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Expansion of Penduline Tit (*Remiz pendulinus*) through Migration and Wintering

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1. Introduction

The status of *Remiz pendulinus* in Western Europe has been revised over the years. The species was, with certain reservations, first considered sedentary (SCHÜZ & HAAS 1955, NIETHAMMER 1937, ORTALI 1978, ZINK 1981) until 1955 (see ZINK 1981); however, later studies proved it to be migratory (GÉROUDET 1954, VAURIE 1959, BAUER et al. 1961).

The migration and wintering of the species in Europe since the analysis in 1961 has been frequently reviewed (MARTENS 1965, ZINK 1981, FRANZ & THEISS 1985, 1987, SCHÖNFELD 1989). Yet, both migration and wintering should be updated, as the species has continually spread over southwestern Europe (VALERA et al. 1990) and has also experienced some shifts in its migration routes and the location of winter quarters (DIEDERICH 1985a & 1985b).

This paper is an overall review of the migration and wintering of *Remiz pendulinus* in western Europe; particularly, it focuses on the relationships between migration, wintering and expansion, and theorizes a process of expansion on these bases.

2. Material and methods

The breeding and wintering areas, and the relative importance of their placements were charted with the program McPaal 1.2 (Micro-computer Programs for the Analysis of Animal Locations, 1985, J. F. BELTRAN pers. com.), designed for the analysis of home range using the Harmonic Mean algorithm. The concentric contours of a home range grouping the percentage of animal locations in these contours can be calculated with this algorithm.

The coordinates of every ringing and/or recovery of the Euring data of *Remiz pendulinus* were converted into Cartesian coordinates, then transferred to a map of the study area, Western Palearctic, and used as animal locations.

150 out of 204 international recoveries available in the EURING Data Bank until 1990 were analyzed, the rest being individuals captured in migration or researched in specific areas that could bias the overall results. The data until 1990 in the Birds Migration Centre in the S.E.O. and ICONA (Madrid) were also considered.

Most of the data for the first years (until 1961) were supplied by the recoveries in BAUER et al. (1961), as the recoveries available in the EURING Data Bank (Tab.) were too few.

Number of locations for each stage and issue. (Figures in brackets are recoveries from BAUER et al. 1961).

Issue	Stage	Locations
Wintering	until Feb. 1961	3 (+ 13)
	Nov. 1961—Feb. 1975	15
	Nov. 1975—Feb. 1985	25
	Nov. 1985—Feb. 1990	50
Breeding	until August 1961	11 (+ 16)
	April 1962—August 1975	12
	April 1976—August 1985	42
	April 1986—August 1990	38
Origin of the Wintering Birds	until 1985	12
	1986—1990	21

The evolution of the breeding areas and winter quarters of *Remiz pendulinus* in Europe was analyzed considering four stages or periods (until 1961, 1961—1975, 1975—1985, 1985—1990), they were all defined according to the shift in the migration routes described by MARTENS (1965) and the spreading waves defined by FLADE et al. (1986).

Finally, the age of the wintering individuals was studied from 81 recoveries and calculated following the EURING criteria. The regular return to the same wintering areas was also estimated on the analysis of 4 EURING recoveries and 42 local recoveries or self-recoveries supplied by ICONA.

Based on the dates of autumn migration and wintering (KIENZELBACH & MARTENS 1964, FRANZ & THEISS 1983, DIEDERICH & LAFONTAINE 1984, VALERA 1988 and others), we consider the winter season to be from the second half of November to February. Likewise, based on the spring migration (BAUER et al. 1961, KIENZELBACH & MARTENS 1964, ZINK 1981) we have taken the breeding season to be from the second week of April to late July in Central Europe, and from the second week of April to the first two weeks of August only for the populations in eastern Austria (Neusiedlersee) (see FRANZ 1988).

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3. Results

3.1. Evolution of the breeding and wintering areas in Europe

Figure 1 (a—c) shows the chronological evolution of the breeding and wintering areas of *Remiz pendulinus* in Europe as calculated from the EURING recoveries, and also the habitual breeding area for every stage or period; since the recoveries for some areas, particularly the Mediterranean one, were too few, the latter is partly based on the literature available.

As FLADE et al. (1986) pointed out, after the expansion in the period 1930—1965, a rest period (1965—1975) set in and the breeding area hardly changed (Fig. 1a). During the last years of the period 1965—1975, a recovery near the mouth of Oder

preluded a new expansion in the north and west (see FLADE et al. 1986). Certainly, during the next period (1975—1985) *Remiz pendulinus* spread its breeding area over all Central Europe (see Fig. 1b). There are records in Sweden, which was previously colonized (FLADE et al. 1986), a new breeding focus appears in the Netherlands and there is a significant spread over the southwest.

Finally, during the last stage (1985—1990) it is in the western Mediterranean region that the breeding areas changed most (VALERA et al. 1990). In Central Europe, it is worth noting the increase of breeding populations in the Netherlands (15.38 % of the recoveries, n = 39; compared with 4.34 % in the previous stage, n = 46). The recovery near Luxembourg suggests breeding in that area, something that DIEDERICH & LAFONTAINE (1984) had already presumed.

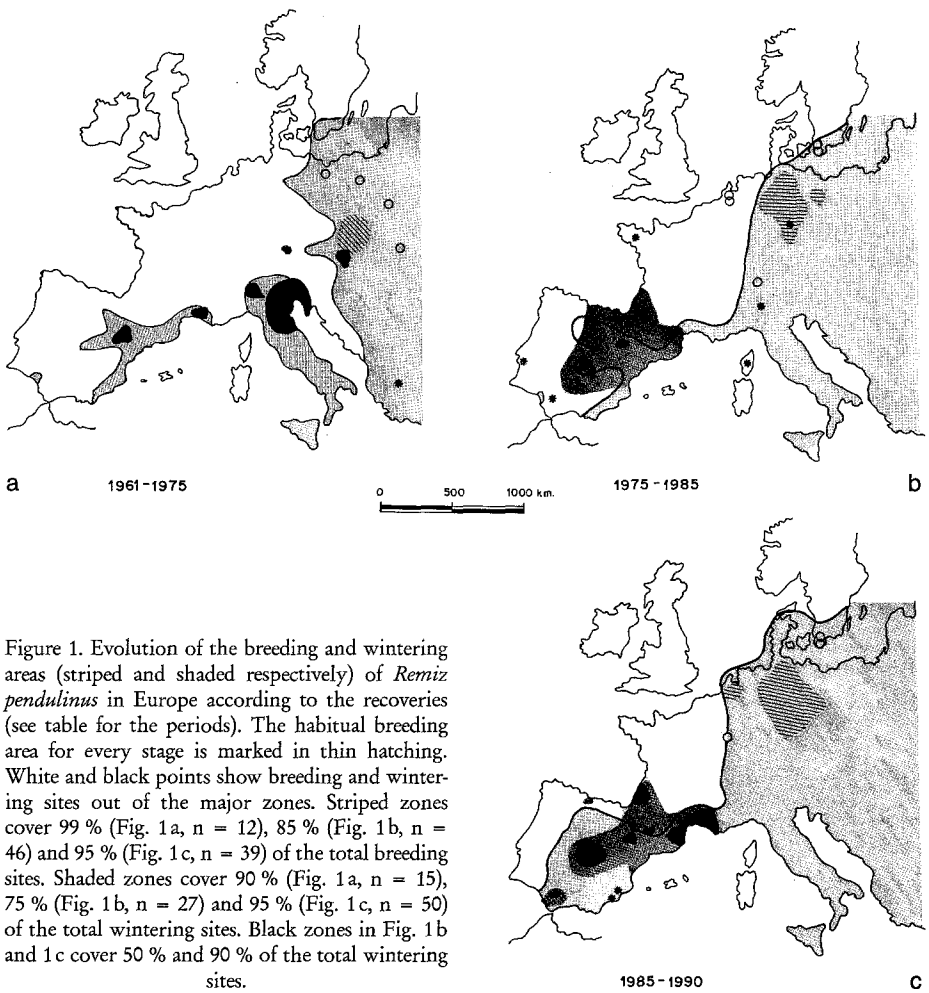

Figure 1. Evolution of the breeding and wintering areas (striped and shaded respectively) of *Remiz pendulinus* in Europe according to the recoveries (see table for the periods). The habitual breeding area for every stage is marked in thin hatching. White and black points show breeding and wintering sites out of the major zones. Striped zones cover 99 % (Fig. 1a, n = 12), 85 % (Fig. 1b, n = 46) and 95 % (Fig. 1c, n = 39) of the total breeding sites. Shaded zones cover 90 % (Fig. 1a, n = 15), 75 % (Fig. 1b, n = 27) and 95 % (Fig. 1c, n = 50) of the total wintering sites. Black zones in Fig. 1b and 1c cover 50 % and 90 % of the total wintering sites.

Similarly, the winter quarters in Europe moved to the west and southwest (Fig. 1). Until the early 60's, the wintering area lay south of the breeding sites, specially in the Neusiedler area (Austria) according to the recoveries (see FRANKE 1955; SCHÜZ & HAAS 1955).

During the next stage (Fig. 1a), which was a rest period in the expansion of *Remiz pendulinus* as a breeding species, there still remained winter quarters south of the breeding areas, but with such a strong tendency to shift westward that there was even a wintering focus in the Iberian peninsula (20 % recoveries in this stage, n = 15). The analysis of the dates of the records of the birds in this period is particularly interesting in relation to time, since the easternmost records date back to the early years of the period (Austria: 1962, 1966; Greece: 1968; Italy: 1965, 1967 and only one in 1972; southern France: 1974 and 1975; Spain: 1971, 1973 and 1974).

The shift of the winter quarters in these years (ca. 1500 km between the habitual wintering areas and the basin of Ebro, Spain) preceded the next expansion stage (1975—1985) of breeding in Europe (FLADE et al. 1986). During the stage 1975—1985, the winter quarters were almost exclusively in southern France and the Iberian peninsula (Fig. 1b).

A quantitative study (though biased, as every study on migration because of the different ringing effort in every region) shows that the rate of recovery in the Iberian peninsula increased from 20 % in the stage 1965—1975 (n = 15) to 74 % in this one (n = 27). This might have been caused by a higher ringing activity, but, in any case, DELIBES et al. (1980) and BASANTA (1974) point out that the amount of records in the season autumn—winter in central Spain increased considerably from 1972 on. Only 10 % out of the latter percentage (74 %, n = 27) can be ascribed to southwestern Spain.

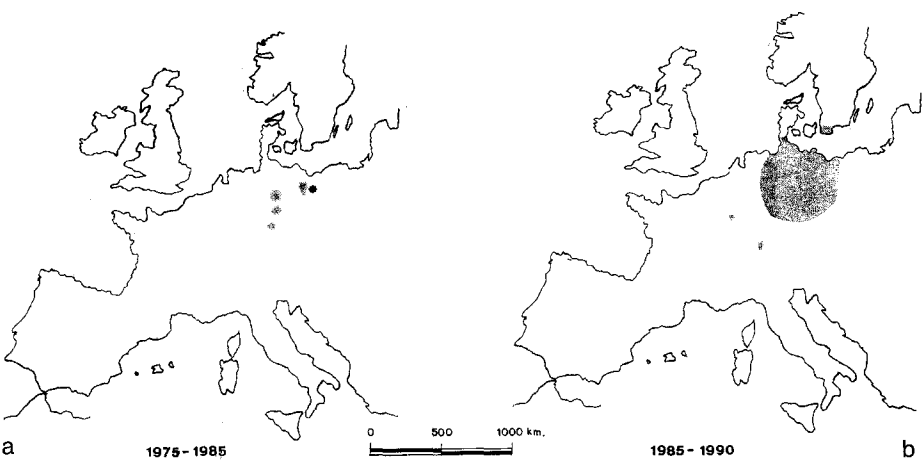

Figure 2. Evolution in the origin of the populations wintering in Spain. a. — Shaded zones cover 99 % (n = 12) of the sites. Black points belongs to the stage 1961—1975. b. — Shaded zones cover 99 % (n = 21) of the sites.

The southernmost recovery, dated at the end of this period, preceded the winter colonization in the following stage.

Furthermore, new winter quarters settled along the Atlantic coast of France and Spain (18.5 % of the recoveries, n = 27).

Short as it may have been, the last period (1985—1990) is particularly significant, as it firmly supported the wintering area in the Mediterranean coast of France (18 % of the recoveries, n = 50) and the furthest southwestern quarters in the Iberian peninsula (amounting to 18.18 % of the Iberian recoveries, n = 33). The Atlantic wintering areas increased only slightly during this period (20 % of the recoveries, n = 50).

3.2 Evolution of the origin of the population wintering in Spain

The evolution of the origin of these populations (Fig. 2) involves a geographical shift. The few data available make it impossible to detail the westward advance of the origin of the populations wintering in Spain, but the fact that the only recovery during 1961—1975 was also the easternmost available record leads us to assume the origin of most of the wintering individuals in Spain at that time. Actually, TRICOT (1967) suggested that part of the breeding population in Germany and Poland may spend the winter in southern France.

The major focus of origin of the birds wintering in Spain does not change in two successive periods: 1975—1985 and 1986—1990. Yet, it is important to note the records in southern Sweden (already colonized in the mid-sixties) during the latter period and, specially, two new populations further west of the central focus that involve a shift in the origin of the wintering populations; this shows, again, the westbound tendency in every stage of the biological cycle.

3.3 Analysis of the age of the recovered individuals

An analysis of the juvenile/adult rate in the recoveries of birds wintering in Spain shows that, as a rule, it is usually juveniles that occupy the new wintering areas. This can be learnt from both qualitative and quantitative data:

— The only individual wintering in Spain (furthest winterquarter) during the period 1961—1975 was a juvenile.

— During the next period (1975—1985) 24 birds were recovered in southern France and the Iberian peninsula. Of these, the only adult belonged to an old wintering area, while the available recoveries in new areas were two juveniles.

— The only recoveries for the same period in the new wintering areas in Atlantic France were 4 juveniles.

— During the period 1985—1990, the rate of wintering juveniles/adults was 2.12 : 1 (n = 25), the rate in the traditional areas being noticeably lower (1.14 : 1, n = 15) than in new ones (9 : 1, n = 10). These deviations were analyzed with Fisher's One-Tailed Exact Probability Test yielding marginally significant differences ($p = 0.065 < 0.1$) that suggest that it is mostly juveniles that appear in new winter quarters.

These results should be taken with certain reservations, since the significance of the test is affected by the greater number of recoveries in traditional areas and, on the other hand, only a low number of them are suitable for this analysis. SCHÖNFELD (1989) proved that greater populations of juveniles winter in recently colonized areas in the Iberian peninsula. Our data verify this tendency.

3.4 Return to previous winterquarters and expansion of the wintering area

The analysis of the data shows that in six cases birds remained in the same wintering locality the same wintering season.

Besides, 36 recoveries showed a tendency to return the same winter quarters in successive seasons; most of them (32) come from approximately the same coordinates where the individuals were originally ringed, with a maximum variation of 37 km. Nine recoveries extended over more than a single season (two seasons for seven of them, and three for the rest).

These data contrast with the two available instances of alternation of winter quarters (see also FRANZ in press).

The difficulties to calculate the age of individuals in winter lead to a shortage of data that makes it impossible to reliably analyze the information on the return to previous winter quarters in relation to age.

4. Discussion

The shift in the migration routes in 1961 (MARTENS 1965) triggered the wintering of *Remiz pendulinus* in southern France and Spain (ZINK 1981, FRANZ & THEISS 1985 and 1987, FLADE et al. 1986).

ZINK (1981) considered the northern part of the western Mediterranean regions to be the major wintering area for the populations from Central Europe; later on, FRANZ & THEISS (1987) extended that range a bit further south, reaching Andalusia. From then on, southern Spain has become in only a few years a customary winter quarter for these populations.

According to FLADE et al. (1986), the new route provided new areas to colonize. From the evolution of the data of autumn migration and breeding in immediately subsequent years, FLADE et al. concluded the existence of a steady alternation between waves of migration and colonization. Our paper confirms such relationship, and also an association between the creation of new migration routes and winter quarters, and the consequent expansion of the breeding area.

The analysis of the recoveries proves the shift in the winter quarters and, particularly, the westward routes of the Scandinavian and German populations for the autumn migration.

This process is extremely dynamic (FLADE et al. 1986), as we can see from new winter quarters (see Fig. 1), like those on the Atlantic French coast (DIEDERICH &

LAFONTAINE 1984, DIEDERICH 1985a and 1985b) and the northern Spanish coast, the latter never having been previously described.

However, this does not seem to affect the traditional route along the Mediterranean coast established in 1961: as ISENMANN (1987) pointed out (and our figures prove), an increase of birds wintering in southern and western France and an important flow reaching even further south can be noticed.

Even considering the increase in the wintering population in northern Italy since the early 80's (FLADE et al. 1986), the total evacuation from the traditional winter quarters in the Balkans (see Figure 1) is noticeable. There are few data from these regions, but we also know that *Remiz pendulinus* winters in Czechoslovakia only very sporadically (HUDEC 1983), even though there are migration routes through the Carpathians (TOPERCER, pers. comm.). Although the ringing effort in these countries may distort the results, we still think that the populations from Central Europe mostly move southwest in the continent for the winter.

On the other hand, the origin of the populations wintering in Spain changed too, moving noticeably westward in a short time as Fig. 2 shows especially with regard to both advanced focuses. As we have stated above, these focuses should be considered the prelude of a general tendency to increase in later years.

It seems, from our results on the age of the wintering populations, that juveniles pioneer the expansion (as BONHAM & ROBERTSON 1975 assumed for *Cettia cetti*) as they move south (and recently also west) for their migration and wintering.

KIENZELBACH & MARTENS (1964) associated long range migrations with juveniles: the higher the density of population in the breeding area, the further the migration reaches the following autumn and the more birds settle in these new areas.

FRANZ (in press) gives proof of changes in the migration routes and winter quarters; it cannot be guaranteed, therefore, that return to the same winter quarters is the rule. Yet, as FRANZ himself suggests, those birds that change their migration routes move along a specific migratory course.

A considerable body of evidence supports the notion that many migratory species return to the same place in successive winters (MOREAU 1972, HERRERA & RODRIGUEZ 1979, FINLAYSON 1980), just the same as our data show for *Remiz pendulinus*. Predictability of food availability in certain places might account for such behaviour.

Description of the expansive process

Figure 1 shows the chronological shift westward in the winter quarters and the shift in the breeding area one stage behind the former. Again, Figure 2 shows a shift in the breeding area of the populations wintering in Spain, i. e., the shift in the winter quarters is paralleled by another one in the breeding areas.

The results of the age of the individuals in new winter quarters may indicate a tendency of the juveniles of the species to lead the winter expansion. Actually,

KIENZELBACH & MARTENS (1964) and SCHÖNFELD (1989) associated breeding abundance with long range migration.

If, as it seems, the species keeps returning to the same winter quarters as a non-exclusive strategy, the whole process would entail a constant advance of the winter quarters (juveniles wintering further than the former generation and keeping a winter quarter to be surpassed by the next generation), which ultimately would mean an advance of the breeding areas in a process of interrelated phases.

Next, then, the relationship between the advance of the winter quarters and the breeding areas should be considered.

The whole process would apparently be a generalization of the process described by WÜST (1986) for the Valley of Main: part of the groups following the course of the river in their migration to the breeding areas in East Germany remained behind and colonized the Upper Main as they moved in a sort of counterdirection (see also FRANZ & THEISS 1983). According to our hypothesis, these individuals would be mainly juveniles; this is attested by SCHÖNFELD's (1989) proof that it is mostly juveniles that, since 1976, have enlarged the breeding range westwards in northern Germany (see Figs. 1a and 1b above), although some adults join them and re-settle in new areas (in fact, geographical links with the birthplace are, for FRANZ & THEISS, 1987, rather an exception). The juveniles, then, would winter farther than their elders.

Expansive strategies proper to the species, such as migration in the breeding season (FRANZ et al. 1987, FRANZ 1988), would also play a role in the expansion. The process is not general in the sense that not all juveniles should behave like this, but those that would, would consequently enlarge the breeding area through their wintering. Besides, as KIENZELBACH & MARTENS (1964) pointed out, the increase in the autumn migration is irregular and largely depends on the fluctuation of the breeding.

The complete verification of this process requires triple recoveries and is, therefore, difficult to carry out.

This paper, thus, shows the close relationship between breeding and wintering seasons for this species. We consider wintering to be key factor that first indicates the process of expansion. This process succesfully accounts for the expansion of *Remiz pendulinus* in the west, but not in the north (Sweden), where the strategies of springtime expansion may prove more important.

Although the ringing and recoveries data are an artefact and in spite of the consequences of the low number of recoveries available, we feel that the analysis of this information is an interesting contribution to the current knowledge of the expansion strategies of this species.

Summary

The migration and wintering of *Remiz pendulinus* in western Europe is updated by analyzing the recoveries available in EURING Data Bank until 1990. The settlement of new winter quarters, the origin of the populations wintering in the Iberian peninsula and the westward shift in the winter and breeding areas, the latter spreading one season slower than the former, are assessed. A process of expansion is suggested based on the association between migration,

wintering and the expansion of the breeding areas; this is supported by the parallelism between the advance and creation of new winter quarters and the advance of breeding areas: as juveniles apparently lead the winter expansion wintering farther than the former generation and as the species keeps returning to previous winter quarters, there is a continuous process of wintering expansion. The colonization of new breeding areas (mostly by juveniles) during the spring migration completes the interrelated process. The wintering, a key factor in the process, becomes, then, a hint of future expansion.

Zusammenfassung

Zug und Überwinterung der Beutelmeise in Westeuropa werden nach den Ringfunden der EURING Databank bis 1990 beschrieben. Im einzelnen lassen sich dadurch belegen: Besiedlung neuer Winterquartiere, die Herkunft der auf der Iberischen Halbinsel überwinternden Population und die Westausbreitung der Winterquartiere und Brutareale, letztere mit jeweils einem Jahr Verzögerung. Der Expansionsverlauf wird als Zusammenhang zwischen Zugverhalten, Überwinterung und der Ausdehnung des Brutareals interpretiert. Dies wird durch den parallelen Verlauf zwischen dem Vorrücken und der Wahl neuer Winterquartiere sowie der Ausweitung des Brutareals bestätigt: Jungvögel scheinen weiter zu wandern als die Vögel der vorhergehenden Generation. Da Winterquartiere im Folgejahr wieder aufgesucht werden, entsteht ein kontinuierlicher Prozeß der Ausweitung des Winterareals. Die Kolonisation neuer Brutgebiete (meist durch Einjährige) auf dem Rückzug im Frühjahr vervollständigt den in mehreren Phasen ablaufenden Prozeß. Das Überwinterungsgebiet als Schlüsselfaktor im Ausbreitungsvorgang liefert somit Hinweise auf weitere Arealausdehnung.

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