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# The geographical variation of the Jay *(Garrulus glandarius)* in Europe: a study on individual and clinal variation*)

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CONTENTS:

## 1. INTRODUCTION.

Ever since it became apparent that terrestrial animals ranging over large continental areas generally showed a certain degree of *gradual geographic variation,* attention has been focused on the colour variation of the Jay, *Garrulus glandarius,* in Europe. Surely the Jays belong to those species of palearctic land birds in which the formation of geographical differences must be considered to be exceptionally favoured: HARTERT (1903—1922; including HARTERT & STEINBACHER 1932) re-

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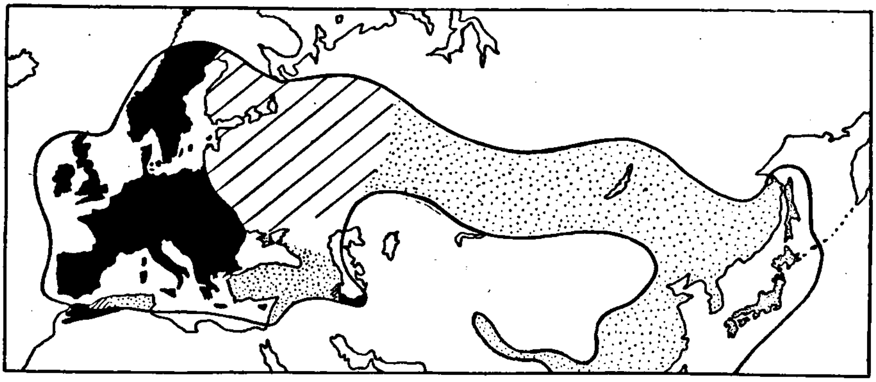

*Figure 1.* Distributional area of the Jay, *Garrulus glandarius*. The area of the group of European subspecies is *black* ; the other subspecies groups live in the remaining parts of the range (*dotted*). Hybrid zones with the European group are transversely *striped*.

cognized as many as 10 European races of the Jay by name, whereas KLEINER (1935—38) in his monographic treatment of the species numbered as many as 9 races in the same region. In several instances of the geographic variation of the Jay the differences are exceedingly striking, e.g. between the reddish brown Jays from Ireland and the dark grey ones from northern and central Europe. Still, the intergradations are so gradual and the individual variation is so unexpectedly large, that the application of subspecific names as a method of expressing geographical variation has proved to meet with serious difficulties. The resulting confusion of names for years has stressed geographical differences being of only minor importance and has obscured others meriting a closer attention.

However, it was not at all for nomenclatorial purposes that this study was started, nor in order to propose a new arrangement of the geographic races of the Jay in Europa. That, in spite of this, these topics have been dealt with in one of the following chapters of this paper must be explained from the fact that the author failed to see a possibility to avoid them. The main purpose of this study was to investigate instances of "*clinal variation*", meaning the presence and the origin of geographical character gradients. "Character gradients in the frequencies or in the expression of variable characters" (DOBZHANSKY 1947, p. 67) occurring in continuous geographical areas have seriously attracted the attention of students of population genetics and of micro-evolution. Hence it seemed worth while to select a suitable subject for a comparison of local individual variation with geographical variation and to study the origin of the clines. This is what the author has tried to do in the course of the present study on *Garrulus glandarius*.

To this study are added some theoretical remarks on the *post-glacial dispersal* of the Jay in Europe. These zoogeographical speculations may not only serve as a back ground to the origin of the development of the clinal variation in the European Jay, but they also intend to add some new evidence for the reconstruction of the history of the dispersal of forest birds in Europe after the last Ice Age. Finally it is the author's belief that apart from environmental influences (temperature, rainfall, vegetation) a close correlation exists between the course of present-day clines in European forest birds and the historic way of the post-glacial dispersal of these birds.

Throughout its total range in the palearctic region, from the Atlantic to the Pacific Ocean, the Jay occurs in a number of subspecies that can be grouped above the subspecies level (fig. 1). For example there is a group of brown-headed Asiatic subspecies with black crown stripes, one of plain brown-headed subspecies, one of black-capped subspecies, and a few others (*cf*. VOOUS 1945). The present study on European Jays deals with the representatives of only one group, *viz*. the vinaceous-grey group with striped heads, having a typically European distribution. In Asia Minor, Tunesia and North Algeria representatives of the black-headed group occur, but the Jays from Cyprus, Marocco and South Algeria belong to the European striped-headed group. Only in eastern Europe brown-headed Asiatic populations have penetrated into the range of European subspecies, resulting in the origin of a large *hybrid zone* in Russia and adjacent countres in eastern Europe. In a special chapter the border zone of hybridisation between these two very distinct groups will be discussed.

## 2. MATERIAL.

A total of 965 specimens of *Garrulus glandarius* from all over Europe has been critically examined, as well as some 100 rather superficially, belonging to 18 museums from 11 different countries and 4 private collections from 3 countries: Zoological Museum Amsterdam (Netherlands), Natural History Museum Basel (Switzerland), Zoological Museum of the University Bergen (Norway), Zoological Museum of the University Berlin (Germany), Museum "ALEXANDER KOENIG", Bonn (Germany), Royal Belgian Institute for Natural Sciences (Royal Museum of Natural History), Brussels (Belgium), Zoological Museum of the University Copenhagen (Denmark), National Museum of Ireland, Dublin (Ireland), "SENCKENBERG" Museum, Frankfort on Main (Germany), Natural History Museum Göteborg (Sweden), Natural History Museum Leiden (Netherlands), British Museum Natural History, London (England), Natural History Museum Malmö (Sweden), American Museum of Natural History, New York (U.S.A.), Zoological Museum of the University Oslo (Norway), Natural History Museum Stavanger (Norway), Royal Museum of Natural History Stockholm (Sweden), Ornithological Institute Zagreb (Yugoslavia); collection HENS (Valkenburg, Netherlands), collection MAYAUD (Saumur, France), collection PAYN (Andover, England), collection SILLEM-VAN MARLE (Bussum, Netherlands).

## 3. ACKNOWLEDGEMENTS.

To all those who kindly and most unselfishly helped the author in gathering the necessary amount of study material, as well as to all those who kindly supplied him with useful information, the author feels himself highly indebted. These are: Dr. D. AMADON (New York), H. BERGMAN (Malmö), Prof. Dr. H. BRATTSTRÖM (Bergen), Dr. B. GOIKOVIC (Serbian Museum of Natural History, Belgrade, Yugoslavia), H. GRÜN

(Salamanca, Spain), Count Dr. N. GYLDENSTOLPE (Stockholm), P. A. HENS (Valkenburg), Dr. H. HOLGERSEN (Stavanger), Prof. Dr. H. JOHANSEN (Copenhagen), Dr. A. VON JORDANS (Bonn), Dr. G. C. A. JUNGE (Leiden), Dr. O. KLEINSCHMIDT (Wittenberg), Z. KLUZ (Museum FRIC, Lázne, Belohrad, Czechoslovakia), G. LAURENT (Remomeix, France), Prinz HANS VON LIECHTENSTEIN (Vaduz), Mag. B. LÖPPENTHIN (Copenhagen), E. D. MAALDRINK (Wierden, Netherlands), J. D. MACDONALD (London), J. G. VAN MARLE (Bussum), N. MAYAUD (Saumur), Dr. E. MAYR (New York), R. NETTERSTRÖM (Bollnäs, Sweden), Dr. O. NYBELIN (Göteborg), Lt. Col. W. A. PAYN (Andover), W. J. PLOWDEN-WARDLAW (Kinloch Rannoch, Scotland), Miss G. ROCHE (Dublin), D. RUCNER (Zagreb), Dr. F. SALOMONSEN (Copenhagen), Dr. J. STEINBACHER (Frankfurt on Main), C. STÖP-BOWITZ (Oslo), Prof. Dr. V. VAN STRAELEN (Brussels), Prof. Dr. E. STRESEMANN (Berlin), Dr. E. SUTTER (Basel), Dr. R. K. VERHEYEN (Brussels), J. WILLGOHS (Fjösanger, Norway).

Important examinations were made during study journeys to the British Museum and to Danish, Swedish and Norwegian collections in 1949 and 1950. For the greater part the expenses of these journeys were supported by the *"Netherlands Organisation for Pure Research"* (z.w.o.), The Hague. The author appreciates it having the occasion of expressing his thanks to Board and Director of this Institution. Not only at home, but particularly in the foreign museums visited, the author has received very great help from his wife, a most pleasant circumstance, which is thankfully acknowledged in this place.

Many hours of discussion with my friend Mr. J. G. VAN MARLE have in the course of more than eight years gradually spread some light in my mind on the variation problems discussed in this paper. I am sure that without the help of VAN MARLE's critical mind the discussion in this paper would have been even more incomplete.

## 4. CLINES.

HUXLEY (1938) introduced the term *"cline"* originally to denote "a gradation in measurable characters". It was intended to be an auxiliary principle in taxonomy and as such it was discussed again more elaborately shortly after its introduction into science (HUXLEY 1939). Much attention was then devoted to the classification of a great number of kinds of clines, but time appeared to be ripe only for the acceptance and full use of the principle expressed by a *"continuous cline"*. Such clines are thought to "occur when the whole population considered constitutes a single inter-breeding unit. The cline is than a continuous line and a biological as well as a geographical reality" (HUXLEY 1939, p. 494). It is in this sense that the term „cline" has received general acceptance and it is in the restricted sense of such internal clines that the word will be used here.

In spite of the fact that in recent years the presence of numerous clines has been indicated, especially by ornithologists, only few of them have been actually described (MURPHY 1951). Instructive, but fragmentary examples have been clearly summarized by MAYR (1942) and DOBZHANSKY (1947).

A cline can be recognized by the gradual geographical change in one or more of the variable characters. Generally this gradual change refers to the average condition of populations and not of individual specimens. As a consequence details of clinal variation can only be studied when the frequency curves of the individual variation throughout most of the range is known (*cf.* Voous 1950). It then will turn out that the study of but few individual specimens cannot contribute to the understanding of a cline, particularly not when local individual variation is large. Therefore, in the present treatment on clinal variation in Jays attention will be focused on geographical differences in the curves of individual variation.

It is well-known that clines occur "most commonly and most typically where continuous series of populations are found, such as in unbroken continental areas" (MAYR 1942, p. 97). The practical result is, that in most of the clines no clear line of separation exists between the races which form a cline. DOBZHANSKY (1947) is right when he states — referring to a cline of the Ladybird Beetle, *Coccinella septempunctata,* that "the populations coming from geographically remote localities are often strikingly different, but intermediate populations are found in the intervening localities, forming a continuous chain of intergradations between the extremes" (p. 72). Everybody will understand that nomenclaturalists can hardly work with clines, especially not, when these cover large areas and connect conspicuous geographical differences. In cases that many of these differences are known in the literature by special subspecific (or even specific) names the whole picture of clinal variation can easily become obscured. As this actually appeared to have happened in the European Jays, this is a further reason why a renewed study of the geographical variation of this species was supposed to be necessary.

From MAYR's statements (1942) we get the impression that according to him most clines are the "results of adaptive power of natural selection by environment" (p. 96). As a consequence most clines can then be expected to occur in regions with many environmental differences. However, MAYR admits that "frequently the cline character seems to be quite independent of environmental gradients" (p. 96). Selection power of the environment (including sexual selection) or the regulation by internal factors must be considered as alternative views regarding the origin of a cline.

The genetical significance of a cline is discussed by MAYR (1942) and DOBZHANSKY (1947). In terms of genetics then a cline is considered to be a gradual variation in the frequencies of genes belonging to a complex of multiple factors. Admitted that this is right, we must search for the cause of this variation in the average number of multiple genes in populations from different localities. We may search into the direction of environmental factors being adverse to individuals carrying certain allele combinations, but it is equally possible that the differences are "based on the instability of certain genes and on the loss of alleles in the border populations of an expanding species" (MAYR 1942, p. 96). Here we denote the same alternative between selection through environment (including sexual selection) and the internal regulations through the instability or the elimination of certain genes (alleles). This problem will be discussed on the evidence provided by the individual and geographical variation of the European Jays.

## 5. THE VARIABLE CHARACTERS.

The great individual variability of European Jays is well-known. It was elaborately described by KLEINSCHMIDT (1893), who, moreover, showed that any correlation is lacking between geographic distribution and (1) the coloration of forehead and crown, (2) the development of the longitudinal black spots on the crown, (3) degree of blue-and-black cross-barring on the tail feathers and on (4) the dark crown stripes. Racial importance was ascribed by HARTERT (1903) and others to the coloration of the upper parts and to a less extent also to the wing length, the shape and length of the bill and the pattern of blue-and-black cross-barring on the primary coverts. In this study attention will be paid to (1) *coloration of upper parts*, (2) *coloration of under parts*, (3) *wing length*. Geographical variation in the length and shape of the bill appeared to be futile (see p. 26).

## 6. METHODS.

In order to compare local individual variation in coloration by means of frequency curves, two standard series were made of specimens covering the total range of the individual and geographical variation of the upper parts; in addition one standard series of variation of the under parts. The specimens have been arbitsrarily chosen out of the whole European range, but considerable care was taken to make sure that each standard specimen represented a gradual and minor intergrade in the total colour scala. The three standard series consisted of 14 and 11 (upper parts) and 10 specimens (under parts), respectively. The colour of each standard specimen was numbered and compared with the first edition of RIDGWAY's "*Color standards and color nomenclature*" (1912). In the course of this study each specimen examined has been directly compared with the standard series and a number for upper and under parts was subsequently assigned to it. This method resulted in the construction of normal frequency curves of every local population from which a sufficiently large number of *breeding specimens* was available for examination. The large numbers of autumn- and winter-specimens present in nearly all study-collections have not been incorporated in my examinations, unless specially mentioned in chapter 10.

## 7. COLORATION OF UPPER PARTS.

The extremes of the colour variation of the upper parts are:

(I) light vinaceous grey: between "*Light Cinnamon-Drab*" and „*Cinnamon-Drab*",

(II) dark reddish brown: between "*Rood's Brown*" and "*Pecan Brown*",

(III) dark grey: almost "*Deep Neutral Gray*".

Intergradations between these extremes are incipient and perfectly continuous and include most of the actual individuals.

Throughout the larger part of Europe the intergrades between light vinaceous grey and dark grey can be arranged in the following colour-classes (A—K):

A = between "*Cinnamon-Drab*" and "*Light Cinnamon-Drab*".
B = "*Cinnamon-Drab*".
D = between "*Russet-Vinaceous*" and "*Sorghum Brown*".
E = between "*Cinnamon-Drab*" and "*Benzo Brown*".
G = "*Brownish Drab*".
I = "*Hair Brown*".
J = "*Neutral Gray*".
K = "*Deep Neutral Gray*".

Reddish brown upper parts occur only in the British Isles and in the countries surrounding the North Sea, in western Germany and in parts of Scandinavia. In these regions the light vinaceous grey extreme has not been found by the author. Instead, the variation runs from a pure reddish brown to a dark grey extreme, with the following colour-classes as intergradients (1—14):

1 = between "*Rood's Brown*" and "*Pecan Brown*".
2 = "*Verona Brown*".
4 = "*Vinaceous-Russet*".
6 = between "*Russet-Vinaceous*" and "*Sorghum Brown*".
8 = between "*Cinnamon-Drab*" and "*Benzo Brown*".
10 = "*Benzo Brown*".
12 = "*Hair Brown*".
13 = "*Neutral Gray*".
14 = "*Deep Neutral Gray*".

TABLE 1.
Geographic variation of upper parts in per cent of specimens examined (*birds collected in the breeding season only*).

| *Region* | *light vinaceous grey tones* | *reddish brown tones* | *dark vinaceous grey and dark grey tones* |
|---|---|---|---|
| Ireland | — | 76% | 24% |
| England<br>Scotland | — | 76% | 24% |
| Netherlands | — | 66% | 34% |
| W. Germany | — | 31% | 69% |
| Denmark | — | 18% | 82% |
| Sweden | — | 5% | 95% |
| Norway | — | 15% | 85% |
| Finland | — | — | 100% |
| Sicily,<br>Italy | 50% | 40% | 10% |
| Yugoslavia | 17% | 34% | 49% |
| Bulgaria<br>Rumenia | 8% | 34% | 52% |
| E. Poland | — | 15% | 85% |
| W. Switzerland | — | 44% | 56% |
| S. Germany,<br>Liechtenstein,<br>N. Austria | — | 13% | 87% |
| Bohemia, Hungary,<br>migrants from Zagreb<br>and Sclavonia | — | — | 100% |
| Sardinia | — | 14% | 86% |
| E. Spain | — | — | 100% |
| W. Spain, Portugal | 50% | 10% | 40% |

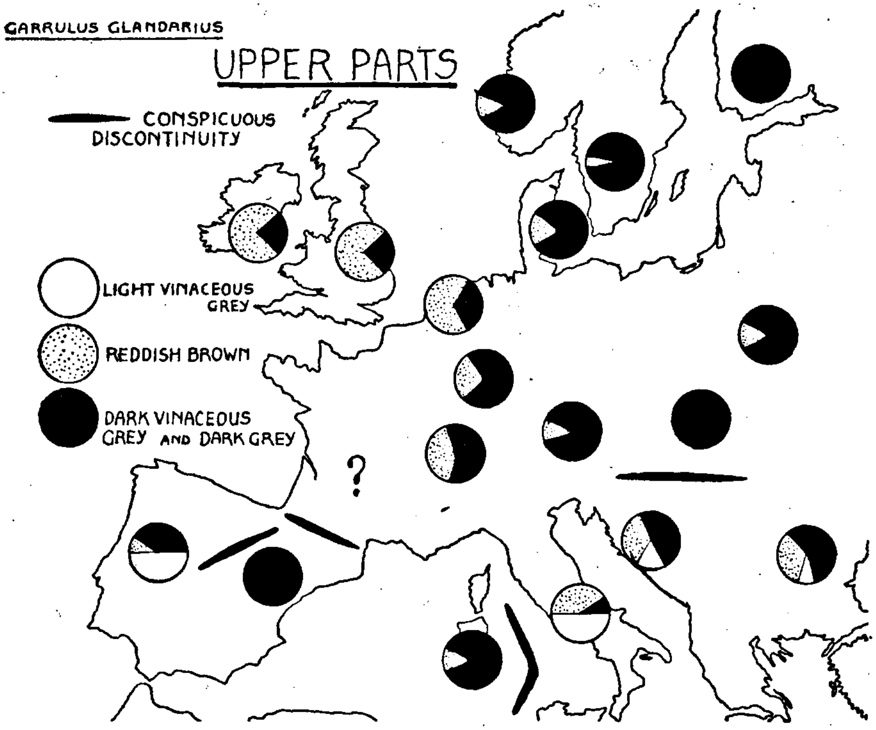

*Figure 2.* Individual and geographical variation of the colour of the *upper parts.*

It appears that the colour of the upper parts is determined by the quantitative proportion of the two types of brown feather pigments known as eumelanine and phaeomelanine. Although actual microscopical examinations of the feathers have not been carried on — an investigation which seems very prospective in view of the results reached by FRANK (1938) with *Parus atricapillus* — it seems that the dark grey colours are caused by the predominance of a large quantity of eumelanines, whereas the reddish brown extremes have a considerable surplus of phaeomelanines. The light vinaceous grey extreme, which is pale and neither pure grey nor reddish brown, seems to be the result of a relatively small quantity of both pigments of which the eumelanine (light grey tones) seems to predominate. All numerous colour shades connecting the above mentioned extremes seem to result from a mixture of the two pigments, differing considerably in the absolute and relative proportions both individually and geographically.

A scheme of the geographic variation of the coloration of the upper parts is given in table 1 and figure 2. The local proportions in per cent of the total number of specimens examined are given for the three main colour classes :

(I) the light vinaceous grey tones (A—B),
(II) the reddish brown tones (C—D ; 1—6),
(III) the dark vinaceous grey and dark grey tones (E—K ; 7—14).

The gradual increase in the proportion of phaeomelanine pigmentation (reddish brown) in the Atlantic countries is a very striking example of a regular cline (fig. 3). The optimum is reached in Ireland, where 76 % of the specimens are of a deep reddish brown tone. The opposite optimum is in Sweden, where grey largely predominates (95 %).

The population in western Norway seems to differ from the Swedish one by the higher frequency of reddish brown upper parts (15 %, against 5 % in Sweden). Unfortunately, Jays are at least very uncommon breeding birds in Norway west from the mountains, where actual breeding cases are unknown (HOLGERSEN, *in litt.* 1951). The influx of migrants from Sweden during the winter season, from which season of course most of the available specimens originated (*cf.* HOLGERSEN 1950), makes it seriously doubtful, whether the frequency curve for Norway (fig. 3) is a somewhat trustworthy reflection of the real condition of an equally doubtful W. Norwegian breeding population.

A second regular cline runs from Italy through southern and eastern France, western Switzerland, southern Germany and Austria, to Bohemia and Hungary, showing a considerable deepening and an increasing frequency of the grey tone (fig. 4). Indeed, the darkest grey upper parts were found in eastern central Europe, where 100 % of the individuals belonged to the grey colour classes, against 10 % in Italy. Evidently the general increase of grey colours into northern direction (Scandinavia) is also part of this cline (Sweden 95 %; Finland 100 %).

A conspicuous and marked change of coloration was observed between the Jays from Hungary and those from Yugoslavia, Bulgaria, and Rumenia (fig. 4). These latter populations tend to be considerably lighter, more browner and less grey, than those from central Europe (grey upper parts in less than 60 %, against in 100 % in Hungary). They are part of a regular cline of increasing greyness, which starts in Italy and terminates in Finland (fig. 5).

The difference in coloration of the upper parts between Jays from Italy and Sardinia is striking and well known (fig. 6). Sardinian Jays are conspicuous by their uniform grey upper parts (86 %, against 10 % in Italy). Not less striking, but never mentioned in the literature, is the difference between Jays from the eastern and the western parts of the Iberian peninsula (grey coloured upper parts occurring in E. Spain in 100 %, against in 40 % in W. Spain and Portugal; fig. 6), not to mention the distinctness between the birds from France and those from south of the Pyrenees.

## 8. COLORATION OF UNDER PARTS.

The extremes of the colour variation of the under parts are:

(I) buffish white, with the pure white coloration of the abdomen conspicuously extended: between "*Vinaceous-Buff*" and "*Tilleul-Buff*",

(II) vinaceous brown without white on the abdomen: "*Fawn Color*",

(III) dark vinaceous grey, sometimes lacking any tinge of vinaceous: "*Drab-Gray*".

Intergradation between these extremes runs into two distinct directions. Starting from a whitish underside variation can be noticed towards either the brownish or the greyish extreme. Both types of variation pass a

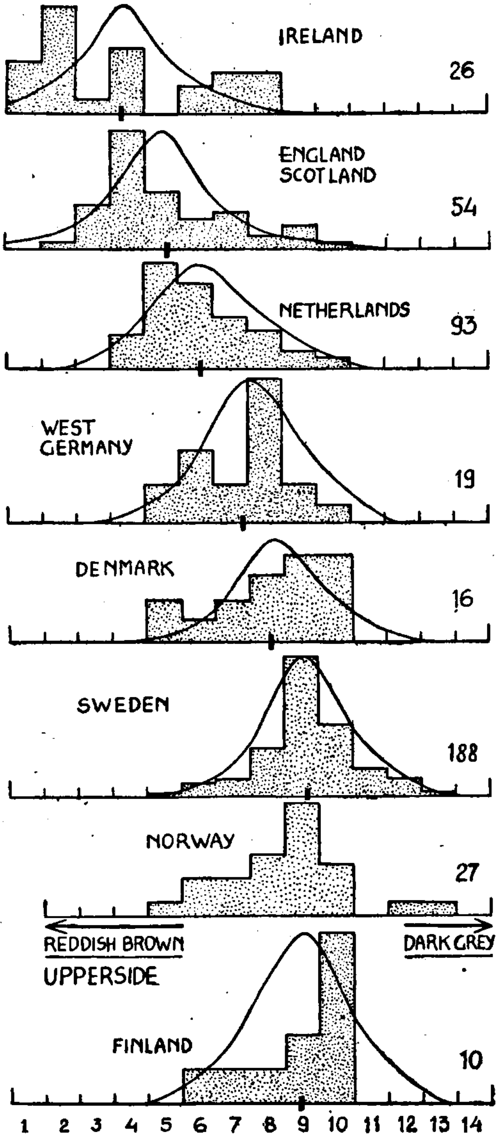

*Figure 3.* Diagrams and frequency-curves of the individual variation of the colour of the *upper parts*. The numbers 1—14 on the horizontal axis denote the 14 colour stages mentioned in chapter 7. The figure to the right of each diagram is the total number of specimens of each locality examined. The lengths of the columns indicate the number of specimens (in per cent) corresponding with a given colour class.

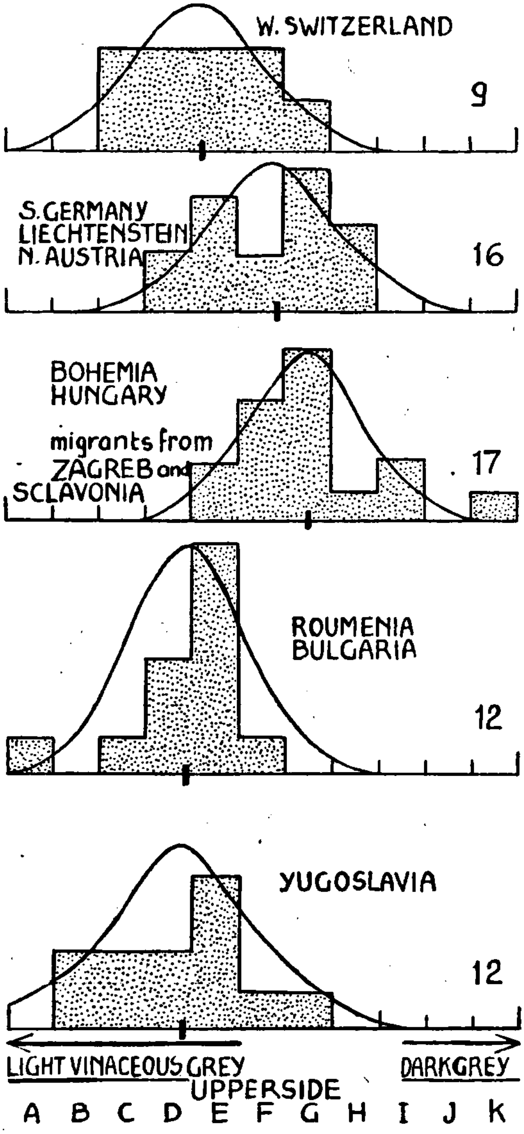

*Figure 4.* Diagrams and frequency-curves of the individual variation of the colour of the *upper parts*. The letters A—K on the horizontal axis denote the 11 colour stages mentioned in chapter 7. For further explanation see figure 3.

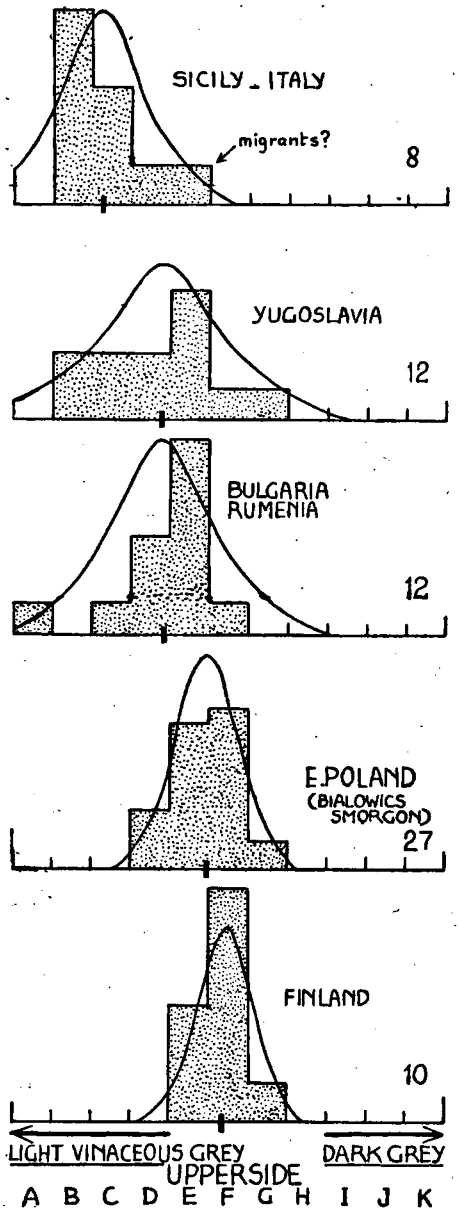

*Figure 5.* For explanation see figure 4.

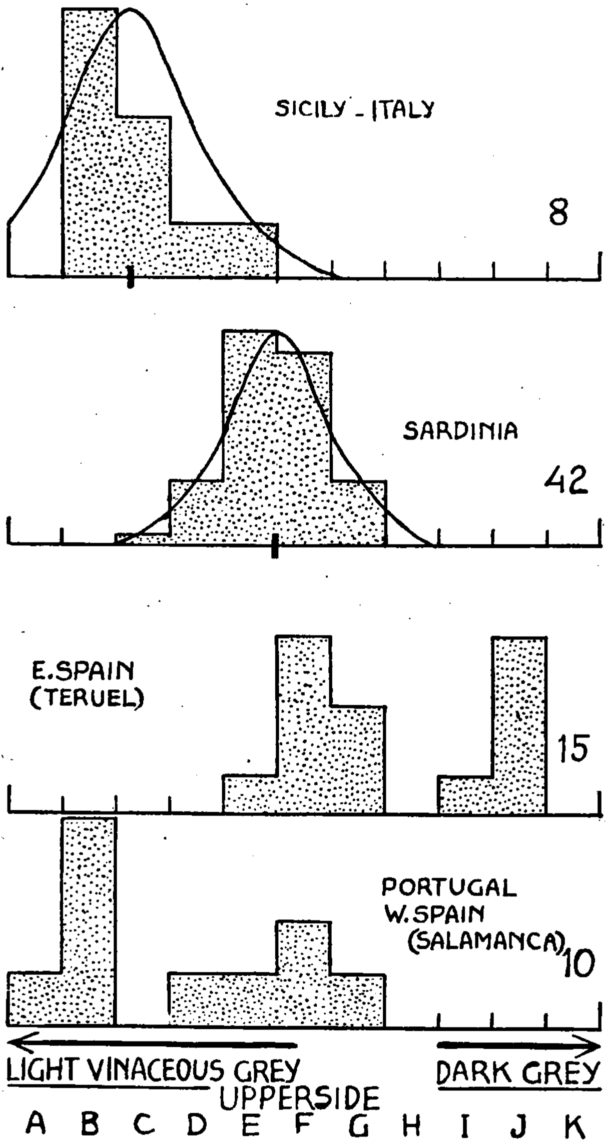

*Figure 6.* For explanation see figure 4.

"*Vinaceous-Buff*" colour gradient, which, therefore, is represented twice in the variation curves (II). However, in each instance only the proportional part if its entry into the curve is made black. The following colour shades of the under parts have been recognized (I—X):

I = between "*Vinaceous-Buff*" and "*Tilleul Buff*".
II = "*Vinaceous-Buff*".
III = between "*Vinaceous Fawn*" and "*Vinaceous-Buff*".
IV = "*Vinaceous Fawn*".
V = "*Fawn Color*".
VII = "*Light Cinnamon-Drab*".
VIII = "*Light Drab*".
IX = "*Cinnamon-Drab*".
X = "*Drab-Gray*".

TABLE 2
Geographic variation of under parts in per cent of specimens examined (*birds collected in the breeding season only*).

| *Region* | *whitish or buffish tones* | *vinaceous brown tones* | *vinaceous grey and grey tones* |
|---|---|---|---|
| Ireland | — | 100% | — |
| England, Scotland | 24% | 61% | 15% |
| Netherlands | 38% | 41% | 21% |
| W. Germany | 11% | 26% | 63% |
| Denmark | 19% | 31% | 50% |
| Sweden | 4% | 26% | 70% |
| Norway | — | 50% | 50% |
| Finland | 33% | 55% | 11% |
| Sicily, Italy | 62% | 26% | 12% |
| Yugoslavia | 32% | 16% | 50% |
| Bulgaria, Rumenia | 33% | 8% | 58% |
| E. Poland | 8% | 31% | 61% |
| W. Switzerland | 33% | 22% | 45% |
| S. Germany, Liechtenstein, N. Austria | — | 31% | 69% |
| Bohemia, Hungary, migrants from Zagreb and Sclavonia | — | 24% | 76% |
| Sardinia | — | — | 100% |
| E. Spain | — | — | 100% |
| W. Spain, Portugal | 50% | — | 50% |

As in the upper parts the coloration of the under parts depends on the relative abundance of the eumelanine and phaeomelanine feather pigments. The pigmentation firstly appears on the flanks and the sides of the breast, extending at last uniformly throughout the whole of the underside. The abdomen, which is pure white in the lighter variants, is the last part of the underside to be coloured with brownish or greyish tones. Chin and throat remain white and are often rather well defined, especially in individuals with a dark underside.

A scheme of the geographic variation of the coloration of the under

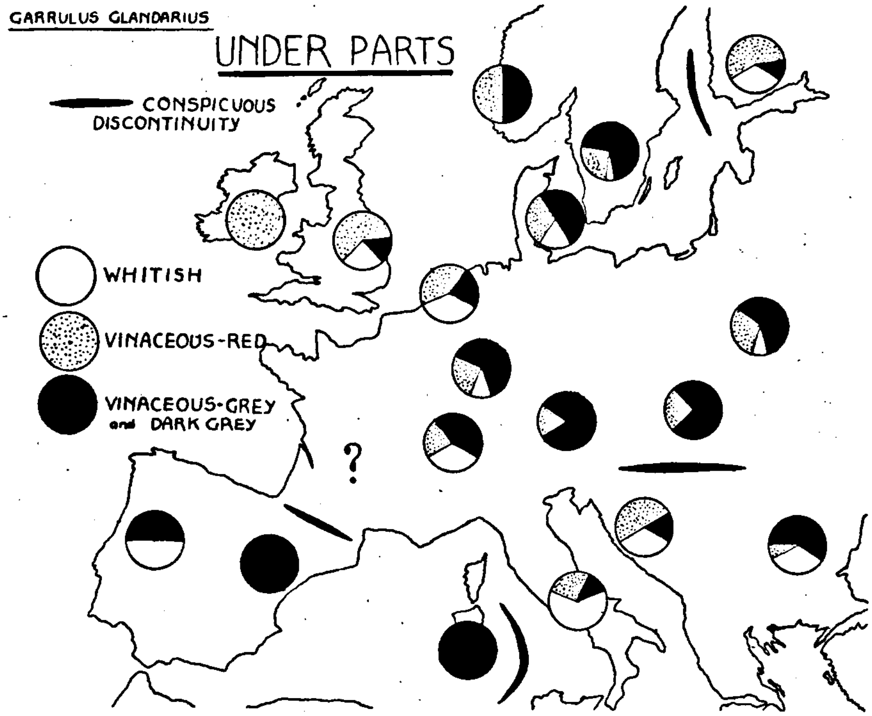

*Figure 7.* Individual and geographical variation of the colour of the *under parts.*

parts is given in table 2 and figure 7. The local proportions in per cent of the total number of specimens examined are given for the three main colour classes:

(I) the whitish or buffish tones (I—II),
(II) the vinaceous-brown tones (III—V),
(III) the vinaceous-grey and grey tones (VI—X).

There is a close correspondence in the geographical variation of the coloration of the upper and under arts; individuals having a generally grey upperside usually show much grey on the underside too.

A regular cline, similar to that noticed for the upper parts, is running through western and northwestern Europe, involving an increase of brownish tones on the under parts in the Atlantic countries (fig. 8). The optimum is reached in Ireland (100 %) and a minimum in Sweden (26 %). Simultaneously a decrease of specimens with whitish under parts is noticed. Again Norwegian birds differ from Swedish ones by the greater frequency of a brownish pigmentation (50 %, against 26 % in Sweden). For the amount of unreliability of the Norwegian curve see the previous chapter.

A second cline, in the figures starting in W. Switzerland and ending in eastern central Europe (Bohemia, Hungary; fig. 9), shows the decrease of whitish under parts (Switzerland 33 %, against 0 % in Bohemia and Hungary) and the almost wholly dominance of dark greyish colours in the terminal populations (76 %).

Marked discontinuities in the geography of the coloration of the under parts are noticeable (1) between Hungary on the one side and Yugoslavia, Bulgaria and Rumenia on the other side (over 32 % of whitish under parts in Yugoslavia. Bulgaria and Rumenia, against 0 % in Hungary; fig. 9.), and (2) between Sweden and Finland (11 % of greyish under parts in Finland, against over 70 % in Sweden). These discontinuities indicate the presence of a third, or East European, cline, starting in Italy and terminating in Finland (fig. 10). This cline shows a certain balance between the three main types of colour variation. In the same region a corresponding cline was found for the upper parts.

Not only on the upper parts, but also on the under parts the Jays from Sardinia are conspicuous by their greyness, differing in this respect greatly from those from Italy (fig. 11). Grey under parts occur in Sardinia in 100 % of the individuals, against in 12 % in Italy. A similar, though slightly less striking difference exists between the populations from E. Spain and those from W. Spain and Portugal (grey under parts occuring in 100 % and 50 %, respectively; fig. 11).

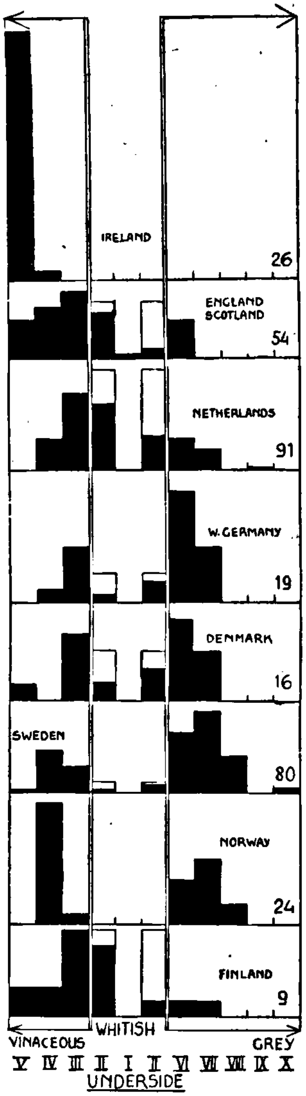

Fig. 8

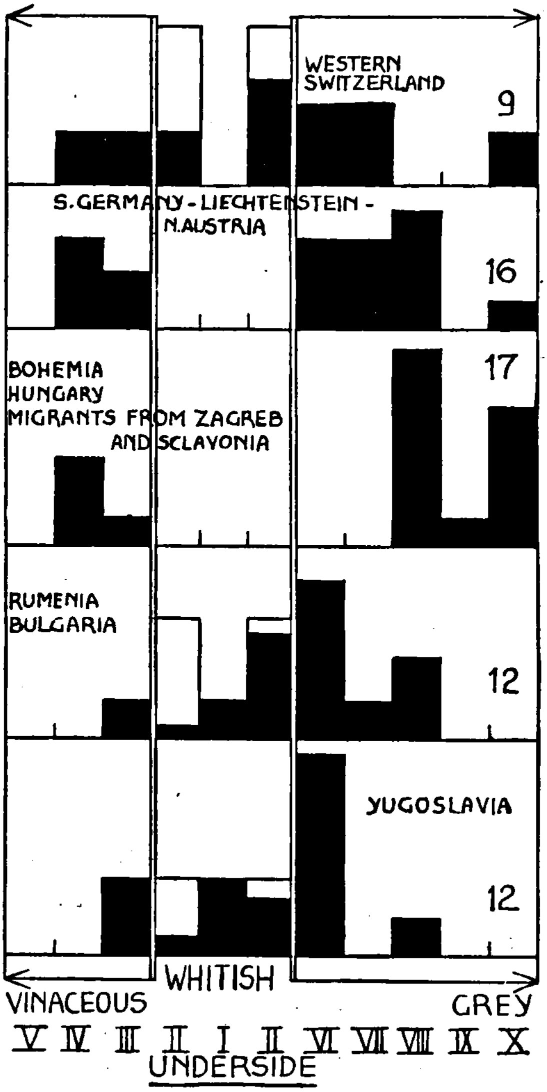

Fig. 9

*Figure 8*. Diagrams of the individual variation of the colour of the *under parts*. The Roman figures I—X on the horizontal axis denote the 10 colour stages mentioned in chapter 8. The figure to the right of each diagram is the total number of specimens of each locality examined. The lengths of the columns indicate the number of specimens (in per cent) corresponding with a given colour class.

*Figure 9*. For explanation see figure 8.

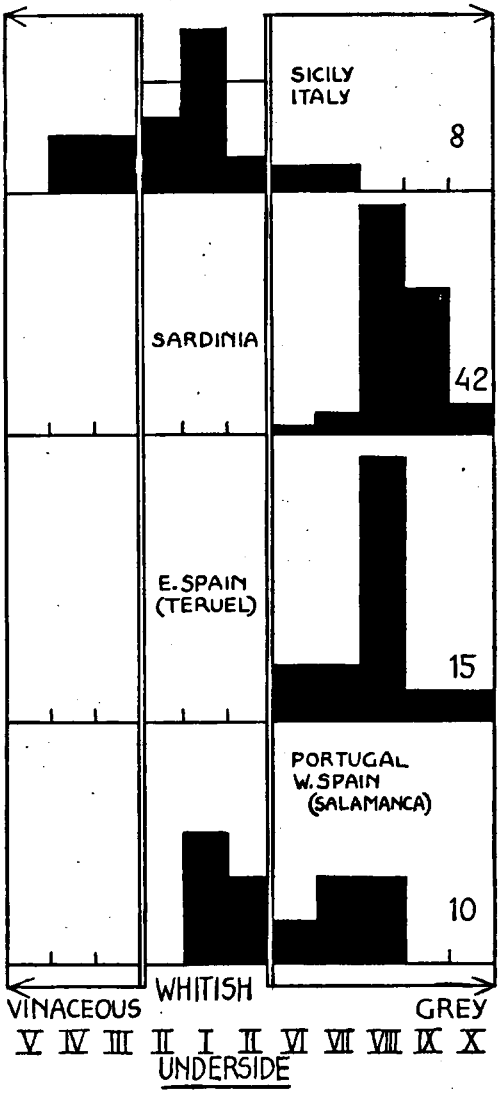

*Figure 10.* For explanation see figure 8.

## 9. DIMENSIONS.

Absolute differences in body size have been measured with the help of the length of the wing. European Jays do not vary much in size geographically, but the individual variation is very large. Females have at the average the wing a few millimeters shorter than males (tables 3—4). The limits of the variation run from 170 (Sardinia) up to 198 mm (W. Germany; Sweden) in males and from 165 (Sardinia) up to 196 mm (W. Switzerland) in females. It is probable, however, that the wing lengths of over 192 mm ascribed to females in reality belong to wrongly

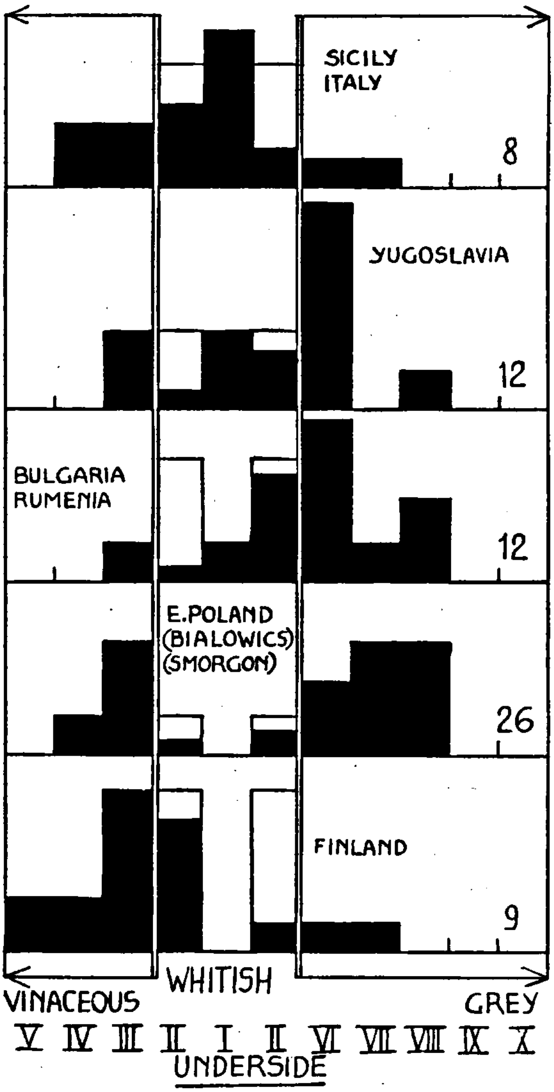

*Figure 11.* For explanation see figure 8.

sexed males. One male (from Denmark), which may be considered abnormal, appeared to be a real *giant,* having a wing of 204 and a tail of 163 mm (length of tail of 9 other Danish males 150—160, average 154.7 mm). It is: ♂, 31 March 1902, Frederiksvaerk, Zealand. Zool. Museum Copenhagen, Ny Kat. 41. 126.

According to the Rule of BERGMAN the smallest birds live in southern Europe (fig. 12). Starting in Sicily and Italy (average wing length of males 176.4 mm) a regular cline can be observed, passing through France, Great Britain, and the Netherlands and ending in Sweden (186.3) and Norway (186.8). In central Europe the mean dimensions are rather

Table 3.
Geographical variation in size. Wing length of males (mm).

| *Region* | *number of specimens* | *variation* | *mean* | *standard deviation* |
|---|---|---|---|---|
| Ireland | 17 | 176 —190 | 183.0 | 4.15 |
| England, Scotland | 20 | 172 —193 | 181.7 | 5.13 |
| W. France | 5 | 177 —184 | 179.4 | 2.50 |
| Belgium | 8 | 174 —191 | 181.2 | 4.47 |
| Netherlands | 47 | 174 —192 | 182.9 | 4.92 |
| W. Germany | 11 | 175 —198 | 185.5 | 5.82 |
| Denmark | 9 | 182 —192 | 187.2 | 2.72 |
| Sweden | 58 | 176.5—198 | 186.3 | 4.68 |
| Norway | 13 | 180 —197.5 | 186.8 | 4.24 |
| Finland | 7 | 179 —190.5 | 184.1 | 5.10 |
| Italy, Sicily | 5 | 172 —184 | 176.4 | 4.34 |
| Yugoslavia | 6 | 186 —196 | 188.8 | 4.34 |
| Bulgaria, Rumenia | 7 | 178 —196 | 187.0 | 6.26 |
| E. Poland | 15 | 178 —194 | 185.7 | 4.47 |
| W. Switzerland | 5 | 182 —193 | 186.8 | 4.07 |
| S. Germany, Liechtenstein, N. Austria | 7 | 183 —195 | 190.3 | 4.11 |
| Bohemia, Hungary, migrants from Zagreb and Sclavonia | 9 | 181 —196 | 186.2 | 4.60 |
| Sardinia | 18 | 170 —183 | 177.9 | 4.75 |
| E. Spain | 7 | 177 —192 | 187.4 | 4.55 |
| W. Spain, Portugal | 5 | 182 —193 | 187.2 | 3.54 |

stable, varying between 186 and 190 mm in males and between 183 and 186 mm in females. In this region no geographical discontinuities are apparant. Similarly, between Italy and Sardinia there are only minor differences (176.4 and 177.9 mm, respectively, in males), as is also the case between the eastern and western parts of the Iberian Peninsula (187.4 and 187.3 mm, respectively, in males). On the other hand the difference in size between birds from north and south of the Pyrenees is noteworthy. Another considerable discontinuity, hitherto unknown in the literature, exists between Italy and Yugoslavia (176.4 and 188.8 mm, respectively, in males). This discontinuity will prove to be of some importance in connection to further distributional speculations.

## 10. THE GEOGRAPHICAL VARIATION.

*Sicily* — Upper and under parts very pale. Upper parts very pale greyish vinaceous, somewhat paler than "*Vinaceous-Russet*". Middle of breast and abdomen almost white, near "*Tilleul-Buff*". Size small. Average wing length of males (including Italy) 176.4 mm. Material examined : 2.

*Italy* — The specimens examined were almost similar to those from Sicily, but the population may be slightly darker at the average. Material examined : 6 (including the type specimen of *Garrulus albipectus*

TABLE 4
Geographical variation in size. Wingt length of females (mm).

| *Region* | *number of specimens* | *variation* | *mean* | *standard deviation* |
|---|---|---|---|---|
| Ireland | 8 | 174 —188 | 179.5 | 4.09 |
| England, Scotland | 27 | 172.5—195 | 180.1 | 4.64 |
| W. France | 4 | 176 —178 | 177.2 | 2.63 |
| Belgium | 3 | 172 —182 | 178.0 | — |
| Netherlands | 43 | 170 —187 | 178.3 | 4.35 |
| W. Germany | 5 | 175 —183 | 179.2 | 2.64 |
| Denmark | 5 | 176 —187 | 180.6 | 3.77 |
| Sweden | 41 | 173 —189 | 181.9 | 3.59 |
| Norway | 9 | 177.5—185 | 181.7 | 2.31 |
| Finland | 3 | 180 —187 | 183.0 | — |
| Italy | 2 | 179 —185 | — | — |
| Yugoslavia | 4 | 182 —192.5 | 186.6 | 4.32 |
| Bulgaria, Rumenia | 4 | 182 —188 | 185.0 | 2 24 |
| E. Poland | 8 | 180 —190.5 | 184.8 | 2.98 |
| W. Switzerland | 3 | 184.5—196 | 186.5 | — |
| S. Germany, Liechtenstein, N. Austria | 5 | 179 —191 | 183.5 | 4.22 |
| Bohemia, Hungary, migrants from Zagreb and Sclavonia | 6 | 175 —186 | 179.3 | 4.10 |
| Sardinia | 21 | 165 —181.5 | 173.7 | 4.24 |
| E. Spain | 7 | 171 —190 | 180.6 | 6.21 |
| W. Spain, Portugal | 5 | 170 —180 | 175.6 | 3.44 |

KLEINSCHMIDT 1920); also a series in the British Museum (including non-breeding specimens).

*Western France* — Resembling Italy, but upper parts tending towards a more reddish brown coloration. Under parts somewhat less pure white, as the flanks are often tinged with vinaceous brown instead of with buffish grey. Size slightly larger at the average. In all characters intermediate between Italy and England. Material examined: 11 (Maine-et-Loire; Loire Inférieure; Finistère, Brittany; in addition a small series in the British Museum). A few specimens from Blois (Loir-et-Cher) in the collection of W. H. PAYN were also exacty intermediate in all regards between Italy and England (only breeding birds examined).

*England* and *Scotland* — Browner above and below than in W. France. Although the characters of several of the French specimens perfectly matched those of British ones, British Jays could most easily be distinguished by their strong tinge of vinaceous or brown on breast and flanks, whereas the abdomen is seldom as white as in W. France. It is possible that Scottish birds are at the average slightly greyer above and darker vinaceous grey below than English Jays. Size as in W. France. Material examined : 54 (Kent; Hampshire; Wiltshire; Herts; Norfolk; Montgomeryshire; York; Perthshire; the specimens originating from all seasons).

*Ireland* — Still more reddish brown than in England both above and below. The colour of the upper parts almost matches "Pecan Brown" or

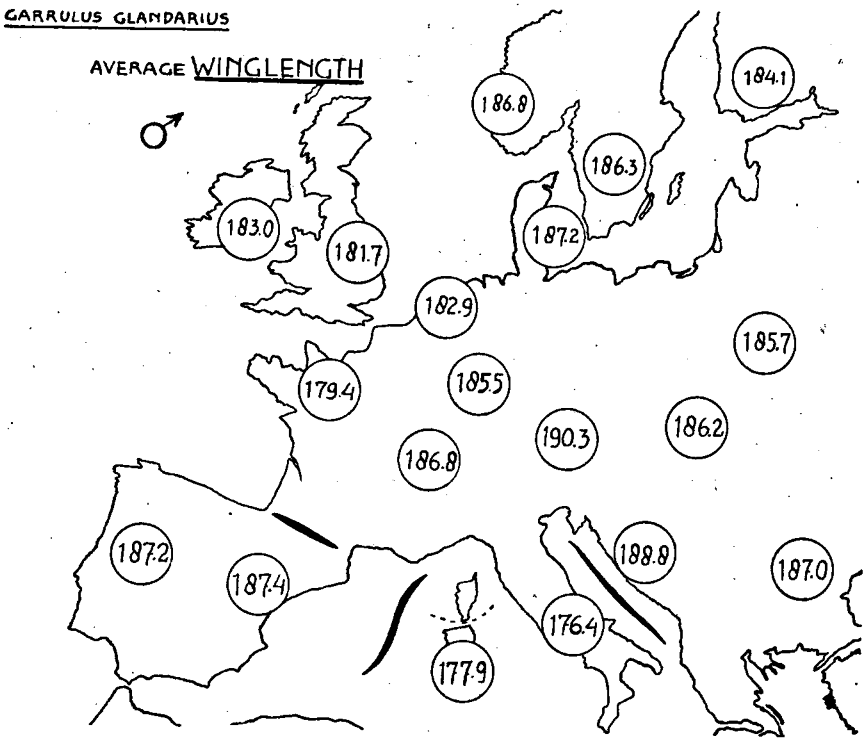

*Figure 12.* Geographical variation of size. The figures denote the average wing length of males.

"Rood's Brown", whereas the under parts tend even towards "Mikado Brown". The series of Irish Jays differed conspicuously from a series of English birds by their reddish brown under parts, reddish brown forehead and sides of the head (including the ear coverts). Size about as in England ; average wing length of males 183.0, of females 179.4 mm. Material examined : 26 (Southeastern and Western Counties ; the specimens originating from all seasons).

*Belgium* — Like W. France, particularly as regards the coloration of the upper parts. Individuals with brown under parts, however, are more frequent than in W. France ; thus, the series resembling more closely a series of British Jays (*cf.* VOOUS 1946). Size slightly larger at the average. Material examined : 14 breeding birds ; in addition 102 specimens collected in fall and winter.

*Netherlands* — Very close to Belgian birds, but the number of individuals with brownish under parts is proportionally smaller. Upper and under parts tend to become greyer (*cf.* HENS 1931). Size very slightly larger at the average than in Belgium. Material examined : 93 breeding birds (April to August inclusive); in addition 148 specimens collected in fall and winter.

*Northeastern France* — Upper parts at the average darker and greyer than in W. France, but the under parts are rather light grey. As a whole very similar to the majority of the specimens from the Netherlands and

W. Germany. Material examined: 7 (St. Dié, Vosges Mts.; from all seasons).

*Western Switzerland* — Upper parts light vinaceous grey, being intermediate at the average between Italy and W. France (between "*Cinnamon-Drab*" and "*Benzo Brown*"). Under parts with more white than in W. Germany, but less than in W. France. Material examined: 9 (Cantons of Basel, Fribourg, Bern, Luzern, Uri, Grisons; from all seasons).

*Western Germany* — Closely resembling Netherlands birds, but individuals with greyish upper parts are of a more frequent occurrence. Brownish under parts are rarer; instead, grey ones predominate. Still, one individual was examined having the under parts as bright creamy white as in Italy (Wesel on Rhine, Westphalia, December 5). Size at the average slightly larger than in the Netherlands. Material examined: 19 breeding birds (Rhine Province; Rhine-Hessen); in addition 27 autumn and winter specimens; also a small series in the British Museum.

*Southern, Central and Eastern Germany* — Upper and under parts at the average greyer than in W. Germany, but less pure and less dark grey than in the northern Alps. S. German Jays tend to be darkest grey. Size at the average rather large. Actual breeding specimens were but scarcely represented in the series available. Material examined: 16 (Black Forest; Upper and Lower Bavaria; Schwaben; Brunswick; Brandenburg; Frankfurt on Oder).

*Eastern Poland/Western Russia* — Upper parts with a more brownish grey tinge than in C. Germany, but darker than in Rumenia. Under parts dark grey; sometimes with a rather strong tinge of brown. A small influx of characters of the brown-headed Russian Jays is unmistakable when examining a series. Size as in C. Europe. Material examined: 41 (Stripuny near Smorgoni; Bialowice; Slonim in Gouvernement Grodno; from all seasons).

*Baltic Countries* — Similar as in E. Poland, but with a stronger tinge of brown, particularly on the under parts; therefore close to Finnish Jays. A strong influence of the brown-headed Jays from Russia is noticeable. Material examined: 10 (Livonia; Esthonia; mostly breeding specimens).

*Finland* — Upper parts as intensively grey as in Sweden, but showing an additional shade of brown. Under parts decidedly more greyish brown than in Sweden, agreeing with the brown-headed Jays from Siberia and the hybrids living in Russia. Size at the average slightly smaller; average wing length of males 184.1, of females 183.0 mm. Material examined: 11 (from all seasons).

*Denmark* — Intermediate in all respects between the Netherlands and Sweden, but tending towards the latter. Very similar to the series from W. Germany, but individuals with light brownish under parts occurred somewhat more frequently. Size as in Sweden, but a real "giant" is mentioned in chapter 9). Material examined: 16 (13 island of Zealand, 1 island of Møn, 2 Jutland Peninsula), but among these were not more than 7 birds taken in the breeding time.

*Sweden* — In all respects closely resembling German birds, but individuals with pure grey upper parts occur even more frequently and the average size is slightly larger. Still, the brownest upper parts of Swedish birds appeared to correspond with the average coloration of the upper parts found in England and Scotland. The average of the coloration of the upper parts is a dark grey (near "*Benzo Brown*"), that of the under parts is a vinaceous grey ("*Light Cinnamon*-Drab"). Average wing length of males 186.3, of females 181.9 mm. Material examined: about 200 (from all seasons).

*Norway* — Upper parts similar to those of Swedish birds, but in the available material individuals with reddish brown upper parts were represented in proportionately larger numbers than in Sweden. A difference with Swedish Jays was furthermore noticeable in the high frequency of brown under parts, particularly along the west coast (where, however, the species is a doubtful breeder). Size similar as in Sweden. As I did not succeed in tracing any Norwegian Jay from the breeding season in the three Norwegian museums visited, the specimens examined originating from October to February inclusive, the diagrams on the individual variaton of the Jay in Norway must be considered as rather inexact. A further detailed study is needed, first of all a tabulation of the breeding localities of the Jay in Norway (see p. 9). Material examined: 31 (13 from the southwest coast; 14 from the neighbourhood of Oslo; 3 without exact locality; in addition one migrant from south-Varanger at 69°30′ northern latitude).

*Liechtenstein* and *Northern Austria* — Upper and under parts darker grey than in W. Switzerland; fairly agreeing with the birds from S. Germany .Material examined: 4 (Liechtenstein), 3 (Hallein, N. Austria). No breeding specimens examined.

*Bohemia* — Upper parts dark grey: generally darker than in Sweden. Under parts a dark vinaceous grey all over, which in some specimens was intensified by the feathers being stained with a dirty dust. Size as in W. Switzerland and in Sweden. Material examined : 6 (near Belohrad; from all seasons).

*Hungary* — As Bohemia. KLEINER (1935—38) could not distinguish between Jays from Hungary and Sweden. Material examined : 2 (Debrecen; Brembergbanya; not from the breeding time).

*Northeastern Croatia* and *Sclavonia* — According to Mr. D. RUCNER (Zagreb), who kindly sent me the material, the specimens examined probably were all migrants, having been collected near Zagreb between Sept. 17 and Nov. 29, 1950, and at Slatina (Podravina) on Oct. 22, 1950. The birds were identical with the series from Hungary and Bohemia in having very dark grey upper and under parts. Upper parts at the average some tinge of "*Brownish Drab*" (standard-series "G"), but the darkest individual was almost "*Deep Neutral Gray*" (standard-series "K"). Under parts as dark vinaceous grey as "*Drab-Gray*" (standard-series "X"). Material examined: 9. — The available Yugoslavian material is too limited to permit a survey on the probable intermixture of the distinct Yugoslavian and Hungarian breeding populations. It is noteworthy that an additional male from Beograd, N. Serbia, from Dec. 17, 1933, had very dark grey upper parts combined with whitish under parts, thus showing a mixture of the characteristics of the Hungarian and the central Yugoslavian populations. If intermediate (mixed) populations really exist they must be sought for somewhere in eastern Steiermark (Graz), from whence, however, no specimens were available for examination.

The manuscript having been finished I received from Mr. D. RUCNER an additional breeding pair, shot at the nest near Zagreb, March 13, 1951. These birds have the pale vinaceous grey coloration of Italian birds (standard-series 'B" and "C", respectively); the under parts are neither whitish as in Italian Jays, nor dark grey as in the migrants from Zagreb and the Jays from Bohemia and Hungary, but are light vinaceous grey in the male and reddish brown all over in the female (standard-series "II" and "IV", respectively). See figures 5 and 10. Wing of male 195, of female 183. The breeding pair is thus very different from the migrants and agrees more closely with the breeding birds from other parts of Yugoslavia.

*Central and Western Yugoslavia* — Different from the migrants collected near Zagreb and in Sclavonia. Upper parts much lighter and more brownish grey; under parts creamy white with a vinaceous grey breast. As a whole the birds are very close to those from Italy, particulary two birds from the island of Krk (Veglia) in the Croatian Littoral and three birds from Crni Lug, Gorski Kotar, W. Croatia. The latter birds have conspicuous cinnamon rufous necks, as in Jays from Crete, but otherwise only rarely found in Europe (*cf.* RUCNER 1949, p. 92—93). KLEINER (1935—38) found three specimens from S. Dalmatia (Nisano and Castelnuovo) almost identical with Italian Jays in coloration. Towards the eastern parts of Yugoslavia the birds seem to grow darker grey at the average, a fact which was independently stated by RUCNER (*in litt.*, 1950). Size as in C. Europe, hence much larger than in Italy. Average wing length of males 188.8, of females 186.6 mm. Material examined: 12 (Island of Krk and Gorski Kotar in Croatia; Crncic and Konjica in Herzegovina; Sarajevo, Odzak and Koseva in Bosnia; Kopaonik Mts. in Serbia; only breeding birds). In addition a small series from N. Serbia in the British Museum.

*Bulgaria* — Similar to Yugoslavia in the pale vinaceous grey upper parts and the whitish under parts, but tending towards a purer grey coloration of the upper parts. VON JORDANS (1940) after having compared 29 Jays from Bulgaria with 4 from the Peloponnesus in S. Greece (Taygetos or Pentedactylon Mts.), found these very similar, although the characteristic light under parts of the Bulgarian Jays in contrast to Greek birds were particularly noticed by him. Material examined: 6 (Pirin Mts.; Rila Mts.; Haskovo on the northern slopes of the Rhodope Mts.; Rhopotamos on Black Sea coast; only breeding birds); in addition a small series in the British Museum.

*Rumenia* — Similar in coloration and size to Bulgarian Jays. Material examined: 6 (Prundu and Rashova in S.E. Rumenia; Bacau in Moldavia; Cernica and Taslan; from all seasons).

*Greece* — Upper parts darker and purer grey than in Bulgaria. Under parts with a distinct vinaceous grey tinge on the breast, but with a whitish abdomen. In all specimens examined the black crown stripes were very broad, showing distinct blue cross bars. Said to be smaller at the average than in Yugoslavia (KLEINER 1935—38). Wing of one female examined: 179 mm. Material examined: 5 (Xechasmeni on Aliakmon River, N. Greece; Mt. Olympus; Platea; breeding birds).

*Crete* — Upper parts conspicuously grey, resembling Greek birds, but of a purer tone, tending towards "*Neutral Gray*". Under parts also grey, being about "*Cinnamon-Drab*". The light reddish brown colour of the hind neck contrasts with the pure grey of mantle and back. Size apparently small. Wing of one male 172.5, of one female 169 mm. Material examined : 2.

*Sardinia* — Upper parts much darker and greyer than in Italy, but less pure grey than in Crete, being at the average about "*Benzo Brown*". Under parts grey, showing a conspicuously narrow range of individual variation. Coloration of under parts at the average between "*Light Drab*" and "*Cinnamon Drab*". Size small, as in Italy. Average wing length of males 177.9, of females 173.7 mm. Material examined : 42.

*Corsica* — Upper parts said to be dark vinaceous ; under parts also with a strong vinaceous tinge. Size rather large. Indeed, the only one specimen examined resembled an intensively pigmented British Jay, but was very different from both Italy and Sardinia, having the upper parts between "*Russet-Vinaceous*" and "*Sorghum Brown*" and the under parts between "*Vinaceous-Fawn*" and "*Vinaceous-Buff*". Wing of one female 185 mm.

*Eastern Spain* — Upper parts very dark grey, darker than in Sardinia ; at the average somewhat greyer than "*Brownish Drab*". Under parts grey, as in Sardinia. Size large, as in C. Europe. Average wing length of males 187.4, of females 180.6 mm. Material examined : 15 (Teruel ; from all seasons). — KLEINER (1935—38) found two specimens from Sevilla, S. Spain, to be different from those from Portugal and C. Spain by having dark grey upper and under parts !

*Western Spain* and *Portugal* — Closely resembling Italian birds in the pale greyish vinaceous coloration of the upper parts ; in addition there is also a tendency towards a more reddish brown tone as in Britain. Under parts as white as in Italy, but with a more or less developed dark greyish breast band. Size as in E. Spain. Average wing length of males 187,2 of females 175,6 mm. Bill at the average 1—2 mm larger and tip of upper mandible somewhat more strongly curved than in E. Spain and C. Europe (average length of the bill measured from nostrils 20,9 (8 males) and 20,0 (9 females), against 20,4 and 19,9 mm in Sweden). Material examined : 7 (Salamanca ; Cintra and Setubal, S. Portugal ; from all seasons). — KLEINER (1935—38) also stressed the similarity of the Jays from Avila, southern Salamanca, and northern Portugal with Italian birds ; these birds being distinct from specimens from southern Spain (Sevilla).

*Pyrenees* — The only two breeding specimens critically examined were intermediate between Jays from France and E. Spain in the coloration of upper and under parts. Wing length rather large : male 194, female 188 mm (Argèles sur Mer, Dept. Pyrenées Orientales ; Fabian, Dept. Hautes Pyrenées).

## 11. THE GENETICAL BASE OF THE CLINES EXAMINED.

Most of the colour clines described above show a gradual and regular shift of the average of the coloration of local populations. Hence they can said to be examples of the regular type of cline. As has been stated earlier, the coloration of the upper and under parts of the Jay depends on the relative and absolute quantities of the two feather pigments, eumelanine and phaeomelanine. As the actual quantity of these pigments in individuals as well as in whole populations varies independently, the very nature of the feather pigmentation may be considered to be the anatomical base of the quantitative character of the colour cline. The method of investigation applicated in this study has not only permitted to formulate the approximate limits of the individual variation in a number of local breeding populations, but has also provided a means to demonstrate the quantitative character of the clines in as much as it appears that all imaginable transitions between the "extreme" colour types actually occur in great numbers. Hence DOBZHANSKY's suggestion (1947) of the typical regular cline, occurring in a continuous geographical area (as in the case of the Jay), having a basal system of *multiple factors* seems very attractive. There is nothing new in the supposition of multiple factors being the genetical base of colour gradients in birds (see also VOOUS 1947), although the fact has never been positively established. Even as a whole the theory of multiple allelomorphism has never been proved by the results of cytological examinations, so that a certain deal of insecurity has to remain in any discussion starting with the acceptance of this theory. The regular trend in European Jays of

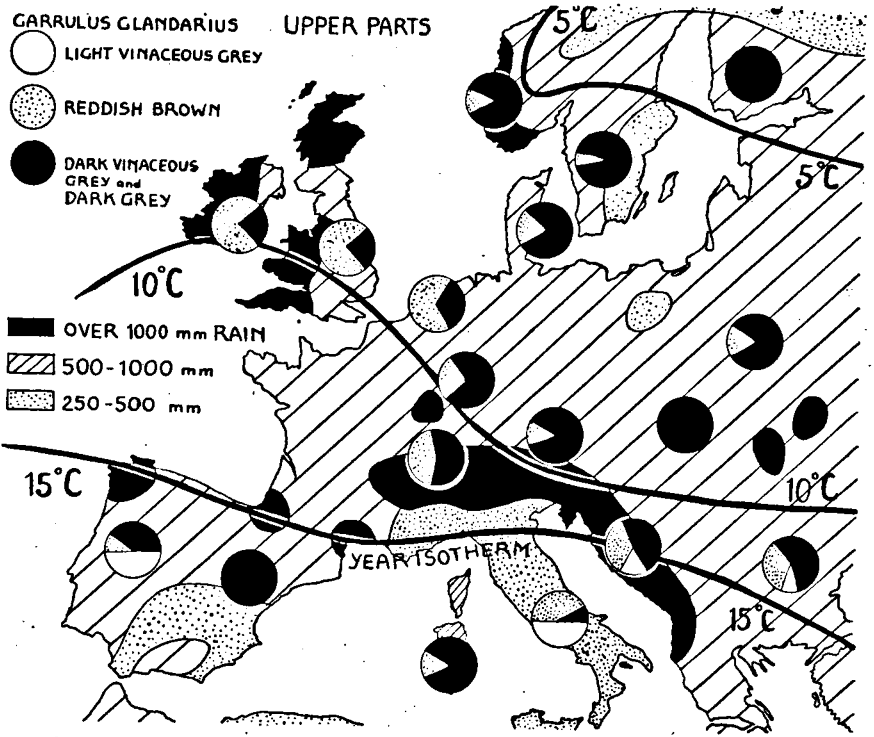

*Figure 13.* Individual and geographical variation of the *upper parts* in relation to mean annual rainfall and mean annual temperature.

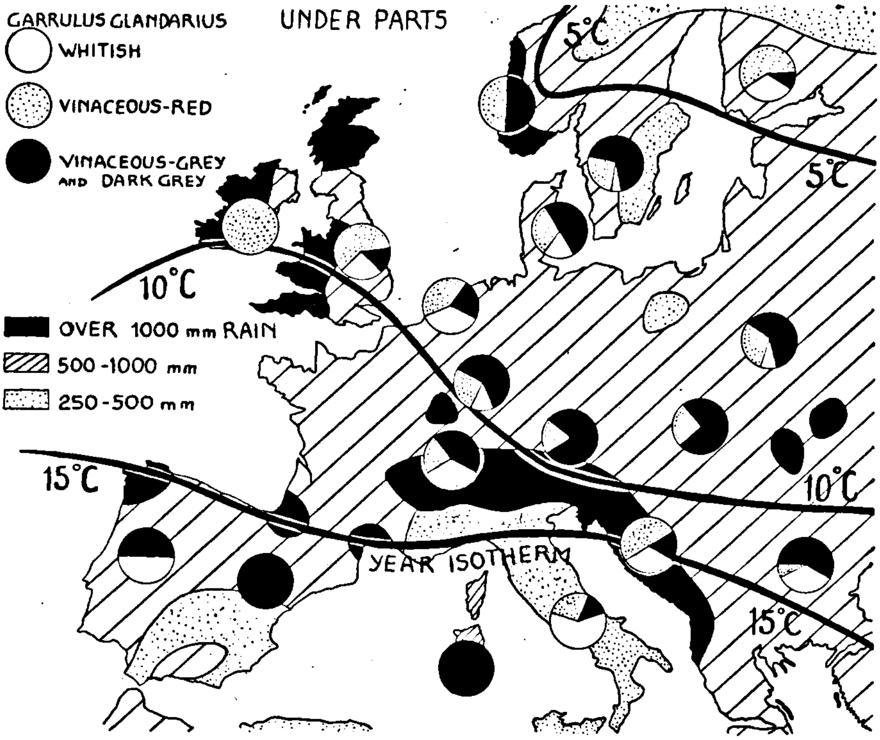

*Figure 14.* Individual and geographical variation of the *under parts* in relation to mean annual rainfall and mean annual temperature.

becoming greyer and more intensively pigmented towards the end of the clines must then be explained by assuming a regular shift in the relative frequencies of the genes (alleles) of a multiple system. Simultaneously certain genes (or their alleles) will gradually come to disappear, resulting in the high frequency of homozygotic conditions of certain genes (either active or recessive) in terminal populations or in isolated areas. Although the hypothesis of gene elimination towards the terminal populations of the clines seems rather well founded, the question of the factors inducing these frequency gradients must now be considered.

First of all it is logical to compare the picture of the character geography of the European Jay with *climatic conditions*, viz., with the mean of the annual rainfall and with the annual mean temperature. From figures 13 and 14 it appears immediately that a correlation between the colour of upper and under parts of the Jay and the temperature is totally lacking, nor is there any conspicuous correlation between the geograpical variation of the coloration and the annual rainfall. Still, the dominance of brown and even reddish brown tones in the Atlantic countries is noteworthy. The occurrence in Norway of much higher frequencies of brown colour tones than in Sweden might also be considered to be indicative of a distinct influence of the Atlantic sea-climate upon the preponderance of individuals with a relative surplus of phaeomelanine pigments. The small increase of individuals with reddish brown under parts in western Yugoslavia where the annual rainfall is rather high, may get a similar explanation. However, since there is no evidence neither to accept nor to deny the direct influence of a humid and mild climate upon actual *individuals* of Jay, we can here only assume that these environmental conditions in one way or another have a possibility of controling the composition of the multiple allele system. These climatic conditions may induce a relatively high *frequency of alleles* favouring the development of the brown feather pigments, and of others suppressing the greyish pigments, but it is not likely that this is the main function of the genes involved. This suggestion also includes the possibility of a local higher frequency of some of the many small gene mutations supposed to occur at random throughout the whole range. The alternative view is that climatic or other direct environmental conditions control the *act of the realisation* of the set of genes present in the multiple system. This means that the action of the genes of inducing the development and the multiplication of the reddish brown pigments would be stimulated in the Atlantic countries, whereas the action of the individual genes for greyish brown pigments would be hindered.

We now have to examine the possibility of a correlation between the clines and the general environmental gradients in Europe. This problem involves the question whether the coloration of the Jay is of an active or an indifferent value in *natural selection*. In this connection e.g. the following direct questions have to be answered:

(1) has it any survival advantage to the Jays from central and northern Europe to be darker and greyer in coloration, instead of being paler and browner, as those inhabiting southern and southwestern Europe ?

(2) would grey Jays be subject of a higher mortality in Britain than the brown Jays actually living there at present ?

The only thing I can say is that, indeed, the habitat of the Jays in Sweden and Norway, being mainly coniferous forests (*Picea*), appeared to me to be darker and more uniformly shaded than the deciduous and mixed forests in western Europe, which are more open and usually show a richness of bright sunny patches. But is it justified therefore to ascribe selective value to the darker and more shaded coloration of the Scandinavian Jays, as well as to the brighter and richer brown colour tones in western Europe ? All these questions not only have to remain unanswered, but we even have to confess that the significance of a quantitative difference in coloration for an individual bird is unknown to us. Thus, we can only try and meet the problem from another angle. We then point our attention towards the fact that *e.g.* among the Swedish Jays, which have for the greater part grey colour tones, some few specimens regularly occur, having a brownish coloration (about 5 % of the specimens examined). The upper and under parts of these specimens appear to fall within those colour classes which are the dominating type in the British Islands. Are these few brownish individuals less equipped to withstand the pressure of environmental and sexual selection, than the average grey-coloured Jay in Sweden ? And what to think about the many intergrades linking these brown extremes with the normal grey Jays ? In view of this situation and the high degree of the individual variation throughout

European populations it seems to me that in this particular case the attack of natural selection cannot be very rigorous.

As direct evidences in favour of the presence of climatic or environmental factors controling the clinal variation of the Jay are lacking, we must finally turn our attention to influences of present cases of *limited directions of gene flow*, as well as to the result of the *historical spread of the species* over Europe. The present continuous range of the Jay in Europe has only been reached after thousands of years of gradual spread of the species in post-glacial times (see next chapter). Thus, although both have originated from glacial refuge populations in southern Europe, the present Finnish Jays certainly have had another distributional history than *e.g.* the Jays inhabiting Great Britain. However, the Jays from France can rely upon a direct historic distributional contact (through the southern North Sea land) with British Jays. As the marginal populations of a continuous breeding area are as a matter of fact subjected to a less regular supply of all gene combinations than those situated in the centre, we may have found in the historic way of *gradual post-glacial dispersal* an additional base of the origin of the clines decribed. Any limit of a cline found (where bordered through a morphological discontinuity by another cline), denotes the end of a particular direction of gene flow (the end of a series of gene-frequency gradients) and thus also the end of a way of post-glacial dispersal.

Regarding the correlation of clinal variation and cytological data it may be of interest to recall the fact that DOBZHANSKY has more than once shown the existence of a correlation between the frequency of chromosome inversions and morphological characters in *Drosophila* populations. CARSON & STALKER (1947) and STALKER & CARSON (1947) have described a correlation between geographical gradients in the frequency of chromosome inversions and the geographical and individual variation of morphological characters in natural populations of *Drosophila robusta*. Thus, a correlation between chromosome patterns and morphological clines seems to occur in certain instances. *Per analogiam* such a correlation might also be present in European Jays. Regarding the possibility of European Jays having adapted themselves to environmental conditions — a theme which was unsuccessfully discussed above — it is interesting to note that according to cytological and morphological examinations and laboratory experiments by STALKER & CARSON (1949) "*Drosophila robusta* may adjust the morphology to the environment in three different ways. 1. It may differentiate into genetically diverse altitudinal or geographic strains. 2. It may undergo rapid genetic adjustment within one locality in response to local seasonal conditions. 3. It may undergo a direct non-hereditary change in phenotype in response to the temperature of rearing" (p. 342). By the absence of cytological examinations and laboratory experiments with Jays we may refer in the following summary on the origin of the clines of the European Jay to the conditions found in *Drosophila*.

1. *As a whole the clines are genotypically defined.*

Remarks — Conspicuously brownish colorations occur in the Atlantic countries (where they are considered by most authors to be induced by climatic conditions : see above), as well as in E. Poland and Finland (not in Germany and Sweden !), proving the genotypic instead of the exclusively phenotypic base ("modification") of the pigmentation.

2. The *geographical gradients of gene frequencies* have a double cause:

a. *The gradual loss of alleles through post-glacial dispersal phenomena.*

Remarks — The presence of sharp discontinuities in some parts of Europe corresponding to zoogeographical dispersal borders and not to climatic or vegetational boundaries is positive evidence in favour of this suggestion.

b. *The genetical adjustment to enviromental conditions through natural and sexual selection.*

Remarks — The high frequency of individuals with a strong phaeomelanine pigmentation in countries with a different origin of their forest fauna, as in Great Britain and in western Norway, can be considered to be circumstantial evidence in favour of this suggestion.

*Size clines* in European Jays, as expressed by the length of the wing, are by far not so instructive as the colour clines. The discontinuities found are of a zoogeographical rather than a genetical importance. Still, the general trend of becoming larger from southwest to northeast is apparent. The genetical base of this agreement with BERGMAN's Rule is not very clear. Most authors ascribe the phenomenon expressed by this Rule to the effect of natural selection, but I fail to see the mechanism of natural selection working on individuals which differ only 1 cm (less than 0.5 %) in the length of their wings (Italy-Sweden).

## 12. POST-GLACIAL DISPERSAL IN EUROPE.

Evidence supporting a theory on the post-glacial distributional history of the Jays in Europe, comparable to earlier theories on this subject (*Dendrocopos, Pyrrhula, Sitta,* also *Corvus monedula* and *Chloris chloris*; VOOUS 1947, 1949, 1950, 1952, VOOUS & VAN MARLE 1953) can be extracted from the following instances:

(1) the limits of the range of the European group of races as opposed to the rangs of the highly distinct races inhabiting Siberia, S.W. Asia, and N. Africa,

(2) the northern limits of the present range in Scandinavia,

(3) the direction of the European clines of colour and size and their local discontinuities.

From these data the following picture of the range expansion of the Jay after the retreat of the last pleistocene glaciation has been developed.

Spreading from a forest refuge in Italy and southern France the Jays colonized the whole of western Europe north of the Pyrenees, including Great Britain and Ireland at the time that these present islands were still part of the continent. Closely combined with this northwestern direction of dispersal a tendency towards a more reddish brown coloration and larger average dimensions gradually started to develop until present day conditions. It is very probable that this process of growing browner and larger is still going on. When central Europe gradually became afforested the extending populations turned northwards from the Alps to the east, spreading through Germany to western Poland and Bohemia, where the further history becomes obscured by the presence of other population strains. Towards the end of this dispersal, which corresponds not only with present day clines, but also with the theoretical results reached by earlier investigations (see above), the gradual increase of grey colours on upper and under parts reaches a most conspicuous optimum in Bohemia and Hungary, where at present the Jays are common in the forests both in the lowlands and in the mountains. South of the Hungarian plains and east of the Carpathians populations of Jays occur, which apparently form part of other clines and hence belong to other distribution strains. Racial discontinuities comparable with those of the Jays living north and south of the Hungarian plains, have been described in all other cases that the character geography of particular, species of forest birds had been studied. The zoogeographical importance if this discontinuity has been more elaborately discussed elsewhere (VOOUS & VAN MARLE 1953). Through Germany and Denmark, where subfossil bones of the Jay have been found in Boreal Time (5000—6000 B.C.), among others together with remains of *Dryocopus martius*, roe-deer, red-deer, elk, squirrels (LÖPPENTHIN *in litt.* 1949), the Jays colonized Sweden and Norway, reaching in the grey Jays from Sweden another end of clinal variation. Although absent as a breeding bird in the mountainous boundary zone between Sweden and Norway, where the European Jay is represented by the "Siberian Jay", *Cractes infaustus*, a species of similar habits, but living in conifer forests (SALOMONSEN 1948), the Jay is found again occupying the particular *niche* in the pine and mixed forests of western and southwestern Norway. According to personal information (a.o. from WILLGOHS and HOLGERSEN 1950 and 1951) the Jay must be here very rare, or may be even absent as a breeding bird at all. However, the available material shows a decidedly more vinaceous brown underside in the Jays collected in western Norway compared with those from Sweden, which might indicate an isolated Norwegian breeding stock (see discussion on p. 9). A steady expansion of the range of the Jay towards the north of Sweden has been noticed all throughout this century (*cf.* ZEDLITZ 1925), but in northern Sweden the species is still considered to be rare (Förteckning over Sveriges Fåglar, 1949). The relatively small number of Jays breeding in Swedish Lapland seems to have originated from Finland, a supposition which was confirmed by Swedish ornithologists (verbal communication). Finnish Jays differ from Swedish Jays by the generally more brownish coloration of the under parts, denoting a mutual isolation of these breeding populations. Contact between the populations from central and southern Sweden with those from Finland (incl. Swedish Lapland) appears to be rather scarce, but still some amount of gene exchange must be present, since specimens from the northern parts of Sweden examined were in some way or another intermediate between those from central Sweden and Finland. These intermediate birds exhibit at least some of the characteristics of the Russian hybrids between the European and the Siberian races; the Finnish population as a whole possessing a strong element of "Asiatic" characters (especially as regards the colour of the underparts, which is strikingly brown).

The striking similarity of the Jays from Sicily and Italy with those from Yugoslavia indicates a narrow contact between these populations during some time of the pleistocene period. However, the present difference in dimensions seems to indicate that gene exchange had come to an end at a rather early time in the post-glacial or even during the last glacial period, but actually we do not know anything about the chronology of this history. From their refuge area in Yugoslavia and Greece the Jays did not cross the Hungarian plains, but as soon as climate and vegetation permitted their expansion they must have spread to the north and northeast, as direct and closely resembling deratives now live in Bulgaria and Rumenia. From here they must have spread much further in northern and northeastern directions, gradually re-populating eastern Poland, Russia and the Baltic countries and Finland. In the larger part of this range the morphological characters have become obscured through the hybridization with Siberian brown-headed populations. The extent of this post-glacial process of hybridization will be discussed separately.

The distinctness of the Jays living north and south of the Pyrenees is noteworthy, but corresponding differences are well-known in other species of forest birds. Apparently the glaciated Pyrenees have acted as a distributional barrier during the last glacial period. At present the Jays from the mountain forests of the Pyrenees seem to be intermediate between those from France and Spain.

Much more surprising are the differences found between the Jays from eastern Spain and those from western Spain and Portugal. They seem to indicate that during the last glacial period distributional barriers (mountains ?) prevented the inter-change of genes throughout the whole of the Iberian Peninsula. At present the Jays are still rather irregularly distributed in Portugal and Spain, occurring both in the Pinsapo Pine forests (*Abies Pinsapo*) in the mountains and in the cork woods in lower altitudes. However, without a detailed study on the distributional history of Iberian land birds (which is eagerly needed) nothing can be added to the interesting problem of the origin of the morphologically distinct populations of the Jay in this region.

All isolated populations in the mediterranean region (Corsica, Sardinia, N.W. Africa, Crete) are practically uniform dark grey above and rather dark grey beneath. These characters seem to result from the most stable of gene combinations to be expected in relatively small populations irrespective of climatic conditions.

## 13. THE BORDER-ZONE OF HYBRIDIZATION WITH THE SIBERIAN RACE IN EASTERN AND NORTHERN EUROPE.

There is nothing particular in the fact that in the zone of contact of the Siberian and the European races a certain amount of hybridization is regularly taking place. Surprising, however, is the fact that the area of hybridization and subsequent seggregation of the characters of these very distinct groups of Jay is as large as the whole of European Russia. It seems superfluous to point to the well-known fact of the large individual variability of the Russian Jays (14 specimens examined), which is the characteristic phenomenon of random hybridization (see: STRESEMANN 1919, VOOUS 1945). What I will try here is to bring together some more information about the western limits of the distribution of the "Asiatic" characters. These latter seem to result from the action of a continuous gene-flow from western Siberia into eastern European populations. How far "European" characters have penetrated to the east would be also most instructive to know, but for the present this escapes to our knowledge. It is clear that only specimens collected in the breeding time can serve the purpose of gathering information about the process of hybridization. However, a regrettable shortage of material has forced me to give the details of all available off-season birds too, and it should be reminded, that Jays are subjected to an irregular straggling, as well as to some migrating, particularly in northeastern Europe.

The Siberian races of the Jay (*brandti, bambergi*) differ fundamentally from the European forms by having the ground colour of the head, hind neck, ear coverts and nasal bristles of a rich rufous brown, instead of vinaceous, buffish white, or white. The under parts are generally brownish grey, which is different from the cold greyish or pure grey coloration found in Europe. The upper parts are dark grey with a slight brownish tinge. Indications of an intermixture of the groups must thus be found in the tendencies of the European Jays towards the above named characters.

*Western Russia / Eastern Poland* (see p. 23) — All 4 specimens from Smorgoni (about 26° east. longitude), collected between August 31 and October 2, had the ear coverts, forehead and nasal feathers conspicuously tinged with rufous. Three of 14 specimens from Slonim (about 25° east. longitude), collected between November 9 and March 24, showed a marked tendency toward Russian Jays in the reddish brown hind neck, upper mantle, ear coverts, forehead and nasal feathers. Of 23 specimens from Bialowice (about 24° east. longitude), collected in November, 7 were by all means indistinguishable from European Jays, whereas the remaining 16 specimens showed slight traces of a rufous tinge on the forehead and the nasal feathers, in addition to some rufous on the ear coverts and the hind neck in at least 5 specimens. All these birds possessed rather brownish under parts, which is another "Siberian" characteristic.

*Baltic countries* (see p. 23) — Over half of the specimens examined (10) had the hind neck and the ear coverts rufous brown; whereas with a single exception (Livonia) all birds showed a marked brown tinge on forehead and nasal feathers. The under parts had a conspicuous tinge of brown, which was strongest in the individuals with the rufous ear coverts and hind neck. The material includes 8 birds from Esthonia and Livonia, collected in the breeding time (April 7—August 16) (mainly in collection JOHANSEN in the Zoological Museum Copenhagen).

*Finland* (see p. 23) — Only 2 (Kuru, Merikarvia) of 11 specimens examined were indistinguishable from Swedish Jays; all remaining birds showing some of the characters of the Siberian birds in a variable degree. These latter specimens, which resembled the Jays from the Baltic countries, originated from: Helsinki (southwest), Kuru (southwest), Merikarvia (west), Kasaböle (west), Kuhmoniemi (east). None of these birds had been taken in the breeding time.

*Sweden* — At least some of the characteristics of the brown-headed Jays were found in 7 specimens from a total of about 200. These birds were conspicuous either by the rufous ear coverts, the rufous hind neck, or the brown tinge on the feathers of the forehead or on the nasal bristles. They are:

| | | | |
|---|---|---|---|
| (1) Ståljäll, Västerbotten (almost 66° North), | ♀, | Feb. 5 | (Göteborg Museum). |
| (2) Gimåfors, Västernorrland, | ♀, | Nov. 6 | do |
| (3) Köpmannebro, Dalsland, | ♀, | Oct. 16 | do |
| (4) Brostorp, Vallarum, Skania, | ♀, | Dec. 1 | (Malmö Museum) |
| (5) Falsterbo, Skania, | ♂, | Aug. 6 | do |
| (6) Kalmar, Småland, | —, | May 18 | (British Museum) |
| (7) Värmland, | ♂, | Feb. 28 | do |

*Norway* — Four specimens from a total of 31 showed some of the characteristics of the Russian Jays. In three of them (2, 3, 4) the coloration of upper and under parts has a dark greyish brown tinge.

| | | | |
|---|---|---|---|
| (1) Nesodden, Oslo, S.E. Norway, | ♀, | Oct. 2 | (Oslo Museum) |
| (2) Eidsvold, S.E. Norway, | ♀, | Oct. 26 | do |

(3) Fana, Bergen, W. Norway, —, Oct. 28 (Bergen Museum)
(4) Fö, Noatun, South Varanger, N. Norway, ♀, Oct. 30 (Stavanger Museum)

It thus appears that at the *Russian/Polish* boundary, between 26° and 24° eastern longitude, about 56 % of 41 specimens showed some of the characters of the Siberian brown-headed Jays. In the *Baltic* countries some 90 % (of 10 specimens) and in *Finland* some 90 % (of 11 specimens) possessed "Siberian" characteristics. These figures generally mark the approximate limit of the Asiatic gene-flow in eastern Europe. *Swedish* and *Norwegian* specimens possessing one or more of the "Asiatic" characters are either migrants from Finland or Russia (as are most probably the Norwegian specimens, which are all from October: about 13 % of 31 specimens), or they are the manifestation of the advancement of the gene-flow through Finland into Sweden and Norway. The influence of this gene-flow in Sweden — if existing at all — must be extraordinarily slight (about 3 % of 200 specimens), but an exact investigation on this subject in the northernmost provinces of Sweden must be very fruitful, particularly since a steady increase of the Jay populations in northern Sweden (probably from Finland!) has been recorded from the beginning of this century onward. At all events some of the Swedish specimens with "Siberian" characters seem to be migrants from Finland or Russia (Falsterbo: August 8!).

## 14. NOMENCLATURE.

In spite of the fact that it is almost impossible to express gradual clinal variation by means of a system of trinominals, an arrangement of what may be called different subspecies cannot be avoided. Care should be taken to understand that real subspecies in the sense of geographic races ought to have well-defined distributional areas, as have the island populations of the Jay in the mediterranean region and the Iberian forms of which the areas are bordered by natural barriers. Although a regular clinal system may (and actually does) result in a considerable geographic variation by distance, distributional borders as a matter of fact do not exist. Of course it is possible to use but one trinominal for each regular cline, but such over-simplificated treatment would undoubtedly meet with several difficulties. Firstly, the cline for the coloration of upper parts does not necessarily correspond with *e.g.* the cline for the under parts, or for size; secondly the terminal populations of a cline can be so distinct as to making it absurd naming them with the same trinominal name (which is considered to express gerographic variation!). In general I have adapted the rule of naming the terminal ends of each cline (when sufficiently distinct), which does not mean, of course, that the populations described under one subspecific name should be constant throughout their range! Now the question remains of deciding in which case the terminal populations have to be considered as sufficiently distinct from each other to separate them in nomenclature. It has been the cause of some mis-understanding, particulary among non-systematicists, that in instances of clinal variation the criteria for the use of trinominals are highly arbitrarily. Recently AMADON (1949) has given a valuable discussion on *"the seventy-five per cent rule for subspecies"*. However, his proposals for the nominal separation of populations showing a distinct geographical trend of variation (only if expressed by frequency curves!) are hardly less subjective than the many conventional decisions. Moreover I fear that most authors will consider the following criteria for separating populations to be too severe and too rigorous.

a) 75 % of the specimens of population A lie below the limits of population B (as defined by the standard range), if

$$M_B - M_A = \text{or} > 3.24\sigma_B + 0.68\sigma_A$$

b) 75 % of the specimens of populations B will exceed the upper limits of population A (as defined by the standard range), if

$$M_B - M_A = \text{or} > 3.24\sigma_A + 0.68\sigma_B\ .$$

M = mean of variation ; $\sigma$ = standard deviation ; standard range = M ± 3.24 .

Following these criteria the geographical variation of the upper parts of the Jay would result in the recognition of only two distinct groups: (1) Italy — (2) Finland, Hungary, and E. Spain. Even such striking differences as existing between Italy and Sardinia, Italy and Sweden, or Italy and England, proved to lie below the limits set up by Amadon. As I failed to find a method for plotting the geographical variation of the colour of the under parts in frequency curves, it is impossible to make use of Amadon's criteria in tracing some acceptable limits of the geographical variation of this character. Regarding the measurements of the Jays, no geographical differences proved to exist in Europe, which would suffice to justify the nominal recognition of geographic populations according to Amadon's criteria. The alternative method of reaching a "75 per cent rule", as brought forward by Amadon (1949), is somewhat more practical. If the limits of $M_A \pm 1.88\ \sigma_A$ and $M_B \pm 1.88\ \sigma_B$ do not overlap it means that 97 % of population A will be separable from 97 % of population B and *vice versa*. The results of this method applicated to the Jay populations in Europe have been plotted in figures 15 and 16. It appears that following this formula of subspecific distinction only Italian populations are separable as regards the coloration of the upper parts from the populations inhabiting Finland, Bohemia, and Hungary. Similarly, differences in size according to these criteria do not refer to more than two instances, viz., (1) the Sardinian populations being materially smaller than those from Spain and Portugal, Yugoslavia, central Europe, and Denmark and (2) the Italian populations being smaller than those from (±) Yugoslavia, S. Germany and Austria, and Denmark.

In view of this lack of success I have not followed Amadon's treatment, sympathatic though it be, but propose to recognize the following names, which try to express the geographic trends of the European Jay in a less rigorous way. It is noteworthy that this arrangement of names closely agrees with a similar arrangement proposed in order to express the geographic variation of the European Nuthatch, *Sitta europaea* (Voous & van Marle 1953). As a result of (1) the gradual and highly overlapping geographic variation and (2) the large individual variation

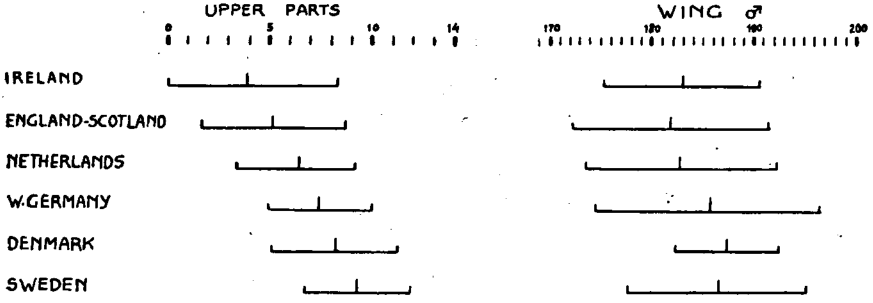

*Figure 15.* Diagram of the individual and geographical variation in western and northern Europe. The average value of the coloration of the *upper parts* (as defined by the 14 colour stages (1—14) mentioned in chapter 7) and of the *wing length* of the males (in mm) are indicated for each locality by a long vertical stripe. The theoretical amplitudes of the individual variation are marked by horizontal lines of 1.88 x standard deviation to the left and to the right of each average.

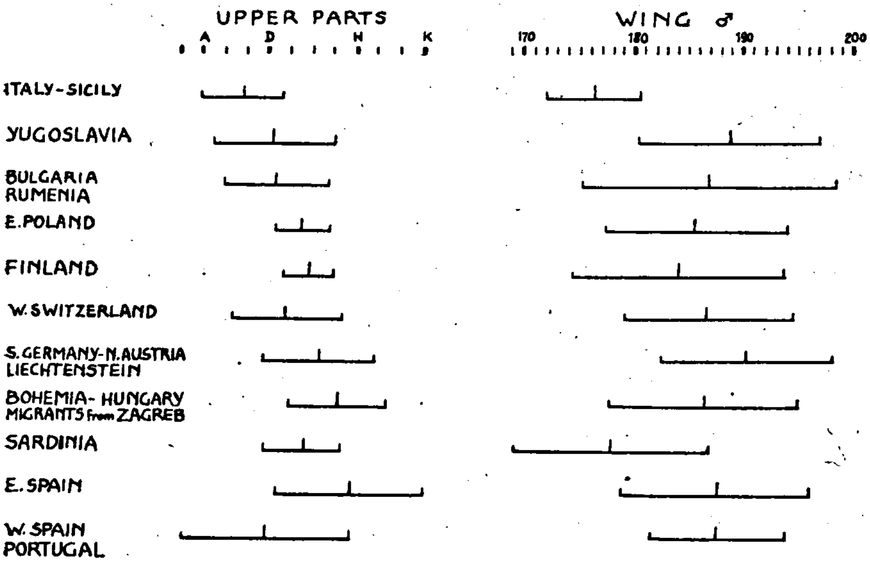

*Figure 16.* Diagram of the individual and geographical variation in southern, central, and eastern Europe. The average value of the coloration of the *upper parts* (as defined by the 11 colour stages (A—K) mentioned in chapter 7) and of the *wing length* of the males (in mm) are indicated for each locality by a long vertical stripe. For further information see figure 15.

in every locality, the type specimens belonging to the names summarized below have but a doubtful significance, even from a purely technical point of view.

## I. FIRST OR SOUTHWESTERN CLINE.

### 1. *Garrulus glandarius albipectus* KLEINSCHMIDT

Falco 16, p. 28, 1920 — Florence, Italy.

Pale vinaceous grey above; very light below, with much white on the abdomen. Size relatively small.

*Range* — Italy and Sicily.

### [*Garrulus glandarius armoricanus* LEBEURIER & RAPINE

Ois. & Rev. Fr. Orn. 9, p. 218, 1939 — Fouesnant, Finistère, France.

Intermediate in a different degree between *albipectus* and *glandarius*, as also between *albipectus* and *rufitergum*. At the average greyer or browner above and below than *albipectus*, with generally less white on the abdomen. As these populations do not agree with Italian, nor with British, nor with central European populations, and as a name is available, they should be known under a separate name, instead of using the symbols *albipectus* $\gtreqless$ *rufitergum* and *albipectus* $\gtreqless$ *glandarius*.

*Range* — France, W. Switzerland, Belgium, Netherlands]

### 2. *Garrulus glandarius glandarius* LINNAEUS

Syst. Naturae X, p. 106, 1758 — Sweden (Uppsala).

Upper and under parts darker and greyer than in *albipectus*. Size larger at the average. I do not see a material difference between the Jays from central and northern Europe. Hence I cannot follow MEINERTZHAGEN (1947) in separating the Jays from central and western Europe under the name *germanicus*.

*Range* — Central Europe, from Germany and E. Switzerland, to Austria, Czechoslowakia, N. Hungary, W. Poland; also Denmark, Sweden, Norway.

## II. ACCESSORIAL END OF FIRST CLINE.

### 3. *Garrulus glandarius rufitergum* HARTERT

Vög. Paläarkt. Fauna (Berlin), p. 30, 1903 — Tring, Herts, England.

Upper parts at the average with a more vinaceous brown tinge, without a contrast between the back, the mantle and the hindneck. These populations are especially characterized by the vinaceous brown colour of the under parts.

Note — I am of the opinion that we can better name the insular British populations separately, than to unite them with the central European birds, as proposed by MEINERTZHAGEN (1947). Besides, the colour of the under parts furnishes in most of the cases a sufficient key for distinction.

*Range* — England, Wales, Scotland.

### 4. *Garrulus glandarius hibernicus* WITHERBY & HARTERT

Brit. Birds 4, p. 234, 1911 — Ireland.

Upper parts only slightly browner than in England, but under parts decidedly richer reddish brown all over; head and sides of the neck also rich brown.

*Range* — Ireland.

## III. SECOND OR SOUTHEASTERN CLINE.

5. **Garrulus glandarius yugoslavicus** *subspec. nov.*

Type : ♀, 9 April 1893, Konjica, Hercegowina, Collected by O. KLEINSCHMIDT. Senckenberg Museum, Frankfurt, nr. 16.632.

*Description* : Resembling *albipectus* in the pale vinaceous grey upper parts and creamy white under parts, but size decidedly larger. Length of wing of 6 males 186—192 (average 188.8), against 172—184 (average 176.4) mm in 5 Italian males.

*Range* — The whole of Yugoslavia, but becoming greyer above towards the east, and in some individuals somewhat reddish brown beneath.

6. *Garrulus glanderius graecus* KLEINER

Bull. Brit. Orn. Cl. 59, p. 71, 1939 — Taygetos Mts., Peloponnesus, Greece.

Upper parts greyer than *yugoslavicus.* Abdomen conspicuously creamy white, as in *yugoslavicus* and *albipectus,* but contrasting with a greyish (vinaceous) breast band.

*Range* — Greece and Bulgaria. Rumenian specimens are very similar, but the exact geographical variation in this country is unknown.

## IV. ISOLATED POPULATIONS IN SOUTHERN EUROPE.

7. **Garrulus glandarius lusitanicus** *subspec. nov.*

*Type* : ♂, 25 April 1947,. Linares de Riofrio, Salamanca, Spain. Collected by H. GRÜN. Zool. Museum Amsterdam Nr. 9477.

*Description* : Upper parts pale vinaceous grey, closely resembling *albipectus* (Italy) with a tendency towards a more brownish coloration. Abdomen bright creamy white, contrasting with brownish grey breast band. Upper mandible perhaps slightly more hooked, butt bill hardly larger than in central and northern Europe. These characters were also noticed by KLEINER (1935—38), who stated that birds from Portugal „näherten sich zu *albipectus* ; auch die Unterseite war ziemlich hell' (p. 202).

*Range* — Western Iberian Peninsula : Portugal and N.W. Spain.

8. *Garralus glandarius fasciatus* C. L. BREHM

Allg. Deutsch. Naturhist. Zeitung, p. 446, 1857 — Sierra Nevada, southern Spain.

Upper parts generally much darker grey than in *lusitanicus,* but particulary distinguished by the dark grey under parts, which are similar to those of *ichnusae.*

*Range* — Eastern and southern Spain.

Note : The type specimen of *fasciatus* is in the American Museum of Natural History in New York. According to KLEINSCHMIDT (*in litt.* 1951), who possesses the diary of ALFRED BREHM's journey through Spain, the type-series has been collected in November 1856 in the Sierra Nevada. One of these specimens later on served as the type of *Garrulus glandarius kleinschmidti* HARTERT (Vög. Paläarkt. Fauna, p. 30, 1903), which is a synonym. Dr. D. AMAMON (New York) kindly examined the type for me and informed me that its upper and under parts are rather dark grey, "being inseparable from many specimens of the typical race (Sweden), including some from such rather distant areas as Hungary" (*in litt.* 1951). In the original description of *fasciatus* it is stated : "*G. glandario similis, sed tergo et pectore obscurior*".

9. *Garrulus glandarius ichnusae* KLEINSCHMIDT.
Orn. Mon. Ber. 11, p. 92, 1903 — Sardinia.
Closely resembling *fasciatus*, and differing mainly by the less variable dark grey coloration of the upper parts and by the smaller size. Much different from *albipectus* (Italy) by grey upper and under parts!
*Range* — Sardinia.

10. *Garrulus glandarius corsicanus* LAUBMANN
Verh. Orn. Ges. Bayern 11, p. 164, 1912 — Corsica.
Differing from *ichnusae* by the deep vinaceous tinge all over the greyish upper and under parts. Said to be larger than *ichnusae*.
*Range* — Corsica.

11. *Garrulus glandarius cretorum* MEINERTZHAGEN
Bull. Brit. Orn. Cl. 41, p. 19, 1920 — Mt. Ida, Crete.
Upper parts pure grey, contrasting with the brown colour of the hind neck. Under parts with a deep grey tinge. Very close to *graecus*, but differing mainly by the lack of white on the abdomen.
*Range* — Crete.

[*Garrulus glandarius severtzovi* BOGDANOV
Vög. u. Säuget. d. Wolga, p. 114, 1871 — Kasan and Simbirsk, European Russia.
Very variable; connecting through hybridization the W. Siberian brown-headed race *brandti* with the European races. In the European colour types the presence of an Asiatic influence can be noticed by a brownish tinge on the under parts, reddish brown (fox brown) sides of the neck and ear coverts, and a reddish brown hue over the frontal feathers, particularly at their bases.
*Range* — European Russia, E. Poland, Baltic countries, Finland. The western limits of the influence of the hybridization have been discussed in chapter 13].

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