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Quantitative bird survey and the short-term fluctuations in numbers.

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The methods used in the quantitative bird surveys energetically carried on during a couple of decades particularly in Finland, as well as the percentage of error with the different methods have attracted much attention (comp. e. g. PALMGREN 1930, MERIKALLIO 1946 and NORDBERG 1947). Thereby, however, the accuracy of the survey work itself has been touched upon almost exclusively. The explanations concerning the possibility of using the obtained values for the purpose of generalization for different years as well as for different areas have, on the contrary, been restricted to very little. The only investigation, in which attention has been paid also to this side is the above mentioned by PALMGREN (1930). He did, in fact, execute linear surveys also along the same survey lines during the summers of 1926 and 1927 using the same method. He came (p. 127—129) to the following conclusions:

„. . . . . . die Zusammenzetzung der Fauna vom einen Jahr zum anderen ziemlich konstant ist . . . . . . Die Variation liegt . . . . . . wenigstens für meine Werte meistens innerhalb der Fehlergrenzen; . . . . . . und daher ist es schwer, einen bestimmten ziffermässigen Ausdruck für dieselbe (oscillation) zu finden. Ein Beispiel einer Jahresvariation, das sogar auf Grund des relativ knappen Materials, das ich jetz vorlegen kann, einen unzweideutigen, ziffermässigen Ausdruck erhält, bietet der Waldlaubsänger *(Phylloscopus sibilatrix)* . . . . Der Vergleich der Prozentzahlen von 1926 und 1927 für Laubwiesen vom SaT beleuchtet indessen einen Umstand, der auf die Zuverlässigkeit der Prozentzahlen einwirkt . . . . . . Der Krammetsvogel *(Turdus pilaris)* hat in den verschiedenen Sommern sehr ungleiche Prozentzahlen, 13.9 bzw. 1.3; der Differenz entspricht jedoch sicher kein so grosser Abundanzunterschied zwischen den beiden Sommern, sondern die Variation beruht auf dem kolonienweisen Hecken des Vogels . . . .“

PALMGREN (op. c.) thus considers these differences mostly as errors in the survey work. In view of the fieldfare he also emphasizes, how the colony bird from the point of view of the method of quantitative bird surveys to a certain extent corresponds to species of birds of a very sparse population, whose quantitative estimation requires wide areas.

Also MERIKALLIO (1946 p. 20) comes to similar results in view of the values of the different years, stating in short: „dass die jährlichen Veränderungen sich .... gleichmässig abgespielt haben."

The extensive and detailed primary records of both these investigations, nevertheless, seem to indicate that the methodic side of the quantitative bird surveys had been left without sufficient attention in view of this circumstance, upon which above all the very slight knowledge of the short-term fluctuations in numbers of small birds may have had an influence. The records mentioned above seem, however, to give valuable possibilities for explaining this problem also. This is seen from the following comparisons, which are based on the primary material of the proper investigations.

In 1926 and 1927 PALMGREN (1930) made surveys of 29 experimental areas. They comprise rather objectively all the principal forest types of Ahvenanmaa. The area of the survey lines totalled 355 ha. In 1926 the number of pairs amounted to 667 and in 1927 to 540, in other words, the value of 1927 was 81.0 $^0/_0$ of the value of the preceding year, and that of 1926 123.5 $^0/_0$ of the value of the following one. They consequently show a clearly declining tendency, the multiplier of the sinking edge (the sinking multiplier $\times$ the value of 1927 = the value of 1926) being 1.24. The corresponding multiplier in view of sporadic species is generally even greater. This depends on one part of the species simultaneously showing a rise and another part on the other hand a drop, which circumstance tends to even the above mentioned average multiplier for all the species. The multipliers of the sinking- and rising curves of the different species (the rising multiplier $\times$ the value of 1926 = the value of 1927) are seen from the following table. In the table only those species are noted of which a total of at least 5 pairs were found in the lines during the one year or the other.

Decreasing species (sinking multiplier)		***Increasing species*** (rising multiplier)	
Sylvia communis	5.0	*Phylloscopus sibilatrix*	7.0
Turdus pilaris	2.7	*Dryobates minor*	5.0
Phoenicurus phoenicurus	2.5	*Pyrrhula pyrrhula*	4.0
Iynx torquilla	2.5	*Parus major*	2.0
Sturnus vulgaris	2.3	*Dryobates major*	2.0
Turdus musicus	1.7	*Scolopax rusticola*	1.8
Parus atricapillus	1.6	*Columba palumbus*	1.5
Certhia familiaris	1.5	*Parus caeruleus*	1.4
Turdus ericetorum	1.5	*Lyrurus tetrix*	1.4
Sylvia borin	1.4	*Sylvia atricapilla*	1.2
Fringilla coelebs	1.3		
Regulus regulus	1.3		
Turdus merula	1.3	***Species, whose stock stayed ± the same***	
Corvus cornix	1.2		
Carduelis spinus	1.2		
Parus ater	1.1	*Emberiza citrinella*	
Muscicapa striata	1.1	*Muscicapa hypoleuca*	
Phylloscopus collybita	1.1	*Phylloscopus trochilus*	

From the above it is seen that several species during the said period were characterized by a clear decline of the stock. The stock decreased in fact for 15 species by not less than 20 %. Another clear group is formed by those (9) species, whose stock increased by not less than 40 %. The stock of 7 of the species had changed between these limits, passing from 1926 to 1927. The changes in the stock were consequently nôt less than 50 % for more than half of the species. They were besides not less than 100 % for $^1/_3$ of the species.

It is interesting to note that systematical totalities are comprised in both these groups. Thus e. g. the thrushes belong to the decreasing species. The same can be said about the genus *Sylvia* except *S. atricapilla* (according to the same records *S. curruca* also shows a decrease). Woodpeckers in their turn belong to the most clearly increasing species (the same applies also to *Dryocopus martius*). To this group thus belong also the pigeons (also *Columba oenas*), the waders (also *Tringa ochropus*) as well as *Lyrurus tetrix*. The titmouses for instance are divided among both groups.

Changes in the stock of such a considerable extent during two consecutive years clearly mark also the dominant values. This is seen by the following table in which the dominant species of a few forest types (dominance > 5 %) are expressed according to surveys executed in 1926 and 1927 (the dominant species characteristic for either year are printed in heavy type):

Type Sanicula, parkland (survey lines 2 and 3; total area 25 ha):

1926:		1927:	
Fringilla coelebs	23.9	*Fringilla coelebs*	31.1
Turdus pilaris	20.9	*Muscicapa striata*	8.9
Muscicapa striata	8.9	*Phylloscopus trochilus*	8.9
Phylloscopus trochilus	7.4		
Sylvia communis	7.4		
Turdus musicus	6.0		

Type Sanicula, grove of deciduous trees (survey lines 1, 4, 8—11, 15 and 16; total area 39 ha):

1926:		1927:	
Fringilla coelebs	25.3	*Fringilla coelebs*	19.8
Sylvia borin	12.0	*Sylvia borin*	9.1
Phylloscopus trochilus	9.8	*Phylloscopus trochilus*	7.4
Turdus pilaris	7.7	***Muscicapa hypoleuca***	6.6
Sturnus vulgaris	6.3		

Type Sanicula, mixed forest (survey lines 1, 4, 6 and 8; total area 23 ha):

1926:		1927:	
Fringilla coelebs	24.7	*Fringilla coelebs*	25.7
Phylloscopus trochilus	7.5	*Phylloscopus trochilus*	10.0
Sylvia borin	7.5	***Phylloscopus sibilatrix***	5.7
Parus atricapillus	6.4	*Sylvia borin*	5.7
Turdus ericetorum	6.4	***Sylvia atricapilla***	5.7
T. musicus	6.4	*Turdus merula*	5.7
Muscicapa striata	5.4	*Erithacus rubecula*	5.7
Turdus merula	5.4		
Erithacus rubecula	5.4		

Type Oxalis-Myrtillus, spruce forest (survey lines 1—6, total area 89 ha):

1926:		1927:	
Fringilla coelebs	37.2	*Fringilla coelebs*	32.8
Regulus regulus	11.1	*Regulus regulus*	11.2
Turdus ericetorum	7.8	*Erithacus rubecula*	8.8
Parus atricapillus	7.2	*Parus ater*	8.0
Erithacus rubecula	6.5	***Turdus ericetorum***	7.2
Parus ater	5.2		

Type Oxalis-Myrtillus, clearing (survey lines 1—3, total area 90 ha):

1926:		1927:	
Fringilla coelebs	32.2	*Fringilla coelebs*	28.4
Regulus regulus	10.3	*Regulus regulus*	9.0
Phylloscopus trochilus	6.9	*Phylloscopus trochilus*	9.0
Turdus ericetorum	6.9	*Carduelis spinus*	6.0
Carduelis spinus	5.8		
Parus atricapillus	5.8		

These comparisons point quite in the same direction as the preceding ones of the abundance values. We can namely state as a striking charactiristic that the decrease of the fieldfare stock with the parkland of the type Sanicula passing from 1926 to 1927 has not been any separate phenomenon, but the same has touched the fieldfares also in other types, although not so sharply. It has thus touched other thrushes, northern willow-titmouse, white-throat, starling etc. Similarly the increase of the *Phylloscopus sibilatrix*-stock during the same time probably could not be considered exclusively separate nor a sequence of an accident caused by the method employed.

If we examine the order of dominance of the different species during the two years, we can establish that the order of the most dominating three species has been the same in two cases, that of the most dominating two species have also been the same in two cases, while in one case only the most dominating species has been the same each year. With three other types, for which the corresponding surveys have also been made, two have only the most dominating species the same, while with one, in the grove-like wet spruce-hardwoods, not even that was the same.

These types and their 2 most dominant species in 1926 and 1927 were as follows:

Type Sanicula, pasture (survey lines 3, 4, 6 and 10; total area **21** ha):

1926:		1927:	
Fringilla coelebs	26.4	*Fringilla coelebs*	27.6
Sturnus vulgaris	9.6	*Muscicapa striata*	10.5

Pine forest growing on rock (survey line 2, area 60 ha):

1926:		1927:	
Fringilla coelebs	22.2	*Fringilla coelebs*	27.8
Anthus trivialis	11.1	*Muscicapa striata*	17.6

Grove-like wet spruce-hardwoods (survey line 3; area 8 ha):

1926:		1927:	
Fringilla coelebs	16.7	*Phylloscopus trochilus*	22.2
Phylloscopus trochilus and 2 other species	11.1	*Fringilla coelebs* and 2 other species	11.1

As average abundance- (pairs/km^2) and dominance-values ($^0/_0$) of all these experimental areas during both these years with the five uppermost species we obtain the following:

	Abundance		Dominance	
	1926:	1927:	1926:	1927:
Fringilla coelebs	53.0	40.5	28.2	26.6
Phylloscopus trochilus	10.7	10.7	5.7	7.0
Turdus pilaris	9.0	3.4	4.8	2.2
Parus atricapillus	8.8	5.4	4.7	3,5
Regulus regulus	8.8	6.5	4.7	4.3

The extensive primary material of MERIKALLIO (1946) offers thus many interesting parallels deserving attention. He has executed linear surveys in southern and central Finland up to lat. 66° N. The survey materials have been arranged by sectors: Turku-, Viipuri-, Vaasa-, Joensuu-, Soviet-Carelia-, Oulu- and Suomussalmi-sectors. In these, with the exception of the Vaasa- and Soviet-Carelia-sectors, he has executed surveys during 2—3 different years. Each year the surveys have comprised many habitat-types characteristic for each sector, although the principal weight has been for the mutual comparison of the values of several years onesided in certain cases (e. g. in Suomussalmi-sector). The surveys during the different years have been made on different survey lines, which have, besides, been of different length. The comparisons below will first be made on the basis of dominance values from all the records of each sector:

Turku-sector:

1941 (total area 60 ha):		1942 (total area 20 ha):		1943 (total area 110 ha):	
Fringilla coelebs	23.9	*Fringilla coelebs*	18.4	*Fringilla coelebs*	14.3
Phylloscopus troch.	17.7	*Phylloscopus troch.*	15.8	*Phylloscopus troch.*	13.8
Sylvia borin	5.3	*Loxia curvirostra*	13.5	*Emberiza citrinella*	8.0
		Parus cristatus	7.9	*Sylvia communis*	5.3
		P. atricapillus	7.1		
		Emberiza citrinella	5.3		
		Muscicapa striata	5.3		
		Oenanthe oenanthe	5.3		

Viipuri-sector:

1941 (total area 190 ha):		1942 (total area 80 ha):		1943 (total area 20 ha):	
Phylloscopus troch.	23.8	*Phylloscopus troch.*	28.0	*Phylloscopus troch.*	16.2
Fringilla coelebs . .	19.1	*Fringilla coelebs* . .	21.6	*Fringilla coelebs* . .	13.3
		Parus atricapillus .	8.9	*Anthus trivialis* . . .	13.3
		Sylvia borin	7.0	*Parus atricapillus* .	10.0
		Muscicapa striata .	6.4	*Sylvia borin*	10.0
		Anthus trivialis . .	5.7		

Joensuu-sector:

1941 (total area 323 ha):		1943 (total area 140 ha):	
Phylloscopus trochilus	25.5	*Fringilla coelebs*	27.3
Fringilla coelebs	22.6	*Phylloscopus trochilus*	11.1
Anthus trivialis	6.1	*Anthus trivialis*	11.1
Parus atricapillus	5.5	*Parus aricapillus*	7.1
		Loxia curvirostra	6.1
		Tetrastes bonasia	6.1

Oulu-sector:

1943 (total area 70 ha):		1945 (total area 120 ha):	
Phylloscopus trochilus	44.0	*Phylloscopus trochilus*	19.8
Parus atricapillus	15.2	*Fringilla coelebs*	17.9
Fringilla coelebs	9.1	*Anthus trivialis*	9.9
Anthus trivialis	6.1	*Parus atricapillus*	6.3
Emberiza rustica	6.1		

Suomussalmi-sector:

1942 (total area 60 ha):		1943 (total area 20 ha):		1945 (total area 60 ha):	
Fringilla coelebs . . .	14.0	*Parus atricapillus* .	25.0	*Phoenicurus ph.* . .	18.9
Phylloscopus troch.	12.0	*Muscicapa striata* .	16.7	*Anthus trivialis* . .	10.8
Loxia curvirostra . .	8.0	*Fringilla coelebs* . .	8.3	*Phylloscopus troch.*	8.1
Hirundo rustica . . .	8.0	*Anthus trivialis* . . .	8.3	*Lyrurus tetrix* . . .	8.1
Parus atricapillus .	6.0			*Muscicapa striata* .	5.4
Anthus trivialis . . .	6.0			*Turdus ericetorum*	5.4
Phoenicurus ph. . .	6.0			*Cractes infaustus* .	5.4
Passer domesticus .	6.0				
Emberiza rustica . .	6.0				

In the sectors of Turku and Viipuri, thus in the most southern parts of Finland, two of the species were the most dominant ones every year; in the Oulu-sector only one, the most dominant species, retained its dominance in both the years; in the Joensuu-sector not even one of the species was the most dominant in two years; and in the Suomussalmi-sector a different species was the most dominant one each year without being dominant at all in one of the cases.

From this it is also seen how accidental the picture obtained of the dominant species of the areas and their mutual preponderance can be in many a case, when the results of surveys from different areas in different years are compared with one another. This is also elucidated by the following table. In this a parallel is drawn, where the composition of the dominant groups is different in spite of the same methods, but in both cases the groups are found to be astonishingly similar from the south of Finland up to the borders of Lapland (the species common in each case for either area are printed in heavy type; the areas in the order S→N):

Viipuri 1943:		Vaasa 1943 (area 100 ha):		Joensuu 1942:		Oulu 1945:	
Phyll. troch.	16.2	***Phyll. troch.***	26.1	***Phyll. troch.***	25.5	***Phyll. troch.***	19.8
Fringilla coel.	13.3	***Fringilla coel.***	15.0	***Fringilla coel.***	22.6	***Fringilla coel.***	17.9
Anthus triv.	13.3	***Parus atricap.***	7.8	***Anthus triv.***	6.1	***Anthus triv.***	9.9
Parus atricap.	10.0	***Anthus triv.***	5.0	***Parus atricap***	5.5	***Parus atricap.***	6.3
Sylvia borin	10.0						

(Ahvenanmaa 1927:)		Turku 1942:		Joensuu 1943:		Suomussalmi 1942:	
Fringilla coel.	26.6	***Fringilla coel.***	18.4	***Fringilla coel.***	27.3	***Fringilla coel.***	14.0
Phyll. troch.	7.0	***Phyll. troch.***	15.8	***Phyll. troch.***	11.1	***Phyll. troch.***	12.0
		Loxia curvir.	13.5	*Anthus triv.*	11.1	***Loxia curvir.***	8.0
		Parus crist.	7.9	***Parus atricap.***	7.1	*Hirundo rust.*	8.0
		Parus atricap.	7.1	***Loxia curvir.***	6.1	***Parus atricap.***	6.0
		Muscicapa str.	5.3	***Tetrastes bon.***	6.1	*Anthus triv.*	6.0
		Emberiza citr.	5.8			*Phoenic. ph.*	6.0
		Oenanthe oe.	5.3			*Passer dom.*	6.0
						Emberiza rust.	6.0

This is interesting also, since it has been explained on the basis of quantitative bird surveys, and to a great extent particularly through the abovementioned surveys, that the most dominant species of birds change substantially in the regions mentioned when moving from south to north (south-west to north-east; comp. e. g. PALMGREN 1942 and MERIKALLIO 1946).

As a third object of comparison of the quantitative bird surveys executed in Finland during different years in the same area the surveys made by MERIKALLIO (1939) on the Heinäsaaret islands in Petsamo (area 278 ha) on the shores of the Arctic Ocean are presented. These surveys have been made in 1921, 1922, 1923, 1928, 1930, 1931 and 1933. Since the surveys have been considerably more deficient in certain years than in others, the years 1921, 1923, and 1928 are chosen from them as years of comparison. Even in this case „some tens“ are mentioned as figure for *Anthus pratensis* in 1921. It has been corrected to 40. The dominant species in the different years have been the following:

1921:		1923:		1928:	
Calcarius lapponicus	42.9	*Anthus spinoletta* . .	68.6	*Anthus pratensis* . .	46.8
Anthus spinoletta . .	42.9	*Anthus pratensis* . .	17.1	*Calcarius lapponicus*	20.3
				Anthus spinoletta . .	7.8
				Anthus rufogularis .	6.2
				Motacilla alba	6.2

In each of these years a different species has thus been the most dominant one.

By comparing for each species the values of the year when the abundance-value was the largest, to the values of the year, when it was the smallest, we obtain interesting additional traits of the surveys made in the areas treated above. According to the above mentioned primary records this comparison will be made with only five of the most general species of each area (the year, when the survey was made, will be mentioned in parenthesis; the multiplier $\times$ the smallest value = the largest value):

	Abundance (pairs/km²)		Dominance (%)		Abundance multiplier	Dominance multiplier
Ahvenanmaa:						
Fringilla coelebs .	53.0 (1926)	40.5 (1927)	28.2	26.6	1.3	1.1
Phylloscopus troch.	10.7 (1926)	10.7 (1927)	5.7	7.0	1.0	1.2
Turdus pilaris . . .	9.0 (1926)	3.4 (1927)	4.8	2.2	2.7	2.2
Parus atricapillus .	8.8 (1926)	5.4 (1927)	4.7	3.5	1.6	1.3
Regulus regulus . .	8.8 (1926)	6.5 (1927)	4.7	4.3	1.4	1.1
			Average		1.6	1.4
Turku:						
Fringilla coelebs . .	45.0 (1941)	27.3 (1943)	23.9	14.3	1.6	1.7
Phylloscopus troch.	33.3 (1941)	28.6 (1943)	17.7	13.8	1.2	1.3
Emberiza citrinella	16.3 (1943)	8.3 (1941)	8.0	4.4	2.0	1.8
Parus atricapillus .	15.0 (1942)	3.3 (1941)	7.1	1.8	4.6	3.9
Anthus trivialis . .	8,3 (1941)	5.0 (1942)	4.4	2.6	1.7	1.7
			Average		2.2	2.1

Viipuri:						
Phylloscopus troch.	62.1 (1941)	25.0 (1943)	28.0	16.2	2.5	1.7
Fringilla coelebs . .	52.1 (1941)	20.0 (1943)	21.6	13.3	2.6	1.6
Anthus trivialis . .	20.0 (1943)	11.3 (1942)	13.3	5.7	1.8	2.3
Parus atricapillus .	17.5 (1942)	12.6 (1941)	10.0	4.8	1.4	2.1
Sylvia borin	15.0 (1943)	11.6 (1941)	10.0	4.4	1.3	2.3
			Average		1.9	2.0
Joensuu:						
Phylloscopus troch.	37.8 (1942)	7.9 (1943)	25.5	11.1	4.8	2.3
Fringilla coelebs . .	33.4 (1942)	19.3 (1943)	27.3	22.6	1.7	1.2
Anthus trivialis . .	10.0 (1942)	7.9 (1943)	11.1	6.1	1.3	1.8
Parus atricapillus .	8.1 (1942)	5.0 (1943)	7.1	5.5	1.6	1.3
Emberiza citrinella	6.6 (1942)	1.5 (1943)	4.4	2.0	4.4	2.2
			Average		2.8	1.8
Oulu:						
Phylloscopus troch.	41.4 (1943)	18.3 (1945)	44.0	19.8	2.3	2.2
Fringilla coelebs . .	16.7 (1945)	8.6 (1943)	17.9	9.1	1.9	2.0
Parus atricapillus .	14.3 (1943)	5.8 (1945)	15.2	6.3	2.5	2.4
Anthus trivialis . .	9.2 (1945)	5.7 (1943)	9.9	6.1	1.6	1.6
Emberiza citrinella	4.3 (1943)	3.3 (1945)	4.6	3.6	1.3	1.3
			Average		1.9	1.9
Suomussalmi:						
Parus atricapillus .	15.0 (1943)	1.7 (1945)	25.0	2.7	8.8	9.3
Fringilla coelebs . .	11.7 (1942)	1.7 (1945)	14.0	2.7	6.9	5.2
Phoenicurus ph. . .	11.7 (1945)	0.0 (1943)	18.9	0.0	∞	∞
Phylloscopus troch.	10.0 (1942)	0.0 (1943)	12.0	0.0	∞	∞
Anthus trivialis . .	6.7 (1945)	5.0 (1943)	10.8	6.0	1.3	1.8
			Average		(5.7)	(5.4)
Heinäsaaret (figures not quite accurate):						
Anthus spinoletta .	360.0 (1923)	9.0 (1928)	68.6	7.8	40.0	8.8
Calcarius lapponic.	144.0 (1921)	18.0 (1923)	42.9	3.4	8.0	12.6
Anthus pratensis .	144.0 (1931)	10.8 (1922)	57.2	4.0	13.3	14.3
Anthus rufogularis	14.4 (1931)	0.0 (1922)	5.7	0.0	∞	∞
Motacilla alba . . .	10.8 (1923)	0.9 (1933)	2.1	0.5	12.0	4.2
			Average		(18.3)	(10.0)

From the collocation it is convincingly evident that the abundance multiplier increases passing from the south toward the north, or rather from south-west to north-east and particularly in the northern parts of the northern hemisphere in an arctic direction (Siivonen 1948 a). The same touches also the dominance multiplier.

It is also important to establish that the dominance multiplier as a rule is just a little smaller than the abundance multiplier, or at the most of the same size. These regularities are also seen from the following table, in which the average abundance- and dominance-multipliers of five of the most frequent species of each area are presented (the areas in the order SW → NW):

	Abundance multiplier	Dominance multiplier
Ahvenanmaa	1.6	1.4
Turku-sector	2.2	2.1
Viipuri-sector	1.9	2 0
Joensuu-sector	2.8	1.8
Oulu-sector	1.9	1.9
Suomussalmi-sector	(5.7)	(5.4)
Heinäsaaret islands	(18.3)	(10.0)

In view of the three most frequent species we come to a quite corresponding, although partly even clearer increase of the abundance multiplier in the order S → N:

	Fringilla coelebs	*Phylloscopus trochilus*	*Parus atricapillus*
Ahvenanmaa	1.3	1.0	1.6
Turku-sector	1.6	1.2	4.6
Viipuri-sector	2.6	2.5	1.4
Joensuu-sector	1.7	4.8	1.6
Oulu-sector	1.9	2.3	2 5
Suomussalmi-sector	6.9	∞	8.8

The increasing tendency of the multiplier in the order S → N is thus evident, although two or three irregularities can be noted. These can, at least partly, depend on the fact that surveys from different areas have been available for different numbers of years, which evidently cannot be placed side by side in view of the course of the fluctuations in numbers, as it will be possible later to presume. We could, namely, not obtain objective material, until similar surveys from at least 3—4 consecutive years were available (comp. p. 54). The presented multipliers can thus approximately correspond to the true multipliers in the above mentioned areas from which the results of three consecutive years have been available (there were 3 such areas). On the other hand it is also to be presumed that the multipliers in their turn from those areas (4 areas), from which there have been survey results only from two consecutive years or from 2—3 separate years, can be even considerably smaller than the true multipliers. This is elucidated by the following comparison, in which the statistics of the yearly catch of gallinaceous birds in the different provinces of Finland are used as objects of comparison (comp. SIIVONEN 1948 b). As multipliers of the neighbouring maxima and minima (the catch of the maximum year: the catch of the minimum year) during the time of the so called rising curves of e. g. 1934—37 and 1939—1942 amongst others the following are obtained (the provinces in the order S→N):

	Tetrao urogallus		*Lyrurus tetrix*		*Tetrastes bonasia*	
	1934—37	1939—42	1934—37	1939—42	1934—37	1939—42
Uusimaa	1.1	2.8	1.3	2.5	1.2	4.7
Turku and Pori .	2.3	2.0	2.4	2.1	2.3	4.6
Viipuri	1.9	2.3	1.8	4.0	1.5	6.8
Kuopio	2.6	1.6	2.7	1.8	2.8	2.8
Oulu	3.2	2.0	3.2	3.5	3.0	4.4
Lappi	3.4	3.4	5.6	8.5	2.8	13.7

Such a multiplier is generally obtained at the rising curve of a maximum during the time of 2—3 years. The multiplier of the sinking curve, which normally is of the same size on the average (exceptionally, e. g. in passing from 1937 to 1939 they can be even many times larger than these; SIIVONEN 1948 b), is on the other hand generally obtained already in 1—2 years (SIIVONEN 1948 a and b, from which also the multipliers of the adjacent years of the rising and sinking curves are seen).

If these multipliers are compared to the corresponding average abundance multipliers in the table on p. 47 of the five most frequent species, they can in principle — many even absolutely — be placed side by side, in other words, one can come to the above mentioned results not only on the basis of the quantitative bird survey records. The multipliers of the gallinaceous birds are, however, in many cases clearly larger than those of the above treated 5 most frequent species. This touches particularly the multipliers of the 1940s (comp. none-the-less, their exceptional nature, SIIVONEN 1948 b). The size of the multipliers of the gallinaceous birds is in harmony with the fact that both of the above statistics of the gallinaceous birds are from four consecutive years, and that each of them comprises one real minimum and a real maximum. The multipliers presented in view of other species on the other hand — maybe with rare exceptions — evidently do not correspond to the true multiplier between the minimum and the maximum, but are probably smaller (comp. above). — Taking such possibilities into consideration, the multipliers can be shown to be large enough to be taken into consideration in each northern area and at least with most of the species. It is also of importance to state, that they increase powerfully starting from the province of Oulu, and obtain very considerable values already in the furthest parts of Lapland — all these regularities characterizing the short-term fluctuations in numbers.

The latest most regularly occurring years of maxima with the gallinaceous birds in Finland were 1923 (with the blackgame 1924), 1927 (with the willow grouse 1926), 1930, 1933, 1937, 1942 and 1945 (SIIVONEN 1948 a and b, in which investigations other regularities in the fluctuations in numbers are also explained). Of other birds only the peak-years of the waxwing until the end of the 1930s are known in Finland (SIIVONEN 1941 and 1948 a). They were 1927, 1931, 1934, and 1937, in other words, the peaks of the waxwings, corresponding to those of the gallinaceous birds in 1930 and 1933, occurred one year later. The similarity is thus evident, although already these comparisons show that by different species the corresponding peaks either join the theoretic maxima (in Finland they are generally situated in years ending in the numbers 0, 3, and 7, type 037; comp. SIIVONEN 1948 a), or are situated directly on the one or the other side of them. The same touches deeper failures, which in their turn are mostly situated in years ending in the numbers 2, 5 and 8. The 1940s have, none-the-less, deviated from this rule, the peaks mostly being situated in years ending in 2 and 5 and the minima in those ending in 3, 4 and 6 (SIIVONEN 1948 b).

Also this regularity of the short-term fluctuations in numbers seems to be reflected by the quantitative bird records treated above, in spite of their brokenness. So, for instance, the blackgame in Ahvenanmaa belonged to species whose stock showed an increase passing from 1926 to 1927. The blackgame thus occurred as a dominant species in 1945 at Suomussalmi. Both these observations concerning the blackgame based on the above presented parallelism are thus in harmony with the Finnish blackgame peaks elucidated in other ways. We cannot exactly consider it as something accidental that e. g. in Heinäsaaret, where the preponderance of the most frequent species in the different years vary very much (comp. p. 45), the preponderance (dominance percentage) of these species were clearly similar during the years 1923 and 1933, corresponding absolutely from the point of view of fluctuations in numbers:

1923:		1933:	
Anthus spinoletta	68.6	*Anthus spinoletta*	37.6
Anthus pratensis	17.1	*Anthus pratensis*	28.1
Calcarius lapponicus	3.4	*Calcarius lapponicus*	18.8

1923 and 1933 were also most clearly general peak-years (a total of 1460 and about 700 pairs) at Heinäsaaret, while on the other hand the values of the general failure of 1928 (comp. p. 49) were the lowest (a total of 380 pairs).

MERIKALLIO's (1946) material from the 1940s offers also in this respect an interesting point of comparison. If we note e. g. the most and the least abundant year of the three most frequent species (*Fringilla coelebs, Phylloscopus trochilus,* and *Parus atricapillus*) in each sector, they are distributed over the different years as follows:

	1941	1942	1943
Maxima	4	7	3
Minima	2	—	9

The maxima of these species even in these broken records (comp. p. 47) occur thus in most of the areas mostly in 1942, and the minima mostly in 1943 (comp. the corresponding years with the gallinaceous birds p. 49). In 1944 MERIKALLIO (op. c.) on the other hand did not make any surveys, so that the values of 1945 are detached. — We come to corresponding results also in respect of many other species.

PALMGREN's (1930) values from Ahvenanmaa in 1926 and 1927 are thus not contradictory to the short-term fluctuations in numbers of the gallinaceous birds and the waxwing. They indicate, on the contrary, that most species of birds recorded in the surveys had a peak-year in 1926 (comp. above e. g. the willow grouse) and part of them in their turn in 1927 (comp. above other gallinaceous birds and the waxwing). The occurrence of 1926 as a year of maximum there is thus not contradictory to the regularity of the short-term fluctuations in numbers viz. that the peak ending in 7 generally changes into one ending in 6 in south direction (type 037 into type 036, comp. SIIVONEN 1948 a).

The increase or decrease of the stock of the different species thus did not necessarily need — at least not exclusively — to be caused by accidental reasons; it is also in full harmony with the quantitative structure of the short-term fluctuations in numbers (comp. above the corresponding traits of the gallinaceous birds as well as SIIVONEN op. c.). Only certain values, e. g. the decrease of *Sylvia communis* and the increase of *Phylloscopus sibilatrix* give the impression of being exceptionally abrupt. The sudden changes in the stock of the last-mentioned species are known, it is true (comp. e. g. SIIVONEN 1936, from which amongst other things the exceptionally steep edged maximum of the year 1934 is seen). They are evidently correlated to the fact that the species in Finland is a typical so-called southern-immigrant (comp. SIIVONEN 1948 a). As to the woodpeckers, as well as to the crossbills (comp. REINIKAINEN 1937), the changes established can scarcely be considered abnormal. — It is not altogether without interest to state that PALMGREN'S (1930) surveys elsewhere in southern Finland occurred during the general failure of 1928 (comp. also above at Heinäsaaret islands).

These few comparisons, and above all the similarities established according to the primary records of the above presented quantitative bird surveys (amongst others the increase of the multiplier from the south toward the north, as well as the noticeable simultaneousness of the peak-years, as well as of the years of failure) together with the structure of the short-term fluctuations in numbers previously described in view of the gallinaceous birds and the waxwing in Finland, thus seem rather decisively to indicate that most of our species of birds fluctuate, following the same laws, some of them more and others less decidedly. This, and its relation to the fluctuations in numbers already known with the gallinaceous birds and the waxwing is, however, difficult to elucidate in detail with numerous small birds on account of the deficiency of the records.

So far as the above-described changes in the stock depend on short-term fluctuations in numbers, as according to the above seems to be presumable at least for the most part, they could probably not generally be considered real disturbances occurring in the biocenosis (here nearest thus in the bird community of the biocenosis). The biocenosis executes, as it is, such changes for most of its members as a totality. This is seen in view of the birds [1]) e. g. from a similar trend of changes in the stock of many species (e. g. the development of the stock in Ahvenanmaa, p. 39), from the considerable dissimilarity in the total quantity of birds in years of maxima and minima (e. g. at Heinäsaaret islands in Petsamo p. 50, and MERIKALLIO's, 1946, records of the 1940s, p. 50), as well as from the fact that the dominance multiplier generally is smaller than the abundance one (p. 47). In biocenosis the phenomenon thus most often reflects as a ± harmonious pulsation of the populations of the different members of the biocenosis. Since the dominance multiplier is, nevertheless, so large — this is in harmony with the fluctuating of the different species at slightly different times — it shows that even a considerable variation in the mutual preponderances can, none-the-less, be shown in view of many a species. Real disturbances in the biocenosis probably need to occur only in such cases, where the years of maxima and minima of such species as have a great influence on the other members of the biocenosis (e. g. predators ⇆ catch) happen to be overlapping with the years of maxima and minima of these other species.

Such a fluctuations in numbers evidently have also been the most essential cause of the great uncertainty that is disclosed by the records of the quantitative bird surveys (this indicates on the other hand the considerable accuracy of the survey work, presupposing that the survey material is sufficiently large). From each of the areas treated above there has in fact been a so large survey material available, that in the totals of records of these the error percentage of the method itself must be considered pretty well evened up. In spite of this the fluctuations in numbers of most of the species have, none-the-less, been very remarkable. It reflects already in the rude structure of the bird community, which can be formed essentially differently depending on the year on which its

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[1]) Comp. SIIVONEN 1948 a, where the same question is passed by also in view of certain other groups of terrestrial animals.

survey has been based. This touches, besides the entire density of the bird community, also very essentially, although a little slighter, the dominance of the different species. In the north, where the fluctuating is much more abrupt than in the southern and central parts of the country, not even the most dominant species of the different years need to be of the same species. Also in southern Finland at the most only two species of the same place clearly differing from one another and also from others in preponderance can preserve their first places. The general organization of the other species is on the other hand very uncertain already in southern Finland. The accidental character of the results of the quantitative bird surveys made is thus shown e. g. by the parallels drawn on p. 44, in which two different dominant groups, explained by the same methods, each occurs almost in the same preponderance from southern Finland up to the borders of Lapland.

On the basis of comparisons made it is also clear by itself that results obtained on the basis of quantitative bird surveys, made at random in view of time and place, cannot be blindly generalized nor, above all, can any too far-aiming conclusions be drawn from them.

According to the above those results of quantitative bird surveys made, that have been most free of errors, have been obtained in view of the relative density of the same species on different types of habitat, under the presupposition that the surveys have been executed for each type in the same district and during the same summer. The abundance of the species on different types of habitat, and their proportion to other species (dominance) are on the other hand not even then fit for generalization. They correspond only to the situation of the year and place, when and where the survey was made. This is a consequense of the short-term fluctuations in numbers not being simultaneous for all the species and in all the areas. If such surveys are executed in different years or in different areas, the possibility of errors in the generalizations made on the basis of them increases already considerably, not speaking of conclusions concerning half or even the whole of the country, e. g. comparisons of the bird fauna of different parts of Finland, of the density of the same species in different parts of the country, changes occurring in the bird-fauna, as well as calculations concerning the numbers of the birds of southern as well as the whole of

Finland (comp. e. g. the generalizations of this kind in PALMGREN 1930 and particularly in MERIKALLIO 1946). In any case the errors of such generalizations based on quantitative bird surveys made at random in different areas in different years (in some areas and with some species downright in years of minima and in others in years of maxima!) must according to the above statement be considerably greater than what it has been considered to be. As it is, the abundance multiplier alone and even that of the dominance is on an average about 2 in southern and central Finland, and about 10 and even more in the most northern parts of Lapland. These correspond thus to a possibility of error percentage of about 100—1000 (± 50—± 500). It is not to be denied, it is true, that great bird-fauna problems have generally even then been reflected — many important regularities have in fact been found out just thanks to such generalizations —, but their accuracy and the force of their occurring, as they appear as results of such generalizations, are in certain cases to be considered either problematic or at least to be in need of control.

These circumstances should consequently be noted, when executing quantitative bird surveys in the future and above all when drawing conclusions on the basis of them — the methods themselves have on the contrary proved to be very practicable. This is absolutely inevitable in order not to endanger the quantitative bird surveys, which have become classical thanks to the investigators mentioned and have attained a leading position in the northern countries, as an exact biological science by generalizing the results too much. If in these surveys one thus endeavours to attain an other aim than that mentioned in the beginning of the preceding paragraph, one should also take the short-term fluctuations in numbers into consideration. In order to reduce the percentage of errors as much as possible, the surveys should be made at least during 3—4 years [1]) dependent on the fluctuating of different species

[1]) The 3-year series is then in most cases the most suitable. At the place of the 4-year cycle (between the two peaks limiting it) no maxima can be contained in the 3-year series. At such a cycle the series should thus be one of 4 years (if it begins from the year following that at which the theoretical 4-year cycle starts). Since the different species of the same area can be of different types from the point of view of the fluctuations in numbers (even if of types close to them; comp. SIIVONEN 1948 a),

occurring at slightly different times, and on the purpose of the investigation, but on account of the diverse heights of the different peaks and minima rather during 10 consecutive years (= the so-called whole cyclic series comprising theoretically 2 ordinary and 1 so-called high-peak; comp. its structure, SIIVONEN 1948 a), each year on the same survey lines, according to the same method, and under the same conditions. Even then the obtained averages only give an idea of a determined phase of the reigning bird-fauna trend of development (comp. e. g. SIIVONEN & KALELA 1937 and SIIVONEN 1948 b) [1]). The same applies also to the use of the yearly statistics concerning catch, etc.

In this manner we obtain also a new significance into the quantitative bird surveys in addition to their considerably increasing accuracy. They open up possibilities amongst others for explaining the short-term fluctuations in numbers of the small birds, the structure of the biocenosis and the mutual relationship between its different members as well as the habitats of different species of birds during the different stages of the fluctuations in numbers, many other ecological etc. relations joining above all the sphere of the short-term fluctuations in numbers (comp. e. g. SIIVONEN 1948 a), which relations must at present still be considered almost unknown.

Literature cited: MERIKALLIO, E., 1939, Heinäsaarten lintukuvakirja. Helsinki. — 1946, Über regionale Verbreitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. I und II Teil. Ann. Zool. Soc. Zool.-Bot. Fenn. Vanamo 12, N:o 1 und 2. — NORDBERG, S., 1947, Ein Vergleich zwischen Probeflächenmethode und Linientaxierungsmethode bei quantitativen Aufnahmen des Vogelbestandes, Ornis Fenn. 24: 87—92. — PALMGREN, P.,

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the length of the series should thus be chosen nearest according to the type, to which most of the species, and above all most of the most dominating species belong. The most reliable results can, nevertheless, be obtained only by the 10-year series, since the considerable differences in height of the different peaks and minima are comprised in them, and the type-differences of the different species will then also be evened.

[1]) MERIKALLIO's (1946) surveys in the 1940s thus occurred during a very exceptional period from the point of view of the short-term fluctuations in numbers. This makes a control of the suitability for generalization of the results obtained on the basis of them still more unavoidable. This with so much more reason, since it has not yet been explained, how the different species have behaved in view of the occurring decline.

1930, Quantitative Untersuchungen über die Vogelfauna in den Wäldern Süd-Finnlands. Acta Zool. Fenn. 7. — 1942, Die Populationsgrösse der Vögel als Evolutionsfaktor. Die Naturwissenschaften 30: 217—220. — REINIKAINEN, A., 1937, The irregular migrations of the crossbill, *Loxia c. curvirostra*, and their relation to the conecrop of the conifers. Ornis Fenn. 14: 55—64. — SIIVONEN, L., 1936, Beobachtungen über die Vogelfauna in Pieksämäki. Kuopion Luonn. Yst. Yhd. Julk., Serie B, 1, N:o 9. — 1941, Über die Kausalzusammenhänge der Wanderungen beim Seidenschwanz, *Bombycilla g. garrulus* (L.). Ann. Zool. Soc. Zool.-Bot. Fenn. Vanamo 8, N:o 6. — 1948 a, Structure of short-cyclic fluctuation in numbers of mammals and birds in northern parts of the northern hemisphere. Papers on Game-Research 1. — 1948 b, Decline in numerous mammal and bird populations in north-western Europe during the 1940s. Ibid. 2. — SIIVONEN, L. & KALELA, O., 1937, Über die Veränderungen in der Vogelfauna Finnlands während der letzten Jahrzehnte und die darauf einwirkenden Faktoren. Acta Soc. F. Fl. Fenn. 60: 606—634.