

## DISTRIBUTIONAL HISTORY OF EURASIAN BULLFINCHES, GENUS *PYRRHULA*

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Recently I have tried to reconstruct the distributional and evolutionary history of the genus *Dendrocopos*, pied woodpeckers (Voous, 1947). The aim of the following study, which is an attempt to reconstruct the course of the same phenomena in the genus *Pyrrhula*, bullfinches, is to ascertain whether the conclusions arrived at in the case of the Palearctic and Oriental members of *Dendrocopos* have a general value. As in the work on *Dendrocopos*, patterns of recent geographical and ecological distribution and of character geography have furnished the basic facts of this study.

The genus *Pyrrhula* has been chosen as the subject of this study because (1) its characteristics, which are well defined, clearly set it apart from other genera; (2) it has only a few members; (3) its taxonomy as well as (4) its geographical distribution do not show conspicuous complications; and (5) its members are exclusive inhabitants of forests, although they regularly descend to the ground for feeding.

Only in the case of the European species was it necessary to make a thorough examination of subspecies. In preparing this part I had the privilege of collaborating with Mr. P. A. Clancey of Glasgow. I am greatly indebted to him for his kind help.

In this paper I have made use of the following terms as defined by Ripley (1945):

*Interspecies*: a species group or sympatric subgenus, containing a group of closely related, geographically overlapping species which have attained physiological isolation in nature.

*Emergent interspecies*: a species group containing a number of closely related, geographically overlapping species with a marginal fringe of hybridization.

*Superspecies*: a species group containing geographically representative species that have developed characters too distinct to permit the birds to be regarded as subspecies.

### MATERIALS AND ACKNOWLEDGEMENTS

With the exception of one species (*aurantiaca*) I have seen specimens of all species of *Pyrrhula*. The total number of specimens examined is 180. These originate from the following museums and private collections, to the authorities of which I am greatly indebted: Amsterdam Museum, Dublin Museum, Leiden Museum, coll. Harrison, coll. Huber, coll. Ten Kate, coll. Sillem-Van Marle. In addition I have to thank the following persons for kind help or valuable information: A. Arcangeli (Turin), Tso-Hsin Cheng (Foochow), P. A. Clancey (Glasgow), E. Dottrens (Geneva), M. S. J. Engel-Ledeboer (Amsterdam), E. Fernández Galiano (Madrid), Director of Genoa Museum, P. Géroudet (Geneva), F. Gudmundsson (Reykjavik, Iceland), N. Gyldenstolpe (Stockholm), J. M. Harrison (Sevenoaks, Kent), J. Huber (Oberkirch, Switzerland), P. Jespersen (Charlottenlund, Denmark), H. Johansen (Copenhagen), G. C. A. Junge (Leiden), O. Kalela (Helsinki), C. G. B. ten Kate (Kampen, Netherlands), G. Laurent (Remomeix, France), B. Löppenthin (Copenhagen), J. D. Macdonald (London), J. G. van Marle (Bussum, Netherlands), N. Mayaud (Saumur, France), E. Mayr (New York), E. Moltoni (Milan), P. O'Connor (Dublin), M. Sassi (Vienna), A. W. Stelfox (Dublin), E. Stresemann (Berlin), E. Sutter (Basel), A. Wollebaek (Oslo).

### CHARACTERS OF THE GENUS *PYRRHULA*

The bullfinches, genus *Pyrrhula*, are cardueline finches related to American goldfinches and purple finches. This genus is at once distinguished by the short, though strongly swollen bill, the short tarsi, the glossy black wing and tail feathers, and the white rump. The tail is distinctly or only very slightly forked and the wings are rather pointed. In most species the males show an orange or red coloration on the under parts. With only very few exceptions the bill is black, the legs and feet fleshy brown, and the irides

brown. A yellowish horn colored bill occurs in *P. nipalensis* (except in the race *waterstradti*) and in *P. leucogenys*. *P. n. waterstradti* is the only form of *Pyrrhula* having yellow irides.

#### THE ORIENTAL BULLFINCHES

##### *Pyrrhula nipalensis* Hodgson

*Characters*.—Head brown, no trace of black mask; tail forked; upper and under side some shade of dull brown, without any lipochromous pigmentation in the male; sexes alike in coloration except for the outer web of the innermost secondary, which is dark red in the male and yellow in the female.

*Subspecific variation*.—The following races have been described: *P. n. nipalensis* Hodgson 1836: Nepal; *P. n. waterstradti* Hartert 1902: Gunong Tahan, east Malay Peninsula; *P. n. ricketti* La Touche 1905: northwest Fukien, southern China; *P. n. victoriae* Rippon 1906: Mt. Victoria, Chin Hills (= *nipalensis* according to Stresemann and Heinrich, 1940); *P. n. uchidai* Kuroda 1916: southern Formosa.

The subspecific variation is very slight and refers to (1) a different degree of pigmentation of the upper parts, which are darker and browner in the birds from south China and from Formosa, and perhaps slightly lighter and greyer in birds from Mt. Victoria; (2) the coloration of the crown, which is dark and has a rather scaly appearance in birds from south China, caused by the relatively large dark centers of the crown feathers, but which is rather pale and hardly spotted in Malayan birds and intermediate in the remaining ones; (3) the extension of the white spot beneath and behind the eye, which is strongly developed in Malayan birds, but almost absent or rather duller in birds from south China; (4) the presence of a black chin, found only in the Formosan race; (5) the white shaft streak on the central rectrices of the Formosan birds, which is unique.

*Range*.—Himalayas, from Gilgit in the West, to Bhutan (Ludlow and Kinnear, 1944) and extreme northern Burma (Adung Valley and Irrawaddy-Salween Divide) (Stanford and Ticehurst, 1938; Stanford and Mayr, 1940) and northwest Yunnan (Rothschild, 1925 and 1926; Greenway, 1933) in the East. In addition, there are four or five isolated ranges: (1) Mt. Victoria, Chin Hills (Stresemann and Heinrich, 1940); (2) the mountains of northwest Fukien and northeast Kwantung (La Touche, 1925) which probably form one continuous area with northeast Tonkin, where the same subspecies has been recorded from Chapa by Delacour and Jabouille (1940); (3) Mt. Arizan in Formosa (Kuroda, 1935); (4) eastern Malayan mountains, in the states of Perak, Selangor and Pahang (Robinson, 1928).

*Biotope*.—Mountain forests, but in the Himalayas apparently generally lower than the zone in which *P. erythrocephala* occurs. Hence it inhabits the broad-leaved forests, rather than the coniferous ones. In the Tung-la Mountains of northwest Yunnan (Greenway, 1933), it is recorded from the fir and rhododendron zone, whereas on Mt. Victoria it inhabits chiefly the broad-leaved zone with evergreen trees covered with mosses, epiphytic ferns and orchids, and with a thick undergrowth. In the same region it has been found in the zone of oak and rhododendron, but it has been observed only rarely in coniferous forests (Stresemann and Heinrich, 1940). In the Malayan Mountains the habitat consists of a xerophytic zone (heath) on the summits of the mountains, where it often occurs in conifers like *Agathis* and *Dacrydium* (Robinson, 1928). In the Himalayas the species has been found breeding up to about 3000 m. altitude, as in the Tonglo Mountains, at the frontiers of Sikkim and Nepal (Baker, 1926); but in Bhutan it does not go higher upward than to about 2700 m., whence it is replaced by *P. erythrocephala* (Ludlow and Kinnear, 1937). In Yunnan, G. Forrest collected birds in July between 2700 and 3300 m. (Rothschild, 1925 and 1926). On Mt. Victoria, Heinrich found it in corresponding altitudes at 2600 and 3300 m. (Stresemann and Heinrich, 1940). Finally, in the east Malayan mountains, it inhabits the zones between about 1400 and 2100 m. on Mt. Tahan, in Pahang (Robinson, 1928).

Its notes are described as quite unlike those of the other bullfinches (Ludlow and Kinnear, 1937; Stresemann and Heinrich, 1940).

*Material examined*.—2 ♂♂, 2 ♀♀: Nepal, Darjeeling, Sikkim (Dublin Mus.; Leiden Mus.).

##### *Pyrrhula leucogenys* Grant

*Characters*.—Glossy black mask; tail forked; upper and under parts brown, without any lipochromous pigmentation in the male; a dark dorsal patch bordering the white rump; ear coverts almost

white; sexes alike in coloration, except for the outer web of the innermost secondary, which is deep red in the male and yellow in the female.

*Subspecific variation.*—The following races have been described: *P. l. leucogenys* Grant 1895: Lepanto, northern Luzon, Philippines; *P. l. steerei* Mearns 1909: northwest Mindanao. Mearns proposed this subspecific separation on the basis of a small difference in wing length, *steerei* being the smaller.

*Range.*—The province of Lepanto in northern Luzon, and the Malindang Mountains (Mt. Bliss) in northwest Mindanao.

*Biotope.*—“Mossy oak forest of mountains” (Delacour and Mayr, 1946:240). Mearns (1909) found it as high as about 1750 m. altitude.

*Material examined.*—1 ♂: northern Luzon (Leiden Mus.).

### *Pyrrhula erythaca* Blyth

*Characters.*—Black mask, bordered posteriorly by a narrow white line; tail forked; in the male the throat is grayish, but the remaining under parts, except the lower abdomen and under tail coverts, are red. Upper parts gray, with an indistinct black dorsal band bordering the white rump anteriorly; in the female the under parts are buffish brown; head and neck are gray, but the interscapular region, scapulars, proximal wing coverts, and upper back are brown; a gray and black band borders the white rump anteriorly.

*Subspecific variation.*—The following races have been described: *P. e. erythaca* Blyth 1862: Sikkim; *P. e. altera* Rippon 1906: Shayang, Chutung Road, west Yunnan, southwest China; *P. e. wilderi* Riley 1918: Eastern Hills, 60 miles east of Peking, Chihli, north China; *P. e. taipaishanensis* Rothschild 1921: Tsinling Mts., Shensi, north China; *P. e. owstoni* Hartert and Rothschild 1907: Mt. Arizan, Formosa (= *P. arizanica* Ogilvie-Grant 1912: same locality).

In the males the following racial characteristics have been noticed: (1) the intensity of lipochromous pigmentation of the under parts, which in eastern Himalayan birds is orange red, distinctly tinged with yellow, whereas in males from northern Burma and western China, including those from the Tsinling Mountains (Jacobi, 1923), the breast is brick red, usually without the slightest trace of yellow; male specimens from Chihli again have the breast distinctly tinged with yellow (Ludlow and Kinnear, 1944); in the Formosan race the red coloration is less developed and reduced to the sides of the breast (Ogilvie-Grant, 1912); (2) the intensity of the coloration of the upper parts, which is said to be darker in birds from northern Burma and western China than in those from the eastern Himalayas and from Chihli (La Touche, 1925); (3) the white band surrounding the black mask, which is widest in the Chinese birds, but almost absent in those from Formosa; (4) the reduction of the light gray of chin and upper throat in favor of the red of the under parts, which is most obvious in Chinese birds.

As regards the females, specimens from northern Burma and western China are said to be darker and browner than Himalayan ones. This is also noticed in females from the Tsinling Mountains (Jacobi, 1923) and from Formosa (Ogilvie-Grant, 1912). Females from Kansu are said to be lighter than those from Yunnan, whereas the type (♀) of *wilderi* (Peking) is somewhat darker (Riley, 1926 and 1930). The restriction of the facial mask in females from the Tsinling Mountains and from Chihli is an additional character of these races.

Finally there is a small variation in size.

From these remarks it appears that geographical variation in this species is mainly quantitative and clinal. Consequently, the ill-defined borders of the races are of no importance to this study.

*Range.*—Mountains of western China, from northern Kansu (Stresemann, *et al.*, 1937) and Tsinling Mountains, through Szechuan and extreme southwest Tibet (Schäfer, 1938), northwest Yunnan (Rothschild, 1926) and the Adung Valley and Myitkyina District of northern Burma (Stanford and Mayr, 1940) to Bhutan and Sikkim (Meinertzhagen, 1927). In the last named regions it overlaps the range of *erythrocephala*, though *erythaca* is very rare west of 92° east latitude (Ludlow and Kinnear, 1944). Also, *erythaca* occurs on Mt. Arizan, Formosa (Kuroda, 1935). It is a rare winter visitor on the eastern Tombs near Peking (La Touche, 1925), but the breeding locality of these winter birds is unknown. In suitable localities in eastern Bhutan, Ludlow found it rather common (Ludlow and Kinnear, 1944).

*Biotope*.—High mountain forests, chiefly of coniferous and mixed types. It has been found in forests of pine (northwest Yunnan: Rothschild, 1921), and spruce and fir (northwest Yunnan: Greenway, 1933), also in mixed forests (southern Tatung Mts., Kansu: Stresemann, 1937; northwest Yunnan: Greenway, 1933), consisting of conifers and rhododendrons (Yunnan: Greenway, 1933; Bhutan: Ludlow and Kinnear, 1944), as also in deciduous growths along mountain slopes, bordering river valleys (Hsifan Mts., western Szechuan: Schäfer, 1938). It has been observed repeatedly to eat the buds of willows, poplars, and birches, as well as their seeds and catkins (Stanford and Mayr, 1940; Ludlow and Kinnear, 1944). Like *erythrocephala* it is a high mountain bird which is mainly found above 3000 m. altitude, as indicated by the following records:

Western Kansu (Min-shan) in May and July, 2700-3000 m. (Lönnerberg, 1924); Szechuan (Hsifan Mts.) even in winter, with a temperature of  $-20^{\circ}\text{C}$ ., up to 3600 m. (Schäfer, 1938); northwest Yunnan (Likiang Range) in summer between 3600 and 4500 m. (Greenway, 1933); northern Burma (Adung Valley) in June and July at 3600 m. (Stanford and Ticehurst, 1938); eastern Bhutan, nesting at 3000 m. (Ludlow and Kinnear, 1944); Sikkim, in January at 3250 m. (Meinertzhagen, 1927); Formosa (Mt. Arizan), between 2100 and 2400 m. (Ogilvie-Grant, 1912); Szechuan, in winter down to 760-1500 m. (Jacobi, 1923).

Various observers in all parts of the range have noticed the resemblance of the call-note of *P. erythaca* to that of both *P. erythrocephala* and *P. pyrrhula* (Ogilvie-Grant, 1912; Schäfer, 1938; Stanford and Mayr, 1940; Ludlow and Kinnear, 1944).

*Material examined*.—1 ♂, 2 ♀♀; Tai-pai-shan, Tsinling Mountains; Likiang District, Yunnan (Leiden Mus.; coll. Sillem-Van Marle).

#### *Pyrrhula erythrocephala* Vigors

*Characters*.—Black mask; tail forked; in the male the head and lower neck, as well as the under parts are orange buff, except the lower abdomen and under tail coverts which are white; sides of the head and upper throat are only very slightly tinged with orange; a narrow gray line bordering the black forehead; remainder of upper parts gray; in the female, under parts and a band posteriorly to the black forehead are pale drab gray; posterior part of crown and the hind neck are golden olive; remainder of upper parts, brownish gray.

*Subspecific variation*.—Although it is stated by Stuart Baker (1926:111) that eastern birds tend to have more saturated colors, there appears to be "so much individual variation and so much overlapping" that no races have been described.

*Range*.—Himalayas, from southern Kashmir and Kangra District, Punjab (Whistler, 1926) to Mt. Yönpu La, in extreme eastern Bhutan (Ludlow and Kinnear, 1944), where it meets the range of *P. erythaca*.

*Biotope*.—High mountain forests, chiefly of conifers. In summer it seems to prefer deep forests of pine, cedar, deodar, juniper, and fir, or mixed forests of fir, birch, and willow (*cf.* Stuart Baker, 1934); in winter it has been found in lower altitudes, frequenting oak and rhododendron forest (Kangra District: Whistler, 1926) and willows along streams (Simla: Jones, 1919). According to Meinertzhagen (1927) it is the commonest bullfinch throughout the Himalayas. Its vertical distribution indicates a high mountain bird. The first Mt. Everest expedition found it in the breeding season (Aug. 17) as high as about 3800 m. altitude (Kinnear, 1922), whereas a nest has been found in Kumaon at about 3600 m. altitude (Baker, 1934), but it seems also to nest on Mt. Yönpu La, eastern Bhutan, which is not higher than about 2600 m. (Ludlow and Kinnear, 1944). From November to January, Meinertzhagen (1927) found it in Sikkim between about 2700 and 3900 m. altitude, but it is also known to descend in winter down to 1100 m. (Stuart Baker, 1926).

Meinertzhagen (1927:383) states that its "plaintive whistle seemed much the same as that of our British bird" (*P. pyrrhula*).

*Material examined*.—5 ♂♂, 5 ♀♀: northwest Himalayas; Nepal; Darjeeling (Amsterdam Mus.; Leiden Mus.).

#### *Pyrrhula aurantiaca* Gould

*Characters*.—Black mask; tail forked; male approaching that of *erythrocephala*, but entire upper parts, including lesser wing coverts, orange buff. Under parts of the same coloration, but generally lighter; female resembling that of *erythaca*, but the under parts are tinged with pale orange rufous

or dull yellow and the upper parts are washed with yellowish brown; no white line bordering the black mask posteriorly.

No subspecific variation occurs.

*Range*.—Kashmir; westward apparently to Gilgit (Biddulph, 1881) and Chitral; also recorded as a breeding bird from Rawal Pindi District (Whistler, 1930); although frequently observed (Stuart Baker, 1926), not yet found as a breeding bird in Simla States and Garhwal.

*Biotope*.—Its partiality to dense coniferous forests has been noticed by several observers. Nests have been found at about 3700 and 3000 m. altitude (Stuart Baker, 1934) in forests of silver fir and birch with luxurious undergrowth. In winter it has been found as low as about 1700 m. altitude (*loc. cit.*). The species seems to be rather locally distributed.

*Material examined*.—None; see color plate in Gould, 1858.

*Distribution and ecology*.—The Himalayas are inhabited by four species of *Pyrrhula*, three of which are known to occur side by side in the Chinese-Burmese section, *nipalensis*, *erythaca*, and *erythrocephala*.

The westernmost representative is *P. aurantiaca*. According to its range it is confined to Kashmir and apparently has not been recorded as a breeding bird from any locality where *P. erythrocephala* breeds, although the latter species nests in Kashmir as well. Biotope (chiefly coniferous forests) and vertical distribution (from 3000 m. upward) are the same in *aurantiaca* and *erythrocephala*.

A considerable overlap of the ranges of *P. erythrocephala* and *erythaca* occurs in the eastern Himalayas. The joint range extends from Sikkim to eastern Bhutan, where the two species nest in the same biotope of chiefly coniferous forests above 2500-3000 m. altitude. Although Ludlow met with the two species in the same localities, *erythrocephala* is just as rare east of latitude 92°E. (mid-Bhutan) as is *erythaca* west of this line (Ludlow and Kinnear, 1944). Thus, one might conclude that interspecific competition acts as a factor preventing further overlap of the respective ranges.

The Himalayan range of the fourth representative (*P. nipalensis*) covers the region inhabited by *aurantiaca* in the West, *erythrocephala* in the middle and *erythaca* in the East. Yet, most observers record *nipalensis* from broad-leaved and mixed forests rather than from a coniferous type of forest. Consequently there is a difference between the other species and *nipalensis* in altitudinal distribution, since the latter occurs usually below 3000 m. altitude. Furthermore, its occurrence in the mountain forests of Yunnan and Formosa side by side with *erythaca* indicates that there is no essential interspecific competition between *nipalensis* and the *erythaca-erythrocephala-aurantiaca* group, in relation to which *nipalensis* acts as a sympatric species.

Since the three species *erythaca*, *erythrocephala*, and *aurantiaca* have close ecological similarities, in contrast to *nipalensis*, it might be of interest to point out that according to several observers, the call-note of the high-mountain group is the same among the three species and closely resembles that of the familiar western European *P. pyrrhula*, whereas the call-note of *P. nipalensis* is described to be rather harsh and remarkably different from the sweet whistle of the other bullfinches.

None of the Oriental and Himalayan bullfinches is migratory, although there are several records of their moving vertically with the season.

*Character geography*.—Three species of *Pyrrhula* from southeastern Asia have black forehead, lores, and chin in both sexes (*erythaca*, *erythrocephala*, *aurantiaca*). I have shown above that these black-masked forms are ecologically alike and that there is a tendency for them to replace each other geographically. Furthermore, in the males of these species there is a tendency toward increase of orange-red pigmentation from east to west: *erythaca*, orange-red breast and flanks; *erythrocephala*, orange-red head and hind neck, throat, breast, and flanks; *aurantiaca*, orange-red back, scapulars, hind neck, head, throat, breast, and flanks.

On account of their linked ranges and the similarity of their color pattern, in addition to a quantitative difference in pigmentation, these forms are here considered as three elements of one interspecies (Ripley, 1945), which will be called the *erythaca* interspecies, "Masked Bullfinch." The tendency toward extension of the red pigmentation of the under parts to the feathers of the upper parts is also found in the males of other species (*P. pyrrhula*), which coincidentally may have brick-red edgings to the feathers of mantle and back.

The adult of *P. nipalensis* is different from those of all other species of *Pyrrhula* in having no black whatever on the head, except that in the race of eastern China, the crown is more strongly indicated because of the dark brown centers of the crown feathers. This brown plumage is remarkable, since it is reminiscent of the juvenal plumage of apparently all species of *Pyrrhula*. The white shaft streaks in the central tail feathers of the Formosan *P. n. uchidai* are without antecedents in the genus, although white patches on the inner web of the lateral tail feathers can be observed frequently in *P. pyrrhula*, especially in the race *cassini*.

The adult Philippine *P. leucogenys* has a black cap and chin, resembling the Palearctic species. The black feathers, however, have a much stronger metallic gloss than in the latter. The white cheeks and ear coverts of *leucogenys* are a rare character in the genus *Pyrrhula*, but it is approached in eastern Malaya by *P. nipalensis waterstradti*, which also has white on sides of the head.

The Oriental and Himalayan species of *Pyrrhula* form a taxonomic unit by possessing a distinctly forked tail and normally developed upper tail coverts. In the Palearctic species the tail is almost square and the upper tail coverts are markedly long. The species are of approximately the same size; *P. nipalensis* is slightly larger than the others. In addition, *P. nipalensis* and *P. leucogenys* have in common a relatively long tail, as indicated by the following measurements of males only:

	Wing	Tail
<i>P. n. nipalensis</i>	85-90 mm.	73-77 mm. (Stuart Baker, 1926)
<i>P. e. erythaca</i>	82-84	67-69 "
<i>P. erythrocephala</i>	76-79	60-64 "
<i>P. aurantiaca</i>	80-83	57-58 "
<i>P. l. leucogenys</i>	79	77 (Leiden Museum)

On the basis of the characters just discussed, *P. nipalensis*, *leucogenys*, *erythaca*, *erythrocephala*, and *aurantiaca* have been united into one subgenus, *Protopyrrhula* (Bianchi, 1906), which, however, has no nomenclatural value.

The eggs of *nipalensis*, *erythaca*, and *erythrocephala* are said to resemble those of *Chloris* and *Loxia* in having a pale greenish white ground color with reddish brown markings, which are most conspicuous in forming an ill-defined ring near the broad end. Those of *aurantiaca* differ in having a white ground color without green tinge (Stuart Baker, 1934; Schönwetter, 1929). Those of *leucogenys* are not known. Since the eggs of the Palearctic species have a bluish ground color, the above remarks once more show that the Himalayan and Oriental bullfinches are closely linked together.

*History.*—Although there are no indications as to the events that have led to the separation between *P. nipalensis* and the masked bullfinches, yet it seems clear that ecological divergences played an important, if not exclusive, role. This conclusion is the more pressing, since *P. nipalensis* shares its range with all three species of masked bullfinches, including *P. e. owstoni* on the island of Formosa. The highly disjunctive range of *P. nipalensis* and its penetration or retreat into isolated subtropical or tropical mountains (Chin Hills; eastern Malaya) justify the conclusion that the specific sepa-

ration between the Brown-headed (*nipalensis*) and the masked bullfinches is of considerable age. The fact that all juvenal bullfinches have a brown head and a uniform brown dress without the red or orange red coloration of the adult males of many widespread species furnishes clear evidence in favor of the assumption that the original bullfinches were uniform brown birds, although with the characteristic black wings and tail and the white rump. The juveniles of at least the European species *P. pyrrhula* have horny yellowish bills, instead of black ones, thus curiously reminding one of the adult of *P. nipalensis*. In conclusion, *P. nipalensis* might be regarded to represent or to resemble most closely the original type of bullfinch from which all other bullfinches have been derived. This form seems to have been but little altered during the long time that has elapsed since the branching off of the *erythaca* interspecies. Its disjunct distribution, however, indicates periods when extermination occurred over large areas.

The generally brown plumage, the isolated tropical range and the mountainous habitat of *P. leucogenys* link it with *P. nipalensis*, although the head coloration of *leucogenys* is quite distinct. The black crown, however, is indicated in the Fukien race *P. n. rickettii*, and the white sides of the head are found in *P. n. waterstradti* of Malaya. Furthermore, *P. nipalensis* and *P. leucogenys* are the only representatives of the genus having the bill yellowish horn with dark culminal ridge and tip, instead of being wholly black, although in *P. n. waterstradti* the base of the bill is leaden color and not horn. The secondary sexual difference in the lipochromous pigmentation of the outer web of the innermost secondary is also the same in both species (red in male, yellow in female). Consequently, there is sufficient evidence in favor of the supposition that *P. leucogenys* is an old side-branch of the *Pyrrhula* stock, more closely related to *P. nipalensis* than to the *erythaca* interspecies. In fact, it might be regarded to be a derivative of *P. nipalensis*, with which it should be united in one superspecies.

The disjunct distribution of *P. erythaca* in eastern China (Eastern Tombs; Formosa) without conspicuous geographical variation reveals the fact that *P. erythaca* must be the older form of the *erythaca* interspecies. Its distribution might be an indication of the Chinese origin of the whole interspecies. The considerable destruction of the forests in most parts of China by human agency may be the cause of the extermination and of the retreat of *P. erythaca* in the mountain forests of western and northern China. Its extermination near the Eastern Tombs (Chihli) was evidently caused by recent deforestation of the country (La Touche, 1925; Bangs, 1932).

The Kashmir representative (*aurantiaca*) has not a single relation with any of the black-headed palearctic forms. On the contrary, it shows clear structural, ecological, and distributional affinities with the Himalayan *P. erythrocephala*, the latter in turn resembling *P. erythaca* of western China. The fact that *aurantiaca* exhibits the most extreme color type of all southern Asiatic bullfinches and possesses the most reduced blue pigmentation (ground color) on its egg shells is in accordance with its extreme western range which is situated at the distributional end of a continuous chain of populations. The divergence between *P. erythaca* and *P. aurantiaca* in coloration and range is perfectly linked by *P. erythrocephala* of the Himalayas. Therefore, the species *erythrocephala* and *aurantiaca* are here considered invaders into the Himalayas from southwestern China.

Unfortunately, the recent distribution of the masked bullfinches does not elucidate the question as to how they diverged originally. Nevertheless, each species has a clear center of dispersal, which, I think, may be located as follows: *erythaca*, mountains of southwestern China; *erythrocephala*, central Himalayas; *aurantiaca*, Kashmir.

## THE EASTERN PALEARCTIC BULLFINCHES

*Pyrrhula griseiventris* Lafresnaye

*Characters and subspecific variation.*—See general discussion beyond.

The following races may be recognizable: *P. g. griseiventris* Lafresnaye 1841: Japan; *P. g. cineracea* Cabanis 1872: Lake Baical (= *cassini* of former authors; see Swarth, 1928); and *P. g. kurilensis* Sharpe 1886: Kurile Islands.

*Range.*—Northern Japan, on Hondo, Seven Islands of Izu (Hachisuka, *et al.*, 1932), Jesso, but absent in the islands of Shikoku and Kiushiu (Jahn, 1942), southern and middle Kurile Islands, north to Ushishiru (Yamashina, 1931) and Sakhalin (Lönnberg, 1908); Amur region (Worobiev, 1937), Manchuria and Korea (Démentiev, 1934), once in Tsu-shima in Strait of Korea (breeding?; Kuroda, 1922), Greater Khingan Mts., west to Transbaicalia (Upper Amur River) and the Kentei (Kozlova, 1933) and Khangai Mts., also Baicalia (Stegmann, 1936), Sajon Mts. and northeast Altai. Nests have been found as far west as Tomsk (Johansen, 1944), and apparently Minussinsk (Sushkin, 1925), whereas Johansen (*loc. cit.*) mentions a summer record from Beresow on the Lower Obj River. In winter it has been found in China, south to Shanghai (very rare: La Touche, 1925), rather frequently in southwest Siberia and exceptionally in southeast European Russia (Orenburg: Sushkin, 1914). The Greater and Lesser Khingan Mts. probably form the boundary between the races *griseiventris* and *cineracea*, but the latter has been found in winter within the range of *griseiventris* (Amur Region: Stegmann, 1931).

*Biotope.*—See general discussion beyond.

*Material examined.*—3 ♂♂, 1 ♀: Lake Baical; Onon River; Upper Yenissei River. 13 ♂♂, 6 ♀♀: Japan (Amsterdam Mus.; Leiden Mus.; coll. Sillem-Van Marle).

*Pyrrhula pyrrhula* (Linnaeus)

*Characters and subspecific variation.*—See general discussion beyond.

The following races may be recognizable: *P. p. pyrrhula* (Linnaeus 1758: Sweden); *P. p. cassini* Baird 1869: Nulato, Alaska (= *kamtschatica* of former authors; see Swarth, 1928); and *P. p. jeniensis* Johansen 1944: Krassnojarsk, Upper Yenissei.

*Range.*—The taiga zone of Siberia, north to the southern Yamal Peninsula (Stschutschja, according to Schuchow, *vide* Johansen, 1944), south generally to 57° N. lat. (Tomsk; Krassnojarsk: Johansen, 1944); the Sajon Mountains, northern Altai (Johansen, 1944) and Baicalia (Kozlova, 1933), to the coast of the Okhotsk Sea, south to Ajan (Démentiev, 1934); also Kamchatka and the northern Kurile Islands (Paramushiru: Yamashina, 1931). Accidentally in the Commander Islands [♂, Bering Island; ♀, Copper Island: June-July (!): Hartert, 1920], St. Lawrence Island [♂, May (!), 1936: Friedmann, 1937] and Nunivak Island (Swarth, 1928), in the Bering Sea; also northwest Alaska (Nulato: Swarth, 1928). Outside the breeding season it has been observed in more southern countries: northern Persia (rare: Sarudny, 1911), Turkestan and Tarbagatai (Démentiev, 1934), Transbaicalia, Ussuri Region (Stegmann, 1931; Kozlova, 1933), northeast Korea (Meise, 1934), northern China (Eastern Tombs, Chihli: La Touche, 1925), and in Sakhalin (Hesse, 1915) and Japan (Hondo: Démentiev, 1934; also one ♀ from "Japan" in the Leiden Museum). The race *cassini* occupies the region east of the mountains of Werkhojansk and Stanovoi, whereas the typical race has been found to the west of it, as far eastward as Yakutia and the Aldan-Maja rivers region (Johansen, 1944). Nevertheless, the species appears to be absent as a breeding bird in the Yakutia region itself, as also in the mountains of Werkhojansk (Tugarinov and Buturlin, 1925).

*Biotope.*—See general discussion below.

*Material examined.*—3 ♂♂, 3 ♀♀: Japan; Onon River; Tomsk; Askabad, Transcaspia (Leiden Mus.; coll. Sillem-Van Marle).

*Distribution and ecology.*—The eastern form, *P. g. cineracea*, has been found nesting within the breeding range of *P. pyrrhula* in the following localities: Kentei and Khangai regions, Baicalia, Sajon Mts., and northern Altai, northwards and westwards to the River Obj (Tomsk) (Sushkin, 1925; Stegmann, 1931; Kozlova, 1933; Grote, 1936; Johansen, 1944). Johansen (1944) mentions summer records as far west as Beresow on the Lower Obj. In the eastern portions of this joint range (Kentei, Khan-



gai) *P. g. cineracea* is by far the commoner of the two, but near Tomsk the situation is just the reverse, *cineracea* being much rarer than *pyrrhula*. In the above countries the two forms have been found according to Sushkin (1925:14) "in the same locality, sometimes one species within some hundred yards from the other, in the same habitat and on the same level." Johansen (1944) found them breeding in the dark taiga of *Picea* and *Abies*, interspersed with birch and poplar. Forests of pure pine near Tomsk are inhabited by *pyrrhula* only, whereas in the eastern Kentei Mountains *pyrrhula* and *cineracea* have been found in bushes and trees near river valleys and in the lower zones of the mixed forest. In the latter countries, however, the higher zones of pine, cedar and larch woods are said to be inhabited by *cineracea* only (Kozlova, 1933). Although there is a considerable overlap in the ranges of *P. g. cineracea* and *P. p. pyrrhula*, yet there appears to be some interspecific competition, resulting in the fact that *cineracea* is much rarer in the West, and *pyrrhula* in the East, whereas the less favorable pure conifer forests are inhabited by the latter species only, which is evidently more eurytopic than *cineracea*. Interspecific competition may be diminished because the forest types preferred are slightly distinct (Johansen, letter, 1948), and that, at all events near Tomsk, the breeding time of *cineracea* starts a few weeks later than that of *pyrrhula* (Johansen, 1944): *pyrrhula*, full clutches between May 9 and June 27; *cineracea*, full clutches between June 1 and July 9. The relatively late breeding season of *cineracea* links it with the Oriental and Himalayan bullfinches, which are also extraordinarily late breeders.

*Character geography.*—All Palearctic bullfinches have a black facial mask and cap (fig. 7). They have only very slightly forked tails and very long upper tail coverts. Consequently, they are here considered to represent the typical subgenus *Pyrrhula*, the "black-capped bullfinches." As compared with *P. griseiventris*, the males of *P. pyrrhula* show a large amount of red pigmentation on the sides of the head and the under parts, which characters remain constant throughout the whole range of the species from Kamchatka to western Europe. Nevertheless, males from Kamchatka (*cassini*) have the upper parts of a more clear gray tone and are on the average smaller than those from central Siberia (*pyrrhula*). In *cassini* the wing of the males measures up to 96 mm., as against 100 mm. in Yukatia males (Johansen, 1944). The white streak on the inner web of the lateral rectrices is much more frequently found in *cassini* than in any other race of *P. pyrrhula*.

*P. griseiventris* is much less constant in its coloration. In Japanese and Manchurian males (race *griseiventris*), the sides of the head are more or less red. The under parts are more variably and slightly red, but in many specimens these are pure gray, without any tinge of red. In the Kuriles a light gray race occurs (*kurilensis*) in which the under side of the males may have only a slight tinge of rosy. West of the Khingan Mountains the species has lost even the slightest trace of red pigmentation, the males being gray, black, and white only (*cineracea*).

Those males of *P. g. griseiventris* showing strongly tinged under parts may be adult birds exclusively, since all three immature specimens, as defined by the wing characteristics given by Drost (1940) and Mayaud (1944) for European birds, have the under parts mostly gray, with only the cheeks and ear coverts dark red.

Several specimens intermediate between *P. p. pyrrhula* and *P. g. cineracea* have been collected in the common breeding ranges. Stegmann (1931) mentions three adult males taken during the winter in southern Baicalia, Khangai and northern Altai. According to Johansen (1944), intermediate birds have been observed frequently near Tomsk, also. These intermediate males resemble the race *griseiventris* (Stegmann, 1931; Johansen, 1944), but by most authors they have been interpreted as hybrids between *pyr-*

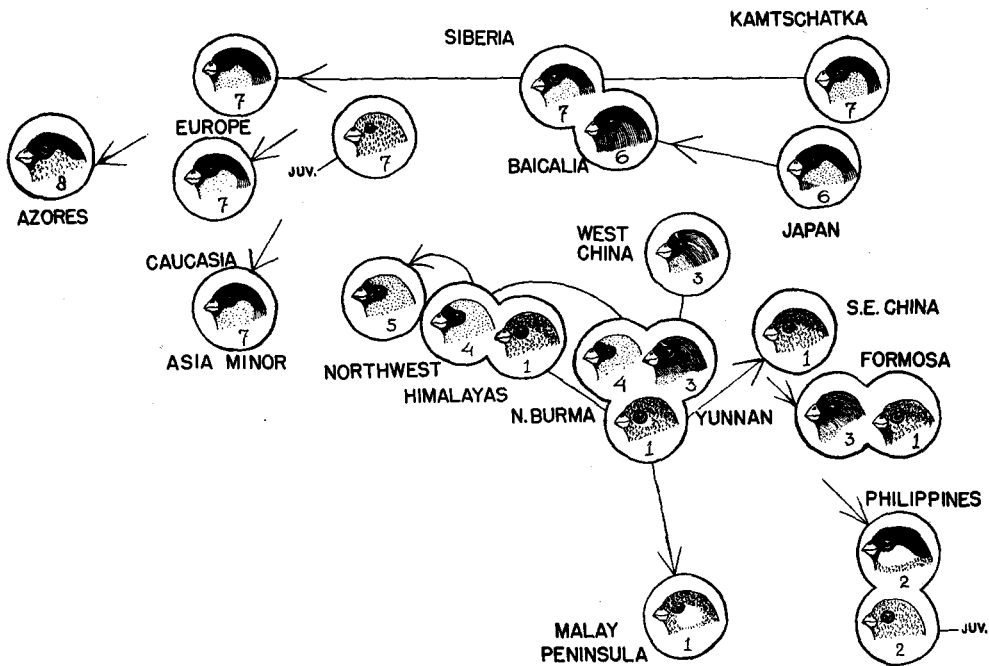


Fig. 7. Diagram of the character geography, not phylogeny, of the genus *Pyrrhula*. Plumage colors other than black are indicated as follows: dots, red; parallel straight lines, gray; wavy lines, brown. The various species are numbered as follows: 1, *nipalensis*; 2, *leucogenys*; 3, *erythaca*; 4, *erythrocephala*; 5, *aurantiaca*; 6, *griseiventris*; 7, *pyrrhula*; 8, *murina*. When circles overlap, the species occur sympatrically.

*rhula* and *cineracea*, although there does not seem to be any convincing evidence of a wild cross between these species. According to Sushkin (1925), the intermediate birds are not hybrids at all, but they exhibit the normal range of variation of the subspecies *cineracea*. A rather wide range of variation within *P. g. cineracea* is in accordance with the fact that in the males of *P. p. pyrrhula* from central Siberia, Johansen (1944) found a slight, but distinct tendency toward variation in the direction of *P. cineracea*, the under side showing a soft raspberry red coloration as in *griseiventris*, rather than the brick red coloration of *pyrrhula*. Consequently, this race *jenisseiensis* (Johansen, 1944), which is based upon winter birds from the Upper Yenisei River (Krasnojarsk), is claimed to represent a transition between *pyrrhula* and *cineracea*, although strongly tending towards *pyrrhula*. However, the parallel action of climate to reduce the red pigmentation may account for the similarity. At all events, the racial characteristics of *P. p. jenisseiensis* seem to be very poorly defined. The only male from Tomsk examined by me (December) closely resembles a series of Scandinavian males, although its under parts are of a slightly clearer vermilion.

Taxonomic distinctness of *P. p. pyrrhula* and *P. g. cineracea* is further indicated by the fact that *pyrrhula* has larger dimensions and a heavily swollen bill, whereas *cineracea* is smaller and has a slender bill like that of the western European birds. According to Sushkin (1925), the few intermediate ("hybrid") specimens have the shape of bill of *P. g. griseiventris*!

There does not seem to be any reason for the assumption (Johansen, 1944) that the race *griseiventris* represents a hybrid population between the forms *cineracea* and *cassini*.

It does not seem to be known if the breeding range of *P. g. griseiventris* is geographically connected with that of *P. pyrrhula*.

*History.*—Contrary to the commonly held opinion, recent Russian geologists (Wojekow, Obrutschew) have found convincing evidence of the occurrence of considerable Pleistocene glaciations in western Siberia and in northern Altai (see the short summary by Johansen, 1943), the intensity of which gradually decreased eastward. In the Altai region, the remnants of three or four glaciation optima have been traced. Nevertheless, there does not seem to be any argument in favor of the extreme view of Reinig (1937), who stated that no Pleistocene taiga refugium in Siberia could have existed. In the case of *Dendrocopos m. major*, I have tried to show that this race must have survived during the last glacial period in local southern Siberian forests which were isolated from both the Manchurian and the Turkestan region (Voous, 1947). The same applies to *P. p. pyrrhula* of Siberia, which, in an unbroken chain of very similar populations, inhabits the northern Asiatic taiga from Kamchatka to the Ural Mountains.

The slight difference in coloration and dimensions between the Kamchatkan and the central Siberian bullfinches is noteworthy. In this respect the distribution of *Dendrocopos major* in eastern Asia should be compared. A conspicuous similarity in the ranges of *P. pyrrhula* and *D. major* is the existence of distinct Kamchatkan races, as well as the fact that the mountains of Werkhojansk and western Stanovoi form the racial boundary. The main difference in the ranges of *P. pyrrhula* and *D. major* is the fact that in the case of *Pyrrhula*, Kamchatka is inhabited by populations closely resembling the Siberian ones and sharply distinct from those of Manchuria, whereas in *D. major* the Kamchatkan race is much closer to that of Manchuria than to that of Siberia. In conclusion it is clear that, at least during the last great Asiatic glaciation, there were three separate refugia inhabited by forest birds: Manchuria, Kamchatka, and central southern Siberia.

Southeast Transbaikalia, which is inhabited by the plain gray *P. g. cineracea*, is known as a glacial refugium of forests or parklands and might therefore be considered to represent the recent center of dispersal of this form. It is also considered by Eller to be the center of dispersal (and consequently a glacial refugium) of a section of the butterfly species-group *Papilio machaon* (Pagast, 1939). The distributional relation between *cineracea* and *pyrrhula* indicates that during the last glaciation they inhabited separate regions. Postglacially they have infiltrated each other's ranges, probably with a certain amount of hybridization. It is known that the northern boundaries of the Mongolian deserts have been richly covered with forests, not only in postglacial times, but also before the last glaciation. As a result the Manchurian populations may have been able to spread into the regions north of the Gobi Desert either during the postglacial, the last interglacial, or an interstadial period. Of these populations, *cineracea* is here considered to represent the direct offspring. The difference between the races *griseiventris* and *cineracea* can be considered to be an argument in favor of the assumption that their genetic separation is older than the postglacial. At all events *cineracea* is taxonomically and historically closer to *griseiventris* than to *pyrrhula*. As *cineracea* and *pyrrhula* inhabit overlapping ranges, they must be treated in nomenclature as distinct species. *Griseiventris* should be incorporated into *cineracea*. Since the ranges of *P. griseiventris* and *P. pyrrhula* overlap with a marginal fringe of hybridization, these species should be called "emergent interspecies" (Ripley, 1945).

The exclusive occurrence of the race *griseiventris* in Manchuria and Japan, which were forest refugia during the Pleistocene glacial periods, reveals the fact that during at least the last great glaciation in northern Asia, these refugia were inhabited by populations resembling the present race. The conspicuous variability within the race *grisei-*

*ventris* is comparable to the variability which seems to be present, for example, in the Manchurian form *Garrulus g. bambergi* (Voous, 1945). This phenomenon might have some historical cause, although there are no indications that the variability originated in the postglacial. Nevertheless, Manchuria acts as a kind of "allele-center," at all events in *Pyrrhula* and *Garrulus*. As in such cases as *Garrulus glandarius*, *Dendrocopos major*, *D. leucotos*, and *D. minor*, the Manchurian populations of *Pyrrhula* represent the stock from which Siberian populations have originated postglacially. From these also the race *P. g. cineracea* arose in postglacial times by losing even the last trace of the red pigmentation still found in the race *P. g. griseiventris*.

A slight similarity exists between *P. g. cineracea* and *P. murina* from the Azores, caused by the absence of any red pigmentation in the male sex. Nevertheless, it appears from the above remarks that there is no basis for the assumption that they are genetically closely related or that their ranges have been once geographically connected. Consequently, I cannot follow Görnitz (1923), who considered *cineracea* and *murina* as the oldest (relict) forms of the genus *Pyrrhula* and who compared them with the geographically disjunct races of *Cyanopica cyanea* of southeast Asia and the Iberian Peninsula.

A zoogeographical element which is probably comparable with *P. g. cineracea* is found in *Dendrocopos major mongolus*. This much disputed race inhabits northern Mongolia and the Kentei Mountains and is said to be intermediate between the Manchurian race *tscherskii* and the Siberian race *major* (= "*brevirostris*"), although sufficiently distinct from both to represent a separate race (see Voous, 1947:18 and 22). The Manchurian-like jays (*G. g. bambergi*) from the eastern Tian Shan Mountains (Voous, 1945) probably also belong to this group of remnants of the old northern Mongolian forest fauna, provided that our specimens of jays did not represent migrants from northern regions!

No taxonomic or distributional fact is known to the author which might serve to clear up the relationship between the Palearctic black-capped bullfinches and the Chinese masked bullfinches. Although it is possible that *P. erythaca* may be extending its range northward into extreme southern Manchuria (see Meise, 1934), no distributional contact between these two groups of bullfinches is known. Nevertheless the resemblance between the juveniles of the Black-capped Bullfinches and the adults of *P. nipalensis*, and the close taxonomic similarity between, for example, the female of *P. leucogenys* from the Philippines and the female of *P. griseiventris* from Japan and especially from the Kurile Islands (Ogilvie-Grant, 1895) may be considered to be a strong argument in favor of the view that the Palearctic bullfinches have spread from an Oriental center. However, the distributional gap and the close relationship of *P. leucogenys* with *P. nipalensis* indicate that the black cap of the Philippine species and the black cap found in the subgenus *Pyrrhula* have probably arisen independently. I can find no indication as to whether or not the subgenus *Pyrrhula* is the direct offspring of *P. erythaca* or of *P. nipalensis*. The black facial mask and the red under parts of the *erythaca* interspecies, in contrast to *nipalensis*, which is plain brown, might be an argument in favor of *P. erythaca*.

From the fact that the black-headed bullfinches are absent as breeding birds in southern Japan (Shikoku; Kiushiu; Riu Kiu Islands) one may conclude that their present range has been occupied only recently. The peculiar jay, *Garrulus lidtshi*, from Amami-oshima and Tokunoshima, Riu Kiu Islands, for example, belongs to a much older group of forest birds, with different representatives in the Caucasian and Hyrcanian regions, as well as in northern Africa. Bullfinches do not occur in northern Africa, and their Caucasian and Hyrcanian races are only slightly differentiated. These facts uphold

the assumption of a relatively recent history for Palearctic members of the genus *Pyrrhula*.

#### THE WESTERN PALEARCTIC BULLFINCHES

##### *Pyrrhula pyrrhula* (Linnaeus)

*Characters*.—Glossy black cap and black chin in both sexes; under parts of males rosy red, upper parts, gray; upper and under parts of females brownish, the upper surface generally more olive than the under parts, which are tinged brownish purple; innermost secondary of males has a gray outer web, part of which may be more or less strongly tinged with red. The latter condition was found in adult birds as defined by Drost (1940) and Mayaud (1944), although odd adult birds have the outer web pure gray and odd juvenal birds may have it red. In most adult females the outer web of the same feather is strongly tinged with drab brown. The plumage of the juvenal birds, which is plain brown, has been discussed in the chapter on the history of the Oriental species.

*Subspecific variation*.—In spite of the large area inhabited, subspecific variation is slight. British and Dutch males have the under parts less bright vermilion than all other European males examined. In Caucasian males (*rossikovi*), especially in South Caspian ones (*caspica*), the under parts are brighter and more orange, less pink, than in any other form of *P. pyrrhula*. The upper parts of the Dutch and British males are of a darker shade of gray than found in the other European males. They are darkest in Scottish mountain birds (*wardlawi*, see Clancey, 1948). The females of the same series have the under parts tinged with brown, although this is more clearly pronounced in British and particularly in Irish birds. In British females the upper parts are of a distinct dark olive brown tinge, although rather grayer in Scottish mountain birds (*loc. cit.*); they are brown in Dutch and German females and grayish brown, or even more gray, in northern European and Siberian birds. Scottish birds (*wardlawi*) have, on the average, smaller and less "massive" bills than other British birds (Clancey, 1947 and 1948). Finally, the white streak on the inner web of the outer tail feathers, which is most frequently found in birds from Kamchatka, is occasionally present in European birds, especially in those from Scandinavia and Russia.

Subspecific variation in size, however, is significant and well known (tables 1 and 2; fig. 8). Various races have long been recognized upon more or less sound bases, but their nomenclature is remarkably confounded (see Stresemann, 1919; Hartert and Steinbacher, 1932-1938; Mayaud, 1939). In establishing subspecific boundaries many errors have been made in the past by the use of non-breeding specimens. In the exhaustive paper of Stresemann (1919), only 44 of 363 listed specimens (12 per cent) were collected in the breeding season; and of 64 Dutch specimens examined in this study, only 10 were more or less certain breeding specimens (16 per cent). Breeding birds, as recognized here, must have been taken between April 8 and August 31. A few British and Dutch specimens considered to represent breeding birds, but taken between April 3 and 8, have been included.

The tables of wing measurements are based upon 186 breeding males and 78 breeding females. As indicated there, the measurements were taken by different workers, but the records have been compiled with the greatest possible care so as to make the measurements strictly comparable.

The tables and figure 8 reveal that the smallest bullfinches inhabit southwestern and western France (average wing of 79.0 mm. in males), a fact which has been recently claimed by Mayaud (1939). In a south-north cline the populations show increasingly larger average measurements, which in the rest of France, Great Britain, Ireland, and the Netherlands vary between 82 and 83 mm. Although the measurements in southwestern and central Germany seem to be generally slightly larger (males, 85.6), there seems to be a decided gap between those, for example, from Lower Franconia (males, 84.3; females, 84) and those from the southern German mountain region (males, 89.4; females, 86.4), where an apparent breeding male is recorded with a wing of no less than 93 mm. (Stresemann, 1919). From those regions eastward, the average measurements increase from 90.0 in males from Bohemia, through 90.4 in the High Tatra Mountains, to 91.3 in the eastern Carpathian Mountains (see Cerny, 1938). One female from the High Tatra Mountains even measures 95 mm. (*loc. cit.*). An increase in average dimensions can also be noticed from France to the Swiss Jura and the Alps. A breeding male taken in the vicinity of Geneva has a wing of 85 mm. and four additional males collected in the same region outside the breeding season measure 82, 85.5, 85.5, 86.5 mm. (Dottrens, letter, 1948), whereas the average measurement of six alpine males has been found to be somewhat more

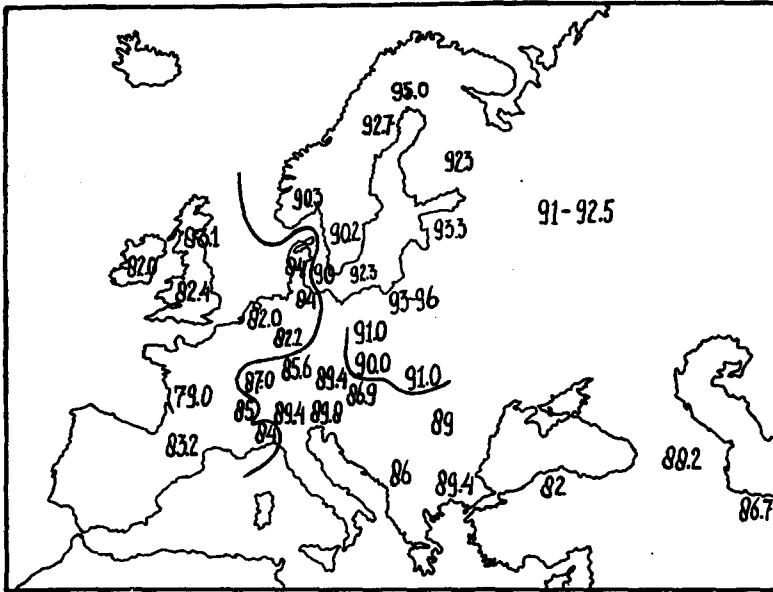


Fig. 8. Geographic variation in average wing length of breeding populations of *Pyrrhula pyrrhula* in Europe.

than 90.0 mm.; intermediate measurements occur in the intermediate areas (see tables). Breeding males from the Vosges (87.0) appear to be larger than those from the neighboring regions of France (Meurthe-et-Moselle: 83.5), a fact to which Hartert (1903) has already called attention. Breeding birds from Spain are not mentioned in the literature, although Ticehurst and Whistler (1928) record the wing measurements of seven males as 80-84 mm. and those of four females as 77.5-80.0 mm. Breeding specimens are absent in the Madrid Museum, but the few Spanish bullfinches that are present measure 80, 81, 81, and 85 mm. in males, 79 and 81 mm. in females (Galiano, letter, 1947). In their smallness these Iberian birds agree with birds from southwestern France. Breeding birds from Italy are also practically absent in the three Italian museums to which inquiries were addressed (museums of Genoa, Milan and Turin). One breeding male from northwestern Italy (Piedmont) has a wing of 84 mm. agreeing with dimensions from western Europe. Random northwestern and mid-Italian specimens have corresponding measurements: males 82-88, average (10) 85.7; females, 82-88, average (5) 83.3 mm. Specimens with large dimensions agreeing with those of the Scandinavian ones have been frequently recorded in Italy, mostly in the Italian Alps (Arrigoni, 1929). In the Milan Museum is a breeding male from Bolzano, Venetian Alps, with a wing of 89 mm. This bird is larger than any western European breeding bird. In the same museum is a male from Zambala, Bergamasker Alps, with a wing of 90 mm. (Moltoni, letter, 1948).

Southeastern European birds (males, 89.4; females, 86.5) appear less regular in the table, although it is clear that they are considerably larger than western European birds, agreeing with those from southern Germany (males, 89.4; females, 86.4). Nevertheless, they are distinctly smaller than those from Scandinavia, with which they have been united by Stresemann (1919), who apparently was confused by the great number of wintering birds of large size. Additional Serbian birds collected outside the breeding season measure 87, 87, 89 in males, 86 and 88 mm. in females (British Museum, data from Macdonald, letter, 1948). The specimens from lower Austria are slightly smaller in males (86.9), although slightly larger in females (87.2); they are larger than specimens from any western European population, except those from the Vosges.

Decidedly larger bullfinches are found in the province of West Prussia, eastern Germany (males, 91.0; females, 89.6), from where the dimensions increase in an easterly direction. Comparably large measurements occur in breeding males from Zealand, Denmark (90). In Scandinavia the average measurements tend to increase from southern Sweden (males, 89.5; females, 88) and southeast Norway

(males, 90.3), northward to Lapland (males, 95.0; females, 90.0). These measurements apparently are the same as those found in Finland (males, 92.3; females, 90.3), central Russia (males, 91-92.5), and Siberia (males, 90-94.5), although Russian and Siberian birds are known with wing lengths up to 100 mm. Wings of Rumanian winter birds have been found to measure as follows: males, 92-97, average (8) 94.4; females, 90-92, average (3) 91.0 mm. (Sassi, letter, 1947; coll. Sillem-Van Marle). These specimens might be referred to northern migrants and not to breeding birds.

In conclusion, it appears that there are three series of populations, each independently showing a slight clinal variation in size. The origins of these series may be located in (1) southwest France and northwest Italy, (2) Yugoslavian and Bulgarian mountains, (3) Russia and northern Scandinavia. The differences in dimensions are more or less sharp and, therefore, can serve as racial characteristics. The birds from central Germany, the southern German mountains, the Vosges, and western Switzerland, as also those from the Carpathian Mountains, might be considered to belong to intermediate populations. These will be discussed in the section on the postglacial history of the species in Europe. Consequently, subspecific names applied to breeding birds from these localities are of doubtful value in nomenclature. It would be advantageous to declare these populations as indeterminate. Bullfinches from southern Germany (males, 89.4; females, 86.4) have apparently the same average wing measurements as southeast European birds (males, 89.4; females, 86.5), so that in order to avoid still more confusion in nomenclature, the name *germanica* (Brehm, 1831: "die deutschen gebirgigen Nadel- und Buchenwälder" = Renthendorf, Thuringia) should be considered to apply to the southern German and eastern European mountain populations, although it would seem to be more in keeping with the evidence to drop the name *germanica* in preference to another name that applies to a stable population instead of to a mixed one. The same situation exists in the use of the name *coccinea* (Gmelin, 1789: Karlsruhe, Baden, southwest Germany), the type locality of which is near the easternmost boundary of the small western European race, but, as *coccinea* has priority over the name *europaea* (Vieillot, 1816: Normandy; Brittany; Anjou; see Mayaud, 1939), it must be used for the western European race.

Apart from the mentioned mixed populations, the wing measurements of the three main groups of populations can be summarized as follows:

	Number of specimens	Males		Number of specimens	Females	
		Range	Average		Range	Average
W. Europe	59	77-87	82.0	23	78-84.5	81.0
S. E. Europe	11	86-92	89.1	2	86-87	86.5
N. and E. Europe	22	89.5-97	92.1	11	86-94	90.0

Although there is no question that the difference in dimensions between the Scandinavian and the western European birds justifies their racial separation, yet the Balkan birds are of intermediate size. However, from a zoögeographical point of view it seems advisable to place the latter birds under a separate subspecific name.

The dimensions of Transcaucasian birds agree with those of southeastern European mountain birds; they are of intermediate size (males, 88.2; females, 87.7 mm.). Measurements of Caucasian birds were not available. Southern Caspian (86.7) and Asia Minor males (82) seem to be slightly smaller. On account of a different tinge of the red under parts in the males, two races have been recognized.

The following names are considered to be the most suitable for the European races: *P. pyrrhula pyrrhula* (Linnaeus 1758: Upsala, Sweden); *P. pyrrhula germanica* Brehm 1831: Renthendorf, Thuringia (Stresemann, 1919); *P. pyrrhula coccinea* (Gmelin 1789: Karlsruhe, Baden, S.W. Germany); *P. pyrrhula nesa* Mathews and Iredale 1917: Tring, Hertfordshire, England; *P. pyrrhula wardlawi* Clancey 1947: Perthshire, Scotland; *P. pyrrhula rossikowi* Derjugin and Bianchi 1900: Caucasia and Transcaucasia; *P. pyrrhula caspica* Witherby 1908: southern coast of the Caspian Sea (Surdabend, Alumdeh).

*Range and biotope.*—(1) *P. p. pyrrhula*. Northeastern Europe, forming a western continuation of the Asiatic range. Through European Russia north to the coasts of the White Sea and in general to latitude 65°N., and south to about latitude 55°N. (provinces of Smolensk, Kaluga, Moscow, Riasan, Kazan, Ufa; see Démentiev, 1934), but absent in the Bialowiss virgin forest (Zedlitz, 1921); the coasts

of the Baltic Sea, mixed and fir forests of East Prussia (Tischler, 1941), northern Poland and north-eastern Germany. In central Germany it meets the small western and the intermediate eastern European mountain races. Here it breeds in the mountains as well as in the lowlands, in parks, gardens, and even in villages. In Scandinavia it inhabits Finland, where its local distribution is determined by the extension of the *Picea* forests, in association with *Regulus regulus*, *Parus ater*, and *Phylloscopus collybita* (Kalela, 1938); the Kola Peninsula up to about 67°N. lat. (*vide* Stresemann, 1919), the *Picea* forests (up to about 67°N. lat.) and to a lesser degree the mixed woods of Sweden, including the island of Gotland (Kolthoff and Jägerskiöld, 1898) and the conifer and more rarely the birch forests of Norway up to 70°N. lat., although it becomes increasingly rare in southern Norway (Lövenskiöld, 1947), as is also the case in southern Sweden. Recently (1934) it has spread from southern Sweden (Skane) to Denmark (Zealand: Jespersen, 1944). Although actual nesting has never been recorded on Bornholm (Löppenthin, letter, 1948), the observations of courting bullfinches in the coniferous woodlands, as well as of family parties with newly fledged young in deciduous and mixed forests, makes it certain that the species is a breeding bird on the island and has been so probably since 1916 (Löppenthin, 1935). The westernmost breeding localities of this race appear to be situated in eastern Pomerania (near Bütow: Niethammer, 1937) and in the province of West Prussia, eastern Germany (Stresemann, 1943). In a less pure state it has infiltrated into the central European mountains, as far west as the Swiss Alps. Apart from its irregular autumn and winter migrations, this race has been recorded from as far south as Asia Minor, Greece (Stresemann, 1919), and Malta (Despott, 1917).

(2) *P. p. germanica*. The mountains of southeastern and central Europe: the submontane (1600 m.), montane, and subalpine (2300 m.) zones of the Rhodope, Perin (Alibotush: Scharnke and Wolf, 1938), and Rila mountains in southern Bulgaria (von Jordans, 1940), where it inhabits, apart from mixed woods, the dense forests of *Picea excelsa*, *Pinus silvestris*, *P. peuce*, and *P. leucodermis*, in association with *Dryocopus martius*, *Loxia curvirostra*, *Fringilla coelebs*, and *Serinus canarius* (Harrison, letter, 1948), as also the subalpine vegetations of *Pinus montana*, *Alnabetula viridis*, *Juniperus nanus*, and *Vaccinium* (von Boetticher, 1919); Greece, Macedonia (Mavrova, July, in mixed wood at 1800 m.: Fehring, 1922), the southern Yugoslavian and northern Albanian mountains, where it is very local and rare (Ticehurst and Whistler, 1932), the Dinaric Alps, and the Balkan Mountains in northern Bulgaria. Furthermore, the mainly coniferous forests (*Abies pectinata*, *A. excelsa*) of the Transylvanian Alps (Mt. Retyezát, 1250 m., June 5: Congreve, 1929), the coniferous mountain forest of Siebenburgen (von Csató, 1885), the Carpathian Mountains, including the High Tatra Mountains, to the mountains surrounding the Bohemian Basin (Cerny, 1938). It is a rare breeding bird on the Bohemian-Moravian highlands and very rare in the Bohemian Basin (Cerny, 1938). It is absent as a breeding bird on the Hungarian plains (Greschik, 1939), but it is this race that is apparently also found in the Austrian, northeastern Italian (Bolzano), and Swiss Alps, where it inhabits, apparently mixed with the race *pyrrhula*, the coniferous and mixed forests (Burckhardt and Wyss, 1947) mostly of the subalpine zone up to the tree-line (Meylan and Haller, 1946), and prefers young fir trees for nesting (Géroudet, letter, 1948). The westernmost records of this race are those from the Swiss Middle Mountains (Canton Lucerne). The breeding specimens with large dimensions found in the Vosges, where they prefer forests dominated by *Picea excelsa* up to 1200 m. alt. (Laurent, letter, 1948) represent perhaps the westernmost infiltration of this or of the northeast European race.

(3) *P. p. coccinea*, *P. p. nesa*, and *P. p. wardlawi*. Western Europe, from the mixed and conifer forests of the Pyrenees (Mayaud, *et al.*, 1936), along the western and northern slopes of the Alps, to southern Germany, where *coccinea* gradually merges into populations with larger dimensions; the whole of France, Belgium, and the Netherlands, although in the latter countries it is rare in the alluvial provinces; also the western half of Germany, east to about Stettin and the Hartz (Niethammer, 1937). Recently (about 1930) in Denmark (southern and central Jutland, and Alsen Island: Löppenthin, 1943; Jespersen, 1944). Also the Channel Islands (Alderney: Thompson, 1921, and 1923; Jersey: Mayaud, 1946; Herm: Mayaud, letter, 1948), and the woods, shrubberies, orchards or large gardens of Great Britain and Ireland (Witherby, *et al.*, 1938), and the conifer woodlands of the mountain regions of Scotland (Clancey, 1948), north to Caithness. These Scottish populations apparently form an ecological race, which, according to Clancey subsists extensively on heather flowers, seeds, etc., and is almost strictly confined to its coniferous biotope. It is absent in the Orkneys (Lack, 1942), although it has spread to some of the Inner Hebrides (Witherby, *et al.*, 1938). It is also a breeding bird in Italy, north of the montane (beech) zone (1000-1850 m.) of Latium (Alexander, 1917). It probably breeds



Table 1  
Wing Measurements of Males of *Pyrrhula pyrrhula* in Millimeters

Localities	Collecting dates	Measurements	Averages	Sources of data
Basses-Pyrénées	Breeding birds	82, 84.5	83.2 (4)	Mayaud, 1939
	May 13, July 7	83, 83.5		Coll. Mayaud (Mayaud)
Gironde	Breeding bird	80.5	79.0 (6)	Mayaud, 1939
Charente Inférieure	"	79		"
Loire Inférieure	"	78, 81		"
Maine-et-Loire	June	77		"
Morbihan	June	78.5	83 (1)	Berlin Museum (Stresemann)
Seine-et-Oise	Breeding bird	83		Mayaud, 1939
Meurthe-et-Moselle	April	82, 85	83.5 (2)	"
Vosges	May 25, 27	84, 89	87.0 (3)	Stresemann, 1919:35
	June 26	88		Coll. Laurent (Laurent)
Kent	April-July	79, 81, 81.5, 82.5,	82.3 (10)	Coll. Clancey (Clancey)
		83, 85		"
Suffolk	May 11, July 7	82, 84	82.5 (4)	Amsterdam Mus. (Voous)
	April 11, May 2	79, 85		Leiden Mus. (Voous)
Yorkshire	May 10-July	79, 83, 83	83.1 (5)	Coll. Clancey (Clancey)
Northumberland	April 25	81		"
Perthshire	June 14, 15	82.5, 83, 87	83.1 (5)	Coll. Plowden-Wardlaw (Clancey)
	April 7, 16	80.5, 82.5		"
Ireland	Breeding birds	79, 79, 80, 80.5, 81,	82.0 (15)	Dublin Mus. (Stelfox)
		81.5, 81.5, 82, 82, 83,		"
		84, 84.5, 85, 85	82.0 (8)	Coll. Sillem-Van Marle (Voous)
	June 10	81.5		"
Netherlands	April 15-Aug. 7	79, 80, 82, 82,	82.0 (8)	Leiden Mus. (Voous)
		83, 84, 84		Coll. Sillem-Van Marle (Voous)
	April 13	82	81.5 (1)	Berlin Mus. (Stresemann)
Westphalia	July 29	81.5		Leiden Mus. (Voous)
Hartz	April	83	83 (1)	Stresemann, 1919:36
Holstein	Aug 3	84	84 (1)	Löppenthin, 1943
Jutland	Aug. 12	84	84 (1)	Stresemann, 1919
Hessen	June 29	86	85.6 (5)	"
Thuringia	June 29	89		"
Lower Franconia	April 8-May 24	82, 85, 86	89.4 (9)	"
Swabia	April 15	93		"
Upper Bavaria	May 5, Aug. 4	87, 87.5	89.4 (9)	"
Bavarian Alps, 1200-1500 m.	July 29-Aug. 2	87, 90, 91, 92.5		"
Bavarian Forest	April 20, May 22	87, 89.5	90.0 (9)	Stresemann, 1919:33
Bohemian Forest	April 10-Aug. 7	88, 89, 90, 90, 90,		Cerny, 1938
		91, 92	90.4 (6)	"
Bohemian Basin	May 22, 28	88, 92		"
High Tatra Mts.	May 13-Aug. 30	87.5, 89, 89.5, 90,	91.3 (10)	"
		92.5, 94		"
Galicia	Aug. 12	93	91.3 (10)	"
East Carpathians	May 4-July 27	86.5, 87.5, 90.5, 90.5,		"
		91, 91.5, 92, 93, 94, 94	84 (1)	Milano Mus. (Moltoni)
N. W. Italy (Piedmont)	April 9	84	89 (1)	"
N. E. Italy (Bolzano)	April 25	89	85 (1)	Geneva Mus. (Dottrens)
Geneva	May 24	85	85.7+ (3)	Mayaud, 1939
Canton Vaud (plains)	April	85, 87		American Mus. (Mayr)
Swiss Jura	Aug. 6	85+	89.7+ (3)	Basel Mus. (Sutter)
Canton Fribourg	May 11	88		Coll. Hubert (Voous)
Canton Lucerne	April 29, May 6	89+, 92+	Stresemann, 1919:35	
Glarus Mts.	April 26	87	89.5, 91	Basel Mus. (Sutter)
Graubünden	May 10	92	90.0+ (6)	"
Engadin	May 30, June 9	89.5, 91		Coll. Clancey (Clancey)
Karinthia, Austria	June 6, July 24	89+, 91.5+	86.9 (7)	Cerny, 1938
Lower Austria	May 1, 3	87.5, 88.5		Berlin Mus. (Stresemann)
	July 11-22	83, 86.5, 87, 87.5, 88	89 (1)	British Mus. (Macdonald)
S.W. Transsylvania,	June 5	89		89.5 (9)
Mt. Retezat	May 27	89.5	89.4 (9)	Von Jordans, 1940
S. Bulgaria	Breeding birds	88, 88, 89, 90, 92		Hartert & Steinbacher, 1932
Rila and Pirin mts.	July 1-2	87, 89.5, 92	86 (1)	British Mus. (Macdonald)
Macedonia	July 15	86	91.0 (11)	Stresemann, 1919:30
S. Yugoslavia, Korab Mts.	May 18-26	89, 89, 89, 90, 90		Berlin Mus. (Stresemann)
West Prussia	April 8-May 20	90.5, 92.5, 92.5, 93	93-96 (5)	Tischler, 1941
		89, 89, 89, 90, 90		Stresemann, 1919:30
		91, 95	90 (1)	Löppenthin, 1935
East Prussia	Breeding birds	93-96	90 (1)	"
Esthonia	May 15-25	90, 94, 96	92.3 (4)	"
Denmark (Zealand)	July 9	90	89.5 (1)	Stockholm Mus. (Gyldenstolpe)
Bornholm	May 8-June 9	90, 91, 92, 96	91 (1)	"
Sweden (Smaland)	April 28	89.5	95.0 (2)	"
Sweden (Upsala)	May 23	91	90.3 (3)	"
Västergötland	April 27-May 29	91, 92, 92, 92, 94, 94,	89.5 (1)	"
Lapland	April 18-25	93, 97	91.2.7 (7)	"
S. E. Norway	June 6-Aug. 5	90, 90, 91	92.3 (3)	Oslo Mus. (Woolebaek)
Finland, South and Central	May	91, 92, 94	92.3 (3)	Heisinki Mus. (Kalela)
Central Russia	.....	91-92.5	91.2.5	Sushkin, 1925
Altai, Siberia	.....	90-94.5	90-94.5	"
Transcaucasia	Breeding birds	88, 88, 88, 89	88.2 (4)	Radde, 1884
South Caspian Mts.	.....	84, 87	86.7 (4)	Witherby, 1910
	May 26	88, 88	82 (1)	Stresemann, 1928
Asia Minor	June 11	82	82 (1)	Kummerlöwe & Niethammer, 1934
Azores	Oct. 15	89	89 (1)	Coll. Sillem-Van Marle (Voous)

Table 2  
Wing Measurements of Females of *Pyrrhula pyrrhula* in Millimeters

Localities	Collecting dates	Measurements	Averages	Sources of data	
Basses-Pyrénées	Breeding birds	80.5, 83	81.7 (2)	Mayaud, 1939	
Meurthe-et-Moselle	April	82, 83	82.5 (2)	"	
Suffolk	April 26-July 21	80, 81, 82	81.0 (3)	Coll. Clancey (Clancey)	
Lancashire	May 11	78.5	80.7 (6)	Leiden Mus. (Voous)	
Yorkshire	May 10-June	78, 79, 82		Coll. Clancey (Clancey)	
Northumberland	April 19, May 29	82, 84.5			
Perthshire	April 10	81.5	82.0 (3)	Coll. Plowden-Wardlaw (Clancey)	
Ireland	April 3, 15	81.5, 83			
	Breeding birds	80, 80, 81, 81, 82	80.8 (5)	Dublin Mus. (Stelfox)	
Netherlands	April 8, 13	79, 80	79.5 (2)	Leiden Mus. (Voous)	
Lower Franconia	April 14	84	84 (1)	Stresemann, 1919	
Upper Franconia	April 27	88.5	86.4 (9)	"	
Upper Bavaria	April 24	86		"	
Bavarian Alps, 1200-1500 m.	July 29-Aug. 2	83, 85, 85.5, 86, 86, 88.5		"	
Bavarian Forest	April 27	89		"	
Bohemian Forest	April 13-16	86, 87, 89, 90	87.4 (5)	Stresemann, 1919:34	
Bohemian Basin	May 22	85			
Sudeten Mts.	Aug. 18	89	89 (1)	Cerny, 1938	
High Tatra Mts.	May 22	95	95 (1)	"	
East Carpathians	May 25-July	85.5, 86, 89	86.8 (3)	"	
Canton Vaud (plains)	April	84	84 (1)	Coll. Meylan (Mayaud)	
Glarus Mts.	April 26	83	86.0 (2)	Stresemann, 1919	
Salzburg	Aug. 1	89			
Lower Austria	May 3	86	87.2 (6)	Vienna Mus. (Sassi)	
"	April-May 3	87, 90			
" (700-1400 m.)	July 14-22	84.5, 87.5, 88			
Rila and Pirin mts.	Breeding birds	86, 87	86.5 (2)	Berlin Mus. (Stresemann) Von Jordans, 1940	
West Prussia	April 8, May 24	91, 92.5	89.6 (6)	Stresemann, 1919:31	
	May 18-26	87, 88.5, 89, 89.5			
East Prussia	Breeding birds	90-93	90-93 (3)	Berlin Mus. (Stresemann) Tischler, 1941	
Bornholm	May 20	89	89 (1)	Löppenthin, 1935	
Sweden (Smaland)	April 28	88	88 (1)	Stockholm Mus. (Gyldenstolpe)	
Sweden (Upsala)	May 23	90	90 (1)	"	
Västergötland	April 27, May 29	90.5, 91	90.7 (2)	"	
Lapland	April 18	94	90.0 (2)	Amsterdam Mus. (Voous)	
Finmark	July 21	86			
S. E. Norway	July 3	90	90 (1)	Oslo Mus. (Wollebaek)	
Finland, South and Central	May	89, 90, 92	90.3 (3)	"	
Transcaucasia	Breeding birds	85, 88, 90	87.7 (3)	Helsinki Mus. (Kalela)	
Azores	October 15	88	88 (1)	Radde, 1884	
				Coll. Sillem-Van Marle (Voous)	

on the Iberian Peninsula, but has never been recorded so (see also von Jordans and Steinbacher, 1941), although the species has been mentioned from mixed oak- and pine-groves in Galicia on May 13 (Ticehurst and Whistler, 1928).

(4) *P. p. rossikowi* and *P. p. caspica*. Caucasian and Transcaucasian mountains, breeding near Tiflis in deciduous forests up to 2200 m. alt. and higher (Radde, 1884), and in the Akhazikh District from 1200 m. upwards (Buturlin, 1906); southern Caspian Mountains, from the beech forests (up to the tree-line) of Talysh (Radde, 1884), to the provinces of Gilan (up to 2000 m. alt.: Stresemann, 1928b), Masanderan and Astrabad; furthermore the Khorassan and the eastern Afghan mountains, bordering the Persian deserts (Desht-i-Kewir: Sarudny, 1911). It ranges westwards to the wet mountain forests of *Picea* and *Abies* of northern Asia Minor (Ilgaz Dagh, Paphlagonia: Kummerlöwe and Niethammer, 1934). It is absent in Crimea (Pusanov, 1933). In this whole area the two races seem to be rare and local breeding birds. In winter, however, the species seems to be quite common, although by far the majority of winter specimens are northern stragglers of the race *pyrrhula*. In wing length, a male and female from Astrabad, Transcaspia (February-March) in the collection of Sillem-Van Marle measure 93 and 91 mm., respectively.

#### *Pyrrhula murina* Godman

*Characters*.—Like *P. pyrrhula*, but upper and under parts in male olive gray with ochraceous brown edgings to the feathers of abdomen and rump; in the female, upper parts are dark olive brown and under parts buffy gray.

*Subspecific variation.*—None.

*Range.*—Azores (eastern San Miguel). Very rare.

*Biotope.*—Formerly orchards and gardens in cultivated areas, where the birds were highly injurious, eating and destroying the blossoms of peach trees. As a result of their destructive habits, their numbers have been seriously diminished by farmers. Moreover, their rareness has attracted a few thoughtless museum-collectors (see Hartert and Ogilvie-Grant, 1905; Murphy and Chapin, 1929 and 1930; Lowe and Bannerman, 1930). At present the remaining (?) birds seem to be restricted to the dense forests (*Juniperus!*) of the mountain slopes. Correia found the species in the same biotope as *Turdus merula*, *Erithacus rubecula*, *Sylvia atricapilla*, *Regulus regulus*, and *Fringilla coelebs*.

*Material examined.*—1 ♂, 1 ♀: San Miguel (Coll. Sillem-Van Marle).

*History.*—The following details in the recent distribution of the European bullfinches may serve as a key to the reconstruction of the postglacial history of the species: (1) Russian and Scandinavian birds are indistinguishable in coloration and dimensions from the Siberian ones. (2) Except for British and Dutch birds, *P. pyrrhula* of Europe does not exhibit any color differentiation, although the geographical variation in size is great. (3) Southeastern European birds are intermediate in size; during the breeding season they are exclusively mountain birds. (4) Birds from western France and Britain are smallest in size. They are forest and parkland birds. (5) Breeding birds with very large dimensions, which match those of the race *pyrrhula*, have been repeatedly found in the Alps. (6) No bullfinches occur in north Africa, the Canary and Cape Verde islands.

Uniform populations of the race *pyrrhula* inhabit the enormous region which extends from Yakutia in eastern Siberia to Scandinavia. Its European range consists mainly of those regions that were covered by inland ice or tundra during the last glacial period. Hence, it is rather certain that *P. p. pyrrhula* is a postglacial Asiatic invader into Europe, as are *Dendrocopos m. major*, *D. l. leucotos* and *D. m. minor* but probably these latter races have had a somewhat different postglacial history (see Voous, 1947). In most parts of its range, *P. p. pyrrhula* is a bird of the taiga, preferring mixed forests in which conifers dominate. The distribution of *Picea excelsa* in many countries has a primary influence upon its local range. The occurrence of occasional large individuals breeding in the Swiss Alps is reminiscent of the occurrence of Greater Spotted Woodpeckers resembling the Scandinavian race *major* in the same region, and of *D. l. leucotos* as a rare breeding bird or accidental visitor in the southern German mountains and in the Alps (Voous, 1947). It seems as if these alpine individuals represent the remnants of those populations which formerly had a more clearly pronounced boreal-alpine distribution. Consequently, one may suppose that during the period that birch and pine (and *Picea* in the East) were the dominant trees in temperate and northern Europe (pre-boreal to boreal time), these bird species had a wide distribution, especially in the eastern and central parts of their range.

The postglacial penetration of these Asiatic populations into Europe was perhaps facilitated by the rapid northward and westward extension of the range of *Pinus silvestris*, which had a main glacial refugium in eastern Europe, as also by the westward extension of *Picea excelsa*, which did not survive west of the Alps (Bertsch, 1935). When in later times the mixed oak forests separated the conifer woods of the central European mountains from those of northern Europe, continuous populations remained in the northern taiga, but the alpine populations became almost isolated.

The postglacial presence of Asiatic bullfinches in Europe is confirmed by the finding of subfossil bones of large dimensions in Hungary (*vide* Geyr, 1919). These rather common remains are referred by Lambrecht to *P. p. major!* They have been found associated with remains of *Nucifraga macrorhynchus!*, *Garrulus glandarius*, *Coloeus monedula*, *Turdus viscivorus*, and *Nyctea*. The rather varying measurements of alpine

breeding bullfinches (wing, males, 85-92; females, 83-90 mm.) lead one to conclude that the Asiatic birds have not been the only bullfinches that managed to occupy the alpine conifer forests, but they suggest that the southeast European mountain birds also succeeded in penetrating into the Alps, thus starting the process of the elimination of the boreal-alpine race *pyrrhula*. Elimination also takes place in the western Alps through the gradual penetration of the small western European race, which, especially in western Switzerland, obscures the racial situation. One might remember that there are also evidences in favor of the assumption that the alpine *Dendrocopos m. "alpestris"* is subject to a similar elimination by a western and central European form ("*arduennus*," *pinetorum*). A breeding specimen of *Pyrrhula* from the low regions near Geneva belonged to the small race; in this locality, however, it is a very rare breeding bird (Géroudet, letter, 1948).

In those countries where the Asiatic *pyrrhula* meets European populations (Carpathian Mts., Poland, southern German mts.), the breeding birds are exactly intermediate in measurements and show a rather wide range of variation (wing of Carpathian breeding males, 86.5-94; females, 85.5-95 mm.). In the same regions corresponding intermediate populations of *Dendrocopos major* are found! Owing to the fact that the geographical variation of *Pyrrhula* can be expressed in average wing lengths, a slightly clearer picture can be made than in the case of *D. major*. The average wing length in eastern European populations decreases from east to west (see Cerny, 1938). Influences of populations with large dimensions are found as far west as in the Bohemian Forest and the Bavarian Alps. Breeding males in the latter locality have wing measurements that equal the mean of Scandinavian breeding birds (92.5 mm.). Some of the rather large measurements which are occasionally noticed in southern German populations might also be caused by a northeast European influence.

The penetration of *P. p. pyrrhula* as well as that of *Dendrocopos m. major* into Scandinavia must have occurred after the melting of the greater part of the Scandinavian ice-cap. It seems that at the initial stage of the Ancylus Lake, which was a primordial stage of the Baltic Sea, Finland was wholly free from land-ice as early as about 7000 B.C. (Zeuner, 1946). Only after that time does there seem to have been enough room for the immigration of forests and forest birds southward along Sweden. This must have happened not before about 6000 B.C. (late Boreal to Atlantic). At the same time hazel, alder, and later also mixed oak forests had occupied the southern part of Sweden, which was at that time connected by land with Denmark, thus separating the Ancylus Lake from the North Sea. It is rather reasonable that an extension of west and central European forest birds into southern Sweden took place during that time, which perhaps is the cause of the phenomenon that southern Scandinavian breeding *P. pyrrhula* tends to be, on the average, slightly smaller than birds from more northern regions and from Siberia, thus resembling the western European race. Nevertheless, the same phenomenon has been established in the distribution of *Dendrocopos m. major*, which is less typical in southern Sweden than in northern Sweden and Finland.

Quite recently the race *pyrrhula* has spread from southern Sweden (Skane), where it is a rare breeding bird, to Bornholm Island (1916) and to the island of Zealand (1934). This new penetration could be established easily owing to the fact that up to these dates no representative of *P. pyrrhula* had been found as a breeding bird in these areas. In the case of *Dendrocopos major* the penetration of the Scandinavian form into Denmark via the same route could be traced less easily. Nevertheless, one should remember that a clear influence of the race *major* could be noticed in a sample of Danish specimens of *D. major*, which proved to be referable neither to typical *pinetorum* nor

to *major*. The Bornholm race of *D. major*, however, proved to be just intermediate between the races *major* and *pinetorum* (Voous, 1947).

An additional characteristic of *P. pyrrhula* and *D. major* is the irregularly occurring autumn migrations, which sometimes involve whole populations. Regular migratory movements may be responsible for the presence of *P. p. pyrrhula* in southeast Europe as a common winter bird. Formerly this led to the conclusion that it was this race that was the breeding one in Bulgaria and Yugoslavia. But in some years it is so extraordinarily abundant (e.g., 1927-28, hundreds in Thuringia, 15-20 thousand in Slovenia: Stresemann, 1928a), that the invasional character of these movements is quite clear. In western Europe the race *pyrrhula* is rather scarce in most winters, but in particular years it is quite common. The year-to-year irregularity in abundance has been noticed from Denmark to France and Great Britain. It is this race that has straggled to the Faeroes (Salomonsen, 1942) and on several occasions even to Iceland (wing, males, 93, 93; females, 89, 90, 90, 91 mm.: Saemundsson, 1929; Gudmundsson, letter, 1948). There seems to be no record of this race from Ireland (Humphreys, 1937). Whether or not all Swiss and Italian bullfinches with large dimensions originate in northern Europe or represent indigenous alpine breeding birds cannot be decided in each case. The frequent occurrence of bullfinches in northern Italy which are conspicuously larger than the majority of Italian specimens is reminiscent of the rather irregular occurrence of the "Scandinavian type" of *Dendrocopos major*, which perhaps also must be referred to alpine breeding birds rather than to northern stragglers.

Although the last glaciation (Würm) did not extend as far south as the penultimate one (Riss), boreal and alpine ice-caps approached each other at a distance of not less than about 53 km. (Firbas, 1939). It is not probable that species of *Pyrrhula* and *Dendrocopos* could have survived in the tundra and dwarf-willow vegetation that prevailed between the ice-caps in central Europe. Consequently, a separation between geographically isolated west and east European populations must be assumed. These populations have smaller dimensions than those which survived in the Siberian refuge (*pyrrhula*). The large dimensions of the latter birds might be an adaptation to the severe continental climate (rule of Bergmann). During the optimum of the last glaciation the remains of subarctic birch and pine forests have been found as far north as the Paris Basin whereas warmth-loving trees occurred in the Etruscan Apennines and in southern France (Firbas, 1939). As a consequence, the glacial refuge of *P. pyrrhula* can be assumed to have been situated in the southern half of France and in Italy.

The apparent postglacial center of dispersal of the race *coccinea* corresponds with this location. Fossil remains of the small race are recorded by Lambrecht (1933) from Pleistocene deposits of Ireland and from northwest Switzerland (Basel). They have also been identified in a bone-breccia from Sardinia, where the species is now absent (*loc. cit.*). After the retreat of the land-ice, the *Pyrrhula* populations followed the subsequent extension of the forests into western Europe, including Great Britain and Ireland. This happened at the time that the English Channel and the Irish Sea still formed land-connections (Boreal). They migrated also north of the alpine range into Germany. In the latter locality they met the Asiatic race *pyrrhula* and formed populations with intermediate average dimensions and a wide range of variation. As in *Dendrocopos major*, *D. minor*, and *Garrulus glandarius*, a slight clinal variation is noticeable in the western European form *P. p. coccinea* which corresponds with the direction of the postglacial extension of the range. The dark coloration of the British and Dutch populations, including those of Alderney Island in the English Channel, but not those of the Island of Jersey (Mayaud, letter, 1948), might be the result of Atlantic climatic conditions, which induce a more intensified feather pigmentation. This type of variation

reaches its optimum in the weakly differentiated race *wardlawi* from the Scottish mountains.

Whether the recent absence of this species and of *Dendrocopos minor* from Denmark has an historical or rather a local cause, I cannot decide. Many other forest birds and deciduous forest trees have actually reached Denmark and have spread to southern Sweden, for example, *Dendrocopos medius*. This must have happened during the time that there was still a land connection between Jutland Peninsula and southern Sweden (Boreal). At this time, in the English Channel and the Irish Sea areas, land connections also occurred (Zeuner, 1946). Quite recently, *P. pyrrhula* has reached Jutland (again?) from the south. Measurements of Danish breeding birds show that the new Danish populations are a continuation of the western European populations.

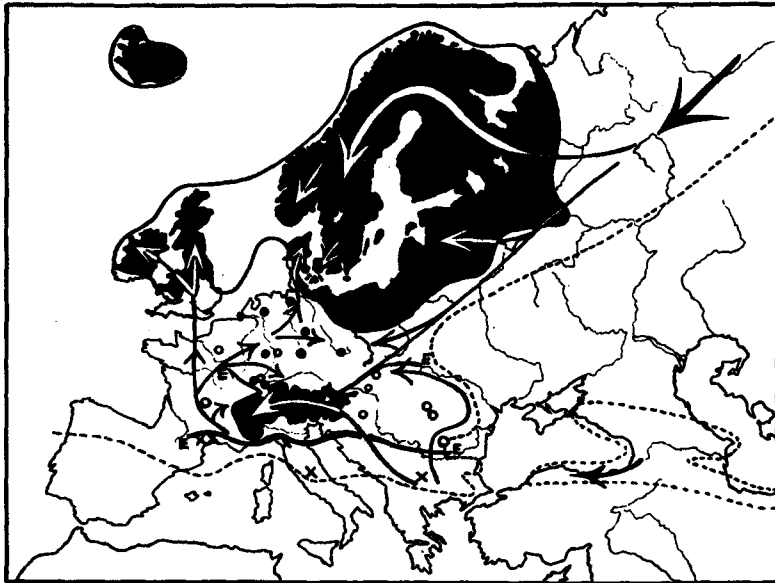


Fig. 9. Postglacial distribution of *Pyrrhula pyrrhula* in Europe. Black areas were covered by land ice during the maximum of the last glaciation. Ice-covered regions in the Caucasus are not indicated. Black spots indicate localities where treeless vegetation is known to have existed during the last glacial period; small circles indicate birch and pine forests of that period; crosses indicate deciduous forest vegetation with warmth-loving trees also of that period (see Firbas, 1939:fig. 6). Two black lines with ends indicated by "E" represent the approximate boundaries of the tundra and birch-pine forests, north to south, respectively. The broken line indicates the southern limits of distribution of *P. pyrrhula* in Europe; in the Caucasus this line indicates approximate range.

Pollen-analysis has shown that forest vegetations survived during the last glaciation in many parts of southeast Europe. The subarctic birch-pine forests in the western Pannonic lowlands and in western Siebenburgen, as well as the deciduous woods in the eastern Serbian mountains (Firbas, 1939), represent the most convincing evidence in favor of the localization of a glacial refugium of forests which were suitable for the existence of *P. pyrrhula*. Originating from this center of dispersal, the birds spread to the mountains surrounding the Hungarian plains and the Bohemian Basin; they apparently also penetrated into the Alps. The southeast European race is a mountain race

everywhere. The wide range of variation in dimensions found in Slovenian and Bohemian birds, as well as in those inhabiting the Alps and the south German mountains, might be the result of the interbreeding of three different waves of populations, which came from the northeast (*pyrrhula*), southeast (*germanica*), and west (*coccinea*). These populations will remain to be an obstacle to any subspecific nomenclature. In the assumption that the central European populations represent "mixed" or "hybrid" ones, I follow Stresemann (1919), although I differ in opinion as to what races actually meet and "hybridize."

In its doubtful occurrence as a breeding bird in the Iberian Peninsula, and in its absence in Italy south of lat. 42°N., as well as in Greece south of lat. 40°N., *P. pyrrhula* exhibits its exclusive partiality to forests or parklands. This absence and scarcity in the Mediterranean region may be correlated with the postglacial retreat of the forests, caused both by human agency and by the general desiccation of the climate. This suggestion is confirmed by Pleistocene fossil records from Sardinia (Lambrecht, 1933), where the species is now absent.

The occurrence of only two slightly distinct races in the Caucasian and south Caspian regions might be considered to be an indication that the bullfinch is a rather recent inhabitant of these regions. The race *rossikowi* still inhabits approximately its last glacial Caucasian refuge. Therefore, *rossikowi* is of a corresponding age as the southeast and west European races. It has the measurements of the southeast European birds, but the colors of the male are slightly brighter and of the female darker. It is the race-analogue of *Dendrocopos major tenuirostris*. Like that race of Pied Woodpecker, *rossikowi* has extended its range westward in Asia Minor (Ilgaz Dagh), where Kummerlöwe and Niethammer (1934) found the species breeding in mossy mountain forests with *Picea* and *Abies*. The collected specimens have the same coloration as *rossikowi*, but they are smaller. These bullfinch populations correspond to *Dendrocopos major paphlagoniae*, which was thought to be a postglacial immigrant from Transcaucasia, although it might be a postglacial relict as well (Voous, 1947). It is unknown if the south Caspian and north Persian race (*caspiica*) is an older inhabitant than *rossikowi*; hence it is not certain that it is comparable with *D. major poelsami*. However, there is one argument in favor of the fact that *P. pyrrhula* inhabited Europe before the last interglacial: its occurrence in the Azores. Although the Azorean form (*murina*) is taxonomically quite distinct from all other races of *P. pyrrhula*, lacking as it does any sexual difference in plumage and a white rump, yet its geographical relations make difficult the assumption that it is not an insular offspring of *P. pyrrhula*. As the Azores are Tertiary volcanic islands which never had any land connection with the continent, the time of the immigration cannot be correlated with any post-Tertiary geological event. The species must have reached the islands by wing as a straggler from Europe (1380 km. west of Cape da Roca, Portugal). This supposition is also necessary for explaining the occurrence of other Azorean breeding birds: *Turdus merula azorensis*, *Erithacus rubecula rubecula*, *Sylvia atricapilla heineken*, and *Regulus regulus azoricus*. Some of the latter species, however, might have reached the Azores via the Canary Islands. In this respect, it is of interest to notice that stragglers of *P. p. pyrrhula* have reached Iceland, crossing the Atlantic Ocean, and that the European *Turdus viscivorus* (Hartert and Ogilvie-Grant, 1905) and *Turdus pilaris* are very rare stragglers to the Azores, the latter species having been recorded only once after a heavy northeast gale (Spolton and Mayaud, 1947).

The taxonomic distinctness of the Azorean Bullfinch, with its hen-feathered male, lack of a white rump, and brown instead of white under tail coverts might suggest that it is a rather old inhabitant, probably older than the last interglacial. This makes it also

possible that *P. p. caspica*, like *Dendrocoptes major poelzami*, represents an older generation than the Caucasian race *rossikowi*.

On these grounds, it might be desirable to treat the Azorean Bullfinch as specifically distinct from *P. pyrrhula*, since this is the only way to indicate close relationship among subspecies of the entire Palearctic region. If this is done, the insular *P. murina* should be united with *P. pyrrhula* in a superspecies.

#### SUMMARY

1. The genus *Pyrrhula* (bullfinches) has an Oriental and Palearctic range; it does not occur in other zoögeographical regions.

2. Bullfinches are inhabitants of forests of various kinds, although not of tropical or subtropical types. In western Europe, they live also in parklands and gardens.

3. The following eight species of *Pyrrhula* are recognized: *nipalensis*, *leucogenys*, *erythaca*, *erythrocephala*, *aurantiaca*, *griseiventris*, *pyrrhula*, *murina*.

4. The Oriental forms have been united in the subgenus *Protopyrrhula* Bianchi, whereas the Palearctic forms have been referred to the typical subgenus *Pyrrhula*.

5. Sympatric species are only found in the Oriental range of the genus (*nipalensis* with *erythaca*, *erythrocephala*, and *aurantiaca*). *P. nipalensis* differs from the other three in biotope and vertical distribution, but *nipalensis* and *erythaca* occur side by side at least in the mountain forests of Yunnan and Formosa.

6. Interspecies (Ripley, 1945), with a marginal zone of overlap, can be recognized in the three Himalayan forms (*erythaca*, *erythrocephala*, and *aurantiaca*).

7. Emergent interspecies (Ripley, 1945), with a marginal zone of hybridization, have been found in the Siberian forms (*griseiventris*, *pyrrhula*).

8. Superspecies, with geographically complementary continental and insular forms, have been recognized in southeast Asia (*nipalensis*, *leucogenys*) and in western Europe (*pyrrhula*, *murina*).

9. Clinal variation occurs most noticeably in the European races of *P. pyrrhula*.

10. The greatest number of sympatric species occurs in the Chinese-Himalayan countries. In Bhutan alone, Ludlow observed the following three species: *nipalensis*, *erythaca*, *erythrocephala*.

11. *P. nipalensis* has been considered to be the most primitive form. Juvenal birds of all members of the genus resemble this plainly colored brown form. It has a rather wide southeast Asiatic range, which is discontinuous.

12. The primitive southeast Asiatic forms occur on the margins of the range of the genus; they inhabit isolated mountain regions in southern Malaya (*P. n. waterstradti*), and the Philippines (*P. leucogenys*).

13. The Japanese and Manchurian bullfinches (*P. g. griseiventris*) are a rather variable form, which, however, does not seem to have originated as a "hybrid" between the gray-breasted *P. g. cineracea* and the red-breasted *P. p. pyrrhula*.

14. The area between Yakutia in eastern Siberia and Norway and Denmark in western Europe is inhabited by one subspecies, *P. p. pyrrhula*, which is constant throughout this enormous range.

15. In Europe three continental races of *P. pyrrhula* have been recognized according to average dimensions: a small form in western Europe (*coccinea*); an intermediate form in southeast Europe (*germanica*), and a large form in north and northeast Europe (*pyrrhula*). Intermediate populations occur in central Europe.

16. The Caucasian and south Caspian races of *P. pyrrhula* (*rossikowi*, *caspica*) resemble the southeast European race rather than the Russian one.



17. The British and Dutch bullfinches show a slightly darkened coloration, which may be caused by Atlantic climatic conditions.

18. *P. pyrrhula* is a breeding bird of Ireland; until quite recently it was absent from Denmark.

19. The virtual absence of the genus in the resident fauna of the Mediterranean region has been correlated with deforestation and desiccation of the climate, rather than with historical distributional events. However, the genus does not appear to have ever reached northern Africa.

20. The Azores, which are Tertiary volcanic islands, are inhabited by a hen-feathered offshoot of the European form. This species (*murina*) is on the verge of extinction.

#### CONCLUSIONS

1. The center of origin and dispersal of *Pyrrhula* and *Dendrocopos* may be situated in southeast Asia (Chinese-Burmese region).

2. Recent distribution and character geography reveal that the Himalayan species of *Pyrrhula* and the "ladder-backed" group of *Dendrocopos* have reached their ranges from the East.

3. The Palearctic species of *Pyrrhula* and *Dendrocopos* originated from some Chinese form, although taxonomy and recent distribution in *Pyrrhula* do not give the clue as to which form this may have been.

4. Manchuria has acted as a secondary center of dispersal of the Palearctic forms of *Pyrrhula* and *Dendrocopos*.

5. An interglacial (or interstadial) dispersal of *Pyrrhula* and of *Dendrocopos major* has taken place from Manchuria along the then forested northern boundary of the Mongolian Desert.

6. During the last glaciation, *Pyrrhula* and *D. major* survived in at least four Asiatic continental forest refugia: Manchuria, Kamchatka, Transbaicalia, and south-central Siberia.

7. Northeast and north Europe have been populated postglacially by birds from the Siberian taiga (*Pyrrhula* and *Dendrocopos*).

8. In accordance with the rule of Bergmann, the Siberian (including the northeast European) birds show considerably larger dimensions than the southeast and western European populations in both *Pyrrhula* and *Dendrocopos*.

9. In both *Pyrrhula* and *Dendrocopos* invasions from Siberia have penetrated into Scandinavia from the north.

10. South Scandinavian populations of *P. pyrrhula*, *D. major*, and *D. minor* show a slight west European influence, which might be the result of a former (late Boreal to Atlantic) northward extension of the range of west European birds.

11. Indications of a penetration of birds from the Siberian taiga into the Alps, resulting in a still recognizable boreal-alpine distribution, have been found in *P. p. pyrrhula*, *D. m. major*, and *D. l. leucotos*.

12. The whole of temperate Europe has been populated by two groups of populations of *P. pyrrhula*, *D. major*, and *D. minor*, having spread postglacially from southeast and southwest Europe, where they survived during the last glaciation.

13. In the central European mountains, the outposts of three glacially separated populations of *P. pyrrhula*, *D. major*, and *D. minor* intermingle, originating from the northeast, the southeast, and the southwest.

14. In the west European element (*P. pyrrhula*, *D. major*, *D. minor*), a distinct clinal variation takes place from northwest Italy and southern France to Denmark. This very gradual variation is hardly worthy of nomenclatural notice. The phenomenon is less pronounced in the bullfinch than in the woodpeckers.

15. British populations of *P. pyrrhula*, *D. major*, and *D. minor* show some racial color distinctions, which may be correlated with Atlantic climatic conditions.

16. Caucasian populations of *P. pyrrhula*, *D. major*, *D. leucotos*, and *D. minor* belong to the same glacial generations as the southeast and southwest European ones. Taxonomically they are closer to the southeast European than to the Russian forms.

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