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On certain morphic characteristics of the Northern European Bullfinch (Pyrrhula pyrrhula).

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Introduction.

It is well known to museum taxonomists, though not to field ornithologists in general, that the bullfinch displays considerable individual variations within single populations throughout the species range. Though apparently a true morphism, part of this variation is, however, more or less quantitative in character. This is true of the dimorphism occurring in the males, some of which are noticeably more brightly coloured on the under-parts than others, as well as of the females some of which are greyer and others browner on the upper-parts of the body. We are not concerned with these variations here.

There are, however, two other morphisms which are more or less purely qualitative in character, i.e. the individual morphs or phases can easily be grouped into distinct classes. The first of these morphisms occurs in both sexes, and is determined by the outermost tail feathers which may or may not be streaked or spotted with white on the inner web. The second one, found only in males, concerns the grey of the mantle, which may be suffused with pink or totally lack this suffusion.

It should be pointed out here that the present author would perhaps never have interfered in this matter, to say nothing of breaking into the discussion on conditions prevailing outside his native country, had not the treatment of the subject (HARRISON 1958) remained regrettably open to criticism as far as the statistical handling of the material, includin that from Finland, is concerned. Due to this statistical error the conclusions drawns are incorrect in some respects and, consequently, no direct comparisons between the Finnish population and those mentioned in Harrison's study are possible on the basis of the figures presented.

The aim of this study is to submit these geographically varying morphisms to a re-examination and to extend the study material for Northern Europe to include Sweden as well as Finland.

Material.

The material studied comprises 41 males plus 26 females from the Zoological Museum of Helsinki University, and 84 males plus 46 females from the Museum of Natural History in Stockholm, or a total of 197 specimens from Northern Europe.

As is usually the case with museum collections, only a comparatively small number of the individuals are from the breeding season: 7 specimens (or 10.3 $^{0}/_{0}$) in the Finnish collection, and 16 specimens (or 12.3 $^{0}/_{0}$) in the Swedish collection (cf. also VOOUS 1949). Among these, only three individuals belong to the white-spotted morph (one male and one female from Värmland, Sweden, and one female from Helsinki, Finland), and not one to the pink suffused variety.

The Finnish material is not evenly distributed over the whole country. Nearly half the specimens $(45\ ^{0}/_{0})$ come from the Helsinki area and neighbouring districts. This is also true to a certain extent of the Swedish material, of which about a third (33.8 $^{0}/_{0}$) comes from the county of Uppland (the Stockholm and Uppsala area). But in general the material is distributed over the southern part of the country from Oulu down to the south coast in Finland, and from Lapland down to Scania (Skåne) in Sweden.

White-spotting on the tail feathers.

As mentioned above, this morphism is distinguished by the outermost tail feathers which are more or less distinctly spotted or streaked with white on the inner web in some individuals. The white marking occurs in both sexes and varies a great deal. It may be heavier on one side than on the other or it may occur on one side only. The size of the streaks ranges from a few mm to more than 2 cm in length in extreme cases. When the spots are small they appear as narrow streaks; when large they are more spot-like taking on an attenuated pear shape. The colour also varies from very slight grey shading to the almost pure white of the large spots.

The proportion of white-spotted individuals within the Finnish and Swedish populations is as follows:

Finland Sweden	17 25	out	of -	a »	total 	of	67 130	or »	25.4 19.2	± ±	5.3 % 3.5 »
N. Europe	42	out	of	a	total	of	197	or	21.3	±	2.6 %

There is a slight difference between the two countries, but it is not statistically significant. As we shall see later, however, their populations form part of a dimorph ratio cline in an east-west direction.

White spotting and sex. — The proportion of white spotting in the different sexes is as follows:

	Finnish	88	9	out of a total of	41 o	or	21.9	±	6.5 ⁰ /0	
	»	₽₽	8	»	26	»	30.8	±	9.1 »	
	Swedish	88	14	»	84	»	16.7	±	4.1 »	
	*	₽₽	11	»	46	>	23.9	±	6.3 »	
N.	European	88	23	out of a total of	125 o	or	18.4	±	3.5 %	
N.	European •	88 99	23 19	out of a total of	125 o 72 ⇒	»	18.4 26.3	± ±	3.5 ⁰∕₀ 5.2 »	

As we can see from the figures the incidence of white spotting is greater among the females in both cases. The difference, however, is not statistically significant.

Exactly the same tendency is to be observed throughout the species range as the material investigated by HARRISON (1958) clearly shows. This is also true of the so-called eastern group (i.e. for populations from the nominate subspecies eastwards), though HARRISON (op. c.) mistakenly suggests just the contrary. His error arises from the incorrect use of the histograms, in which the absolute number of the specimens possessing the characteristic was used to determine the »incidence» presented, and no attention was paid to the total number of specimens studied in each group. By correcting the error we arrive at the pertinent facts which are in good agreement with the general picture prevailing elsewhere (see the figures presented on p. 84). The difference between the sexes is very clear and statistically significant in both cases ($\chi^2_{(1)} = 18.69$, P=< .001; and 32.03, P=< .001 respectively).

One point still deserves attention. Not only is the incidence of white spotting higher in the female sex, but it has also been observed that the largest spots are to be found in the females, whose spots are, on an average, more heavily marked than those of the males. In the Finnish and Swedish material considered jointly, the proportion of large spots to small spots was 9:10 in the females and only 4:19 in the males. The difference, however, is not statistically significant $(\chi_c^2 = 3.08, P = .10 - .05, 1 \text{ d.f.}).$

Thus, our conclusion is that white spotting on the tail feathers, in itself varying in extent and in intensity of colour, displays quite a marked sexual dimorphism, in that the penetrance is considerably higher among the females. The expressivity is also different, being far less among the males. These tendencies are found throughout the easternmost populations, across the Finnish and Scandinavian areas to Western Europe and the British Isles.

White spotting and geographical distribution. — The characteristic in question represents quite a typical case of a geographically varying morphism. The following figures referring to the »eastern» and »western» populations have been computed from the histograms given by HARRISON (1958) who divided his total material into two groups. The first of these comprises the subspecies from the nominate race eastwards, i.e. pyrrhula (syn. jenisseiensis) cassini, griseiventris (syn. kurilensis, rosacea), rossikowi and caspica; the second concerns the following western subspecies: germanica, coccinea, europaea and pileata (syn. nesa, wardlawi). The proportion of the morph within these separate groups and within each of the sexes is as follows:

white spotted	\$ \$ \$ \$	31 25	out	of a 	total 	of	158 49	or »	19.6 51.0	± ±	3.2 ⁰ /0 7.2 »
Eastern populations		56	out	of a	total	of	207	or	27.1	±	3.1 %
white spotted	88 99	21 40	out	of a	total	of	247 128	or or	8.5 31.3	± ±	1.8 %/0 4.1 »
Western populations		61	out	of a	total	of	375	or	16.3	±	1.9 %

As can be seen from the figures above and from those relating to the Scandinavian populations (see p. 83), the proportion of white spotted individuals varies considerably with geographical location. Arranged in order from east to west we get the following picture:

Eastern p	opulations	$27.1 \pm$	3.1 %	white spotted
Finnish	>	25.4 ±	5.3 »	»
Swedish	*	19.2 ±	3.5 »	»
Western	*	16.3 ±	1.9 »	»

Thus, there is a decreasing cline from east to west. It should, however, to be noted that HARRISON'S »eastern group» also included the races *pyrrhula*, *rossikowi* and *caspica* in addition to the more eastern races, within which the incidence of white spotted individuals is the highest, especially within the Kamchatkan subspecies *cassini* (see e.g. VOOUS 1949 and HARRISON 1958). It is, therefore, probable that the proportion within the easternmost populations is higher than indicated. The cline running from Western Europe through the Fennoscandian populations towards the east is apparently steep along its eastern slope too. In any event, the difference (10.8 %) between the outermost populations mentioned above is clear and statistically significant ($\chi^2_{(1)} = 9.66$, P=< .005).

As the opposite western end the cline also appears to be comparatively steeps as can be seen from the figures presented above. Though not statistically significant ($\chi^2_{(1)} = 3.24$, P= .10-.05), the difference $(9.1 \ 0/0)$ between the Finnish and Western European populations is guite appreciable. The position of the Swedish population, within the cline in question, does not appear clearly enough from these figures. But if we examine the Swedish material in more detail we realize that there is an appreciable difference in the polymorph ratio between the southern and northern populations of that country. The specimens taken from the counties of Skåne, Halland, Småland and Öland (34 in all) represent the southern population in our material, and those (96 in all) originating from the counties of Värmland and Södermanland northwards represent the northern population (there is only one specimen from the central region of West- and East-Götland and Bohuslän). The indicence of the morph within these two separate areas is as follows:

white spotted &	33 22	14 out 8	of a total of 	67 oi 29 →	20.9 ± 27.6 ±	± 4.9 % ± 8.3 »
northern population		22 out	of a total of	96 oi	22.9	± 4.3 %
white spotted a	\$ \$ 2 Q	0 out 3	of a total of 	17 or 17 »	0.0 17.6 <u>+</u>	⁰/₀ 9.2 →
southern population		3 out	of a total of	34 or	· 8.8 ±	= 4.8 º/o
			$\chi^2_c =$	= 3.29,	P = .10	05, 1

The difference $(14.1 \ ^{0}/_{0})$ is indeed fairly large though statistically not quite significant. It shows that the polymorph ratio cline probably changes fairly abruptly somewhere in Sweden between 59° and 57°N.

It would appear from these figures that the incidence of the morph is comparatively high within the western populations of Europe. If we examine each sex separately we get the following interesting picture of the spatial changes of the morph ratio:

	males	females			
Eastern populations	19.6 ± 3.2	51.0 ± 7.1			
Finnish —»—	21.9 ± 6.5	30.8 ± 9.1			
N. Swedish —»—	20.9 ± 4.9	27.6 ± 8.3			
S. Swedish —»	0.0	17.6 ± 9.2			
Western	8.5 ± 1.8	31.3 ± 4.1			

It is apparent that the incidence of white spotted individuals tends to rise in both sexes, but especially among the females of the western populations. This challenges us to a further scrutiny of the conditions prevailing in Western Europe. We must investigate the circumstances which reverse the cline in the west.

For this the histograms presented by HARRISON (1958) serve as a basis. HARRISON (op.c.) suggested that the incidence of the morph is greater among the females of the two western insular races, *nesa* (Great Britain and Ireland) and *wardlawi* (Scotland) as compared with the races of Continental Europe, *coccinea* and *germanica*. This again was based on a misuse of the histograms and led him, in this case too, to erroneous conclusions.

The relevant figures computed from the histograms presented by HARRISON (op.c.) for each of the four races mentioned are as follows:

			spec	imens
	males	females	white	total
germanica	10.4 ± 4.4	15.4 ± 10.01	5 + 2	48 + 13
coccinea	11.1 ± 4.7	22.2 ± 7.9	5 + 6	45 + 27
nesa	10.7 ± 3.4	13.2 ± 2.7	9 + 21	84 + 159
wardlawi	15.2 ± 6.2	52.9 ± 12.1	5 + 9	33 + 17

There is no appreciable difference between the populations as regards the male sex. As the statistical calculation for the females shows, there is no significant difference between the English populations (ie: *wardlawi* and *nesa*) and those of Continental Europe $(\chi_c^2 = 0.05, 1 \text{ d.f.})$ or between the former and *coccinea* $(\chi_c^2 = 0.15, 1 \text{ d.f.})$ as suggested by HARRISON (op.c.). But what is most interesting is the fact that within the Scottish population (*wardlawi*) the incidence of the morph (52.9 ± 12.1) is distinctly different from that of the subspecies *nesa* (the difference is statistically significant with P=0.03 %, using Fisher & Yates' exact test for 2×2 contingency table) and from those of the continental subspecies *coccinea* $(\chi_c^2 = 8.04, 1 \text{ d.f.})$ and *germanica* (P=4.18 %, Fisher & Yates' exact test for 2×2 contingency table).

As we can now see, the apparent reversal of the cline is based on the subspecies *wardlawi*, not on the more southern *nesa* which represents the western end of the continental cline.

In conclusion, there are no grounds for the supposition made by HARRISON (1958) that where the species inhabits a wider, i.e. contiguous distributional area, the incidence is less. We cannot agree that insularity or the discontinuity of distribution would be correlated to the morph ratio in this special case. The subspecies *wardlawi* is an exception, but the subspecies *nesa* indicates that insularity as such cannot be the sole explanation.

Pink suffusion in the males.

The pink suffusion of the mantle represents a morphism limited to the male sex. It varies a great deal, from small pink zones on single feathers to a dense suffusion over the whole of the mantle. Due to this quantitative variation it is somewhat difficult to draw a demarcation line between the morph and the »normal» type. We have decided to classify individuals with a pink suffusion in one feather only as »normal» (three Swedish specimens out of a total 84 males), and those with more as belonging to the pink suffused morph. The proportion of males possessing a pink suffusion on the mantle within the Finnish and Swedish populations is as follows:

Finland	9	out	of a	total	of	41	or	21.9	±	6.5 %)
Sweden	13		»			84	*	15.5	±	3.9 »
N. Europe	22	out	of a	total	of	125	or	17.6	±	3.4 %

There is no appreciable difference between the Finnish and Swedish populations ($\chi_c^2 = 0.41$, 1 d.f.). Furthermore, the Swedish population seems to be uniform without any appreciable difference between the northern and southern populations as was the case with white spotting.

Pink suffusion and geographical distribution. — The pink suffusion of the male is considered to be an eastern characteristic as it commonly occurs in the Kamchatkan subspecies cassini and in P.p. griseiventris (HARRISON 1958). Here again, however, exact figures are lacking.

It is a curious accident that the percentages of the morph, within both the Finnish and Swedish populations, are nearly exactly the same as those relating to white spotting in the males from the same areas. Though we do not attach much importance to this accident, it may well indicate, however, that the respective populations belong to the eastern group in this respect too.

It is possible that they also form part of a decreasing cline from east to west. In any event, the figures computed from the histograms presented by HARRISON (1958, Fig. IV) show that the incidence of pink suffused males is considerably less within the western populations of Europe (coccinea + nesa + wardlawi treated together), viz. 17 males out of at total 247 or 6.9 ± 2.6 %. The difference (10.7 %) between the Western European and the Northern European populations is statistically significant ($\chi^2_{(1)} = 9.05$, P=.005-.001).

As regards the so-called eastern group in HARRISON's study the incidence of the morph in question is surprisingly low, even lower than that of the western group, viz. 9 males out of a total or 158 or 5.7 ± 3.4 %. This is in strong contradiction to our data on the conditions prevailing in Northern Europe and probably within the eastern group in general. This controversy can be explained in two different ways: Either there is a great difference in opinion about what degree

of pink suffusion constitutes a separate morph or, more probably, there are several populations having very low incidence included in this group.

In any event, there is no support for HARRISON's suggestion (op. c.) that the western group has a greater incidence of the pink suffused morph than the eastern populations. Even the histograms in his Fig. IV do not support this view.

Thus, our conclusion is that at least within the northern group of the species the incidence of the morph steadily decreases from the eastern populations (cassini, griseiventris) westwards across the nominate race to the Western European representatives (coccinea, nesa, wardlawi) of the species. It may well be that the subspecies wardlawi also tends to be more "eastern" in character in this respect as is the case with the white spotted morph. The relevant figures, however, are lacking and further study would be rewarding here.

Discussion.

The morphisms in the Bullfinch represent a fairly typical geographically varying polymorphism with more or less clear polymorph-ratio clines sloping in certain geographical directions over large parts of the species area. In such cases, as experience shows, the character gradients (morph ratio clines in this case) are usually more or less clearly correlated with certain environmental gradients, thus revealing the adaptive nature of the morphic variation or its firm correlation with some other (cryptic) adaptive features of the species. Such being the case, the morphic species effectively serve as ecological indicators, which register very sensitively the possible sudden changes in the slope of the ecological gradients (VOIPIO 1956, 1957). When, on the other hand, no ecological changes are discernible within zones marked by a sudden jump in the morph ratio cline, it is a sign of a secondary contact between the populations thus casting light on the chorology of the populations in question (VOIPIO 1961 a, b). It is, therefore, only natural that in the morphism of the Bullfinch there are also some interesting relations which deserve to be studied.

Our knowledge is too scanty, it is true, to detect clearly defineable zones of sharp slope of the morph ratio cline correlated with environmental gradients. But in two instances the material studied reveals more than the mere fact that there is one or probably two decreasing

89

clines of the morph ratios from east to west within the northern group of the Eurasian Bullfinches.

The first of these concerns the Swedish populations within which a relatively sudden change of the morph ratio is discernible in South Sweden between 59° and 57° North. Though statistically not quite significant, there still remains more than 90 per cent probability that the populations on the two sides of this zone of change are morphically different. This corresponds exactly to the established fact that the South Scandinavian Bullfinches are slightly smaller, on an average, than the more northern birds thus showing a slight west European influence. According to VOOUS (1949) the explanation for this phenomenon might be in the extension of the Western and Central European forest birds into southern Sweden during the late Boreal period. If so, there is a secondary contact zone between two population waves pushing from opposite directions. This is also reflected in the relatively sudden jump in the polymorph ratio cline. The supposed chorological relations of the Scandinavian Bullfinch population thus receive additional support from its polymorphic constitution.

The second case deserving special attention concerns the Scottish population *wardlawi* regarded by some authors as a weakly differentiated race not deserving a special subspecies name (see e.g. VAURIE 1956, 1959). In its dimensions and colouration this subspecies decidedly belongs to the western group derived from the southwestern refuge and represents, together with *nesa*, the northwestern offshoot of this group (Voous 1949). This being the case, one would expect that its morphic structure would also be, if not identical with that of the western Bullfinches and especially with that of *nesa*, yet a direct continuation of the decreasing cline of the white spotted morph. But such is not the case; instead of that the cline becomes reversed.

Two explanations may be offered for this. Either there are selective forces at work or the increased morph ratio is based on immigrants from the more remote populations characterized by a higher incidence of the morph. Owing to the lack of data it is difficult to decide between these two possibilities. The latter seem, however, to be more probable because of the ecology of the Scottish birds which are »almost strictly confined to ... coniferous biotope» (VOOUS op.c., p. 67). But so is the case also as regards the northern Fennoscandian populations which are characterized by »irregularly occurring autumn migrations, which sometimes involve whole populations» (VOOUS op.c., p. 72). As has been pointed out by various authors (e.g. VOOUS op.c., HARRISON 1958) these migrations, sometimes in the nature of invasions, are well-established in Great Britan and Central Europe. One must therefore allow for the possibility of a gene flow from Scandinavia into the northern parts of the British Isles. The ecological similarity as regards the biotope of the populations concerned may be the factor which allows the northern migrants to settle down here and there in the coniferous zone.

Summary.

Two separate morphisms of the Bullfinch have been examined: the white spotting of the outermost tail feathers occurring in both sexes and the pink suffusion of the mantle occurring in the males only.

The study is based on material comprising 197 specimens from the Northern European populations which makes it possible to compare them with those of Western Europe studied by other authors.

The white spotting displays quite a marked sexual dimorphism in that the penetrance is considerably higher among the females. The expressivity is also different being far less among the males.

These tendencies are to be seen throughout the whole species range, i.e. the incidence of the morph is higher among the females in all the populations so far studied.

The proportion of the white spotted individuals varies geographically. There is a decreasing cline from east to west.

Within the Swedish population a relatively abrupt jump in the morph ratio cline is discernible between 59° and $57^{\circ}N$. It probably reflects the secondary contact zone between the northern and western Bullfinch populations which slightly differ in other taxonomic features also.

The Scottish population (subsp. *wardlawi*) which is to be regarded as the northwesternmost offshoot of the western group shows a reversal of the cline. A slight gene flow from the irregular immigrants of the northern populations with the same ecological requirements as regards the biotope may be the correct explanation for this.

The pink suffused morph is probably also relatively more common within the eastern populations from which a decreasing cline runs through the Fennoscandian populations into the Western European countries. No stepped zones nor any reversals are to be seen in this cline. As regards the Scottish population the material, however, does not allow any precise conclusions in this respect.

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Selostus: Pohjoiseurooppalaisten punatulkkupopulaatioiden eräistä polymoriisista piirteistä.

Kirjoituksessa tarkastellaan kahta punatulkulla esiintyvää, toisistaan riippumatonta polymorfista ominaisuutta. Näistä toinen koskee uloimpien pyrstösulkien valkotäpläisyyttä, jota esiintyy molemmilla sukupuolilla. Toinen koskee taas pelkästään koirailla esiintyvää muuten harmaan manttelin punaista vipevöintiä, jota eri vahvuisena tavataan muutamilla yksilöillä.

Pyrstösulkien valkotäpläisyydessä on havaittavissa varsin selvä sukupuolien välinen ero sikäli, että se esiintyy huomattavasti yleisempänä ja myöskin voimakkaampana naarailla kuin koirailla. Tämä ero on todennäköisesti vallalla koko lajin asuinalueella, sillä kaikissa tähän asti tutkituissa populaatioissa valkotäpläisten naaraiden prosenttiluku on ollut korkeampi.

Valkotäpläisyyden prosenttisessa edustuksessa esiintyy selvää maantieteellistä muuntelua. Kysymyksessä on aleneva kliini Itä-Aasiasta Fennoskandian kautta Länsi-Eurooppaan.

Ruotsin eteläpuoliskossa 59. ja 57. leveysasteen välillä esiintyy kliinissä suhteellisen nopea hyppäys. Tämä vyöhyke todennäköisesti vastaa taksonomisesti toisistaan myös muissa suhteissa vähäisessä määtin eroavan pohjoisen ja läntisen punatulkkupopulaation välistä sekundaarista kontaktivyöhykettä.

Länsieurooppalaiseen punatulkkuryhmään taksonomisesti kuuluvassa Skotlannin populaatiossa kliinin kulku muuttuu päinvastaiseksi. Tämä johtuu mahdollisesti siitä, että invaasionluontoiset syksyiset muutot Skandinaviasta Brittein saarille yhdessä immigranttien ja Skotlannin residenttien punatulkkujen samanlaisten biotooppivaatimusten kanssa saavat aikaan vähäisen geenivirran pohjoisesta käsin Skotlannin havumetsäalueelle.

Myöskin punaisen vipevöinnin prosenttisessa edustuksessa on havaittavissa vastaava aleneva kliini idästä yli Fennoskandian alueen. Tässä kliinissä ei kuitenkaan ole havaittavissa hyppäysvyöhykkeitä eikä kääntymistä kulussaan vastakkaiseksi.