the first arrivals — usually in the second week of May — to the last departures in mid-August. An average of 14 hours a day was spent in the field during the period of active breeding, from mid-May to mid-July. Nests were most easily found at the building stage, as revealed by the frequent journeys of the females. They were not visited more than four or five times during breeding, so as to avoid making tracks leading to them.

Times used are GMT + 1.

3. — *WEATHER CONDITIONS DURING EACH BREEDING SEASON*

The kind of open habitat where Marsh Warblers breed is greatly influenced by changing weather conditions, particularly rainfall. Consequently, the annual variations in the development of the herbaceous vegetation were reflected noticeably in the breeding density and breeding patterns of this species. The weather conditions of each of the three seasons of the population study are summarised below, together with a table of rainfall data from the Cointe meteorological station, 4 km distant from the study area (Table I).

1975 : May is quite dry, except the first 9 days. From 12 to 13 May, the wind changes from W to S and temperature rises from 5 to 15° C : the first Marsh Warblers come back on 13. (Similarly in 1974, the first Marsh Warblers appeared on 10 May after a change in wind direction from E to S and a rise in temperature of 10° C). June is increasingly wet : frequent long rains with a drop in temperature are recorded in the second half of the month until 2 July. This cold wet period has an unfavourable effect on breeding. The heavy rainfall of July is in fact concentrated in a few storms and temperatures are higher than in June (ave. daily mean 18.7° C against 15.6° C).

TABLE I

Means of rainfall (mm) in spring over the period 1833-1975 and total rainfall in each spring from 1975 to 1977 ; from the Cointe (Liège) meteorological station.

	May	June	July
General mean	61	68	75
1975 : monthly total	25	53	102
per 10-day period	22, 3, 0	8, 19, 26	67, 20, 15
1976 : monthly total	29	11	84
per 10-day period	3, 11, 15	9, 1, 1	0, 26, 58
1977 : monthly total	46	80	59
per 10-day period	23, 16, 7	34, 39, 7	4, 10, 45

1976 : May is as dry as in 1975, but especially so in the first 10 days when it is also very hot (maxima above 30° C). The development of the herbaceous vegetation is obviously delayed and the first Marsh Warbler is only noted on 16. June is, apart from the first four days, unusually hot and dry, and so is the first half of July. Development of perennials has ceased prematurely — e.g. tufts of *Tanacetum vulgare* are 50 cm below the 1975 level — and some trees (mainly *Betula alba*) already wither in early July. Storms in mid- late July arrive too late for the vegetation to regenerate.

1977 : The May rainfall is still below average but much higher than in the other years, particularly during the first 20 days. The vegetation grows rapidly and the first Marsh Warblers return on 10. June is very wet, but rain mainly falls at night or in the forms of storms (7 and 9 June). The vegetation is luxuriant. July is warm and sunny until 12, then rather wet.

4. — *THE BREEDING SEASON AND CYCLE*

4.1. SETTLEMENT PATTERNS (Fig. 1) AND BREEDING DENSITY

Results are based on daily checks of newly-arrived birds, a large proportion of them being marked as soon as they settle into their territories. To clarify the situation, I am dealing separately with the settlements of those birds who eventually breed and of non-breeding individuals. The latter consist of a “ floating ” population of territorial birds, the males

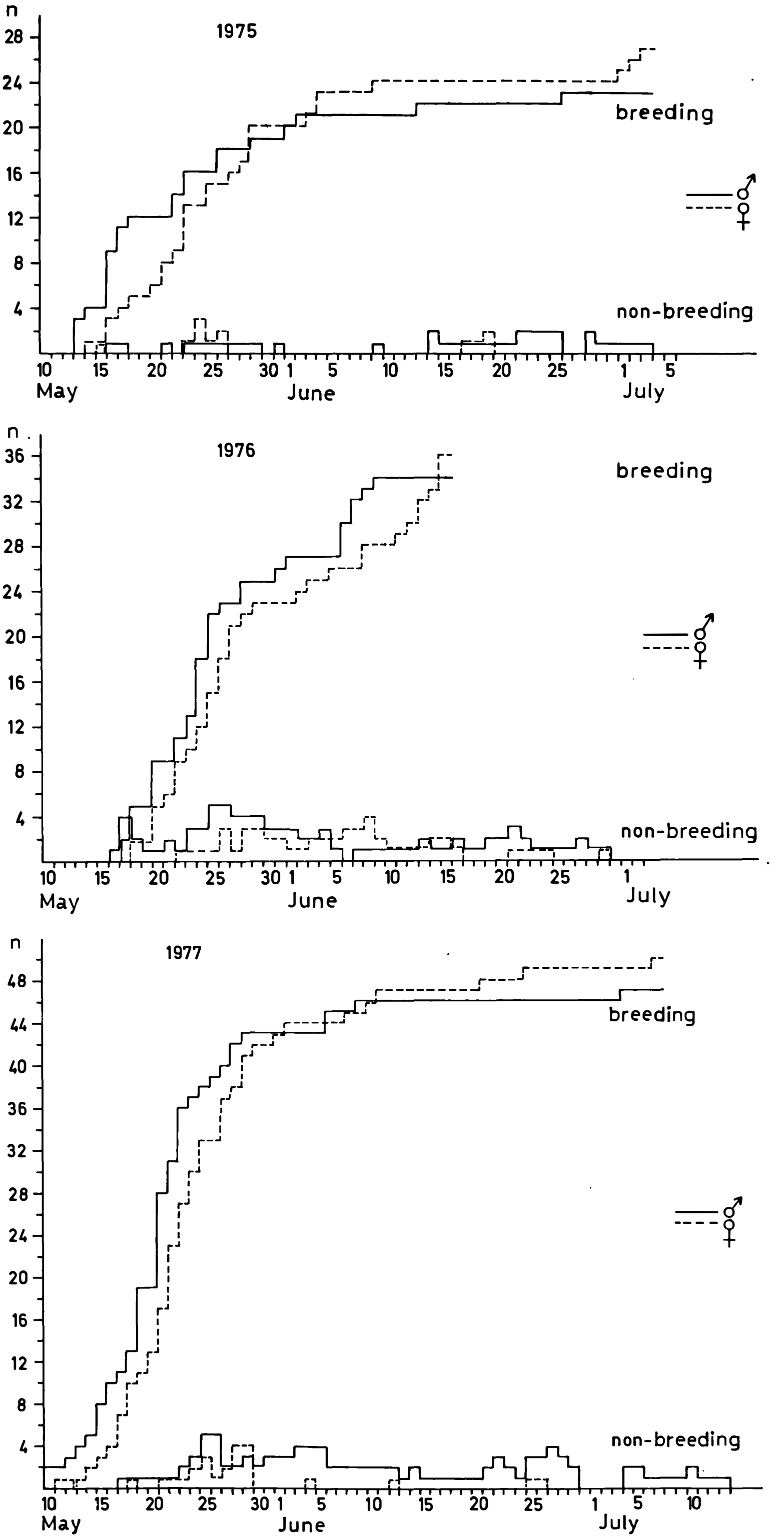

Figure 1. — Settlement patterns of the breeding population and daily total of non-breeding territorial birds. The sample is partial in 1975, complete for all but one pair in 1976 and 1977 ; n = cumulative total of individuals.

being unmated or only temporarily paired to females who disappear without having laid. Non-territorial migrant birds are not taken into account.

In 1975, daily checks of arrivals could be carried out only in part of the study area. In 1976 and 1977, the whole population was under control, the exact arrival dates being known for all birds — except for one pair each year which settled sometime in May. At the end of the settlement period, the breeding population is in fact less large than shown in Fig. 1, for some birds have already abandoned their breeding territories in the course of the cycle. These individuals have not been excluded from the totals, so as not to mask the peaks of arrivals. Breeding females are always slightly more numerous than breeding males, since some males are bigamous or breed in succession with two different females, the first one having disappeared or been predated on the nest.

4.1.1. *First arrivals.* — The Marsh Warbler is one of the last migrant species to return to the European breeding quarters. Coming from East Africa through the Middle East, the first birds reach the Russian coasts of the Black Sea at the end of April and the central areas of Russia around mid-May (Dement'ev & Gladkov, 1954). In Switzerland, the first normal arrivals are noted early May (Géroudet *in* Glutz Von Blotzheim, 1964), and in western Germany mid-May (Schucking, 1965) as in Poland (Ferens, 1949). In southern England, at the western limit of the range, the first singers are generally recorded after 20 May (Walpole-Bond, 1933 ; Sharrock, 1976). Finally, Marsh Warblers reach their northern breeding quarters in Sweden (Wingstrand, 1949 ; Jacobsson, 1964) and Finland (Eriksson, 1969) during the last week of May.

In Belgium, the first returns are often noted early May, and in the Liège area in particular, nearly always during the second week of May (other observations apart from this study). In 1974 and 1975, the first males return on 10 and 13 May, after a sudden improvement of the weather. In 1976 despite hot temperatures and many clear nights in the first half of the month, the first Marsh Warbler appears on 16 May, but drought had delayed the development of the vegetation. In 1977, frequent rain and mist early May does not prevent Marsh Warblers from returning as early as 10, the herbaceous vegetation growing rapidly as a result of rain.

4.1.2. *Duration and patterns of settlements (Fig. 1).* — In 1976, the settlements of breeding birds extend over a period of 30 days with the last male and female appearing on 9 and 15 June respectively, whereas in 1975 and 1977 the settlement period is much more protracted, covering respectively 52 and 59 days, with the last birds appearing early July. The annual variations in the environmental conditions probably account for these differences : the drought of June 1976 stops the growth of the vegetation at an unusually low level whereas after the abundant rains of June 1975 and 1977, herbaceous tufts continue to develop until early or mid-July.

Settlements are not uniformly spread throughout the season : the bulk of the population arrives in the second half of May. In 1976, over 2/3 of the breeding birds settle from 18 to 28 May ; in 1977, half of the males arrive within 5 days — from 19 May — and half of the females within 7 days — from 21 May. Peaks of arrival often occur after clear, windless nights, but not always so. Thus important arrivals occur from 19 to 21 May 1977 despite rainy weather and a northerly wind. Possibly these birds had reached areas only a short distance from Liège prior to the depression of 19 May. In a Swiss locality, Wiprachtiger (1976) also recorded the bulk of arrivals late May. He assessed the total length of the settlement period to be about 10 days : this is almost certainly an underestimation due to irregular coverage in time and to the fact that he was dealing with unmarked birds.

The Meuse valley is an important migration route, and at times from late May to early June, the study area has been invaded at dawn by migrant Marsh Warblers moving through, usually northwards (“ creeping migration ”). The dates of major passage movements have not always coincided with the arrival peaks of breeding birds, which suggests that migration patterns may differ according to the origin of the populations.

There is some evidence that some birds settle some time after their arrival, that is after a period of wandering or local dispersal. The last indications of true migration — capture of fat individuals, observation of “ creeping migration ” — are noted in the middle of June. Later settlements are probably the result of local wanderings. Thus, all three of the breeding females appearing for the first time after mid-June who could be caught before egg-laying showed an old brood patch, attesting to an earlier breeding attempt elsewhere. On the other hand, none of the females caught on arrival before mid-June had a brood patch. Some local wandering has also been noted earlier in the season : several males changed territories within the study area a day or two after their arrival in May. Local dispersal is further exemplified by the following observations : an important arrival of Marsh Warblers, future breeding birds and migrants mixed, took place on the morning of 16 May 1975 ; one of three males caught in the same net established a territory on the spot while the other two disappeared to settle respectively at 400 m and 8 km to the south (retrap of the latter by M. Raick, pers. comm.).

4.1.3. *Interval between arrival of males and females.* — Arrivals of females follow very closely those of males (Fig. 1). On average, males get paired 3.3 days after they settle (n = 112), or 2.8 days after, if one takes into account the first female accepted in the territory (which is not always the future breeding partner). Fig. 2 shows that most males are paired a day or two after their arrival. In many other migrant species, males precede females by a much longer interval. In England, Catchpole (1967) observed a gap of 10 to 15 days between the arrivals of the first males (late April) and of the first females of Reed and Sedge Warblers *Acrocephalus schoenobaenus*. Brown & Davies (1959) in England, and Springer (1960) in Germany, also found that in the Reed Warbler, early males remain unmated much longer than late males, as the bulk of females arrive only late May. By contrast, the first Marsh Warbler males return much later than male Reed Warblers, that is when the vegetation is developed just enough to shelter the first nests. Feeding conditions might be difficult earlier on.

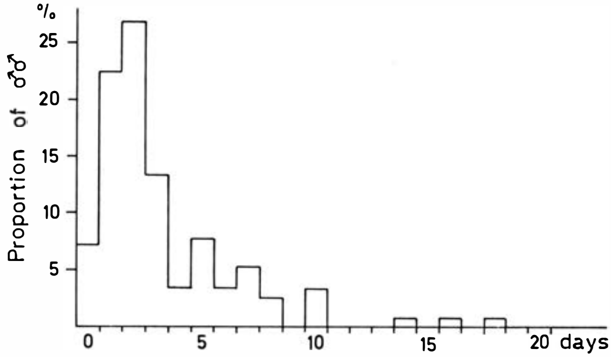

Figure 2. — Duration of the celibacy period of breeding males (from arrival to pair formation).

4.1.4. *Return dates of individuals related to age.* — The return rate of breeding birds from year to year is very low (Dowsett-Lemaire, 1978). From the small sample available, it appears that birds of two or more years of age generally return early. All of the 14 old females whose return dates is known exactly came back in May and 32 out of 35 old males reappeared in the first half of the settlement period. Consequently, most of the unringed birds arriving in the second half of the period are probably first-year birds. Through lack of returns of ringed juveniles, the extent of the overlap between arrivals of the two age classes is not known. Only one immature male caught in August (1975) came back the following year, on 25 May.

A few individuals (seven males, two females) reoccupied the same zone for a third season : those adults of 3+ years came back on about the same dates as in the previous season.

Early returns of older birds to the breeding quarters are observed in most migrant species (e.g. Kluijver, 1935 ; Conder, 1956 ; Ficken & Ficken, 1967 ; Darley *et al.*, 1971 ; Bairlein, 1978). However, it does not seem to be the case in some populations of Pied Flycatcher *Muscicapa hypoleuca* where first-year birds come back as early as older ones (Curio, 1959 a). Young Marsh Warblers leave the breeding grounds a few weeks after the adults, and consequently reach their autumn and winter quarters in Africa some time after the adults (Dowsett-Lemaire, 1979 b). A complete moult is undertaken during the brief stay in the winter quarters, and the fact that first-year birds start moulting later than older birds could justify their delayed spring departure for Europe.

4.1.5. *Annual variations in breeding density.* — The density of breeding pairs and of the extra females of bigamous males varied annually as follows :

1975 : 12.3 pairs + 0.2 female/ha
1976 : 10.6 pairs + 0.6 female/ha
1977 : 13.6 pairs + 0.9 female/ha.

Thus breeding density was lowest in 1976, an exceptionally dry season with underdeveloped herbaceous vegetation and rather scattered nest-sites, and highest in 1977, the wettest season of the three with luxuriant vegetation and abundant nest-sites.

4.1.6. *Non-breeding territorial birds.* — The importance of the non-breeding population expressed in daily totals of birds does not seem great when compared to the breeding population (Fig. 1). This is because most birds do not stay more than one to a few days. The longest sojourns are 31 and 42 days for males, and 14 days for a female who disappeared after having built three nests in succession. The relative importance of a floating non-breeding population was greatest in 1976, with respectively 22 and 15 non-breeding males and females against 35 and 37 breeding ones, and lowest in 1977, with 26 and 11 non-breeding males and females against 48 and 51 breeding ones. Most temporarily settled birds occupied normal territories rich in nest-sites and thus played an important role in territorial competition. Exactly 1/4 of the males were temporarily mated and a little more than 1/3 of the females were involved in nest-building activities before disappearing. The following examples illustrate how different individuals have occupied the same territory in succession :

1) In 1976, one territory was occupied by two males and three females in succession, two of the three females working at the same nest one after the other. Thus on 17 May, a male (returning from the previous year) settled there, and paired on 22 ; the female built a nest which got wet from rain and that she abandoned. She started another nest from 2 to 4 June then disappeared ; her male also deserted the territory, on 6 June, and on that same day was replaced

by a male newcomer. The latter was paired on 8 to a female who actively built for two days before disappearing. The male got a second female on 15 June who completed the unfinished but solid construction of the previous female. A brood was successfully raised in this nest.

2) Still in 1976, the neighbouring territory was occupied by two pairs successively ; the first pair (whose female had started a nest) left on 1 June, and the next day the same territory was taken over by another pair who bred normally.

3) In 1977, a territory was occupied by three males and three females in succession. One male settled there on 24 May and paired on the same day. The female deserted after having completed a nest from 26 to 29 May. The next female was first observed on 20 June, but a second male interfered and the female went from one male to the other alternately. The first male eventually neglected by the female left on 22 June, and the female left in turn on 25 June without having built anything (I later found her breeding some 500 m distant). The second male disappeared on 28. Lastly, on 6 July, a third male took over the area and paired on 7 to a female who built a nest and laid.

Several cases as complex as those detailed above were observed each year. On the whole, it is not clear why so many birds desert their territories after a short while. At the beginning of the season, a certain instability could be justified by the persistence of the migratory impulse. But even some of the old males coming back to their previous territories in early May have deserted them after a day or two (Dowsett-Lemaire, 1978). Later in the season, such unsettled birds are probably local wanderers and some of them may have bred or attempted to breed elsewhere. There is no doubt that at least a few individuals do not breed at all in the season, such as those who stay for long periods and disappear when their chances of finding a mate elsewhere are rather remote. But the proportion of truly non-breeding birds in a population cannot be estimated as most birds stay only for a few days and their subsequent behaviour is unknown. It is likely that this proportion was higher in 1976 (when breeding density was lower) than in the other years, since the total number of temporarily settled birds was relatively (to the number of breeding birds) more important. Similarly, temporary settlements in 1976 extended beyond the period of settlements of breeding birds, whereas the two periods were simultaneous in 1975 and 1977 (Fig. 1).

To conclude this section, it can be said that settlement patterns of Marsh Warblers represent a complex and dynamic phenomenon, and much would be overlooked or misunderstood without daily checks of individually marked birds. Moreover, numbers of territorial (breeding) birds as assessed by the standard methods of bird censusing would certainly be largely underestimated in this species, in particular because of the spread of arrivals over a long period and the rapidity with which males get paired and therefore fall practically silent. A clear underestimation of numbers by counts of singing birds was proved for some marshland species by Bell *et al.* (1968) by using data from detailed population studies for comparison. The census results were especially poor for the

Reed Warbler, a species whose biology and behaviour are similar to those of the Marsh Warbler in many respects.

4.2. FROM CELIBACY TO PAIR FORMATION

All territories contain a certain amount of dense low vegetation — herbaceous tufts, *Rubus* or *Polygonum cuspidatum* — which is suitable for nest-sites, and some bushes or small trees (at least one, occasionally only a few dry tall stems) used as song posts. Food is collected mainly in herbaceous vegetation in and out of the territory, extraterritorial excursions being frequent (Dowsett-Lemaire, 1980).

All males are very active as soon as they return on migration. Early settlers are rather mobile in their initially large territories, but as the season progresses, newcomers occupy smaller territories. By late May and early June, it is of common occurrence to see birds settle at dawn in a particular bush and sing there for hours without moving. Around midday, however, they start exploring the surroundings of their song post. Some males sing again actively in the evening and throughout the night. The song of the Marsh Warbler is of a continuous type, and of an extraordinary variety due to its richness in extraspecific imitations. I have analysed elsewhere (Lemaire, 1974, 1975 ; Dowsett-Lemaire, 1979 b) the structure and the imitation range of this unusual song.

As already seen (Fig. 2), the arrivals of females follow closely those of males. The behaviour of a male who accepts a female into his territory changes in a spectacular way, the most striking feature being the decrease (sometimes complete cessation) of vocal activity. Pairs are usually formed very quickly at dawn. In a short time, partners seem already used to each other, the male following the female closely in her exploration of potential nest-sites. The male sometimes plunges into a tuft to inspect it after the female has just left it, or utters short bursts of song from the top of clumps just visited by his partner. A female busy exploring tufts often wanders beyond the initial boundaries of the territory until she reaches the limit of the neighbouring territory. As the first reaction of the neighbour (even if he is still unmated) is usually aggressive, the female turns back towards the territory of the male who has already accepted her.

Most females settle early, but I have seen the occasional one wandering around and entering territories later in the morning until midday. The following example details the first reactions of a male to the intrusion of a female into his territory :

This male returned on 18 May (1975). He was paired on 23 May, but the female disappeared in the middle of the next day. The male resumed active singing in the evening and was singing continuously the next morning, perched high in a *Robinia* when, at 9.00 hrs, a female entered his territory. She flew low for a few metres towards him but stopped some 8 m from his song post and started inspecting tufts of *Aster* sp. The male continued to sing for a few minutes without noticing her, then as soon as he got sight of her, he flew straight over and perched 1 m distant, stretching his neck at the " intruder ". She reacted by puffing out her body plumage and uttering a short grated song, then carried on her explorations. Her attitude had the effect of calming him instantly, and he started escorting her silently 2 m behind. The female began a nest the next morning in a tuft of *Urtica* 10 m from where she first arrived.

Short grated songs are often used by females soon after their arrival as a means of keeping an aggressive male at a distance. Later, such songs are used as territorial warnings towards intruders or as contact signals with the partner (Dowsett-Lemaire, 1979 c). As this kind of vocalization seems exceptional in males, it can help to some extent to identify the sex of birds. It is clear that males must recognize the morphologically similar females from their behaviour : unlike intruding males, females do not fly away when approached by territorial males, do not sing (except for short grated songs), do not perch high and in full view as they are usually busy exploring herbaceous tufts. Even to the human eye, slight differences in silhouette can be perceived with some experience : females appear rounder and behave less nervously than males, with more placid attitudes and slower movements.

The acceptance of a female by a male is not always as quick as in the above example. Some individuals remain aggressive for an hour or two, or even longer until the next day as in the following example :

This male did not accept his female for the first two days and continued to sing like an unmated bird. Each time he caught sight of her, he pounced at her with neck and bill stretched forward, and the only way she could avoid his attacks was to dive into the huge, single clump of *Urtica* in the territory which obviously attracted her irresistibly. As soon as she climbed out of the clump, he would attack her again. He was, however, less aggressive and nervous in the afternoon, when he half tolerated her, and he accepted her definitively from the third day onwards.

Between the two extremes of quick acceptance and prolonged aggressiveness, some males, namely those who receive a female in their territory the very morning of their own arrival, continue to sing for a few hours without really paying attention to her. Reciprocally, the female does not seem to care much about the male, contenting herself with the exploration of the vegetation around the song posts. These observations clearly show that females are not primarily interested in the owners of territories but in the potential nest-sites available there. The song of the unmated males is likely to be the clue that leads them to an explorable area. The various examples described above also emphasize the variety of individual temperaments.

In principle, large territories contain a greater choice of nest-sites than smaller ones. The importance of nest-site availability to attract females and facilitate pair formation is also expressed by the fact that males with large territories get mated more quickly on average than males with smaller ones (Fig. 3 B). Mating success (rapidity of mating) is significantly correlated with territory size ($r = 0.5$, $n = 27$, $t = 2.88$ with $P < 0.01$). On the other hand, the size of the song repertoire (expressed in number of species imitated, which should be a reflection of the variety of song motifs per time unit) has no influence on the behaviour of females (Fig. 3 A ; $r = 0.07$, $n = 23$). Though significant, the correlation between territory size and mating success is not very strong, as other factors such as the vocal activity of the male could influence the choice of passing females. The relative position of the territory might also be important : a small territory is that much closer to others and its owner could benefit from the vocal activity of other males increasing the overall attraction of the area. Some males indeed got mated the very morning of their

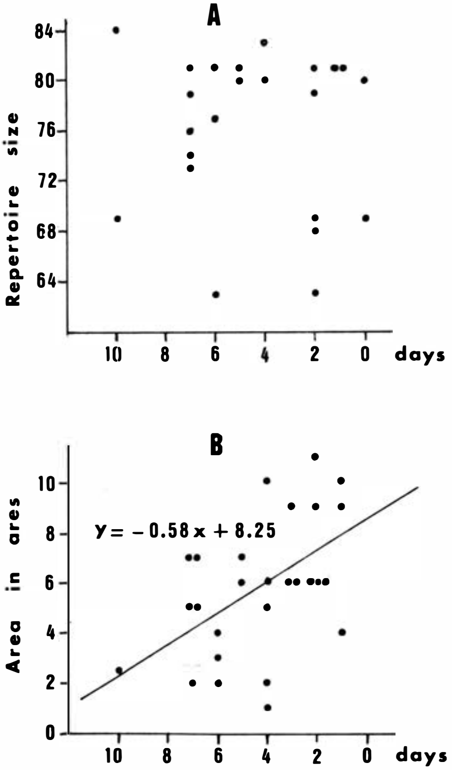

Figure 3. — Relationship between mating success (number of days for a territorial male to get mated) and : (A) the size of the song repertoire (in number of species imitated) ; (B) the size of the territory. Fourteen data for (A) concern the same males as in (B).

arrival, without having had the time to acquire any sizeable territory. This seemed to happen when females were arriving in such numbers that all bachelors had a chance simultaneously, whatever the size of their territories. Territory size or nest availability (in species where unmated males build nests) are known to influence mating success in several species (e.g. Howard, 1974 ; Garson, 1980).

4.3. SELECTION OF THE NEST-SITE AND NEST-BUILDING

4.3.1. *The selection of the nest-site.* — This seems to be the responsibility of the female. Within a few hours after their arrival, many females already show a preference for a particular area of the territory, spending most of their time inside certain tufts, and they start building there shortly after. The selected nest-site is sometimes situated outside the territory initially occupied by the unmated male.

In a few particular territories covering more or less the same area from year to year, different females (as proved by ringing) succeeding each other season after season used exactly the same tuft to establish the nest. This suggests that in a given situation, different individuals have the same concept of the optimal nest-site. I have already related earlier how, in the same season, two females succeeding each other in the same territory worked at the same nest. A similar case occurred in another territory, the second female completing the construction five days after the first female had left. In both cases, the dry weather had kept the framework of the nest in very good condition.

Many territories certainly contain several potential nest-sites, and I have seen some females, lingering on in a particular area one day, suddenly change their minds and start building elsewhere the next day. It even happened once that in a territory containing two fairly similar big clumps of *Urtica* at 40 m from each other, a female started building in the two clumps simultaneously. She was bringing a few twigs into one then the other alternately ; after two days, she abandoned one of the skeletons and finished the other.

4.3.2. *The role of the sexes in nest-building.* — Some authors (Walpole-Bond, 1933 ; Garling, 1934) claim that they saw both members of the pair taking part in nest-building, but most observers (including Géroudet, 1963 ; Wiprachtiger, 1976) have never seen a male involved in the work. Obviously the participation of the male is only marginal : in the building of over 100 nests watched with sufficient attention, I saw a male take part only once. For two days, male and female worked together at an outline that was abandoned afterwards, and the female alone built another nest 2 m distant, in the same clump of *Urtica*. The very occasional participation of the male has been observed in several passerine species where normally only the female builds (Tinbergen, 1939 ; Nice, 1943 ; Hinde, 1952 ; Olivier, 1959). As Hinde (1952) remarked, it shows that in fact " Both sexes possess the nervous mechanism necessary for nest-building ", but females are much more motivated.

Males show a variable interest in the work of their partners : some stay apart ; others escort the female on nearly all her journeys and inspect the nest after she has left the tuft to collect more material. Most males stop following the female systematically after the first day, but start again to escort her closely towards the end of building, showing then more interest in the female herself than in the nest — she will soon be ready for copulation.

4.3.3. *Beginning and duration of nest-building.* — Females start building soon after their arrival, sometimes on the very same day, most often the next day (Fig. 4). For some time before actually starting to build, they are often seen pulling twigs from stems without tearing them off, or carrying nest material for short distances before dropping it.

The nest is usually completed in four days (Fig. 5). Replacement nests are always built more quickly than first ones, often in three days instead of four. I only saw once a female using the material of her first nest (which had been robbed) to build the second one ; this habit seems much more widespread in the Reed Warbler (Brown & Davies, 1949). Some females started to lay a replacement clutch on the third day of active nest-building. From the laying of the second egg, no building activity was observed, except in one case when a female brought a tiny sprig to the nest the day she laid her third egg. Later, even damaged nests are not repaired.

Building activity varies throughout the day : many females are very active in the early morning, but some more so around

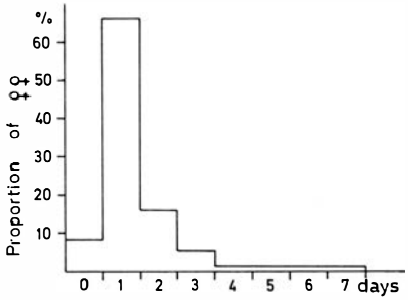

Figure 4. — Number of days between the arrival of females and the start of nest-building (n = 95 females).

midday, bringing twigs every 3-4 minutes. They then stop working for an hour or two, or more, at other times of the day. When the nest is nearly completed, the visits to it are more spaced out.

4.3.4. *Structure of the nest.* — The general structure and the size of the nests of Marsh Warblers are well known and described in many works. Here, it is enough to remember that these warblers are able to exploit a variety of nest-sites in modifying the nest structure — namely the way it is bound to its supports — according to the type of vegetation it is built in. In herbaceous tufts, they are suspended laterally to a few stems and not supported from below. But in *Rubus, Polygonum cuspidatum* and other bushes, nests are often set into a fork and not suspended, which recalls the structure of nests of *Sylvia* warblers.

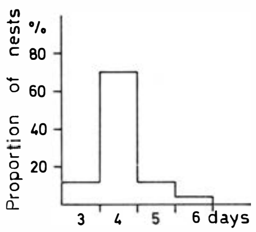

Figure 5. — Duration of nest-building (n = 56 nests).

The nest is made of essentially vegetable matter, mainly dead twigs of perennial plants of the previous season. I have occasionally found bits of wool haphasardly woven into the rim. Lastly, one female curiously fixed a large piece of white toilet paper into the outside wall ; this unusual adornment made the nest very obvious from a distance and the clutch of 5 eggs was robbed soon after being laid.

4.3.5. *Annual variations in the distribution of nest-sites.* — Table II presents the distribution of nest-sites in different types of vegetation in three successive seasons. A binomial test was applied to the three main categories of sites (herbaceous tufts, *Polygonum cuspidatum, Rubus* pure or mixed) to confirm that :

- in 1976, the proportion of nests built in herbaceous tufts is significantly less than in the other two seasons ($P < 0.01$), and the proportion of nests in *Polygonum cuspidatum* is significantly greater ($P < 0.01$). The proportion of nests in *Rubus* is significantly greater than in 1977 ($P < 0.001$) but not than in 1975 ;

TABLE II

Distribution of nest-sites in 1975, 1976 and 1977.

Nest-sites	1975		1976		1977	
	Number of nests	Prop. (%)	Number of nests	Prop. (%)	Number of nests	Prop. (%)
Herbaceous tufts	25	64.1	15	37.5	42	71.2
Polygonum cuspidatum	4	10.2	12	30.0	7	11.8
Herb. tuft + *P. cuspid.*	—	—	—	—	4	6.8
Pure *Rubus*	1	20.5	1	30.0	2	8.5
Rubus + herb. stems	7		11		3	
Sambucus n.	1	2.6	1	2.5	—	—
Ligustrum v.	1	2.6	—	—	—	—
Cornus s.	—	—	—	—	1	1.7
Total	39		40		59	

— the years 1975 and 1977 show a similar distribution of nest-sites except as regards the proportion of nests in *Rubus* which differs significantly ($P < 0.05$).

An herbaceous tuft with thick stems is the favoured nest-site of the Marsh Warbler. But the drought of 1976 affected the herbaceous vegetation more than any other type of vegetation, and the Marsh Warblers adapted themselves to this exceptional situation by building more in secondary sites, notably *Polygonum cuspidatum.* They also made ample use of *Rubus,* but they did so too in 1975 which was not a dry year. Clumps of mixed or pure *Rubus* were present in 25-30 % of all territories from year to year ; thus in 1975 and 1976, it seems that Marsh Warblers used them wherever available. They could not do so in 1977 because the *Rubus* were in very poor condition as a result of the underdeveloped shoots of the 1976 summer. On the other hand, clumps of *Polygonum cuspidatum* thick enough to hide a nest were present in 45-50 % of all territories from year to year but were obviously neglected when the preferred natural herbaceous site was available. Still, the presence of this plant probably helped to limit the decrease of the breeding density in the dry season of 1976 by providing replacement nest-sites. Other local breeding birds make even more use of this introduced plant as a nest-site, namely the Blackbird *Turdus merula,* Garden Warbler *Sylvia borin,* Dunnock *Prunella modularis* and Linnet *Carduelis cannabina.*

The herbaceous plants with thick stems used as nest-sites include 12 species of perennials occasionally mixed with thinner grassy plants such as *Galium aparine, Convolvulus* sp., *Lamium album* and various graminaceae. Of the 107 nests built in herbaceous growth, pure or mixed with *Rubus* or *Polygonum cuspidatum,* 47 were in pure tufts of *Urtica dioica* and 30 others in mixed *Urtica.* Thus *Urtica* pure or mixed were used for 72 % of the 107 nests. It is indeed the dominant herbaceous species in the area. The next four most common perennials used in pure or mixed tufts were *Tanacetum vulgare* (14 %), *Artemisia vulgaris* (11 %), *Eupatorium cannabinum* (7 %) and *Carduus crispus* (6 %).

4.3.6. *Nest-heights.* — Nearly 3/4 of the nests are situated between 20 and 60 cm (Fig. 6). The lowest nests (20 cm) were built in tufts of *Urtica* at the beginning of the season (mid-May) and the highest one (2 m) in a clump of *Polygonum cuspidatum* in June. Nests in the latter situation are relatively high : the mean for 23 nests is 102.6 cm against a mean of 52.7 cm for the 115 nests in other types of vegetation. In the herbaceous growth, the highest nests (120 cm) were found in *Urtica* at the end of the season.

The mean nest-height did not vary much annually ; in 1976, the mean height of nests in herbaceous tufts was 44.3 cm ($n = 15$) against 54.2 cm ($n = 25$) in 1975 and 49.6 cm ($n = 42$) in 1977, but the differences are not significant.

As the vegetation is developing in the course of the season, nests are built higher (Table III). The differences in mean nest-height between the first and second half of the season are significant in 1975 (Student's t test, $P < 0.05$) and in 1977 ($P < 0.01$) but not in 1976, when several early nests were built high in *Polygonum cuspidatum,* thus reducing variations in height during the season. Schulze-Hagen (1975) demonstrated the existence of a linear correlation between the height of the nests and that of the tufts containing them. Small mammals are probably the main predators of clutches and broods, and high nests should therefore be safer. The mean height of the 19 robbed nests measured in this study (53.4 cm) is indeed lower than that of the 119 non-robbed nests (62.3 cm) but not significantly so. In his study, Schulze-

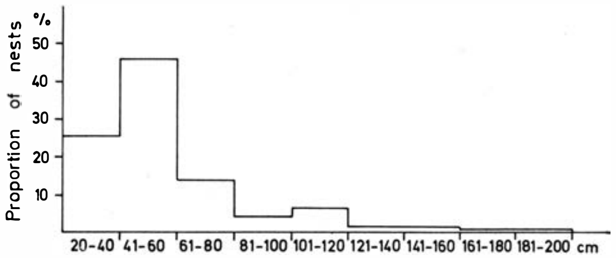

Figure 6. — Distribution of nest-heights (n = 138 nests).

TABLE III

Seasonal increase in nest-heights. The nest-building period is divided into two halves.

	Mean nest-height in cm
1975 : 18.5-13.6 / 14.6-11.7	57.8 (n = 30) / 77.2 (n = 9)
1976 : 19.5- 6.6 / 7.6-26.6	61.5 (n = 29) / 75.9 (n = 11)
1977 : 14.5-10.6 / 11.6- 9.7	52.6 (n = 49) / 79.5 (n = 10)

Hagen (1975) states he found a significant difference ($P < 0.05$) between sample means, which seems surprising since they only differ by 3 cm (55-52 cm).

4.4. COURTSHIP DISPLAYS AND COPULATION

The courtship behaviour of the Marsh Warbler has not, as far as I know, been previously described. Howard (1907-1914) gives only a brief description of the female's precopulatory display.

I have seen only three males starting some display movements in following the female as early as the day of her arrival. Most males display actively for just two or three days at the end of the period of nest-building, with a maximum intensity the day before the first egg is laid. The day on which egg-laying starts, the males (with but a few exceptions) will have become suddenly quiet and any exception will have stopped displaying by the next day. The first displays of the male consist of just a slight vibration of the wings done more or less regularly or by fits and starts ; the bill is closed. Next, the wings are vibrated further from the body and more intensely, and the bill is kept half open ; the bird frequently emits longs fragments of subdued song. In the most intense displays (as observed prior to copulation or in any case the day preceding the start of egg-laying), the vibrating wings are extended widely and the bill is fully open so that the bright orange throat is exposed, but the bird is now silent ; the tail is sometimes raised to 45°. Some males display asymmetrically, vibrating one wing after the other.

Wing vibration is the most frequent common character of male passerines' displays (Andrew, 1961), and even in other respects -- the position of the bill and tail — the postures of male Marsh Warblers do not differ markedly from those of other Sylviinae. I have shown elsewhere (Lemaire, 1977) that courtship displays are sufficiently similar between the closely related Reed and Marsh Warblers so as not to act as an ethological barrier against hybridisation.

I observed copulation in only four pairs, and in each case it took place around midday (10.15, 12.00, 13.00 and 14.00 hrs) on the day preceding the start of laying. Copulation lasts only a few seconds and is initiated by the female joining the male and presenting briefly the solicitation posture — wings vibrating, head and tail slightly raised. Before that, the male could be seen displaying for long periods near the nest — either singing subduedly with a half open bill, or silent with the bill fully open — or undertaking circuits on the edge of the territory, singing briefly and loudly on each perch. Given the number of hours spent observing the courtship behaviour of many pairs without seeing more than one copulation in four pairs, it seems likely that in this species copulation occurs only once before the laying of the clutch. Very few males still display on the day of the laying of the first egg. Even if some pairs attempt to mate again on that day, copulation is far less frequent than in many passerines which are known to mate on several days from nest-building to laying and even several times a day (see e.g. Tinbergen, 1939 ; Nice, 1943 ; Verheyen, 1968).

Apart from their own females, males also show interest in their neighbours', and pay frequent visits to them especially when the latter are preparing to lay. They can even indulge in display and subdued song near the nest while the " legitimate " male is away. Some females remain indifferent while others react aggressively and chase the visitor. Males stop these courteous visits at the latest when they start feeding their young, by which time they have also stopped singing. However interested males seem to be in the neighbouring females, no-one ever adopted a female who had been deserted by her partner in the course of the breeding cycle.

4.5. EGG-LAYING

4.5.1. *Seasonal patterns of laying activity.* — Without exception, it was found that females lay in the early morning at the rate of one egg per day, and from 3 to 5 eggs per clutch. Most start laying very soon after having completed the nest (Fig. 7), that is some six or seven days after their arrival. The shortest period recorded between the arrival of a female in a territory and the start of laying is three days : this female was caught on 24 June 1977 in a territory where she had spent five days without building a nest ; the next day, she moved 500 m further to pair with another male, started building immediately and laid the first egg of a 5-egg clutch on 28 June ! An interval of three days between nest destruction and relaying was also recorded once, in July 1975. Intervals of four days between a female's arrival (or clutch destruction) and the start of laying are known in at least five cases in the 3-year study. Since an increase in female weight is already noticeable four days before the start of laying (Dowsett-Lemaire & Collette, 1980), suggesting that the formation of a clutch takes at least four days, the performance of the two females who managed to prepare a clutch in three days (while actively building a nest) remains puzzling.

Wiprachtiger (1976) claimed he found a relationship between temperature and laying activity in the population he studied, in so far as he believed that he saw peaks of laying activity occurring four days after peaks of temperature. However, his results expressed in Fig. 2 of his paper are far from conclusive. In my population, it was not possible to establish a relationship between daily variations in temperature and laying activity. Peaks of laying activity are in fact dependent on peaks of female arrivals, and the seasonal evolution of laying activity parallels the evolution of female arrivals with a shift of six or seven days. As an example, the high peak of laying in the last few days of May 1977 (Fig. 8), particularly on 27 and 28 May, is a consequence of the numerous arrivals of females from 21 to 23 May (Fig. 1). Similarly, the slight annual variations in the start of laying are related to the date of arrival of the first female (Fig. 9). For the Pied Flycatcher, Curio (1959 b) also found a strong correlation between the timing of female arrivals and that of laying. This does not exclude the possibility that the average temperature over a certain period may not have an effect (presumably via the food supply) on the laying activity of females. While the average temperature increases from May to July, it was found that later in the season, newly-arrived females start laying on average slightly more quickly than those arrived earlier in the season. In 1976, females arriving from 18 to 31 May started laying on average 7.5 days after their arrival (n = 18), and those arriving from 1 to 15 June started on average 6.0 days after (n = 13). In 1977, 41 females arriving from 13 to 31 May started laying on average 7.1 days later, and 8 females arriving from 1 June to 7 July started on average 5.9 days later.

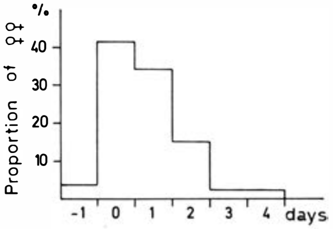

Figure 7. — Time elapsed between the end of nest-building and the laying of the first egg (n = 73 females).

Fig. 8 represents the evolution of the laying activity in the course of each season. The data for 1975 are not quite complete for the beginning of the season so that the May figures should have been slightly higher. The coverage was complete in 1976 and 1977. In 1977, a sharp peak of laying activity took place late May- early June, that is a week after the bulk of female arrivals. The main peak is a bit later in 1976, due to the delayed settlements. A smaller second peak appears in the third week of June 1976, subsequent to the arrival of several females from 11 to 15 June. No normal second clutch was attempted, and only some of the lost clutches or broods were replaced.

The laying period covered 56 days in 1975 (20 May - 14 July), 37 days in 1976 (24 May - 29 June) and 54 days in 1977 (20 May - 12 July). In 1974, the first egg was laid on 18 May (by a female back on 11 May) but the end of the season is not known.

In 1975 and 1977, the bulk of late clutches are replacements (Fig. 8) : I have considered here not only clutches relaid in the

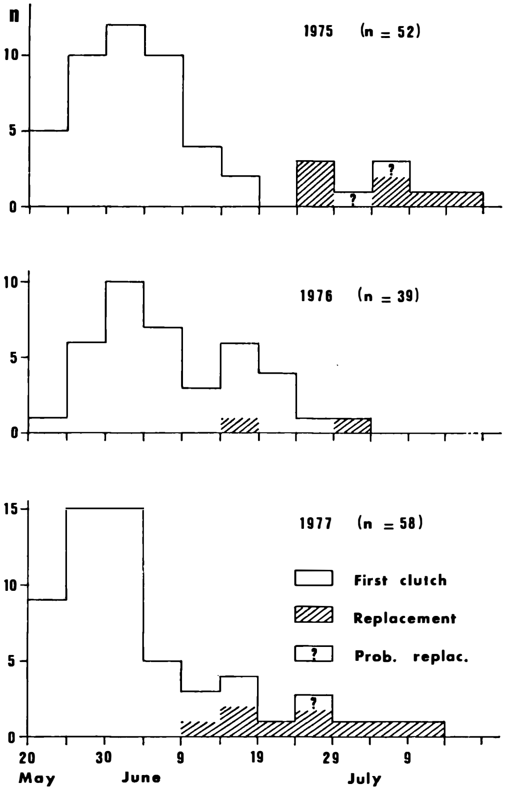

Figure 8. — Seasonal patterns of laying activity expressed in number of clutches (= n) started per 5-day period.

same territory, but also clutches of late-arriving females for which the presence of an old brood patch before laying indicated a previous nesting attempt elsewhere. Not all late-arriving females could be caught before laying, but given the date and the general pattern, such late layings are more likely to be replacements and are designated by a ? (probable replacement) in Fig. 8. The last certain first clutch — laid by a female who had no brood patch when caught on arrival — was started on 24 June (1976).

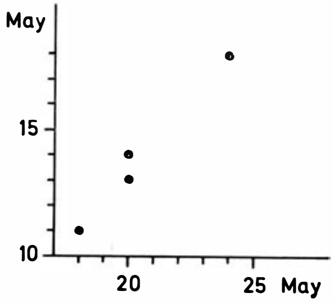

Figure 9. — Relationship between the date of arrival of the first female (ordinate) and the date of the first egg laid (abscissa) in each of four successive seasons (1974-1977).

Marsh Warblers replace lost broods far less often than lost clutches. Only two of 26 broods lost in the three seasons (by predation or starvation) were replaced. All the other pairs deserted. By contrast, 14 of 23 lost clutches were replaced in the same territory. Thus pairs having lost their brood as early as mid-June deserted even if other nest-sites were available locally, whereas many females replaced lost clutches in July as late as 14 July. One female (in 1977) laid as many as four clutches in succession in the same territory. The only two cases of brood replacement took place in June 1977, in large territories rich in nest-sites. As already mentioned before, the vegetation was particularly luxuriant in that wet month.

4.5.2. *Clutch-size.* — Table IV shows the proportions of the various clutch-sizes in the three seasons. The mean annual clutch-size remained constant in the period of study. Clutches of 6 eggs are occasionally recorded in this species (Witherby, 1943 ; Géroudet, 1963 ; Wiprachtiger, 1976) but none was found here. Clutches of 4 and 5 eggs are in equal proportion and have a similar chance of success (59.5 and 60.0 % respectively, expressed as percentage of eggs laid producing fledglings) while 3-egg clutches are less productive (50.0 %).

In Switzerland (Lucern area) and West Germany (Rhineland), Wiprachtiger (1976) and Schulze-Hagen (1975) both found an

TABLE IV

Clutch-size in 1975, 1976 and 1977.

	Proportion of clutches (%) with 3	4	5 eggs	Mean size	Total sample
1975	12	44	44	4.3	41
1976	5	47	47	4.4	38
1977	9	47	44	4.3	57
Total	9	46	45	4.3	136

average clutch-size of 4.6 eggs, with a clear preponderance of 5-egg clutches — 66 % in the two areas. The differences in distribution of the various clutch-sizes between their data and mine are significant (χ^2 test, $P < 0.001$). The reason for this is obscure. In some species, an increase in clutch-size has been found from western to eastern Europe (Lack, 1947), but the longitudinal differences between the areas concerned are minimal. In addition, the habitat where Schulze-Hagen carried out his study is very similar to that of the Liège area.

4.5.3. *Seasonal variation in clutch-size.* — The mean clutch-size decreases seasonally (Fig. 10) from 4.9 to 3.7 eggs per clutch from late May to the second week of July. Similarly, Schulze-Hagen (1975) found an average decrease of 1.2 (from 5 to 3.8 eggs) over the same period.

Replacement clutches usually contain one egg less than the previous one. This was not always so in 1977, however, where at least three of seven females laid as many eggs or even one more in their replacement clutches. One female who made three replacements laid successively : 4 — ? (nest destroyed before completion) — 5 — 3.

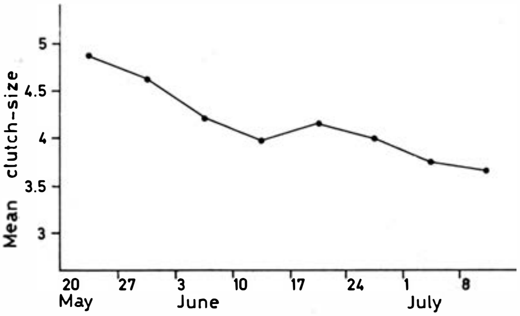

Figure 10. — Seasonal variation in clutch-size.

Clutches of 3 eggs are few overall. Eight out of 12 are in fact first clutches, some laid early in the season (from 24 May) ; this may be an individual characteristic. Therefore the decrease in mean clutch-size depends mainly on changes in the proportions of 4 and 5-egg clutches : the proportion of 5-egg clutches decreases weekly from 90 % of all clutches to 0 % before the end of the season. The overall latest 5-egg clutch was started on 28 June (1977), two weeks before the end of the laying period.

A seasonal decrease in clutch-size has been observed in many bird species in temperate latitudes — among the Sylviinae, in the Wood Warbler *Phylloscopus sibilatrix* (Lack, 1950), several *Sylvia* warblers (Mason, 1976), the Reed Warbler and the Great Reed Warbler *Acrocephalus arundinaceus* (Havlin, 1971). It has often been suggested, and proved in some cases (e.g. Perrins, 1965, for British Great Tits *Parus major*) that more food is available for early than late broods so that it is advantageous for late females to lay smaller clutches. But the evidence for the adaptive significance of a seasonal decrease in clutch-size is still very vague or even contradictory in many species of nidicolous birds and all nidifugous birds (Klomp, 1970). In the Marsh Warbler, a study of weights of nestlings of different brood-sizes would be desirable ; the difference in survival of early and late young is not known as the recapture rate of young birds is practically nil. In any case, it was already shown that 4-egg clutches (which predominate at the end of the season) are as successful as 5-egg clutches. Expressed otherwise, the fledging success of broods born during the last week of June and in July (75.4 %, n = 114 young) does not differ significantly from that of broods born earlier (73.6 %, n = 360 young). It is obvious that the supply of insect food in the herbaceous vegetation decreases in the course of July and August as the various perennials come into flower and dry out. But simultaneously, Marsh Warblers shift progressively to woody vegetation — namely *Salix caprea* — to look for food.

Perrins (1970) questioned why, in species where large early broods are more successful than late ones, a large proportion of pairs breed later " than the date at which they could most successfully raise their young ". He suggested that dates of laying may in fact be determined by the dates when females are able to find enough food to form eggs, and that the spreading of the laying period over a season is due to physiological variations in the females. Perrins seems convinced that late females would have raised more young had they bred earlier ; but this is perhaps not so in a dense population. Some pairs of Marsh Warblers bred in July in areas previously occupied and defended by other pairs ; simultaneous early breeding would not have been possible. On the contrary, the spread of laying reduces competition and allows a larger number of pairs to breed than if all females laid simultaneously.

4.6. INCUBATION

4.6.1. *The start of incubation.* — The female's brood patch starts developing just before or at the laying of the first egg and looks completely defeathered at the laying of the third egg. At the beginning of laying, the female, occasionally the male, pays brief visits to the nest at protracted intervals, unless it is raining in which case the female covers the eggs as long as necessary. She also covers them at night. Proper incubation seems to start at the laying of the third egg in 3 and 4-egg clutches, and at the third or fourth egg in 5-egg clutches (see further 4.6.4). There is then a sudden increase in the proportion of day time during which the eggs are brooded — from almost nothing to 57 % of day time as measured in 15 hours of watching at various nests. From the second day of incubation, eggs are brooded for an average of 93 % of day time — as measured in 28 hours of watching.

4.6.2. *The role of the sexes.* — Howard (1907-1914) states that incubation is shared by both partners who relieve each other at regular intervals, but Walpole-Bond (1933), Géroudet (1963) and Schucking (1965) consider that the share of the male is less. I found that, apart from the bigamous males and of course those who had deserted, males brood as much as their females by day from the second day of incubation (about half of them do not yet brood on the first day). I checked regular change-overs in more than 100 pairs : in 28 hours of watching at 20 nests, the incubation time was exactly shared between the sexes — 50.6 % by the males and 49.4 % by the females. Only the females seem to brood by night.

Partners relieve each other at regular intervals, usually between 10 and 30 minutes, on average every 20 minutes. The male often utters a short burst of song when approaching the nest, which provokes the departure of the female. Similarly, some females utter a short grated song just before relieving the male, or even in the nest at the end of an incubation session as if to call the male to replace them. Change-overs vary in discretion according to the pair, time of day etc. Contact songs are less often used in bad weather. Some pairs are extremely unobtrusive and silent, reaching the nest through the vegetation (and not hopping on tops of tufts like others), and the non-brooding partner feeding hidden inside the clump. Life seems to have deserted the territory.

Males occasionally sing briefly while on the eggs : either when an intruder crosses the territory, or at my own intrusion into the territory, or apparently to make contact with the female who answers with a grated song. They are sometimes distracted from their brooding activities by the defense of the territory. A particular male who was about to relieve his female had to spend another 20 minutes singing and chasing an intruder. During that time, the female left for only 7 minutes to feed and look at the intruder then returned to brood.

It is remarkable that males are so assiduous at incubation, since they do not have a brood patch. In this respect, the situation is rather confusing in male passerines, where there seems to be little correlation between the brooding behaviour of males and the presence of a brood patch (Skutch, 1957). Males of many species who share incubation do not have a brood patch (Bailey, 1952) whereas some birds (e.g. *Empidonax* flycatchers) who do not incubate have one (Skutch, 1957). Incubating males of only a few species are known to develop a full brood patch (e.g. nutcrackers *Nucifraga* spp. [Mewaldt, 1952 ; Swanberg, 1956]) or an incomplete one, less well vascularized than that of females (e.g. *Sylvia* warblers [Spencer & Mead, 1978 ; pers. obs.]) and Starling *Sturnus vulgaris* (Feare & Burham, 1978).

Whereas clutches brooded by both members of the pair are covered for 93 % of day time on average, females abandoned by their partners and who have to brood alone stay on the nest for 60 to 75 % of day time. The few data I have suggest that the duration of incubation is probably the same in the two situations. Skutch (1962) showed that in closely related species where the proportion of day time incubation varies according to the participation of the male, the duration of incubation is similar. Skutch concluded that, since the participation of the male does not accelerate the process of incubation (and thus does not reduce the period during which eggs are exposed to predation), the brooding behaviour of males must be considered as of no adaptive significance. However, females helped by their mates must be at an advantage by having more time off to feed.

4.6.3. *Influence of weather on incubation behaviour.* — It is well known that birds spend less time brooding as the temperature increases (Skutch, 1962). The influence of the external temperature on the length of incubation sessions was also proved experimentally by von Haartman (1956) in the Pied Flycatcher.

In the Marsh Warbler, it is obvious that change-overs are tightly synchronised in cold and rainy weather, whereas in sunny, hot weather, birds are less assiduous. One bird often leaves the nest before it is invited to do so by its partner, and some males, after having given the warning song nearby, carry on singing for a few minutes before going to the nest. Finally, rather peculiar behaviour was observed in a female in the heat of June 1976 : whenever I sat to watch the nest, I saw her interrupting her brooding sessions by a 5 minute outing, returning to the nest just before the male, apparently unaware (he was coming back from excursions outside the territory), came to relieve her.

4.6.4. *The duration of incubation.* — The duration of incubation from the last egg laid to the last egg hatched is known in 19 cases to 1/4 day of accuracy and is distributed as follows : 12 days (n = 2), 12.5 days (n = 3), 13 days (n = 11) and 13.5 (n = 3). An infertile clutch was brooded by both members of the pair for 25 days before being abandoned. Géroudet (1963) and Schucking (1965) give, respectively, a duration of 12 to 14 and 13 to 14 days. Wiprachtiger (1976) calculated a period of 11.5 to 13.5 days, considering that incubation did not start before the laying of the last egg.

Hatching of 4 or 5-egg clutches was spread over a period varying from a few hours to one day, or more in at least one 5-egg clutch. In one case measured accurately, the last egg of five hatched 9 hours after the first one ; although the adults had apparently started incubating with the laying of the third egg, proper incubation could not have begun before the laying of the fourth one. In another 5-egg clutch, incubation did start at the laying of the third egg since the fourth and fifth ones hatched, respectively, one and two days after the first three.

4.6.5. *Activities of birds when not brooding.* — Only a small part of the time off the nest is spent in feeding. Males often wander outside their territories, in their neighbours' territories or in neutral zones which they will exploit later to collect food for the young. I have seen or caught some males as far as 200 to 400 m from their nest. Females are overall more sedentary and devote much time to the maintenance of their plumage. In hot sunny weather, many males spend most of their free time singing in peaceful chorus with their neighbours. Concerts occur discontinuously with a periodicity related to that of the incubation change-overs and are most intense during the hot midday hours (see Dowsett-Lemaire, 1979 c).

Incubation is certainly the stage of breeding at which life is easiest for Marsh Warblers. Both sexes put on weight, particularly the females who fatten up considerably (Dowsett-Lemaire & Collette, 1980). These reserves will be used up rapidly during the feeding of nestlings.

4.7. YOUNG IN THE NEST.

At the hatching of the eggs, the birds' behaviour changes remarkably : the territory is no longer defended and males stop singing. Some late settling males have, however, already ceased singing before this stage.

Until now, the territory seemed sufficient to provide most of the food required by the adults, although some feeding also took place during extraterritorial excursions. On the other hand, food for the young will be sought largely outside the initial territory, in areas of dense herbaceous vegetation exploited in common by neighbouring pairs (see Fig. 1 C in Dowsett-Lemaire, 1980). Herbaceous tufts around the nest are also investigated ; birds with initially small territories in unsuitable vegetation such as *Polygonum cuspidatum* must collect relatively more food outside than birds with better territories, richer in herbaceous vegetation. Some fly over hay-fields or vegetable gardens to reach suitable feeding grounds as far as 150 m from their nests. They are also tolerated inside occupied territories as long as they do not venture too close to the nest. Each parent has its routine, exploring from three to five feeding localities and always using the same flight lines between them and the nest.

The parent birds are usually more discreet now in taking turns at the nest than during incubation. At the early stage of feeding, a very brief warning song is still used by some males when approaching the nest. Food is brought to the nest for the young as soon as the first egg has hatched and the shell is carried away before the next egg hatches. Infertile eggs are left untouched but dead nestlings less than 7 days of age are usually removed.

4.7.1. *Brood-size.* — Table V shows the proportions of the different brood-sizes observed. The mean brood-size (4.1) is only slightly lower than the mean clutch-size (4.3), a few eggs being lost through falling out of the nest or infertility.

4.7.2. *Hatching season.* — As for laying, hatching is spread over several weeks per season, that is from 5 June to 28 July in 1975, 9 June to 14 July in 1976, and 5 June to 21 July in 1977 — the last clutch laid should have hatched on about 27 July but was upset by a storm. Following the peak of laying in late May, the peak of hatching is around mid-June : 14/33 and 21/46 hatchings took place from 12 to 18 June in 1976 and 1977 respectively. The second half of June is thus a very active period for feeding at the nest.

4.7.3. *Feeding rates.* — I spent a total of 62 hours noting the frequency of feeding journeys to broods of various ages and

TABLE V

Brood-size for the three seasons 1975-1977.

Proportion of broods (%) with					Mean size	Total sample
1	2	3	4	5 young		
1	5	16	37	41	4.1	111

various sizes (from 3 to 5 young), devoting usually one hour per brood at any time. Fig. 11 shows that feeding frequencies increase with the age of nestlings until they reach a maximum of 22-23 feeds per hour from the age of 7 days to fledging. A curve of the same pattern — increase then plateau — is observed in many species (Ruiter, 1941 ; Nice, 1943 ; Gibb, 1955 ; Curio, 1959 b ; Royama, 1966 ; von Treuenfels *in* Fouarge, 1968 ; Seel, 1969 ; Welsh, 1975). The increase in feeding frequencies in the Reed Warbler (Brown & Davies, 1949) parallels the increase in nestling weight (Dyrcz, 1974), as also observed in several other species.

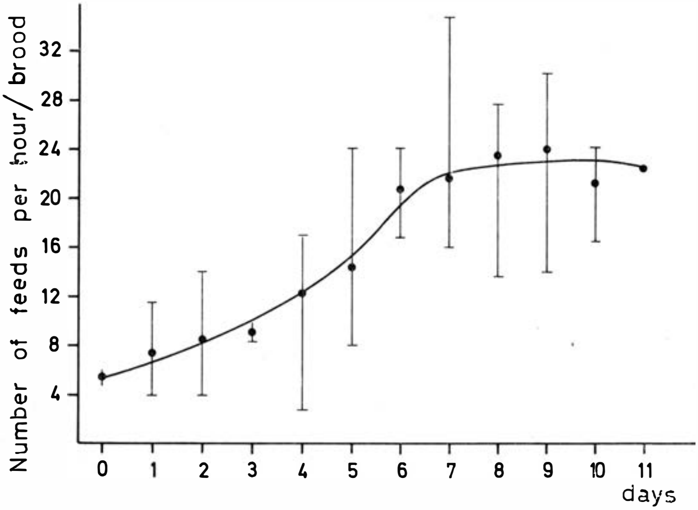

Figure 11. — Feeding rates according to the age of broods of 3 to 5 young. Means are represented by dots.

I did not weigh Marsh Warbler nestlings to avoid disturbance, but in most broods, they seem to reach their final body size at the age of 6 ½ - 7 ½ days when the feeding rate stops increasing.

Variations in the feeding rates for broods of the same age depend of course on numerous factors, of which not the least important must be the number of feeding adults and the weather — influencing the amount of time spent brooding and food availability. The low rate of 3.6 feeds per hour for a brood of four days (Fig. 11) is due to a female feeding alone in cold rainy weather ; two of the three young eventually died of starvation. The feeding activity is reduced at dawn and late in the evening, but as far as I could check, does not vary much between 8.00 and 18.00 hrs. The curve shown in Fig. 11 might have a slightly different pattern if the weight of food and not the number of feeds had been considered : from the age of 3 - 4 days, nestlings receive quite a few large prey items. However, small prey (particularly aphids) forms an important part of the diet for young of all ages. As found in other species (e.g. the House Sparrow *Passer domesticus* [Seel, 1969]), the feeding frequency for broods of the same age does not seem to increase with the number of nestlings in nests of 3 to 5 young ; data are not sufficient, however, for a statistical analysis. As an example, I noted that in the same area and in the same period in June 1977, a brood of 3 young and one of 5 received the same number of feeds per hour — that is from 25 to 30 feeds at the age of 7 to 9 days. The young of the two broods were at the same stage of development and left the nest at the same age. Royama (1966) demonstrated in the Great Tit that the heat loss is greater in small than in large broods ; therefore, a nestling in a small brood needs more energy than in a large brood to maintain its body temperature.

4.7.4. *The food for the young.* — Marsh Warblers catch a variety of insects and spiders that they pick from the stems and leaves of plants. They only occasionally catch prey on the wing. No time was available for a detailed study of the diet of nestlings, but some information could be obtained from direct observation of the adults' behaviour. Aphids are probably one of the main constituents of the diet of nestlings of 1 to 3 days, and continue to be an important element at later stages. At the age of 3 days, the young are already able to swallow prey as big as the butterfly *Coenonympha pamphilus,* although such prey only becomes frequent one or two days later. The largest item I have ever seen eaten was a *Pieris* sp. on which a nestling of 7 days nearly choked itself. Marsh Warblers take advantage of temporary infestations of insects on some plants : in 1977 for example, *Heracleum sphondylium* were invaded by aphids from late June to mid-July. Some pairs then collected at least half of the feeds on *Heracleum,* catching almost everything that was available (a lot of aphids, small Diptera, Coleoptera) but the ladybirds *Coccinella septempunctata* also very abundant seemed usually to be avoided. I only saw for certain a male Marsh Warbler carrying one to his young on two occasions, but I did not see whether the young accepted it. The repulsive flavour of *Coccinella* spp. usually makes birds avoid them. Henry (1978 a) noted some larvae and adults in the diet of young Sedge Warblers, but none in that of young Reed Warblers (Henry, 1978 b). They are also very rarely recorded in the diet of *Sylvia* warblers (Warden & Bibby, 1978).

4.7.5. *The role of the sexes in feeding and brooding.* — Both sexes seem equally active in feeding : in pairs where the sex could be identified, males contributed to 52.8 % of 492 feeds. However, there is considerable individual variation : in some pairs, one of the adults of either sex may bring food up to 10 times more often than its partner, and also decrease or increase its share of feeding during the nestling period.

As detailed elsewhere (Dowsett-Lemaire, 1979 a), the disappearance of one member of the pair, particularly the male, during the nestling stage or even before is not infrequent. Most females left alone managed to raise at least part of the brood successfully, and the few males deserted by the female after the brood was 5 days old also succeeded in raising young.

The proportion of time spent brooding the nestlings by day decreases with the age of the brood. The young are no longer covered from the age of 7 days, except during heavy rain. Until then, the brooding activity of the parents is of course much dependent on the weather. On average, the share of males is less (37 %) than that of females (63 %), as measured out of a total of 13 hours of observation. Nestlings start growing their wing feathers and various tracts of body feathers at the age of 6 - 7 days, which probably ensures enough protection from then on. In two species of *Spizella* with a very short nestling period as in the Marsh Warbler, Dawson & Evans (1957) showed that nestlings become progressively homeothermic during their first week.

4.7.6. *Age of broods at fledging.* — Most broods leave the nest at the age of 10 or 11 days (Fig. 12), if the age of the older nestlings (forming the whole or at least the majority of the brood) is taken into account only. In fact, the process often takes several hours, with the (presumably) youngest nestling leaving last, occasionally the day after the others. The average length of stay varies little with brood-size, that is from 10.8 to 11.1 days for each of the three main brood-sizes of 3 to 5 young. The two broods that fledged at the age of 13 days (with 3 young each) had been underfed and their development delayed. The fledging of a brood can start at any time of the day. Two broods (excluded from Fig. 12) were accidentally expelled from the nest at the age of 7 ½ and 8 days respectively, and managed to survive, probably thanks to favourable weather conditions at the time.

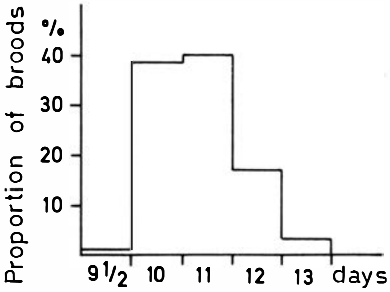

Figure 12. — **Age of broods at fledging (n = 65 broods).**

4.8. THE FLEDGLING PERIOD.

4.8.1. *The division of the brood between the parents.* — If the two members of the pair have remained together so far, it is now, at the fledging of the brood, that they part irrevocably, each taking charge of some of the young and feeding the same ones until independence is reached. The selection of the young to be cared for by each adult occurs when they leave the nest, as described in the following example :

On 19 June (1974), at the age of 11 days, a brood of 5 left the nest over a few hours. The nest was situated in a clump of *Urtica* near a small *Sambucus nigra*. The first young jumped out at 9.00 hrs into the thick growth around the nest and was immediately adopted by its father who, from then on, stopped visiting the nest. The male also fed the second and third chicks as soon as they came out one and two hours later, respectively. At 11.10 hrs, I guessed, from the weak calls of the young and the journeys of the father, that the first chick was 10 m from the nest in *Urtica* and grass, the second 5 m behind, whereas the third one had moved in an opposite direction, in thick grass, already 10 m from the nest. The father was feeding one chick four or five times before switching to another. At 13.00 hrs, the fourth chick left the nest and was taken in charge by the female who also continued to feed the last one until it jumped out an hour later, to remain in the care of its mother. Two days later, the two fledglings fed by the female were still only 2 m from the nest, hidden at the bottom of the *Sambucus* tree, whereas the other three were already more than 50 m away, beyond the limit of the initial territory. The male had irrevocably lost contact with his female.

The fledging process was observed in several other broods, where the older young were sometimes taken in charge by the female. In one brood of 4, the female adopted the third chick out whereas the male took charge of the first 2, and also the fourth one who left the nest several hours after its brood mates. Broods of 5 have always been divided into two groups of 2 + 3 (never 1 + 4), and broods of 4 into groups of 2 + 2 or 1 + 3. It is questionable whether the number of young taken in charge by an adult can be related to the feeding effort of the parent bird at the nestling stage : three adults of either sex who adopted 3 of the 4 or 5 young of their brood had done very little feeding so far, but a male who took charge of 3 of 4 young had done most of the feeding before.

Broods of 2 have never been shared between the parents ; in seven such cases, only one adult remained to feed the fledglings. Parent birds already left alone before the brood fledged, have of course to continue to feed the whole brood until independence. Thus the number of fledglings fed by single adults varies from 1 to 5, but is most often 2 or 3. Even if a brood of 5 is in the charge of the same adult, the brood mates spontaneously separate into at least two groups (2 + 3) or three (1 + 2 + 2) distant from each other by 10 - 20 m or more.

The sharing of the brood between the two parents is of course advantageous : in case part of the family is discovered by a predator, the rest of the young hidden elsewhere are likely to escape it. This behaviour has however been rarely noted in passerines

(Tinbergen, 1939 ; Snow, 1958 b ; Nolan, 1978 ; Smith, 1978). In a multi-brooded species like the Blackbird, only the last brood of the season is divided between the parents (Snow, 1958 b) ; and in a *Dendroica* warbler with occasional second broods, the male feeds all the fledglings if the female prepares a second brood (Nolan, 1978). The insufficiency of observations at this stage of breeding is probably responsible for the scarcity of such records.

The young Marsh Warblers leave the nest by climbing up stems and jumping (using their diminutive wings as a parachute) or can even run on the ground. They will be unable to fly for a few more days. They disperse quickly after fledging, into low bushes or thick tufts ; some chicks have covered up to 20 m within an hour after leaving the nest. The parents locate them by their weak " chrah " calls, repeated at intervals. It is during the nestling and fledgling period that the adults are most prone to give the high-intensity alarm call (a loud rattle " krrret ") when disturbed, and also other alarm or distraction calls or short songs (see Dowsett-Lemaire, 1979 c).

4.8.2. *Dispersal of the family groups.* — The two family groups from the same brood lose contact with each other soon after fledging as they usually disperse in opposite directions. Overall, I have succeeded in following the daily movements of 60 family groups, often until the emancipation of the young. It appears that only a minority of groups stay in the immediate surroundings of the nest — and rarely more than one of the two groups from the same nest. Most (at least two thirds) disperse outside the initial territory, moving 30 - 40 m or more from the nest up to 100 - 150 m distance. Some groups move along a large circuit which will bring them back to the initial site at the end of feeding. Lastly, a few groups — perhaps more than it seems, as I completely lost track of several groups — wander much further, even more than 500 m away from the nest, and do not hesitate to cross large unsuitable areas, of pure grass for example, to reach new feeding grounds. Thus a 18 day old fledgling and its father left the breeding territory to be discovered 500 m further three days later ; they had crossed 400 m of hay-field and vegetable fields. Another family group of 3 young fed by their mother had covered a distance of 100 m through a field of hay 1 m high at the age of 15 days (thus before being able to fly), to reach a large clump of perennials already exploited by the parents at the nestling stage. The physical performances of such very young chicks are somewhat surprising, as well as their high tolerance of heavy rain and storms in open habitat. The survival rate of fledglings until their independence is indeed very high (see later).

Family groups often move in a direction taken previously by the parents to collect food. It seems that the initiative of choosing a certain direction of movement is taken by the young ; I have never seen an adult behaving as if it was trying to call the young over to a particular spot.

4.8.3. *Development and behaviour of the fledglings.* — From fledging to independence, i.e. usually in 15 to 19 days, the young Marsh Warblers develop very quickly : the wings grow from about 35 - 40 mm (measured in only one brood) to over 64 mm and the tail from almost nothing to about 50 mm. The body plumage is also in active growth. At the age of 16 or 17 days, they become able to fly over short distances of 3 or 4 m, but do so only when they are disturbed. From the age of 18-19 days, they can fly straight over 10 m, and at 22 days, fly about as well as the adults. In the first week following fledging, they usually remain hidden in low thick vegetation. However, in sunny weather, they enjoy sun-bathing in the open as long as they are left undisturbed. After the age of 20 days, they move about more openly, sometimes following closely the adult who feeds them. Begging calls become louder with age but are uttered irregularly, mainly when or after moving. Noisy parties of fledglings following their parent have been observed only a few times with young 20 - 24 days old. I once saw 26 day old brood mates (about to become independent) calling and chasing each other in a curious low flight from bush to bush : this may have been a playful activity.

The parents feed their young very frequently in the first few days after fledging, probably as often as during the last days in the nest. I observed groups of 2 or 3 young of 13 to 16 days receiving food at the rate of one feed every 2 or 3 minutes, sometimes one per minute. The chicks are then completely unable to feed themselves. At the age of about 18 days, they start showing an active interest in their environment and pick at various small objects (leaves, twigs), catch them and turn them around in their bill, or even hammer them on a stem as if to "kill" them. At about 20 days, many young are able to pick food up properly and swallow it, particularly in the form of aphids (which must be a relatively easy prey) which they catch in *Salix* or herbaceous plants without any apparent difficulty except that their movements are slower than adults'. At other times, they sit motionless, just waiting to be fed by their parent. At 23 - 24 days, all young practice self-feeding to some extent, from two to a few days before becoming completely independent. The rate of feeding by the adults must have decreased considerably during the second week after fledging, but this was not measured accurately.

The reaction of young birds before possible danger is sometimes awkward. At my intrusion for example, small young of 13 to 15 days, still unable to fly, have sometimes made themselves conspicuous by hopping about and calling on tops of tufts, instead of remaining hidden and silent. However, they generally escape the predation of small mammals.

4.8.4. *Fledglings at independence.* — I determined the moment young become independent by following the movements of identified family groups from day to day until, one morning, I found the young, without the adult. It seems that the adults leave at night. The young from the same group often remain together for one or two more days, if not more, and when they move around, communicate by the juvenal location " chrah " calls or by " tec " calls. Family groups become independent at 26 to 31 days (Fig. 13), a third of my sample at 29 days. The average age at independence of family groups of 2 young (28.2 days, n = 17) does not differ from that of 1 young (28.2 days, n = 9) or from that of groups of 3 young (28.5 days, n = 10), and so the duration of parental feeding does not depend on the number of fledglings in the care of each adult.

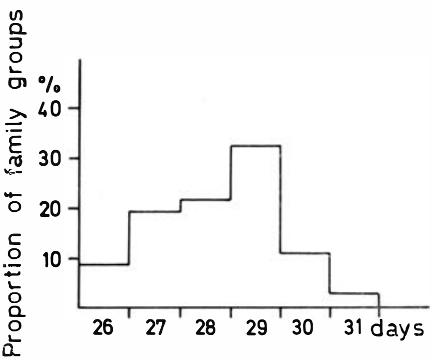

Figure 13. — Age of fledglings at their emancipation (n = 37 family groups).

In his study of fledgling Spotted Flycatchers *Muscicapa striata,* Davies (1976) found that the young switch to self-feeding when it becomes more profitable than begging (as the adults become more reluctant to feed them) and then become independent of their parents altogether. He later proved experimentally with young Great Tits (Davies, 1978) that once the young are able to start feeding themselves — about 8 days after fledging — the process leading to independence can be initiated more or less quickly as the parents become mean, i.e. reluctant to feed, at a more or less early stage. Marsh Warblers are certainly well able to collect some food on their own at the age of 22 - 24 days, and how soon they become independent after that may depend mainly on how reluctant the adults become to feed. However, they experience a difficult time at independence, since on the first day they undergo a sudden loss of weight : from 1.1 to 3.6 g, on average 1.9 g or 13 % of their mean evening weight of 15.0 g (n = 8).

Each year, it is in the first few days of July that the first independent young are noted. In the field, even at a distance, it should be relatively easy for trained observers to distinguish them from adults : their spruce fresh plumage of a warm brown contrasts with the more olive and quite worn out adult plumage. In 13 out of 18 fledglings caught within a day of their independence, the development of the wing was just completed, and was nearly so in the 5 others. In most, the tail had still to grow from one to a few mm, to reach a final length of 50 to 54 mm. On the other hand, the growth of the body plumage was far from complete. Young Reed Warblers handreared by Davies & Green (1976) had also practically completed the development of the wing and tail feathers at about 30 days of age.

4.9. THE DEPARTURE OF ADULTS.

4.9.1. *The incidence of body moult.* — Apart from very few exceptions (in July 1977) all adults disappeared irrevocably at the emancipation of their young. At that stage, the adults appear to be in a more or less advanced state of body moult and females start refeathering the brood patch. The earliest dates on which moulting birds were caught are 27 and 28 June : respectively a male on the last day of incubation and a female with fledglings 21 days old ; they had only just started, with some new feathers growing in the upper- and under-tail coverts. The latest known bird to start moulting is a female who showed no sign of moult on 29 July, but had started when recaught on 2 August, her nestlings being 5 days old. Most birds start during July, at various stages of the breeding cycle, from the incubation onwards. Individual differences in the timing of body moult have been noted even between birds at the same stage of breeding at the same time (as between members of the same pair). Two recaptures of moulting birds show that the process can develop rather quickly. A male caught on 6 July (with fledglings of 23 days) had a few feathers growing on his flanks and upper- and under-tail coverts, and was already in very active moult all over when recaught four days later (the day before he left the area). Another male feeding 6-day old nestlings on 17 July was in full active moult ; he was recaught 10 days later with far fewer feathers growing mainly on the back and head. Thus in this case, body moult was nearly complete before the bird left the area in early August.

Body moult must consume little energy since it overlaps with the task of feeding young or the process of fattening up for migration. Moult of the body plumage also takes place before migration in the Reed and Sedge Warbler (Tyson & Pepler, 1976), and in the Aquatic Warbler *Acrocephalus paludicola* (Heise, 1970).

4.9.2. *The start of migration.* — I noticed the earliest signs of " autumn " migration on 6 and 7 July 1977 when I saw quite a few adults which were unringed (and thus most likely foreign to my population) crossing the study area in a southerly direction, flying from bush to bush and feeding briefly on the way. Putting up nets three days later, I indeed caught five passage birds in heavy moult, two of which were quite fat ; the females had half refeathered brood patches. When I put up nets on 14 July 1975, migrant birds were also caught. It is likely that most of the adults leaving their breeding areas at the emancipation of their young, from the second week of July onwards, are about ready to migrate. Some of the birds I caught at the end of their stay (as early as 14 July) were fattening up (Dowsett-Lemaire & Collette, 1980). With such an early start, it is not surprising that the first Marsh Warblers are already noted in northeastern Africa in mid-August.

In 1975 and 1976, none of the adults leaving as their young became independent was subsequently seen in that season. This was true for all but six of the breeding birds in 1977 : after emancipating their young relatively early in the first half of July, five birds (of which a female) were seen again in the area from one to a few days later, and a male was resighted two weeks later. Two males sang again briefly for a day or two, and most interestingly, another male resettled in a new territory and uttered persistent early morning song from 10 to 14 July before leaving. Thus, part of the population delayed its departure, although by the same time (second week of July) other birds were already migrating. Such behaviour may have been influenced by the exceptional luxuriance of the vegetation in July after a very wet month of June. It is in July 1977 that J. François *(in litt.)* apparently obtained the first proof of a normal second brood in this species in a French population (Doubs).

4.9.3. *Length of stay on the breeding grounds.* — Most adults stayed for less than two months, from their arrival to the emancipation of their single brood. In taking into account only birds who succeeded in their first breeding attempt — which is the majority — and who did not desert the territory before the end of the cycle, the sojourn of males averaged 55.2 days (from 51 to 63 days, $n = 19$) and that of females 52.5 days (from 48 to 58 days, $n = 18$). It was shown earlier that females arrive on average three days after males.

Considering the birds who undertook replacements, the longest stay I recorded was 85 days (in 1977) : this was by a female who, after having lost or abandoned three clutches in succession, raised the young of the fourth one ; her male left when the brood fledged, after a sojourn of 70 days.

4.10. THE DISPERSAL OF YOUNG AFTER THEIR EMANCIPATION.

After acquiring independence, juveniles disappeared from the area more or less soon, according to local habitat conditions. In

1976, the herbaceous vegetation was drying out very quickly and the usual July flush of aphids in *Salix caprea* did not occur. Nearly all young disappeared as soon as emancipated, and in four ringing sessions from 15 July to 11 August, I caught only three juveniles aged 29 to 33 days — i.e. recently emancipated. No passage birds were noticed.

The situation was quite different in 1975 and 1977, as higher rainfall made the habitat more hospitable. From mist-netting data, it seems that at least half of the local young remained for one week, and some up to two weeks, after their emancipation. The oldest local young caught were 42 and 43 days old respectively in 1975 and 1977. The first juveniles from outside (unringed) were noted on 19 July 1975 and 21 July 1977 ; such birds were regularly caught until early or mid-August and the age of the first ones caught (19 July) was estimated to be at least 35 days.

In July 1975, the shift of feeding sites from the herbaceous vegetation to small trees occurred progressively so that in the second half of the month most birds were feeding in *Salix caprea.* The only perennials still exploited then were the late-flowering ones, such as *Artemisia vulgaris, Eupatorium cannabinum, Solidago gigantea* and some others. In 1977, an even higher rainfall maintained the herbaceous growth in a luxuriant state, and by the end of July (28) I counted that at least half of the Marsh Warblers were still present in perennials such as those cited above and also *Heracleum sphondylium, Vicia cracca* and *Melilotus* spp. particularly well developed in that wet summer.

None of the 15 independent juveniles recaught up to their departure had completed the growth of the body feathers, even past the age of 40 days, although from the age of 35 days the process seemed near its end. For example, a young of 40 days caught on 2 August 1975 had only three or four feathers growing on its throat and back ; another juvenile of 43 days caught on 22 July 1977 was growing the last few feathers on its back and flanks. The latest-born local young recaught in 1976 (on 11 August, at the age of 33 days) was already completing its body plumage development, with the last feathers growing on its flanks. It may be that young born late develop relatively more quickly but my data are insufficient to confirm this. Berthold *et al.* (1970) clearly showed in two *Sylvia* warblers that the age at which the processes of plumage development occur is earlier and their duration shorter the later the birds are born. Although a partial post-juvenile moult is known to occur in many Sylviinae before migration (Snow, 1967), including the Reed and Sedge Warbler (Tyson & Pepler, 1976), my present data do not suggest that it takes place in the Marsh Warbler on the breeding grounds, where the stay is of course particularly short.

After the loss of weight at emancipation, the young remain lean for at least a week. At about 36 or 37 days, they start accumulating fat during the day, but they lose it overnight. Thus, they do not seem prepared to undertake migration for at least two weeks, if not more, after emancipation. Those who leave the birthplace earlier must simply disperse locally, perhaps in search of better feeding places to fatten up. Humid clumps of *Salix* spp. on the edge of marshes along the river Meuse, for example, bear far greater concentrations of Marsh Warblers in summer than the dry study area. Some controls support this, including one of a young ringed by me as a nestling in June 1977 and recaught 71 km to the NW on 6 August at the age of 55 days.

5. — *BREEDING SUCCESS*

5.1. BREEDING SUCCESS AND PRODUCTIVITY.

The breeding success was known for all nests in 1976 and 1977, and a little over half of them in 1975. The proportion of successful nests — i.e. producing at least one fledgling — varied from 60.0 % in 1975 and 60.3 % in 1977 to 74.4 % in 1976, and averaged 64.2 %.

TABLE VI

Breeding success and productivity.

	1975	1976	1977	Total	Mean
Eggs laid	171	168	252	591	
Hatching success (%)	81.3	81.6	76.2		79.2
Fledging success (%)	64.8	84.7	72.4		73.7
Breeding success (%)	52.6	69.0	55.2		58.4
Ave. number of young fledged/nest	2.3 (n = 40)	3.0 (n = 39)	2.4 (n = 58)		2.5 (n = 137)
Ditto/pair or female	2.5 (n = 37)	3.2 (n = 37)	2.7 (n = 51)		2.8 (n = 125)

The overall productivity (Table VI) is expressed as the mean number of fledglings produced per pair or female, since there was a slight excess of breeding females over males. The seasonal productivity per pair or female is not much higher than that per nest since only a few of the lost clutches or broods were replaced (as discussed earlier). Breeding success was highest in 1976, for reasons considered below.

5.2. CAUSES OF BREEDING FAILURE.

The causes of failure are detailed in Table VII. Desertion of whole broods led of course to starvation, so that the overall proportion of nestlings dying of starvation is 13.5 %.

5.2.1. *Predation.* — This is usually the most important cause of breeding failure in small birds, accounting for up to 90 % of the losses (Lack, 1954 ; Delius, 1965 ; Cody, 1971 ; Catchpole, 1974 ; etc.). But this factor is not especially important here, particularly for clutches.

It is not certain that potential avian predators (Jays *Garrulus glandarius* and Magpies *Pica pica*) ever caused damage to a nest. On the other hand, a number of indications suggest that Weasels *Mustela nivalis* were involved in many cases. Most nests were robbed by night and left undamaged. The average height of robbed nests is only 53.4 cm ; most of them must have been of easy access to Weasels without having to be pulled down. Five adult females disappeared at night together with their clutch or brood, except that once the clutch was found broken (presumably by the female when she was caught). The rate of predation was not evenly distributed in the area : 10 of 21 predated nests were in the same territories over the years, whereas elsewhere some very exposed nests were successful. In 1977, five of the eight robbed nests were in adjacent territories possibly visited by the same predator.

The age of the predated broods varied from 2 to 9 days. Although nestlings start showing fear of strange objects at the age of 6 ½ - 7 days, the fright reaction is not developed enough to ensure escape of predators after that age. I experienced this myself by being able to ring a few broods of 8 or 9 days without causing pre-

TABLE VII

Causes of breeding failure (in % of all eggs laid or young hatched) for 123 eggs lost and 123 nestlings lost.

	Eggs (%)	Nestlings (%)
Predation	4.9	12.0
Desertion	4.4	8.6
Starvation of younger nestlings	—	4.9
Unhatched eggs	5.2	—
Destruction by man	4.6	—
Storm - wind	1.7	0.2
Unknown	—	0.6
Total	20.8	26.3

mature departure from the nest. Two broods of 7 ½ and 8 days flushed from the nest accidentally proved, however, able to survive.

5.2.2. *Desertion and starvation.* — A total of six clutches were deserted, three of them after having been uncovered by a storm. Two pairs continued to brood for several days after the nest-site had been damaged, before deserting the nest and territory altogether. In the third case, incubation had not yet started, so that the nest was abandoned straight away and the female rebuilt elsewhere.

A total of 11 broods were deserted, seven of them in the period 21 June - 2 July 1975 when heavy rainfall and cold temperatures had apparently caused a food shortage. The seven abandoned broods (from 2 to 5 young each) were from 6 to 9 days old, so were at a stage when a maximum feeding effort was required from the parents. The desertions occurred at night, the young were found dead and cold in the morning. Four of the male parents were seen again in the neighbourhood, but none of the females. Interestingly, desertions took places in zones of grouped territories (where the feeding grounds are shared between several pairs) and not in isolated territories. Similarly, in 1977, two broods were abandoned during a spell of cold wet weather in an area of very high density (7 pairs in 0.25 ha). Two more broods were deserted by their only parent (female), the male having disappeared during egg-laying.

Desertion of broods associated with bad weater is probably not rare in Sylviinae : in England, in five *Sylvia* species, it is the main cause of failure after predation (Mason, 1976). In Czechoslovakia, Havlin (1971) found several broods of Great Reed Warbler a week old deserted in bad weather.

Most younger nestlings of other broods who died of starvation did so in the first few days following hatching, and in the same bad weather periods during which all cases of brood desertion occurred. Two females feeding alone in June 1975 succeeded in raising only one young out of 3 and 5 respectively.

5.2.3. *Unhatched eggs.* — Of the 31 eggs that did not hatch, 28 were infertile and three contained a dead embryo. Most often, only one egg per clutch may be infertile, but once I found 3 eggs infertile out of 4, and I also found three clutches of 4 entirely infertile. In each case, the male had proved his fertility on other occasions ; so it must have been the female who was barren, unless copulation did not succeed. Two of the clutches were abandoned after about a week of incubation (but one was half upset by an unknown factor). The third one was brooded by both members of the pair for 25 days until only one egg remained ; during this period, 3 of the 4 eggs had disappeared one by one as they were drying out inside — presumably carried away by the adults as they broke.

The proportion of eggs lost through infertility is similar to that found in several other passerines (Ricklefs, 1969) or slightly less (Seel, 1968 ; Havlin, 1971 ; McGinn & Clark, 1978).

5.2.4. *Other factors.* — Habitat destruction by man and bush fires destroyed six clutches. Only one clutch was completely upset by a storm ; a brood of 8 days was also upset by a storm but survived. Two very violent storms in June 1977 caused very little direct loss (three eggs fell out) but about 15 nests had sunk lower down and were more or less uncovered ; among them, three clutches were later deserted, and one clutch and two broods predated.

5.2.5. *Conclusion.* — Overall, predation and desertion/starvation of nestlings are the main causes of failure (Table VII). Predation of nestlings affected the breeding success mainly in 1977 when 18.8 % of all young hatched were taken against 7.9 % in 1975 and 6.6 % in 1976. On the other hand, breeding in 1975 suffered from a high desertion/starvation rate of 26.6 % because of unfavourable weather, as against 6.5 % in 1976 and 8.8 % in 1977. Although breeding success was highest in 1976, the overall productivity remained lower than in other years because of a low breeding density : the population of 35 males and 37 females produced 118 fledglings against 139 raised by 48 males and 51 females occupying the same 3.5 ha in 1977.

Mate infidelity is high in the Marsh Warbler, particularly in males (Dowsett-Lemaire, 1979 a). However, breeding success of single parents is overall 59.0 % (n = 100 eggs laid), which is not significantly different from the breeding success of pairs sharing the breeding duties (58.2 % from 491 eggs laid).

In his West German population, Schulze-Hagen (1975) found an overall breeding success of 69.1 %, from 1369 eggs of 297 nests studied from 1969 to 1973. Hatching success (79.2 %) is exactly the same as in my population, but fledging success is higher (87.2 % against 73.7 %). This difference is essentially due to the fact that Schulze-Hagen never found a brood deserted. In addition, he discovered a few clutches parasitised by the Cuckoo *Cuculus canorus,* but that was a very small factor of failure (2.2 %). The Marsh Warbler does not seem to be a frequent host to the Cuckoo even where the latter is common. In an area of Switzerland where Cuckoos are quite common, Wiprachtiger (1976) did not find any parasitised nest in a total of 101 clutches. In this Swiss population, hatching success was 83.5 %, but fledging success is not known. The Reed Warbler seems to be a much more frequent host to the Cuckoo, being very heavily cuckolded in some places (Wyllie, 1975).

5.3. SURVIVAL OF YOUNG FROM FLEDGING TO INDEPENDENCE.

I was able to count the number of young still present just before emancipation in 44 family groups. In the period of 15 - 19 days of post-fledging dependence, 88 out of 94 young Marsh Warblers survived (= 93.6 %). Four of the six young that disappeared belong to a brood that suddenly vanished the day after fledging.

The survival rate of young Marsh Warblers seems much higher than in several other species for which comparative data exist. In a population of Blackbirds (protected from cats), Snow (1958 a) found that 66 % of the fledglings survive until independence. About half of the young Stonechats *Saxicola torquata* of a British population disappear during the three weeks after fledging (Phillips, 1976), and about half of the young Winchats *S. rubetra* die in the week following fledging (Gray, 1974). In another British study, Delius (1965) estimated that only 22 % of young Skylarks *Alauda arvensis* survive from fledging to independence. Broods of tits *Parus* spp. and *Phylloscopus* warblers are also largely decimated in spells of cold wet weather. By contrast, young Marsh Warblers resist adverse weather remarkably well, and, hidden as they are in thick vegetation, are well concealed to predators.

5.4. DISCUSSION.

Schulze-Hagen (1975) showed that the figures of breeding success he obtained for his population of Marsh Warblers are higher than in most other species of Sylviinae or other passerines with open nests. Another way of assessing breeding output in various species is to compare the overall productivity per nest, which I show in Table VIII for some Sylviinae species. The Marsh Warbler population that Schulze-Hagen studied certainly produced more fledged young per nest than the other species considered, but the productivity of my population compares well with that of the other *Acrocephalus* or *Sylvia* species. The Reed Warbler is the least successful breeder of all, and this is due to a high predation rate : Catchpole (1974), working on a British population, showed that the predation rate of Reed Warbler nests situated in *Phragmites* is twice as high as that of nests built in thick herbaceous tufts. Similarly, in a West German locality where Reed and Marsh Warblers breed side by side, breeding success is lower in the former species as its less well concealed nests built in *Phragmites* are more accessible to predators (C.K. Catchpole, *in litt.*). The comparative data in Table VIII must, however, be considered with some caution as some pairs of warblers other than Marsh may be double-brooded. As an example, the proportion of Reed Warbler pairs raising a second brood per

TABLE VIII

Breeding productivity in some Sylviinae species, with the number of nests in ( ).

Author	Species	Ave. number of young fledged/nest
Present study	*Acrocephalus palustris*	2.5 (125)
Schulze-Hagen (1975)	*A. palustris*	3.2 (297)
Catchpole (1970)	*A. scirpaceus*	1.5 (94)
Havlin (1971)	*A. scirpaceus*	2.2 (50)
Dyrcz *(in litt.)*	*A. scirpaceus*	1.5 (385)
Havlin (1971)	*A. arundinaceus*	2.7 (177)
Dyrcz *(in litt.)*	*A. arundinaceus*	2.1 (277)
Catchpole (1970)	*A. schoenobaenus*	2.7 (72)
Mason (1976)	*Sylvia communis*	2.7
	S. atricapilla	2.6
	S. borin	2.1
	S. curruca	2.6
	S. undulata	2.3

season is 10, 22 and 29 % in populations studied by Havlin (1971), Catchpole (1970) and Franzisket (1955).

Schulze-Hagen (1975) suggested that the high breeding success of the Marsh Warbler must be the origin of the general increase in numbers and the extension of its range northwards on the continent in the last few decades (see Dowsett-Lemaire, 1978). The only marginal population that does not seem very healthy is that of southern England which has been decreasing for about 25 years (Sharrock, 1976). British ornithologists attribute that decrease to the disappearance of natural habitats. On the continent, however, where natural habitats (such as humid valleys of *Filipendula ulmaria* and *Salix* spp.) have also become scarce in many places, Marsh Warblers are thriving in all sorts of artificial herbaceous habitats, including cereal fields locally. More studies are needed to know if breeding success is usually higher than in other species, and if the high starvation rate of nestlings that I recorded in 1975 — responsible for a lower breeding success than in the German population — is of an exceptional nature or not. The overall success and spread of the species can also be linked to a high survival rate in general — there is an indication of this in the very high survival of fledglings — and of course to pioneering dispositions and the capacity to adapt to artificial habitat.

6. — *CONCLUSION*

Since they are adapted for exploiting a type of vegetation of late development, Marsh Warblers have a very short breeding season. It was shown that they do not spend more time on the breeding grounds than is strictly necessary to raise one brood ; most birds staying less than two months. If the length of each journey across Europe is estimated at two weeks, it means that they spend in Africa three times as much time as in Europe. Females who fail at the first breeding attempt are reluctant to relay, especially if failure occurs at the nestling stage. The apparent discovery of a normal second brood in a French population in 1977 (J. François, *in litt.*) must remain exceptional, but it occurred in a more humid habitat than my study area, with possibly a more protracted productivity. The mate of the female who relayed was not identified by François, but from my own observations on the breaking up of pairs at the fledging of the brood, it is likely that remating with another male occurred between broods. In my population, only one male temporarily resettled in July 1977 after having raised his share of the first brood to emancipation, and after a separation of more than two weeks from his female who raised elsewhere the rest of the family.

The annual variations in the start of breeding at temperate latitudes can be related to a number of factors such as spring temperature, food supply, environmental changes, etc. (Immelmann, 1971). In the Great Tit for instance, the onset of breeding is correlated with tree leafing and the appearance of some insects, two factors themselves correlated with spring temperatures (Slagsvold, 1976 ; Leclercq, 1977), but the direct factor influencing breeding was shown experimentally to be the food supply (Kallander, 1974). In the Marsh Warbler, annual variations in the onset of breeding were slight and directly correlated with the dates of first arrivals. The latest first arrivals were recorded in May 1976, the hottest month of May in Western Europe in the period of study. Therefore temperature is unlikely to have a major influence on the progression of migrants to their breeding grounds. On the other hand, the drought associated with the heat wave caused a delay in the development of the herbaceous vegetation, and the first Marsh Warblers appeared only when perennials were sufficiently wellgrown to support the first nests. Since Marsh Warblers exploit this type of vegetation not only as nest-sites but also for food, it is not clear which of the two factors — the state of the herbaceous tufts as a visual clue or the abundance of food — is involved in determining the onset of breeding. Annual variations in the termination of breeding were more pronounced and are more likely to depend on visual clues than on food. When laying stopped in late June 1976, food was indeed abundant, with a maximum of pairs feeding nestlings, and apparently more plentiful than in the other years — when broods suffered from a higher rate of starvation in the cold wet weather of the same period. However, the vegetation was showing the effects of drought and did not experience the resurgence of growth recorded late June-early July 1975 and 1977, when laying extended until mid-July.

The Marsh Warbler is essentially a sociable species, with a system of small clustered territories, competing for suitable nest-sites (which are in limited supply) whereas food (not so localized) can be searched for largely outside the territory. The breeding territories are defended for only part of the cycle, i.e. until the hatching of the brood in the earliest pairs, at a time when new settlements are practically finished (Dowsett-Lemaire, 1980). Until then, interrelations between neighbours are frequent — cf. visits by males to their neighbours' females — and the sociable temperament of the species expresses itself in a most original way in the group singing of males at the incubation stage. Triggered by certain weather conditions, this striking activity does not appear functional (Dowsett-Lemaire, 1979 c). On the other hand, it was suggested elsewhere (Dowsett-Lemaire, 1978) that the sociability of the Marsh Warbler must contribute to the successful spreading of the species ; only factors of social attraction can explain the rapid rate at which Marsh Warblers are able to colonise new habitats.

SUMMARY

This paper describes and discusses the eco-ethological aspects of breeding in the Marsh Warbler *Acrocephalus palustris,* through the various stages of the breeding cycle. This is based on an intensive study of a colour-ringed population, varying annually from 35 to over 60 pairs in the period covered — 1974-1977. The habitat consists of a few ha of dry filled-in grounds with a thick herbaceous vegetation dominated by *Urtica dioica.*

The arrivals and settlements usually extend from the second week of May to early July, but the bulk of birds arrive in the second half of May. The arrivals of females follow very closely those of males (Fig. 1). In the hot and dry 1976 season, the development of the herbaceous vegetation was much reduced : the settlement period was thus 3 - 4 weeks shorter than in other years, the breeding density was lower (10.6 pairs/ha against 12.3 and 13.6 in 1975 and 1977) and the proportion of territorial non-breeding birds was higher.

Unmated males defend a small territory containing potential nest-sites. They become almost silent at pair formation. This process takes place when a female stops in the territory to prospect nest-sites. Most males are mated a day or two after their arrival

(Fig. 2). Territory size (but not the song repertoire) influences to some extent the rapidity with which a male gets mated (Fig. 3).

The nest-site is selected by the female, who then builds alone a nest usually completed in four days (Fig. 5), starting most often on the day following her arrival. In 1975 and 1977, the majority of nests were built in thick herbaceous tufts, but not in 1976 when more nests were situated in vegetation less affected by drought, such as the artificial sites of *Polygonum cuspidatum* (Table II). The average nest-height increases seasonally (Table III) as the vegetation continues its development.

Males display actively for two or three days, mostly the day preceding the start of laying, when copulation was observed once in a few pairs.

Most females start laying as soon as the nest is completed (Fig. 7). The seasonal patterns of laying activity parallel those of the female settlements with a shift of 6 - 7 days. The peak of laying is recorded in the last days of May and first days of June (Fig. 8) following the peak of arrivals a week earlier. Few of the lost clutches and almost none of the lost broods were replaced ; no second brood was attempted. Overall, laying was recorded from 18 May to 14 July, but in 1976 the period was three weeks shorter than in the other years.

Clutch-size varies from 3 to 5 eggs, averaging 4.3 eggs (Table IV), and decreases seasonally (Fig. 10). The spreading of laying must be advantageous as it reduces the pressure of the population on the environment per time unit. Small late clutches are as successful as large early ones.

Incubation usually starts before the laying of the last egg in 4 and 5-egg clutches, and lasts from 12 to 13.5 days. Males brood by day as much as females, although they do not develop a brood patch. Partners relieve each other regularly, on average every 20 minutes.

The territory is no longer defended at the hatching of the brood if not earlier, and males stop singing. Food for the young is largely collected in communal feeding grounds outside the initial territory. Feeding rates increase with the age of the brood to reach a maximum of 22 - 23 feeds per hour from the age of 7 days (Fig. 11). On average, males feed as much as females but brood less.

Most broods leave the nest at the age of 10 or 11 days (Fig. 12), several days before being able to fly. The two members of the pair part irrevocably when taking charge of some of the young as they fledge ; they feed the same ones until independence. Most family groups disperse far from the nesting territory. Fledglings start feeding themselves at the age of about 20 days. They become completely independent at 26 to 31 days (Fig. 13).

Almost all adults left the breeding area as soon as their young became emancipated. Most of them were then in a state of active body moult. Adults succeeding in their first breeding attempt stayed on average less than two months. There is evidence that the " autumn " migration starts in the second week of July.

A proportion of the young remained in the area for up to two weeks after emancipation. They cannot fatten up then, and the growth of the body plumage continues after that of the wings and tail ; it is (almost) completed at independence. They are probably not able to undertake movements of more than local dispersal in the two or three weeks following emancipation. In the course of the summer, they feed progressively more in small trees, mainly *Salix* spp., than in the herbaceous vegetation which is drying out.

Breeding success averages 58.4 % (79.2 % hatching success x 73.7 % fledging success) and was highest in 1976 (Table VI). An average of 2.5 young was produced per nest. Predation of broods by small mammals and desertion/starvation of nestlings in bad weather are the main causes of failure (Table VII). Survival of young birds from fledging to independence is very high (94 %). Breeding success is discussed in relation to the current increase in numbers and extension of the species's range.

To conclude, a very condensed breeding cycle and a system of small clustered territories are obvious adaptations to the exploitation of a locally very dense habitat of short productivity. It is suggested that visual environmental clues (i.e. the state of the herbaceous growth) are the most likely proximate factors determining the timing of breeding.

RESUME

Cet article décrit et discute les aspects éco-éthologiques de la nidification chez la Rousserolle verderolle *Acrocephalus palustris,* le cycle reproducteur étant analysé stade par stade. La population étudiée (marquée de bagues de couleur) a varié annuellement de 35 à plus de 60 couples (1974-1977). L'habitat consiste en quelques hectares de terrains de remblai secs où domine l'ortie *Urtica dioica.*

Les installations se déroulent en général de la deuxième semaine de mai à début juillet, mais le gros de la population se fixe dans la seconde moitié de mai ; les arrivées de femelles suivent de près celles des mâles (Fig. 1). Au printemps sec et chaud de 1976, la végétation herbacée est moins développée : la période d'installation est raccourcie de 3-4 semaines par rapport aux autres années, la densité de la population nicheuse est moindre

(10,6 couples/ha contre 12,3 et 13,6 en 1975 et 1977) et la proportion d'individus non-nicheurs temporairement cantonnés est plus forte.

Les mâles célibataires défendent un petit territoire contenant des sites de nid potentiels. Ils se taisent pratiquement lorsqu'une femelle pénètre dans leur territoire pour prospecter les sites de nid ; c'est ainsi que le couple se forme. La plupart des mâles s'accouplent un jour ou deux après leur arrivée (Fig. 2). La dimension du territoire (mais non l'étendue du répertoire vocal du mâle) a une influence sur la rapidité des accouplements (Fig. 3).

L'emplacement du nid est choisi par la femelle ; elle se charge seule de la construction qui dure généralement 4 jours (Fig. 5), commençant le plus souvent le jour après son arrivée. En 1975 et 1977, la majorité des nids sont construits dans des touffes herbacées, mais pas en 1976 où davantage de nids sont situés dans un type de végétation moins affecté par la sécheresse, comme les *Polygonum cuspidatum* (Tabl. II). La hauteur moyenne des nids augmente au cours de la saison (Tabl. III) avec la croissance de la végétation.

Les mâles paradent activement pendant deux ou trois jours, surtout le jour qui précède le début de la ponte et au cours duquel la copulation a été observée une fois seulement chez quelques couples.

La plupart des femelles commencent à pondre dès que le nid est terminé (Fig. 7). Les pics d'activité de ponte de la population sont observés les derniers jours de mai et premiers jours de juin, suivant les pics d'arrivées de femelles une semaine plus tôt (Fig. 8). Dans l'ensemble, les pontes ont été commencées du 18 mai au 14 juillet, mais en 1976, la période est plus courte de trois semaines que les autres années. Presque aucune nichée et peu de pontes perdues ne sont remplacées ; il n'y a pas eu de seconde ponte normale. La grandeur des pontes varie de 3 à 5 œufs (moyenne = 4,3 œufs, Tabl. IV) et décroît au cours de la saison (Fig. 10). Les pontes tardives (plus petites) ont le même taux de succès que les pontes précoces (plus grandes). L'étalement des pontes sur la saison doit être avantageux puisqu'il réduit la pression de la population sur le milieu.

L'incubation dure de 12 à 13,5 jours et commence avant la ponte du dernier œuf dans les pontes de 4 ou 5 œufs. Les mâles prennent une part égale à l'incubation pendant la journée, bien qu'ils ne développent pas de plaque incubatrice. Les partenaires se relaient régulièrement, en moyenne toutes les 20 minutes.

Les mâles cessent de chanter au plus tard à la naissance des jeunes, et le territoire n'est plus défendu. Une grande proportion de la nourriture pour la nichée est recherchée en dehors du territoire initial, en zones neutres. Les fréquences de nourrissage augmentent avec l'âge de la nichée pour atteindre un plateau de

22-23 becquées par heure après l'âge de 7 jours (Fig. 11). En moyenne, les mâles nourrissent autant que les femelles mais couvent moins.

La plupart des nichées quittent le nid à l'âge de 10 ou 11 jours (Fig. 12), plusieurs jours avant de pouvoir voler. Les parents se séparent définitivement à l'envol des jeunes, chacun s'occupant d'une partie de la nichée et nourrissant les mêmes petits jusqu'à l'indépendance. Les jeunes commencent à se nourrir seuls vers l'âge de 20 jours et deviennent complètement indépendants à l'âge de 26 à 31 jours (Fig. 13).

Pratiquement tous les adultes quittent les lieux de la reproduction aussitôt qu'ils ont émancipé leurs jeunes. La plupart sont alors en mue active des tectrices. Les adultes qui réussissent leur première tentative de reproduction restent en moyenne moins de deux mois sur place. La migration « d'automne » commence la deuxième semaine de juillet.

Certains jeunes restent encore dans la zone de naissance une ou deux semaines après l'émancipation. Ils sont incapables de s'engraisser et la pousse des tectrices continue alors que les ailes et la queue ont (presque) achevé leur croissance à l'indépendance. Ils ne peuvent sans doute commencer à migrer que quelques semaines après leurs parents. Au cours de l'été, ils se nourrissent progressivement plus dans les arbustes (*Salix* spp. surtout) que dans la végétation herbacée qui se fane.

Le succès de la reproduction est en moyenne de 58,4 % (79,2 % à l'éclosion x 73,7 % à l'envol) ; il était le plus élevé en 1976 (Tabl. VI). En moyenne, 2,5 jeunes sont produits par nid. La prédation des nichées par les petits mammifères et la mort des jeunes par désertion/manque de nourriture (par temps pluvieux) sont les principales causes d'échec (Tabl. VII). La survie des jeunes de l'envol à l'indépendance est très élevée (94 %). L'augmentation actuelle des effectifs de la Verderolle et l'extension de son aire de nidification sont discutées à la lumière des observations sur le succès de la reproduction.

En conclusion, un cycle reproducteur très resserré et un système de petits territoires groupés sont des adaptations évidentes à l'exploitation d'un milieu localement très dense et à productivité de brève durée. Il est suggéré que ce sont très probablement des caractères visuels de l'environnement (le développement de la végétation herbacée en particulier) qui déterminent de façon immédiate l'époque de la nidification.

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