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SUOMEN LINTUTIETEELLISEN YHDISTYKSEN JULKAISEMA
UTGIVEN AV ORNITOLOGISKA FÖRENINGEN I FINLAND

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Secondary intergradation of the Blue-headed and Grey-headed Wagtails (*Motacilla f. flava* L. and *Motacilla f. thunbergi* Billb.) in South Finland.

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Introduction.

The extremely lively discussion centering around the Yellow Wagtail complex has already produced several theories intended to explain the apparently hopeless confusion in the genetical structure of the species in question. The oldest assumption of »spontaneous» and »parallel» mutations especially favoured by the German ornithologists (see e.g. GROTE 1937) has been severely criticized by WILLIAMSON (1955), who points out that this theory, when applied consistently, leads to impossibilities and thus cannot explain the whole situation. He also emphasizes the importance of the so-called »migrational drift» and secondary intergradation, and points out that these phenomena make it unnecessary to base speculation on any such assumptions as the mutation theory and the »genetic lability» theory (TUCKER 1949). It seems that there are two major series of primary intergradation. The first is the cline *M.f.simillima-M.f.zaissanensis-M.f.thunbergi*[1], in which there is to be found a reduction of the eye-stripe and darkening of the head (especially of the lores and ear-coverts) from east to west. The present author cannot avoid the impression that the black-headed race *M.f.feldegg* also belongs to this series: the geographical and morphological gap between it and *M.f.thunbergi* is possibly due to the Ice Age and the expansion of the nominate race from Europe towards the east. In this cline, the length of the

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[1] In this paper, the nomenclature of WILLIAMSON (op. cit.) has been followed.

hind-claw decreases from east to west. The other cline starts with the nominate race, which is very like *M.f.simillima.* During the expansion eastwards an elimination of alleles took place (see JOHANSEN 1946), which led to a paler head colour and so produced the races *M.f.beema* in the Kirgizh Steppe region and the almost white-headed *M.f.leucocephala* in Outer Mongolia. The westernmost race *M.f. tschukchensis* is obviously due to a minor clinal step (from *M.f.simillima).* Other races are products of secondary intergradation: *M.f.superciliaris(M.f.beema×M.f.feldegg)* in the Aral-Caspian region, *M.f.dombrovskii(M.f.flava×M.f.feldegg)* in South Poland, Galizia and the south of Russia and probably the South-European races *M.f.cinereocapilla* and *M.f.iberiae*[1] (also *M.f.flava×M.f.feldegg).* The resident Egyptian race *M.f. pygmaea* has so much in common with the South-European races that it must be regarded as a result of the same hybridization as these. MEINERTZHAGEN (1954) and GLADKOV (1954) mention that the nominate race and the Grey-headed Wagtail also intergrade in Northwest Russia and the observations of ARMINGTON (1949) in South Sweden show that hybridization occurs there too. In Finland, it has been known ever since HORTLING's (1928) time that many specimens cannot be identified either as the Grey-headed or the Blue-headed Wagtail, which are the only ones breeding in Finland. According to MERIKALLIO (1955), 85 % of the Finnish Yellow Wagtail population belongs to *M.f.thunbergi* and the rest to the nominate race, whereas LEHTONEN (1955a) gives the figures 97 % and 3 %, respectively. However, both of them admit that hybrids occur very commonly; thus the mere division into two types cannot clarify the situation, since in modern taxonomy we must study populations, not types (MAYR 1942). The only objective method, therefore, is that accepted by LUNK (1952, p. 8): »In studying the specimens, I first considered size and color, temporarily disregarding present subspecific conditions.»

Material and methods.

Classification of the specimens. The extreme types occurring in Finland are *M.f.thunbergi* and *M.f.flava,* the »typical» specimens of which represent the ends of the series of types, as they are

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[1]) See also MAYAUD 1952.

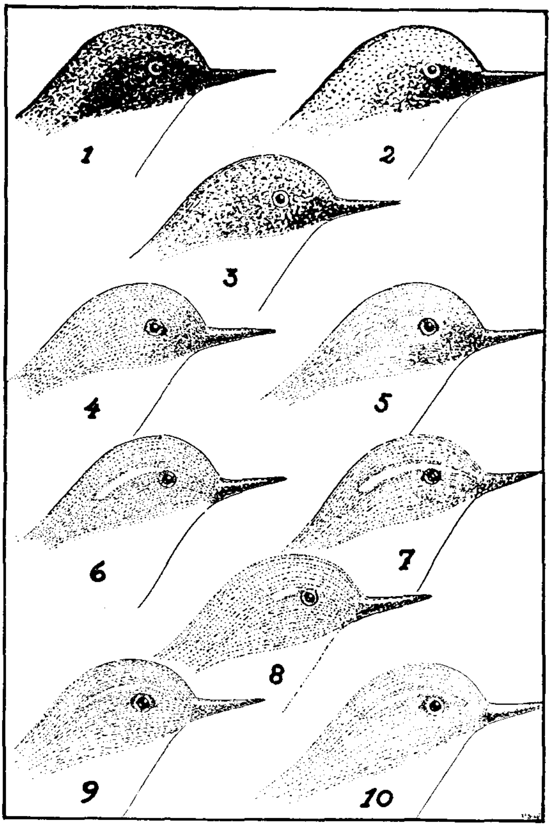


Fig. 1—10, showing types of males (1—7) and females (8—10). See pp. 3—4.

described in the handbooks (e.g. Peterson-Mountfort-Hollom 1954). A »typical» male of the Grey-headed Wagtail is seen in Fig. 1, and Fig. 7 represents the nominate race (the eye-stripe, however, is only about 80 % of that of a »typical» specimen). Figs. 2—6 are examples of intermediary types. Since the gradual darkening of the head from *M.f.flava* to *M.f.thunbergi* is not as easily recognized as the presence of pure black or pure white, the areas of these colours have been taken as the basis of the classification of males. As a rule, the male has black on the lores and ear-coverts or a white eye-stripe or neither of these. I have seen only two males which had at the same time black lores and ear-coverts and an eye-stripe reduced to a little spot behind the eye. These specimens have been placed in type 1 (see below). In the field, I had 10×50 field glasses with T-optics, and the area of white or black was estimated for every specimen. The 100 per cent area of black is that of a »typical» Grey-headed Wagtail (Fig. 1) and the 100 per cent area of white, respectively, that of a »typical» Blue-headed Wagtail (in Fig. 7 the area of white is only about 80 %). The classification of males is as follows:

Type	Black		White
0	100—60 %		—
1	60—20 %		—
2	20 %	or	— 20 %
3	—		20—60 %
4	—		60—100 %

Fig. 1 represents type 0, Fig. 2 type 1, Figs. 3—5 type 2, Fig. 6 type 3 and Fig. 7 type 4.

The identification of females is often considerably more difficult than that of males (see, for example, JOHANSEN 1946). The distinction between the two races in question, however, is comparatively clear (see the colour plate in GRANT & MACKWORTH-PREAD 1952). The Grey-headed Wagtail has no eye-striple or only a reduced one, whereas the Blue-headed Wagtail female has nearly as well developed an eye-stripe as the male. In classification, the size of the eye-stripe has been taken into account. In the following table, 0 means the absence of the eye-stripe and 1 the amount of white in the »typical» Blue-headed Wagtail.

Type	Eye-stripe
0	0—1/3
1	1/3—2/3
2	2/3—1

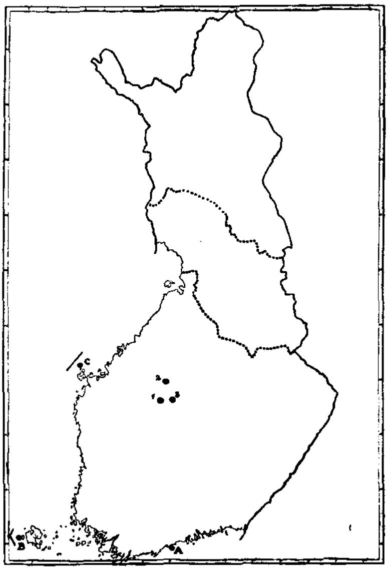
Figs. 8—10 represent these types.

The populations studied. The study area proper is situated in the watershed zone of Suomenselkä and consists of parts of the communes of Perho, Karstula, Soini and Saarijärvi. In this area, three sections have been studied in 1955, two of which (1. and 2. in the map on page 5) lie in the highest parts of the watershed zone and one (3. in the map) 20 km. east of this zone. A characteristic feature of the watershed is the great proportion of peat land, especially of open swamps, which are the most suitable habitats for the species in this district (see SAMMALISTO 1955). In the first section, 25 % of the total area consists of open swamps, and in the second section, the respective figure is 50 %. The amount of cultivated land is very small (1 % and none respectively). In the third section the proportions are quite different: of the total area of the section only 1 % consists of open swamps and 20 % of cultivated land.

The census was started as soon as the pair-formation had begun. In the year under review the spring was exceptionally late and breeding pairs were not noted before 27. V. The census was continued throughout the month of June. In the watershed zone, the total population cannot have been much greater than the number of pairs noted, since all open swamps were carefully censused in the nestling period, when it is not difficult to find the adult birds. In the settled area, however, the small patches of field were not taken into account; furthermore, in the early breeding period the species spends a more hidden life and therefore some pairs may have been overlooked. However, the pairs observed certainly comprise much more than half of the total population and therefore amply represent the population of this section.

During the spring migration in Karstula, 124 males were examined.

Only very few of observations made in other parts of the country could be treated in terms of the classication used for the study area proper. I have found observations of only 7 males, 4 made in the surroundings of the lake Oulujärvi (HORTLING 1928) and 3 in the surroundings of Oulu (22. 6. 1955, my own material). The collections in the Zoological Museum of Helsinki contain 23 males in breeding plumage; thus the whole material



Map 1. The shifting area of the vegetation zones (bounded by the dotted lines), the study areas (1, 2 and 3, see on page 4), and the observation places for migration: A = Helsinki, B=Signilskär, C=Valassaaret/Valsörarna, 3=Karstula.

consists of only 30 males. The number of females is much too small (11) for a detailed study. However, I have had at hand the data of **Merikallio**, who (oral comm.) has divided the males into two groups, the »northern» type consisting of my types 0—2 and the »southern» type my types 3—4. **Lehtonen** (1955b) has used a different classification and therefore his material cannot be much treated here.

The length of the hind-claw of all the museum specimens has been measured.

The segregation into types.

The study area proper. In all, 135 pairs were found.[1] Of these, 127 males and 75 females have been seen well enough for identification of type. In only 58 pairs were both sexes identified, since it could not always be decided which birds belonged to the same pair.

The segregation of the males was as follows (in all tables, the types are in the order 0, 1, 2 ... from the left):

3 19 82 19 4

The result is an almost ideal binomial curve. The proportion of the »pure» types (0 ond 4) is only 5.5 %, whereas 65 % of all specimens belong to type 2, which is the clearest intermediary form (in the following, by intermediary type is meant only this type, whereas 0, 1, 3 and 4 are regarded as »pure» types). The proportions of types are different in the watershed zone and in the settled area, as the following statistics show:

Watershed zone	—	6	39	4	1
Settled area	3	13	43	15	3

The number of intermediary specimens is proportionately greater in the former than in the latter. This comparison does not reveal the true situation, which appears only when we compare the populations of swampland and cultivated land. The following table shows that there is no vital difference between the swamplands of the watershed and the settled area ($\chi^2 = 0.62$):

Swamps of the watershed	—	6	39	4	1
Swamps of the settled area	—	2	19	1	1

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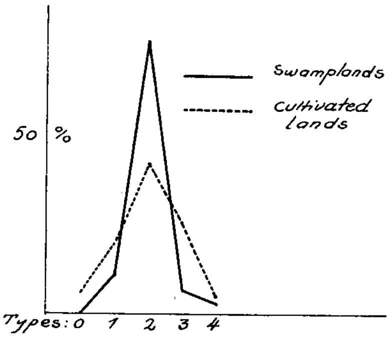
[1] This indicates great population fluctuations, since the density is only 0.8—0.9 pairs/km^2, whereas **Merikallio** (1955) gives the figure 1.5 for Suomenselkä.

Therefore, there is no possibility of error in the following comparison:

Swampland	—	8	58	5	2
Cultivated l.	3	11	24	14	2

The difference is considerable (see also Diagr. 1) and statistically significant ($\chi^2 = 20.28$; 4 degrees of freedom). The proportion of the intermediary type is 80 % on swampland but only 45 % in cultivated biotopes.



Diagr. 1. The segregation of types (males) on swampland (continuous line) and on cultivated land (dotted line).

Attention has also been focussed on the call-note. According to the Finnish field-guides (e. g. LEHTONEN 1955a), both races call *pssli* (or *fjsi*), but the Grey-headed Wagtail also a rough *rssli* (or *rsliu*). Since most pairs were watched only for the short time necessary for identification of type, the following statistics may be misleading in the sense that they probably underestimale the number of *rssli* + specimens (those having the *rssli* note). The possibility of error, however, is the same for each type.

rssli+	1	10	22	—	—
% of all	33	55	26	0	0

The small percentage of type 0 is obviously due to scarcity of material, but the difference between types 1 and 2 is significant ($\chi^2 = 4.53$; 1 degree of freedom). It is therefore obvious that the two races differ from each other in the call-note and that the difference becomes apparent even in the intermediary forms.

The segregation of the females is as follows:

17 40 18

The comparisons give results similar to those for males:

Watershed zone	5	24	4
Settled area	12	16	14

Swamps of the watershed zone	5	24	4
Swamps of the settled area	5	4	1

In the latter statistics, the difference (in contrast to males) is almost significant ($\chi^2 = 5.41$; 2 degrees of freedom). Therefore the following statistics may be misleading, although the difference there is significant ($\chi^2 = 8.69$; 2 degrees of freedom):

Swampland	10	28	5
Cultivated -.	7	12	13

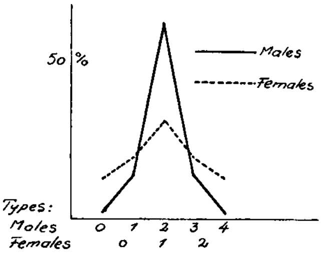
No attention has been paid to the call-note of the females.

The segregation of males and females cannot be directly compared with each other, but with an interpolation this becomes possible:[1]

Males	3	19	82	19	4
Females	8	16	25	17	9

The segregation of the females is much more even than that of the males ($\chi^2 = 23.34$; 5 degrees of freedom. See also Diagr. 2). No difference in this respect is to be found between swampland and cultivated land:

Swampland	Males	—	8	58	5	2
	Females	4	11	18	9	1
Cultivated 1.	Males	3	11	24	14	2
	Females	4	5	7	8	8



Diagr. 2. Comparison between the segregation of the males (continuous line) and of the females (dotted line).

For instance, the ratio of males to females in the percentage of the intermediary type is on swampland 1.9 and on cultivated land 2.0.

The following segregation of pairs was found for the 15 possible combinations of types:

		Males				
		0	1	2	3	4
Females	0	—	2	7	1	1
	1	1	4	19	5	1
	2	2	3	9	3	—

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[1] In this connection, linear interpolation has been used, since it gives results which differ not too much from given by the accurate (parabolic) method.

The correlation coefficient (— 0.14) is not significant.

The segregation of the males noted during the spring migration was as follows:

15 24 59 18 8

The difference from the breeding population is significant ($\chi^2 = 13.77$).

The whole country. The segregation of the males is as follows:

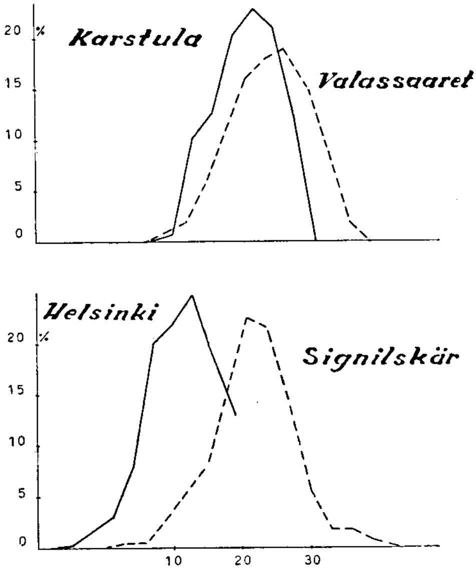
8 3 13 3 3

The intermediary type is here, too, the most frequent. Of the specimens of type 0, most (6) were north of the 65th parallel, as was expected. A more detailed comparison between the different parts of the country is not possible, since the material is too meagre. The proportion of types 0—2 is 80 %, which agrees very well with the figure (85 %) given by MERIKALLIO (op.c.). LEHTONEN (1955b) has obviously included many (probably all) specimens of my type 3 in the northern race, which makes it impossible to compare his results with mine.

The length of the hind-claw has been measured for both the males and the females, which show no essential difference (average values 9.7 and 9.55 mm., respectively). The average value for 31 specimens during the breeding season is 9.65±0.10 mm., and the length varies from 8.2 to 10.7 mm. This is in good accordance with the results of JOHANSEN (op.cit.) who gives for the nominate race the variation amplitude from 8 to 9.5 mm. and for *M.f.thunbergi* from 8 to 10.5 mm. The material is too small for correlation calculations. A male with a 12 mm. long hind-claw taken from Yyteri on the coast of the Gulf of Bothnia during spring migration is in the collections of the Zoological Museum of Helsinki. The length of the hind-claw is thus that of some eastern race, and the head colour is nearest to the East-Siberian race *M.f.zaissanensis*. It is to be noted that all aberrant Yellow Wagtails observed in Finland *(M.lutea lutea,* TENOVUO in press, *M.f.feldegg,* HILDÉN 1955, and the present *M.f.zaissanensis)* are of eastern origin, which is in good accordance with the »migrational drift» theory of WILLIAMSON (op.cit.).

The spring migration in Finland.

According to earlier authors, the Grey-headed Wagtail migrates later in the spring than does the nominate race (see e.g. WILLIAMSON, op.c.). The difference, according to ROSENBERG (1953), is about two weeks in South Sweden. In Karstula, the migrating specimens represented the intermediary population (see page 9) and in the archipelago of Vaasa (Valassaaret), according to HILDÉN (oral comm.), the specimens, with few exceptions, are »typical» Grey-headed Wagtails (much black on the lores and ear-coverts). For comparison, observations on spring migration at Helsinki and the ornithological station on Signilskär have also been taken into account (see map on page 5). Since by day migration is not very active (the species migrates largely by night, see e.g. SMITH 1950 and SPAEPEN 1951), both birds seen on migrating flight and resting specimens have been included. The values for Helsinki have been calculated by dividing the number of specimens observed by the number of hours of observation; at Signilskär and Valassaaret the observing has been fairly continuous and therefore the numbers have been treated as such. Since the number of migrating specimens at Valassaaret varies very much from year to year, the course of migration has first been calculated separately for every spring and the average curve has been constructed from the percentages so obtained. At Karstula, the numbers are based on a constant daily excursion route. At Signilskär, the observations were made in 1933, 1935 and 1953—54 (173 specimens), at Valassaaret in 1951 and 1953—55 (660 specimens), at Helsinki in 1948—55 (420 specimens) and at Karstula in 1955 (440 speci-



Diagr. 3. The spring migration of Yellow Wagtails at four points in South Finland.

mens). The values are calculated for three-day periods and are arithmetically smoothed. In this way the double-peakedness' due to the non-coincidence of the migratio nof the males and the females is eliminated. The course of migration is seen from Diagr. 3. Because of the complicated way by which the curves have been obtained, many inaccuracies may have come into them, and therefore an accurate statistical comparison of the curves is not warranted. The possibilities of error in the following comparison, therefore, cannot be estimated.

The curves show a marked difference between the two migration routes Signilskär-Valassaaret and Helsinki—Karstula. The migration seems to be about a week earlier in the latter than in the former. That the difference between Helsinki and Signilskär is greater than that between Karstula and Valassaaret, is obviously due to the lateness of the spring in 1955.

Discussion.

MEKIKALLIO's (1955) map (on his page 52) seems to afford evidence that there is a cline in the proportions of the races from south to north. My own observations at first sight seem to support this hypothesis: the material (127—10 = 117 males) from the Suomenselkä watershed (the rest, 10 males, are from Lake Finland in the commune of Saarijärvi) gives the percentage 84 for types 0—2, whilst the respective figure given by MERIKALLIO (op.c.) is 82 %.

There is, however, another possibility, which is based on the fact that the intermediary type is much more frequent on swampland than on cultivated land. The intermediary type is the most numerous one on all biotopes; thus the proportion of this type plays a decisive role when we divide the specimens into two groups only, as has been done above. The greater the proportion of intermediates, the more frequent does the northern race appear to be.

The proportion of the »northern» type in the settled area of the district studied is 76 %, whereas the respective value in Lake Finland, which is very similar in the biotope frequencies to the settled area in question, is, according to MERIKALLIO (op.c.), only 66 % (see the map on his page 52). The difference is probably due to the influence of the population of the watershed zone, if not to paucity of material.

Among the migrating specimens at Karstula the proportion of the »northern» type is 79 %, which is very near MERIKALLIO's value (80 %) for the coast of Bothnia. The frequency of the »northern» type is also very similar to that of the study area proper, but this is not due to the similar proportion of intermediates (48 % in the migrating and 65 % in the breeding population) but to the greater proportion of the »pure» (0—1) northern types in the migrating (32 %) than in the breeding (17 %) population. There are two possibilities to explain this: either much of the Lapland population migrates through the country or the migrating population is under the influence of northern populations in its breeding area.

The Yellow Wagtail population in South Finland is thus clearly polymorphic, as a result of secondary intergradation between the nominate race (coming from the southwest) and the Grey-headed Wagtail (coming from the east), and mating seems to occur without any appreciable selection between the races. Furthermore, there is a clear difference in polymorphism between the swampland and cultivated land populations, the intermediary type being more numerous in the former than in the latter. It is possible that the swampland population, on the one hand, and the population of cultivated land, on the other hand, are similar throughout the southern half of Finland. The differences in the frequencies of the types may be due to the discontinuities in the distribution of these two biotope complexes. It is to be noted that the proportion of types 0—2 is greatest in those territories which are the most swamped, namely in Suomenselkä, Maanselkä and the coast of Bothnia. It is remarkable that the value for the coast of Bothnia is nearly the same as for Maanselkä and Suomenselkä, although the boreal element of the bird fauna is far less represented on the coastland than in the watershed zones (MERIKALLIO, op.c.). On the south coast of Finland, LEHTONEN (1955b) has observed only 3 males of the »pure» nominate race (roughly representing my type 4) out of a total of 190 males¹), which is in good accordance with my observations (4 of 127). A cline is to be found only when the polymorphic population is under the influence of a

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¹) The biotopes in this investigation were largely marshes which show features of both open swamps and fields.

»pure» race, as in the northern parts of South Finland, or when two territories very different in regard to biotope conditions are close to each other, as in the boundaries of watersheds and settled areas.

In Finland, the confusion thus seems to be due to the fact that certain ornithologists (the earliest authors and TENOVUO 1954) regard the intermediary type as the nominate race, whilst others (LEHTONEN 1955a and b, MERIKALLIO 1955) refer them to *M.f. thunbergi.* The boundary between the northern race and the polymorphic population is not easy to determine, since we do not know in which cases MERIKALLIO's values are based on »pure» northern types and in which cases on intermediates. However, the museum material seems to justify the assumption that the demarcation line runs somewhere in the border area of the vegetation zones of South and North Finland (KUJALA 1936, see map on page 5). The earlier authors (e.g. HORTLING 1929) were thus right in the sense that the 65th parallel is a demarcation line. However, it does not concern the Grey-headed Wagtail and the nominate race, but the Grey-headed Wagtail and the intermediary population. The southern boundary of the polymorphic population obviously runs somewhere in the Baltic.

A similar colour polymorphism has been detected by VOIPIO (1950) in the Finnish squirrel *(Sciurus vulgaris)* population. This polymorphism, however, is clearly clinal, with a leap in the border area of the vegetation zones; no differences are to be found between different biotopes. In addition, the steps between the colour phases are much greater in the squirrel than in the Yellow Wagtail, which shows a most gradual variation.

The intermediary type seems to be better adapted to the conditions on swampland than the other types. Otherwise it would be difficult to explain why the swampland population of the settled area is similar to the population of the watershed zone.

In the search for an explanation, the effect of the microclimate comes to mind. The arctic microclimate of open swamps must be very unfavourable for the survival of the fledglings. It is possible that the intermediary type has developed a physiological mechanism more resistant to the influence of the cold, and that the genes responsible for this mechanism produce, as a by-product, the adaptively neutral head colour. A physiological correlation (TIMOFEÉF-

RESSOVSKY 1940) thus seems to be involved; good analogies are to be found in *Drosophila* (CUNHA 1949) and *Colias* butterflies (HOVANITZ, 1953), for example. The cases of polymorphism established in birds (e.g. MAYR & STRESEMANN 1950, SOUTHERN 1945) are probably also adaptive. In all these cases, however, only one or a few pairs of genes are involved; the gradual variation in the Yellow Wagtail and the segregation according to the binomial curve indicate that the inheritance of head colour in the Yellow Wagtail is polygenic. Lately polymorphism due to linked polygenes has been found in some populations of *Drosophila melanogaster* (DOBZHANSKY 1951). It is quite possible that the polymorphism of the Yellow Wagtail, too, is based on such polygenic complexes, the effect of which seems, in addition, to be stronger in males than in females in regard to head colour.

According to the handbooks (e.g. ROSENBERG 1953), the Grey-headed Wagtail breeds in a comparatively woody terrain, whereas the Blue-headed Wagtail favours fields and marshes. According to my own observations (SAMMALISTO 1955) in South Finland the species in limited in its breeding on peat land to the boundaries of open swamps and woodlands (especially of pine swamps). SEISKARI (1954) also states that the species is infrequent on pure pine swamps of South Finland. The intermediary type thus seems to be intermediary in its ecological demands also. In its migration, likewise, it differs from the northern race, but probably not much from the nominate race (see page 10).

In inter-racial hybrids, the chances for preadaptation are good because of great variation amplitude. However, it is quite possible that no preadaptation at all is involved in the occupation of new biotopes, since owing to the plasticity of the habitat selection mechanism, the variation due to population pressure may be greater than that based on heredity (SVÄRDSON 1949). The only possible reason would thus be an increase in reproductivity (see also PEUS 1951 and KALELA 1955). In the present case, however, it seems obvious that the intermediary type is preadapted and that the right *biotope* must have been found by the trial and error mechanism. A systematic investigation of the ecology of Yellow Wagtails in other zones of secondary intergradation could give an answer to the question of whether in some cases the *new genotype* had been arrived at by the trial and error mechanism.

The secondary intergradation of *M.f. flava* and *M.f. thunbergi* has produced a number of types, and in fact in South Finland one could find specimens which could be referred (if judged solely by the head colour) to any other race except *M.f. feldegg* and *M.f. superciliaris*. In other zones of secondary intergradation the situation seems to be very similar: for instance, the intermediates between *M.f. feldegg* and *M.f. cinereocapilla* found by TICEHURST and WHISTLER (1932) in Albania resemble very much the Grey-headed Wagtail (the authors regarded these specimens as »aberrant»). As WILLIAMSON (op.cit.) has already pointed out, the confusion is due only to the secondary intergradation and to a small extent to »migrational drift»; genetically the Yellow Wagtail complex seems to be no more labile than other species are.

For acknowledgements and valuable criticism I wish to express my gratitude to Prof. E. SUOMALAINEN (Genetical Institute, University of Helsinki) and Dr. P. VOIPIO (Zoological Museum, University of Helsinki). The races not breeding in Finland I have an opportunity to study by the courtesy of Dr. E. STRESEMANN, of the University of Berlin, who has kindly sent 36 specimens from the collections of the Zoological Museum, Berlin. The treatment of migration would not have been possible without recourse to the archives of the biological society Societas pro Fauna et Flora Fennica and observations made by the students K. AULA, O. HILDÉN, E. KAJOSTE, J. MIKOLA, M. RAUTKARI and H. ÅKERBLOM. The figure plate on page 3 has been drawn by Mr V. SORSA, M. Sc. For my study I have received a grant from the Finnish Zoological and Botanical Society Vanamo.

Summary.

A racial and ecological investigation of a Yellow Wagtail population in South Finland has been made in 1955. In addition, material of other authors and Museum collections has been used to clear up the racial conditions of the species in the whole country. The results show that the population of South Finland south of the 65th parallel is in a state of balanced polymorphism (the mating seems to happen at random between the types), the heterozygote» (the intermediary form between the nominate race and *M. f. thunbergi)* being the most frequent in all biotopes. However, the

proportion of intermediates is much greater on swampland than on cultivated land. This indicates that the intermediary form is better adapted to the swampland than the other types. The reason may be a physiological mechanism more resistant to the arctic microclimate (the survival of fledglings!) of open swamps than that of the »pure» races. The genes responsible for the physiological mechanism in question produce as a by-product the adaptively neutral head colour: a physiological correlation is thus involved. The proportion of the »pure» races is very small (about 5 %) throughout the southern half of the country.

The intermediary population migrates through the country about a week earlier than the Grey-headed Wagtail population of Lapland, which migrates along the Gulf of Bothnia.

The secondary intergradation in Finland has produced types inseparable from distant races. The situation seems to be the same in other zones of secondary intergradation, too. Thus the apparent confusion in the genetic structure of the species seems te be largely due to secondary intergradation and not »genetical lability». »Migrational drift» also has a role to play. All clearly aberrant (i. e., not resulting from secondary intergradation) Yellow Wagtails found in Finland are of eastern origin, which fits in well with the »migrational drift» theory.

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Selostus: **Keltavästäräkin ja pohjan keltavästäräkin sekundaarisesta vaihettumisvyöhykkeestä etelä-Suomessa.**

Keltavästäräkkirotujen pään väri vaihtelee täysin mustasta melkein valkoiseen (keltapäiset rodut viedään nykyään useimmiten omaan lajiinsa). Vaihtelu johtuu pääosaltaan ns. primäärisestä intergradaatiosta, joka saa aikaan populaatioiden vähittäisen muuttumisen niiden vaellussuunnassa ulkoisista tekijöistä riippuvien valinnan edellytysten samalla vähittäin muuttuessa. Keltavästäräkin levinneisyysalueella on todettavissa kaksi tällaista kliiniä, ja kun eri kliineihin kuuluvat rodut ovat paikka paikoin vaelluksensa aikana joutuneet toistensa asuma-alueille, on tuloksena ollut ns. sekundaarinen intergradaatio: rodut risteytyvät keskenään kapealla vaihettumisvyöhykkeellä. Näin on syntynyt muutamia uusia rotuja.

Kirjoittaja on tutkinut etelä-Suomen keltavästäräkkikantaa sekä museoaineistosta että maastossa kesällä 1955 Suomenselän vedenjakajaseudulla ja siihen rajoittuvilla asutusalueilla Karstulan, Perhon, Soinin ja Saarijärven pitäjissä. Tyyppijaossa on otettu koirailla huomioon sekä mustan että valkean värin alan laajuus päässä, naaraissa taas huomiota on kiinnitetty vain silmäkulmanjuovan laajuuteen. Koiraat on jaettu viiteen tyyppiin, joista »puhdasta» pohjoista rotua esittää kuvataulun kuva 1. Muita tyyppejä (1—4) esittävät kuvat 2—7, jolloin viimeksimainittu edustaa »puhdasta» eteläistä rotua. Tyypillisintä rotujen välimuotoa (tyyppiä 2) esittävät kuvat 3—5. Naaraat on jaettu kolmeen tyyppiin (0—2), joita edustavat tässä järjestyksessä kuvat 8—10 (ensiksimainittu »puhdas» pohjoinen rotu).

Sekä koiraiden että naaraiden jakautuminen tyyppeihin osoittaa, että välimuotoja (tässä tyyppi 2) on tutkimusalueen kannassa eniten (koiraista 65 % ja naaraista 55 %). Lisäksi kävi ilmi, että soilla välimuotoa on suhteellisesti huomattavasti enemmän (koiraista 80 %) kuin pelloilla (koiraista 45 %). Pariutuminen eri tyyppeihin kuuluvien koiraiden ja naaraiden välillä näyttää tapahtuvan ilman minkäänlaista valintaa. Yksilölliset erot ovat naaraiden välillä paljon pienempiä kuin koiraiden välillä (diagr. 2.). Myös Karstulassa kevätmuuton aikana nähdyistä koiraista suurin osa oli välimuotoa. Koko maan käsittävässä ainaistossakin välimuotoa on eniten (43 %). »Puhtaista» pohjoisen rodun yksilöistä suurin osa on 65:nnen leveysasteen pohjoispuolelta.

Erimielisyydet rotujen levinneisyyssuhteista maassamme johtuvat siitä, että runsaslukuinen välimuoto viedään milloin eteläiseen (Tenovuo ja vanhemmat käsikirjat), milloin pohjoiseen rotuun (Merikallio ja Lehtonen). Itse asiassa lienee niin, että koko etelä-Suomen populaatio n. 65:nnen leveysasteen eteläpuolella on pään värin suhteen monimuotoinen siten, että välimuodot ovat yleisimmät ja »puhtaat» rodut häviävänä vähemmistönä. Tätä tukee Lehtosen toteamus, että »puhdasta» eteläistä rotua oli hänen etelärannikolla tutkimistaan 190 koiraasta vain 3, mikä hyvin sopii yhteen keski-Suomen havaintojeni kanssa (4 127:stä). Näennäiset erot rotujen runsaussuhteissa selittyvät siten, että toisilla alueilla pohjoisen rodun runsaus Merikallion käyttämän rotujaon mukaisesti (kirjoittajan tyypit 0—2 viety pohjoiseen rotuun) tulee suuremmaksi kuin asutusalueilla, koska välmuoto on soilla hyvin runsaslukuinen.

Välimuoto näyttää sopetutuneen pesimään soilla (nimenomaan nevan ja metsämaan reunavyöhykkeessä) paremmin kuin »puhtaat» rodut, millä saattaa olla tekemistä pienilmastoseikkojen kanssa. Biotoopinvalinnassaan välimuoto on siis intermediaarinen, sillä pohjan keltavästäräkki pesii huomattavan metsäisillä mailla, ja nimirodun asuinalueita ovat niityt ja viljelysaukeat. Myös muuton kannalta (diagr. 3) etelä-Suomen välimuotopopulaatio on intermediaarinen siinä mielessä, että se keväällä muuttaa n. viikkoa aikaisemmin kuin Pohjanlahden kautta muuttava Lapin kanta, kun taas nimirotu etelä-Ruotsissa on muutossaan n. kaksi viikkoa edellä pohjan keltavästäräkkiä.

Sekundaarisen intergradaation tuloksena syntyy kaukaisiakin rotuja muistuttavia yksilöitä: pään värin mukaan arvostellen (joka maastossa on melkein ainoa tuntomerkki) voisi sanoa keski-Suomessa pesivän kaikkia muita lajin 13:sta rodusta paitsi mustapäisiä M. f. feldeggiä ja M. f. superciliarista. Esimerkkejä samanlaisesta on muiltakin sekundaarisen intergradaation alueilta. Sitä paitsi on suuri merkitys muuttoharhautumilla: keltavästäräkkirodut ovat talvipuvussa hyvin paljon toistensa näköisiä ja jotkin linnut saattavat seurata »väärän» rodun yksilöitä niiden asuinalueille. Suomessa on myös tavattu tällaisia: itäsiperialainen M. f. zaissanensis, kaakkoinen M. f. feldegg ja keltapäiseen lajiin kuuluvista roduista Kirgiisiaroilla pesivä M. lutea lutea. Kaikki ovat siis alkuperältään itäisiä, mikä tukee muuttoharhautumateoriaa, koska laji on itäinen muuttaja. Sen sijaan olettamus, että kysymys olisi »mutanteista», tuntuu erittäin epätodennäköiseltä eikä missään tapauksessa voi selittää kaikkia epäselvyyksiä keltavästäräkin rotusuhteissa.

Über die Expansion des Karmingimpels, *Carpodacus erythrinus* Pall., während der letzten Jahre in Finnland.

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Der Karmingimpel gehört zu denjenigen Kleinvögeln, die zumal in den letzten zehn Jahren ihr Verbreitungsgebiet in Finnland auffallend rasch erweitert haben. Es sind demnach von Jahr zu Jahr immer zahlreichere Mitteilungen über Besiedlung neuer Orte durch diesen südöstlichen Vogel eingelaufen, namentlich aus den westlichen Teilen des Landes. Es mag darum motiviert erscheinen, die augenblickliche Verbreitung des Karmingimpels innerhalb der gegenwärtigen Staatsgrenzen Finnlands in Kürze zu beleuchten. REINIKAINEN (1939) hat seinerzeit die Brutbiologie und Verbreitung des Karmingimpels in Finnland bis zum Jahr 1939 einer eingehenden Betrachtung unterzogen, und sein Aufsatz bietet demnach ein vortreffliches Vergleichsmaterial im Hinblick auf die Verhältnisse in der seitdem verflossenen Zeit. Karte 1 zeigt das Vorkommen des Karmingimpels im Lande gemäss den Untersuchungen von REINIKAINEN.

Vorliegende Zusammenstellung gründet sich auf verfügbare Angaben in der Literatur, ebenso sind zahlreiche Angaben über Nistlokale des Karmingimpels aus den Beringungsprotokollen für die Jahre 1940—55 zu entnehmen gewesen. Ergänzende Angaben sind ausserdem aus dem sog. Palménschen Archiv im Zoologischen Museum der Universität Helsingfors sowie aus der kürzlich gegründeten Nistkartothek der Finnischen Wissenschaftssozietät erhalten worden. Im Frühjahr 1955 sandte das Zoologische Museum eine