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Does the Willow Warbler, *Phylloscopus trochilus* (L.), belong to those species of birds fluctuating greatly in number.

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In a recently published article PYNNÖNEN (1948) established that during the summers of 1943 and 1944 the willow warbler occurred „in considerably larger numbers than previously" on the island Kukkosensaari comprising 38 ha and situated near the city of Joensuu in East Finland. The willow warbler density was at that time 84,2 brace/km^2. An estimate made on the same island in the summer of 1948 gave, however, as a result only 5,3 brace of willow warblers/km^2, so that the population of willow warblers had dropped to $^1/_{16}$ in the course of only a few years. PYNNÖNEN mentions in a supplement to his article that he had „noticed the willow warbler population in the summer of 1948 to be less numerous than usual, at least in certain places, in Central Finland also" (comp. also PYNNÖNEN 1949 and SOVINEN 1949).

An excellent occasion for a more detailed investigation of this highly interesting and far-reaching phenomenon of population dynamics (comp. SIIVONEN 1948 c) — according to MERIKALLIO (1946) the willow warbler is, besides, our commonest species of bird — was offered in the summer of 1949, when, in order to obtain records for the purpose of comparison, census work on small birds was added to the census work on game to be made at fixed times at certain so-called control stations of the Game Research Institute along fixed lines marked out in the ground (transects).

The census of small birds was carried out in mixed forests and spruce forests of the OMT- and the MT-types. The transects of each station were 15 km long (10 km at one station only) corresponding to 60 ha (40 ha).

The work was carried out according to detailed directions kindly given by Dr. E. Merikallio, and thus done in the same manner as in the censuses of the bird fauna made by him (Merikallio 1946) and Palmgren (1930) [1]). The censuses were made by ornithologists experienced in field work and particularly in the censusing of birds (Dr. E. J. Valovirta, T. A. Putkonen, M. A., T. Sovinen, M. A., T. Lampio, assistant, R. Tenovuo, teacher, as well as Messrs H. Suomus, M. Sovinen and P. Sovinen, students of zoology at the University). In the following only the results obtained from the nine stations of southern and central Finland will be dealt with, since these stations offer an opportunity for examining the occurrence of the willow warbler in the whole of South and Central Finland in addition to Merikallio's (1946) special area (the eastern half of South and Central Finland). The control stations to be noted are situated in the following places: Mynämäki, Helsinki, Lammi, *Imatra*, Ähtäri, *Leppävirta*, *Ilomantsi*, *Haapajärvi* and *Kuhmo*. The stations printed in italics give the best average picture of Merikallio's special investigation area. At these nine stations the bird fauna of the above-mentioned forests was estimated on a transect totalling 130 km, corresponding to 520 ha. The corresponding figures for the stations roughly corresponding to Merikallio's special investigation area, totalled 75 km and 300 ha. The crossbills have not been taken into consideration in the dominance values calculated on the basis of the results of the census; Palmgren (1930) has ignored them also.

According to these censuses the densities and dominances (brace/km^2 and $^0/_0$ of the whole bird fauna) of the willow warbler in the summer of 1949 in mixed and spruce forests of OMT- and MT-types at 9 stations in southern and central Finland were as follows:

	Dens.	Domin.		Dens.	Domin.		Dens.	Domin.
Mynämäki	0,0	0,0	Imatra	15,0	5,9	Ilomantsi	6,7	6,8
Helsinki	16,7	5,7	Ähtäri	6,7	6,3	Haapajärvi	3,3	2,9
Evo	3,3	2,1	Leppävirta	1,7	3,5	Kuhmo	0,0	0,0

The willow warbler density as well as the dominance were thus exceptionally low in the summer of 1949 all through Southern and Central Finland, the density fluctuating at the different stations from 0,0 to 16,7 brace/km^2 and the dominance from 0,0 to 6,8 $^0/_0$. The corresponding values in the whole of South and Central Finland were on an average 6,2 brace/km^2 and 4,1 $^0/_0$ and in the eastern half of South and Central Finland on an average 5,3 brace/km^2 and 4,3 $^0/_0$. The corresponding values obtained by

[1]) In order to obtain more exact results a transect breadth of 40 m is, however, used in the census series now started. In the previous investigations it has been 50 m.

PYNNÖNEN (1948) in the summer of 1948 on the island Kukkosensaari in East Finland were 5,3 brace/km² (and 3—4 %?), in other words of the same magnitude.

These figures differ sharply from those obtained by PYNNÖNEN (op. c.) in the summers of 1943 and 1944, viz. 84,2 brace/km² and 32,0 %. Nor are these figures isolated. This is seen from the extensive census of the bird fauna made by MERIKALLIO (1946) in the eastern half of South and Central Finland.

Of the extensive census of the bird fauna in different parts of South and Central Finland executed by MERIKALLIO 1941—43 and 45, principally in 1942—43 we shall note only his census made in 1942 in the eastern half of South and Central Finland in mixed forests of OMT-type as well as in mixed and spruce forests of MT-type, since these forests correspond most nearly to just those forests where the census work was done in the summer of 1949. In the following we shall make use of the mean values obtained by MERIKALLIO for these types. The transects used by him in these forests totalled 29 km, corresponding to 143 ha. Since MERIKALLIO has also taken the crossbills into account, his dominance values are slightly smaller than those in the censuses made by PALMGREN (1930) and in those just carried out.

In 1942 MERIKALLIO obtained the following density and dominance values for the willow warbler in mixed and spruce forests of OMT- and MT-types in the eastern half of South and Central Finland:

	Dens.	Domin.		Dens.	Domin.
OMT mixed forest	69,5	29,3	MT spruce forests	24,0	18,0
MT „ „	46,2	24,5	Above mentioned forests on an avarage	46,6	23,9

If these values are compared to the corresponding values now obtained, the conclusion must be drawn that a very considerable change in the density of the willow warbler population in the eastern half of South and Central Finland — and also in the whole of South and Central Finland [1]) — has occurred within a few

[1]) The density and dominance values of the willow warbler were high in all the other sectors investigated by MERIKALLIO (also in those of West Finland) except in the most north-easterly one of Suomussalmi (the census was made there in 1942—43 and 45) and in the most easterly ones of the Karelian Border and East Karelia (in 1943; comp. also SOVERI 1942), where the willow warbler densities were 6,4, 7,9 and 3,1 brace/km², corresponding to the dominance 9,1, 11,0 and 5,8 %. Whether there was a minimum of willow warblers in the frontier zones in these years, or if these values reflect a local peak, or other value, cannot be decided since records for comparison are lacking.

years' time; the density in the forests represented in the eastern half of South and Central Finland has decreased to $^1/_9$ and the dominance to $^1/_5$—$^1/_6$. The difference is considerable even if the values now obtained are compared only to those obtained by MERIKALLIO in 1942 in a forest less suited (spruce forest of the MT-type) to the willow warbler. The corresponding proportions are then $^1/_4$—$^1/_5$ and $^1/_4$.

On the other hand we can state that the present scarcity of willow warblers is not unique in this country, but that such a phenomenon is known also from the summer of 1928. This is seen from the extensive census carried out in that year by PALMGREN (1930) in the eastern half of South Finland.

These investigations took place at Padasjoki, Sortavala and Suistamo, and should represent at least approximately the average in the eastern half of South Finland as well as the most southern part of MERIKALLIO's special investigation area. The transects are situated in mixed, spruce and pine, and spruce forests of OMT-type as well as in mixed, and spruce and pine forest of MT-type. The structure of the forests thus corresponds in this case also to the above-mentioned forests of MERIKALLIO, and to those forests in which the present census was made. Mean values obtained for OMT- and MT-types will be used in the following. In the forest of this structure PALMGREN had transects totalling 37 km, corresponding to 187 ha. This as well as the two previous censuses must thus be considered so extensive that the deficiencies of the method of estimation can be considered to be evened out in them.

PALMGREN likewise obtained in 1928 an average willow warbler density of 6,1 brace/km^2 and an average dominance of 4,3 % in mixed and spruce forests of OMT- and MT-types in the eastern half of South Finland — astonishingly similar values to those obtained in the census just made. The census carried out by the writer (SIIVONEN 1936) at Pieksämäki in Central Finland (the area is situated near the middle of MERIKALLIO's special investigation area) in the same year in a certain mixed forest of OMT-type rich in birds (willow warbler dominance 11,4 %, MERIKALLIO's corresponding value in 1942 being 29,3 %), seems to show that this scarcity was also an extensive one in this country.

The years 1934—36 seem in their turn to be characterized by a rather high willow warbler density (comp. e. g. SIIVONEN 1936, KALELA 1938, PALMGREN 1942, PUTKONEN 1942 and PYNNÖNEN 1943). Since the willow warbler density and dominance were low, none-

the-less, in certain other areas (e. g. SOVERI 1940 for 1934 and 35, and VÄLIKANGAS 1937 for 1935), one cannot obtain as clear a picture of this period as in the former cases in spite of the numerous investigations of the time. The difficulty is increased by the fact that it is impossible on the basis of these local investigations to make comparisons in forests of the same structure, as in the former cases. From other years there exist only sporadic, local census investigations of the bird fauna on the basis of which no generalisations comparable with the previous ones can be made.

The fluctuations in the willow warbler population, however, are evident from the foregoing. Neither can they be considered as isolated phenomena. If one compares, for instance, the results obtained from roughly the eastern half of South and Central Finland with MERIKALLIO's (1946) results obtained from the same areas in 1942, one finds that in the summer of 1949 the populations of all the other species (except the chaffinch) dominant in forests of OMT- and MT-types (comp. MERIKALLIO op. c., percentage of dominance not less than 5) — including the migratory birds (comp. ROWAN 1931) — was also remarkably lower than in the summer of 1942 (the density- and dominance coefficients [1]) in parentheses): *Anthus trivialis* (5,5 and 3,3), *Parus atricapillus* (2,3 and 1,2) and *Sylvia borin* (13,1 and 7,1) as well as for example *Phylloscopus sibilatrix* (2,4 and 1,3). The corresponding coefficients for the willow warbler are 8,8 and 5,6. The proportions are the same, if the density and dominance values obtained by PALMGREN (1930) in 1928 for the same types in the eastern half of South Finland are compared to those of MERIKALLIO for 1942 mentioned above: in 1928 the density of all the dominant species was also considerably smaller than in 1942 (the density- and dominance coefficients in parentheses): *Anthus trivialis* (2,6 and 1,6), *Parus atricapillus* (8,0 and 4,3), *Phylloscopus trochilus* (7,6 and 5,6) and *Sylvia borin* (8,2 and 4,4).

In examining these values, nevertheless, it should be noted that MERIKALLIO's density and dominance values for species other than the willow warbler, are generally taken only from the OMT- and MT-types (the mean values obtained by MERIKALLIO for both these types are noted as such), of which about $^1/_3$ are deciduous woods and about $^1/_{12}$ pine forests. Since they thus consist, however, of about 60 % of mixed and spruce forests belonging to the OMT- and MT-types from which the above-mentioned values for the

[1]) MERIKALLIO's value divided by the value now obtained.

willow warbler are obtained, such large coefficients as these cannot be explained only as a result of the concurrence of types of another structure, but each of these coefficients probably mainly reflects mere fluctuations in the population. The dominance values: 30,1, 35,8 and 26,9 % obtained by MERIKALLIO e. g. for willow warbler in deciduous forests of OMT- and MT-types and in pine forests of MT-type respectively also indicate this. His corresponding mean dominance value in mixed and in spruce forests (23,9 %) is $^4/_5$, $^2/_3$ and $^9/_{10}$ respectively of the above-mentioned values, in other words at most only $^1/_3$ smaller than they. The dominance of *Anthus trivialis* is according to MERIKALLIO the same in needle tree and deciduous forests. The ratio of the dominance values of *Parus atricapillus* in needle tree and deciduous forests is similarly $^3/_4$ only. Of all the above-mentioned species, only for *Sylvia borin* is this ratio considerable ($^1/_{12}$).

The gallinaceous birds had a peak year in 1942 and a minimum year in 1949 and in 1928 (comp. SIIVONEN 1948 a, b, and c, and 1949 a). Other peak years of the gallinaceous birds in the 1940's occurred in 1945 and 1948 (comp. SIIVONEN op. c.). These fluctuations in the numbers of the gallinaceous birds belong according to the present opinion to the sphere of short-term fluctuations in numbers. It is thus possible that the considerable fluctuations in the population of willow warbler and of other species referred to may also be a similar phenomenon (comp. SIIVONEN 1948 c), although, for lack of detailed and fully comparable series of observations, it would be too bold draw this conclusion, at least for the present.

The populations of some other species, e. g. *Carduelis spinus, Parus cristatus, Aegithalos caudatus, Regulus regulus, Muscicapa striata, Phylloscopus collybita, Turdus ericetorum* and *Erithacus rubecula*, has been according to the census work made in 1949 considerably higher than according to MERIKALLIO (1946) in 1942. In 1949 *Regulus regulus, Turdus ericetorum* and *Muscicapa striata* were even dominant species in the forests referred to above in the eastern half of South and Central Finland. *Phylloscopus collybita* and *Erithacus rubecula* were also dominants in the same forests in the eastern half of South Finland in 1928 (PALMGREN 1930).

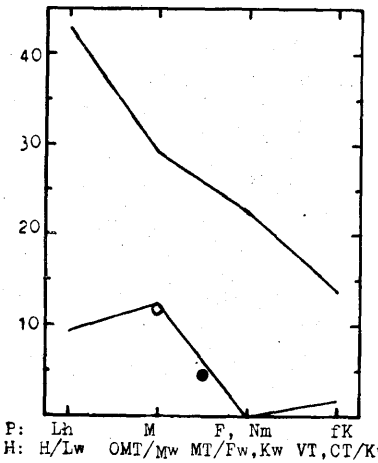
Even these differences, obviously applying at least to the eastern half of South and Central Finland, cannot be interpreted — at any rate entirely — as due to the different structure of the transects. Thus MERIKALLIO counted on all his transects of the types OMT and MT (totalling 49 km = 245 ha) only 6 brace of *Turdus ericetorum*, 4 brace of *Phylloscopus collybita*, and 2 brace ot *Regulus regulus* and *Erithacus rubecula* each, though 29 km (= 143 ha) of these transects were of mixed or spruce forest. Even if all these brace had been found in such parts of the transects, the density of each species would nevertheless remain below 5 brace/km² (1.2 — 4.2 brace) corresponding to dominance values 0.7 — 2.2 %. As the above species are

all more or less typical species of spruce forests, it may be mentioned that the density of *Muscicapa striata*, a species that has increased in numbers too, is according to MERIKALLIO 1.9 times higher in deciduous forests than in spruce forests; the corresponding dominance coefficient is 1.2.

It seems thus that these species also fluctuate rather greatly, even if they do not coincide with the fluctuations of the willow warbler. Since the above detailed censuses have given the following total bird densities in the described cover types: 1928 124, 1942 185, and 1949 122 brace/km², it seems to be possible that the year 1942 has been a general peak year and the years 1928 and 1949 on the other hand, general years of decline, as in the gallinaceous birds (comp. above). That is to say, the fluctuations of most species, even if not always quite simultaneous, only slightly overlapped oneanother (comp. also SIIVONEN 1949 b). It is to be hoped that this, like many other so far open questions, will receive further elucidation, when the present census series have been continued for some years more.

In diagr. 1 the dominance values of the willow warbler in different forest types during the declines of 1928 and 1949, and the peak of 1942 are compared. The values given there, it is true, do not originate from quite the same districts and perhaps not even from forest types of quite the same structure. The diagram is, however, so clear that it is obvious from it that in some cases the willow warbler may during the declines be quite absent in those types least favoured by it (spruce, spruce and pine, and pine forests). During the peak its occurrence is on the other hand, remarkably more equally divided between all the different forest types. The dominance may then reach, even in types most unfavourable for the willow warbler, values of the same magnitude as in the best types during the decline. This fact cannot be interpreted in an other way than that the species so-to-say retires to its optimal environment during the decline (the willow warbler to deciduous or mixed forests) and spreads out during the peak to types even less favoured.

The extreme values for these species should not, properly speaking, be communicated merely from three isolated years (1928, 1942 and 1949, comp. SIIVONEN 1948 c). Many of these coefficients are, however, a great deal larger than the coefficients presented for the gallinaceous birds, which have in fact been calculated from the values of numerous successive years i. e. from the values of the absolute minima and maxima of the fluctuations in numbers (comp. SIIVONEN 1948 b, and c). As a partial reason at least for the difference one might suggest that the coefficients presented for the



Diagr. 1. The dominance (%) of the willow warbler in the different forest types (for abbreviations and descriptions of the types, P:, see PALMGREN 1930 and M:, see MERIKALLIO 1946) during the declines of 1928 and 1949 (the lower curve at Åland in South-West Finland in 1928, comp. PALMGREN op. c.; ● in the eastern half of South Finland in 1928, comp. PALMGREN op. c., and in the eastern half of South and Central Finland in 1949 according to the present study; o at Pieksämäki in the eastern half of Central Finland in 1928, comp. SIIVONEN 1936) as well as during the peak of 1942 (the upper curve in the eastern half of South and Central Finland, comp. MERIKALLIO op. c.).

gallinaceous birds are based on statistics concerning the catch. Since it can be presupposed that the levy of the fowl at peak time has been slight compared to the total population and has risen greatly relatively at the time of the minima, the coefficients presented for the fowl do not necessarily mirror the real steepness of the fluctuations in numbers but only indicate them in part.

A couple of explanations have been advanced to account for different willow warbler densities. According to MERIKALLIO (1946) the notably low willow warbler densities and dominances established by some other investigators „sind wohl unzweifelhaft auf das Konto unvorteilhafter Biotopverhältnisse zu führen". PYNNÖNEN (1948), on the other hand, points out the possibility that the reason for the remarkably great density of the willow warbler which he found in 1943—44 was „that the quantity of branches, leaves and needles of the trees increases with the growth of the woods. This has caused an increase of the insect fauna, and thus possibilities of sustenance for a greater number of the species in question have ensued". This, however, is contradictory to the fact that the willow warbler population on the selfsame island Kukkosensaari — as has been shown above — had dropped in the summer of 1948 almost to extinction without the forests having (according to Pynnönen) changed appreciably during these years. These explanations, with PYNNÖNEN'S opinion, presented in the same paper, that the great fluctuations in numbers of the populations of fieldfare and redwing

would be „dependent on the degree to which these birds were allowed to hatch in peace", etc. as well as all the very varied opinions suggested by shooting experts for the reasons for the scarcity of game from time to time (comp. e. g. HASTINGS 1948) do not, however, suffice, as is seen even from what has been said above alone, to prevent one at all from regarding these phenomena as connected in any way with the very sphere of the short-term fluctuations in numbers.

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