BIRD BANDING

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CHANGES IN GEOGRAPHIC RANGES IN THE AVIFAUNA OF NORTHERN AND CENTRAL EUROPE IN RELATION TO RECENT CHANGES IN CLIMATE

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Until very recently it has been generally assumed that changes in geographic ranges of species of animals occur, as a rule, very slowly, indeed almost imperceptibly. Increasing knowledge, however, has revealed many cases which, during the course of a few decades, have shown very striking changes in limits of geographic range which are independent of human influences. Apparently the recent decades have been unusually favorable for the development of such changes. The apparent basis for this will be considered in subsequent parts of this treatise.

It is evident that light can be thrown on many theoretical questions of zoogeography and population dynamics by the study of such changes in geographic range. Reference may be made to the relation of these phenomena to population genetics since a considerable role is generally attributed to "population waves" as a factor in evolution. The fundamental problem at present, however, is to study the frequency and intensity of the recent faunal changes and to formulate an interpretation of their causes. The present paper will serve to supply additional elucidation for the latter.

THE AVIFAUNAL CHANGES

The present paper is concerned with several recent striking changes in geographic ranges of certain birds of northern and central Europe. Both northern and southern limits have changed, and this is true not only of the breeding areas but also of the winter quarters of many species. (See, *e.g.* Siivonen and Kalela, 1937; Merikallio, 1946.)

In the following account, however, only changes in the northern limits of the breeding areas will be considered, since they are the best known. The period of time under consideration begins about the middle of the last century. Certain changes in range which are peculiar to the immediate past will be discussed separately in a subsequent section.

NORTHERN EUROPE. Changes in the northern limits of distribution of southern birds, particularly in the southern parts of northern Europe, have been summarized in a number of papers (Jägerskiöld, 1919; Ekman, 1922; Lönnberg, 1924; Kivirikko, 1925; Siivonen and Kalela, 1937; Kalela, 1938; Siivonen, 1943; etc.). As to their general nature, reference may be given to the investigations which have been carried out in the Kokemäenjoki River region (Kalela, 1938). This region embraces a considerable part of southern Finland (60°36′ — 62°51′ N; 21°27′ — 25°18′ E; an area of about 27,000 square kilometers). The northern limits of the geographic ranges of 25 species occur in this region. In Table 1, only those are included which (1) have increased and extended their ranges northward, or which (2) have decreased and receded southward.

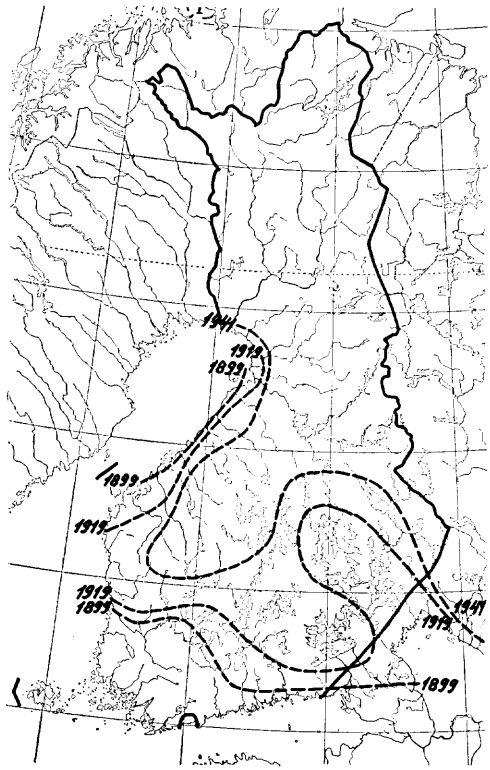

Fig. 1. *Vanellus vanellus*: Extension of the continuous area of breeding in Finland.

The increasing component consists of 11 species (44 percent of all southern species). It has been possible to establish the occurrence of these changes taken as a whole, since about 1870–1890. Information concerning their extent throughout Finland is recorded in Figures 1–3. The Polecat, *Putorius putorius* (Linnaeus), has been included, since the history of its change in range is particularly well-known (Kalela, 1940, 1948). The fact that the direction of expansion in Finland is in this case northwestward depends merely on the fact that we are dealing with a terricolous species; in general, a northerly or northeasterly expansion is characteristic in northern Europe.

The decreasing component consists of six species (24 percent of all the southern species). The decrease seems to have begun at the turn of the century at the earliest. The changes from a quantitative point of view are not as extensive as that of the expanding species; only in the case of the Corn Crake, *Crex crex* (Linnaeus), and the Quail, *Coturnix coturnix* (Linnaeus), are they of approximately the same order of magnitude.

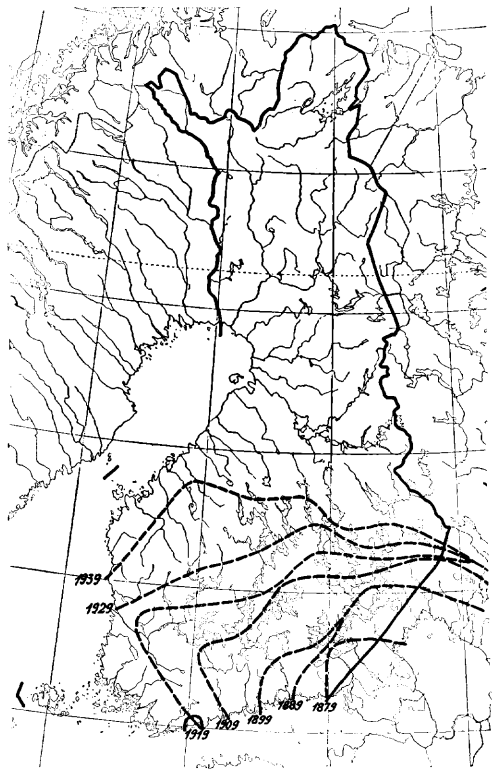

Fig. 2. *Turdus merula*: Extension of the continuous area of breeding in Finland.

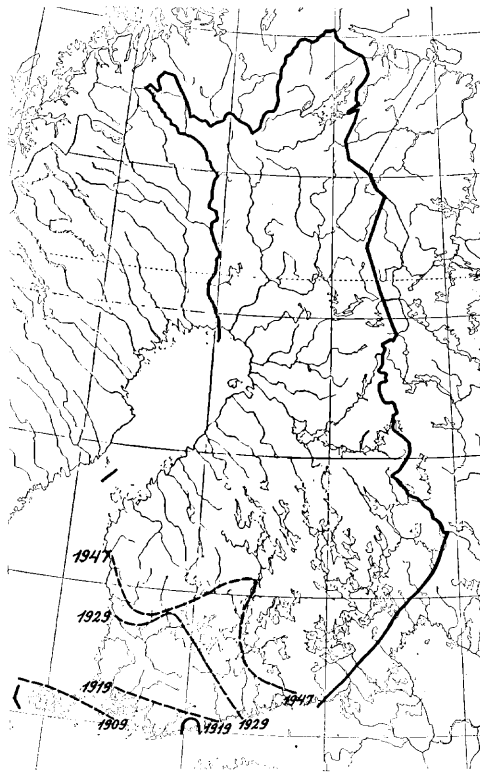

Fig. 3. Polecat, *Putorius* (*Mustela*) *putorius*: Recent spread into Finland (After Kalela 1940.)

CENTRAL EUROPE. Since it becomes immediately apparent from a superficial examination of the literature that recent changes in the fauna farther south, in central Europe, differ considerably from those of northern Europe, a survey (Kalela, 1946a) has been made, chiefly by use of Niethammer's (1937–1942) handbook of the changes in the southern avifauna of Germany. These changes, which also appear in Table 1, have, in general, occurred since the middle of the previous century.

Omitting those which are specifically alpine, there are 32 species whose northern limits occur in Germany or practically coincide with its northern border. (As a result of the recent expansion, certain species have extended somewhat farther north.)

Of the above-mentioned 32 species, only six (19 percent) have increased and expanded. The greatest change is shown by the Serin, *Serinus canaria* (Linnaeus), which at the beginning of the previous century still did not breed in Germany, and which since then has become a breeding bird in practically the entire country. (Mayr, 1926, with maps.) Although not comparable in extent

with that of the Serin, there have been marked expansions in the range of the Crested Lark, *Galerida cristata* (Linnaeus); Black Redstart, *Phoenicurus ochrurus* (Linnaeus); and the Gray Wagtail, *Motacilla cinerea* Tunstall.

No less than 14 species (44 percent of all the southern ones) have displayed a more or less marked recession of their northern limits. Maps are not available to show the extent of their changes in central Europe. Figures 8 and 9, which show the decrease in the Roller, *Coracias garrulus* (Linnaeus), in southern Sweden, should, however, be considered since, as will be shown subsequently, the pattern of change in range of this species resembles the receding species of Germany very closely although its area extends somewhat farther north.

Thus we find in Germany, which here represents central Europe and the deciduous-forest zone, that the relative numbers of southern species which have expanded or receded are opposite to those of southern Finland, which represents the southern part of northern Europe and the southern part of the coniferous-forest zone. The fact that the beginning of the changes was not simultaneous in all cases is not considered here.

If we attempt a causal analysis of the above trends in the faunal changes in northern and central Europe, two groups of external factors require consideration: (1) *the direct or indirect influence of mankind;* this will be outlined briefly in the following section; and (2) *climatic factors* with which the present paper is chiefly concerned. The question, whether in any particular case expansion may depend on mutations which have arisen in the populations of the species concerned, cannot be considered here. Most of the problems discussed below have been treated more completely in the cited papers of the author and other investigators.

THE INFLUENCE OF MAN

To illustrate the significance of this group of factors for the avifauna of northern Europe, the following data from my investigations in southern Finland may be quoted (Kalela, 1938). Of the 149 species of breeding birds of the Kokemäenjoki River region, at least 43 (29 percent) have profited from the changes which man has produced in the vegetation or the landscape; 14 species are completely dependent on cultivated land and have only been able to colonize the region following the advent of man. The activity of man has, directly or indirectly, had a detrimental effect on at least 27 species (18 percent); three species have been exterminated in this century.

As to the effect of civilization on the avifauna of central Europe, I must express myself with greater reservation since I do not know the circumstances from personal experience and it is rather difficult, in many cases, to obtain a clear picture from the records given in the literature..

Since the cultivated land in central Europe and in the southern part of northern Europe is the result of centuries of gradual develop-

TABLE I

Expanding and Receding Species of the Southern Element in the Avifauna of Southern Finland and Germany with the Principal Periods of Arrival in Spring, and Breeding and Wintering Areas (p. r. = permanent resident. VI_1 = June 1-10; VI_2 = June 11-20, etc.)

	Arrival in Spring	Full Clutch; (2) = two broods annually	Principal wintering areas of the central and northern European populations
Southern Finland, expanding species			
Podiceps cristatus cristatus (Linnaeus) (Great Crested Grebe)	IV_3-V_1	V_3-VI	Black Sea, Mediterranean, western part of central Europe
Aythya ferina (Linnaeus) (Pochard)	IV_{2-3}	V_2-VI_1	Mediterranean, British Isles, western part of central Europe
Fulica atra atra Linnaeus (Coot)	IV	V	Central Europe, Mediterranean, southern part of central Europe
Vanellus vanellus (Linnaeus) (Lapwing)	III_3-IV_2	IV_3-V_1	Western part of central Europe, British Isles, Mediterranean
Larus ridibundus ridibundus Linnaeus (Black-headed Gull)	IV_{1-2}	V	Mediterranean, western part of central Europe, British Isles
Strix aluco aluco Linnaeus (Tawny Owl)	p. r.	IV	Central Europe, southern part of northern Europe
Corvus frugilegus frugilegus Linnaeus (Rook)	III_2-IV_1	IV_3-V_1	Southern and western part of central Europe, British Isles, Mediterranean
Coloeus monedula monedula (Linnaeus) (Jackdaw)	III_2-IV_1 in part p. r.	V_{1-2}	Central Europe, British Isles, southern part of northern Europe
Parus caeruleus caeruleus Linnaeus (Blue Tit)	p. r.	V_2-VII (2)	Central Europe, southern part of northern Europe
Turdus merula merula Linnaeus (Blackbird)	III_3-IV_1 in part p. r.	V_1-VI (2)	Central Europe, British Isles, southern part of central Europe
Carduelis carduelis carduelis (Linnaeus) (Goldfinch)	III_2-IV_1 in part p. r.	VI_{1-2}	Central Europe, southern part of northern Europe
Southern Finland, receding species			
Coturnix coturnix coturnix (Linnaeus) (Quail)	V-VI_1	VII	Mediterranean, northern and central Africa
Porzana porzana (Linnaeus) (Spotted Crake)	V_{2-3}	V_3-VII	Mediterranean, northern and tropical Africa
Crex crex (Linnaeus) (Corn Crake)	V_3-VI_1	VI_2-VII	Tropical and southern Africa, Mediterranean
Oriolus oriolus oriolus (Linnaeus) (Golden Oriole)	V_3-VI_1	VI_3-VII_1	Eastern and southern Africa
Hippolais icterina (Vieillot) (Icterine Warbler)	V_3-VI_1	VI	Tropical Africa
Carduelis cannabina cannabina (Linnaeus) (Linnet)	IV	V_2-VII (2)	Central Europe, Mediterranean

TABLE I (Continued)

Germany, expanding species	Arrival in Spring	Full Clutch, (2) = two broods annually	Principal wintering areas of the central and northern European populations
Galerida cristata cristata (Linnaeus) (Crested Lark)	p. r.	IV-VI_2 (2)	Central Europe
Remiz pendulinus pendulinus (Linnaeus) (Penduline Tit)	p. r.	IV_3-	Central Europe
Phoenicurus ochrurus gibraltariensis (Gmelin) (Black Redstart)	III_1	IV_2-VI (2)	Mediterranean
Regulus ignicapillus ignicapillus (Temminck) (Firecrest)	III_3-IV	V-VII_2 (2)	Mediterranean
Motacilla cinerea cinerea Tunstall (Grey Wagtail)	III in part p. r.	IV_1-VII (2)	Central Europe, Mediterranean
Serinus canaria serinus (Linnaeus) (Serin)	III_3-IV occasionally p. r.	V_1-VII (2)	Mediterranean, southern part of central Europe
Germany, receding species			
Ardea purpurea purpurea (Linnaeus) (Purple Heron)	IV	V -	Western, eastern, southern Africa
Nycticorax nycticorax nycticorax (Linnaeus) (Night Heron)	IV	V -	Central Africa
Aythya nyroca nyroca (Güldenstädt) (Ferruginous Duck)	III_3-IV mostly p. r.	V_2-VI_3	Central Europe
Circaetus gallicus gallicus (J. F. Gmelin) (Short-toed Eagle)	IV	V_{1-2}	Central Africa
Porzana pusilla intermedia (Hermann) (Baillon's Crake)	?	V_2-VII	Northern and central Africa?
Otis tetrax tetrax (Linnaeus) (Little Bustard)	mostly p. r.	V_2	Central Europe
Chlidonias leucoptera (Temminck) (White-winged Black Tern)	V_{1-2}	VI	Tropical and southern Africa, southern Asia
Gelochelidon nilotica nilotica (Gmelin) (Gull-billed Tern)	IV_3-V_2	V_3	Tropical and eastern Africa, southern Asia, northern Africa
Merops apiaster Linnaeus (Bee-eater)	IV_3-V	V_3-VII	Tropical and southern Africa
Panurus biarmicus biarmicus (Linnaeus) (Bearded Tit)	p. r.	IV_2-VII (2)	Central Europe
Monticola saxatilis (Linnaeus) (Rock Thrush)	IV_1	V_2	Western and eastern Africa
Lanius minor Gmelin (Lesser Gray Shrike)	V_{1-2}	V-VI	Southern and southwestern Africa
Lanius senator senator Linnaeus (Woodchat Shrike)	IV_3-V	V-VI	Tropical Africa
Petronia petronia petronia (Linnaeus) (Rock Sparrow)	p. r.	V-VI (2)	Southern part of central Europe

ment, such reviews as that cited above for southern Finland are not directly concerned with the problem treated here. The following kinds of influences of civilization are pertinent to the period under investigation which coincides approximately with the "Age of Industrialism": (1) *Intensification of agricultural methods;* (2) *Drainage of marshland*, especially in central Europe; (3) *Increase in the area of coniferous forest* in central Europe as the result of planting; (4) *Increase in area of ruderal vegetation* as a result of the development of the network of traffic; (5) *Development of hunting weapons;* (6) *Protection.*

THE EXPANDING SPECIES. The relation of the increasing southern element of southern Finland to civilization has been treated fairly thoroughly in an earlier paper (Kalela, 1938). Among the species concerned many are more or less confined to habitats occurring only in cultivated districts. The possibility, however, that the activities of man could represent the fundamental factors in the recent expansions can be considered seriously only in the case of the Goldfinch, *Carduelis carduelis* (Linnaeus), which is dependent, because of its feeding habits, on the ruderal vegetation. During the last hundred years, man has hardly produced any fundamental changes in the environment of the remainder of the species.

One would commit no great error, in supposing much the same to be true of the advancing southern element in Germany. A species whose recent expansion has quite commonly been connected with cultural measures is the Crested Lark, *Galerida cristata* (Linnaeus). In fact, there is no doubt that the habitat requirements of this species, which occupies dry habitats supporting ruderal vegetation, have been very much favored, among other things, by the recent development of the network of railways. However the fact that once previously, in the sixteenth century, *Galerida cristata* occupied a wide range in Germany, makes it highly unlikely that the recent expansion depends chiefly on cultural factors. The culture-conditioned spread of the coniferous forests may have played an important role in the expansion of the Firecrest, *Regulus ignicapillus* Temminck (Schnurre, 1921).

THE RECEDING SPECIES. The intensification of agricultural methods has clearly played an important role in the decimation of *Coturnix coturnix* and *Crex crex* in northern Europe (Lönnberg, 1940; Svärdson, 1944). The increase of the former in the immediate past, however, indicates that other factors, too, are concerned in the changes of its population. Cultural factors might not have been accountable for the fluctuations in population of the other species belonging to this group, perhaps partly with the exception of the Linnet, *Carduelis cannabina* (Linnaeus).

On this basis the question of the extent to which the decrease of the central European species of this group depends on the activities of man is especially difficult to ascertain. As examples of species whose recession is due partly to cultivation may be mentioned the Short-toed Eagle, *Circaetus gallicus* (Gmelin) (direct persecution); the Purple Heron, *Ardea purpurea* Linnaeus; and *Nycticorax nycticorax* (Linnaeus) (drainage of marshland). On the other hand the fact

that some species, such as the Lesser Gray Shrike, *Lanius minor* Gmelin; the Woodchat Shrike, *Lanius senator* Linnaeus; and the Rock Thrush, *Monticola saxatilis* (Linnaeus) have, after a century of retreat, displayed clear signs of increase is much more simply explained by factors other than cultural.

Even if the influence of civilization cannot yet be adequately ascertained, it is scarcely unsound to say that it has not played the chief role in the faunistic changes in question; the positive displacement obviously depends chiefly on other factors and the negative displacements can only be attributed in part to cultural factors.

Before attention is directed to the discussion of climatic factors, it should be emphasized that, although cultural factors have played a role of more or less importance in the distributional dynamics of certain species such as *Coturnix coturnix* and *Galerida cristata*, it is assumed that other factors are operative in the changes in geographic range in both cases. The influence of climatologic factors, as will be seen subsequently, becomes predominant. Of course there are cases where the importance of one factor so obviously dominates that it seems superfluous to look for other causes. But in the present state of our knowledge it would be wrong simply to eliminate further factors, climatic, for example, from the discussion of a species in whose dynamics the influence of one group, cultural, for example, has been established. Neither group of factors mentioned excludes the other in any way. For this reason all of the above-mentioned species are also treated in the following discussion whether or not it may be possible to show that their changes in range have been affected by civilization.

INFLUENCE OF THE RECENT CHANGES IN TEMPERATURE

As is well known, data which have been collected from various parts of the world, show clearly a general change of climate since the beginning, and especially since the latter half, of the previous century. (See, *e. g.*, Kincer, 1933; Wagner, 1940.) The basis of this change consists of the increased intensity of general atmospheric circulation. One of the results of this is an equalization in temperature over the entire earth. Consequently the temperatures in the high latitudes have increased (Figure 4). Since the greatest difference in temperature between the poles and the equator occurs in winter, the change is far more striking in winter than in summer. In the following account, an examination will be made to ascertain whether the peculiarities of the temperature changes may be factors in the changes in the fauna of northern and central Europe. Changes in other climatic factors, particularly in atmospheric humidity, and their eventual significance for changes in geographic ranges of birds will be considered later.

THE EXPANDING SPECIES. It is clearly shown in Table 1 that the expanding portion of the avifauna of southern Finland consists in part of permanently resident species and in part of migrants which arrive early in spring—in March and April. The breeding

season is in most cases early, considering the position in northern Europe. The beginning occurs in the majority of species in April and May.

The situation in central Europe is very similar. Of the six expanding southern species in Germany, two, *Galerida cristata* and the Penduline Tit, *Remiz pendulinus* (Linnaeus), are typical permanent residents. The remainder are migrants which arrive early in spring; this applies above all to *Motacilla cinerea* (a part of whose population winters in Germany) and *Phoenicurus ochrurus*.

Let us consider the above facts in relation to the temperature changes in the two regions. Figure 5 gives the mean monthly temperatures in southern Finland (Helsinki) for the period 1831-1935. It is very striking that late autumn, winter and spring *have under-*

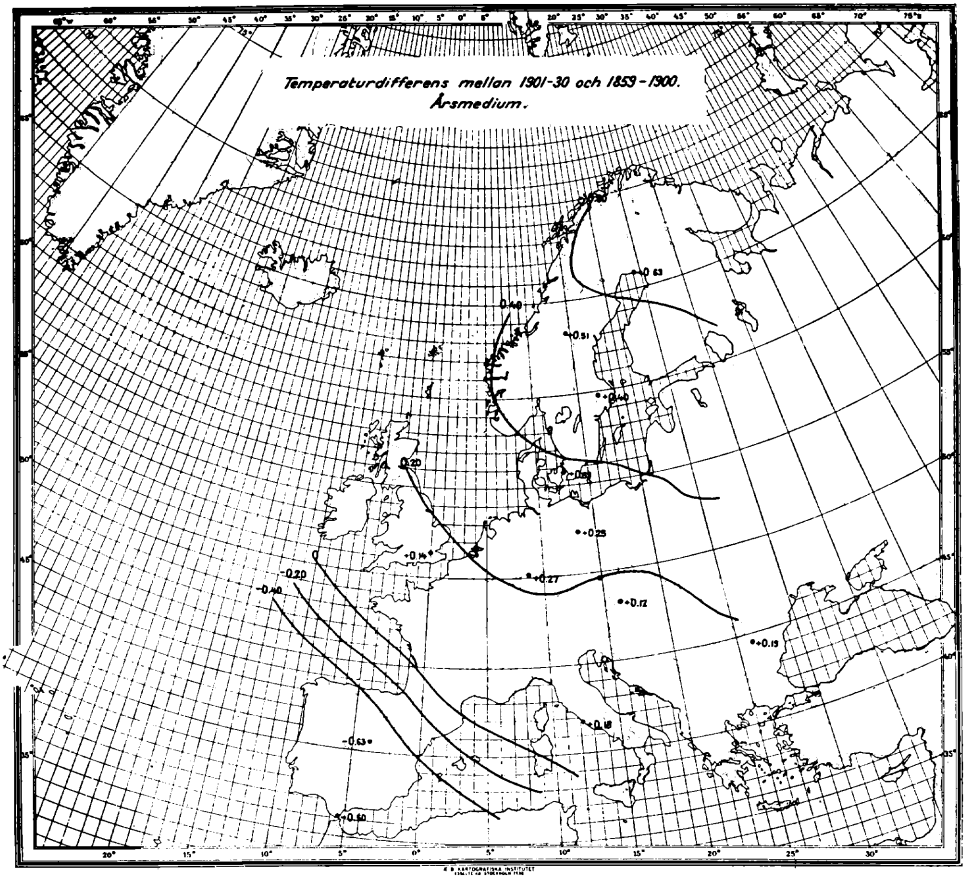

Fig. 4. Temperature difference between 1901-30 and 1895-1900, yearly mean values. (From Ångström 1939.)

gone a rapid rise of temperature during the same period as the expansion of the above-mentioned permanent residents or early spring migrants. (Siivonen and Kalela 1937; Kalela 1938; etc.). Figure 6 which gives the corresponding mean temperatures for Vienna [1] during the period 1827-1937, shows that the situation in central Europe has been fundamentally the same. Although the increase in winter temperatures has been much less marked there than in northern Europe, the coldest months, December and January, have become noticeably warmer, and to some extent the same is true also of early spring, March, in central Europe.

THE RECEDING SPECIES. Since this group of species is much more strongly represented in central Europe than in northern Europe, we will consider first the facts as they concern central Europe. Of the fourteen receding species of central Europe, four are permanent residents but the remainder, that is the great majority, are typical migrants. It is noteworthy that the latter birds, contrary to the expanding migrants, arrive markedly late, in April and May, considering the position of central Europe. (There are other differences, too, between the two groups of migrants, which will be considered.) Breeding occurs in May, June and July.

The six retreating southern species of southern Finland, also are (excepting *Carduelis cannabina*) typical "summer birds," that is, species which arrive noticeably late in spring and which breed only in the summer months. It is at once evident that the relation of the receding typical "summer birds" to the recent temperature changes must have been quite different from that of the permanent residents and the early spring migrants (Kalela 1938). At any rate they could not enjoy the benefits of the warmer winters and early springs. Of more direct significance is another important circumstance which is very clearly seen today in central Europe. As shown in Figure 6 *the summers in the middle of central Europe became strikingly cooler during that time period when the decrease in the species under consideration took place.* The situation in northern Europe (southern Finland) is not as clear. Here the summer temperatures considered as a whole display no marked changes. However the most important breeding season, June, in northern Europe too has grown somewhat cooler since the turn of the century simultaneously with the decline of the species considered. (See Figure 10.)

The general trend of the changes in avifauna in relation to the recent temperature developments may be summarized as follows:

(1) The recent developments in temperature indicate, with the exception of the immediate past, both in northern and central Europe, *a change towards a more maritime climate;* the winters, and especially

[1] The temperatures for Vienna have been used here, since a correspondingly long continuous series from Germany is not available to me. They are no doubt applicable also to southern Germany. In this connection it should be observed particularly that of the receded southern species mentioned, about half are characteristic of southern Germany. In northern Germany the temperature changes have of course been less different from those in northern Europe than have those in Vienna. Nevertheless the summers have grown cooler since the middle of the previous century, for instance in Berlin. This is true in particular of June. The increase in winter temperature has been more pronounced in Berlin than in Vienna. (See Wagner 1940; Kalela 1946 a.)

in northern Europe, the springs too, have become warmer; the summers have grown cooler in central Europe. In the southern part of northern Europe, although there has been no great change, June has become cooler. Correlated with this change in temperature there has developed an *expanding element of the avifauna* consisting of permanent residents and early spring migrants and, on the other hand, a *receding element* consisting of typical migrants which arrive late in spring and which breed exclusively during the summer months.

(2) Corresponding to the divergence in the changes of temperature between northern and central Europe there is a marked difference in the relative numbers of expanded and receded species in both regions.

OTHER EUROPEAN REGIONS. The recent changes in the avifauna of the British Isles have been considered by Alexander and Lack (1944). Jespersen (1946) has published a corresponding survey for Denmark. In both investigations, temperature is considered, among other factors, as a cause of the changes in fauna, although no decisive importance is attributed to it. Alexander and Lack point out that the cause of the changes is in many cases unknown. Space does not allow a detailed consideration of these problems although the following remarks can be made. Both the British Isles and Denmark lie in a zone where the increase in winter

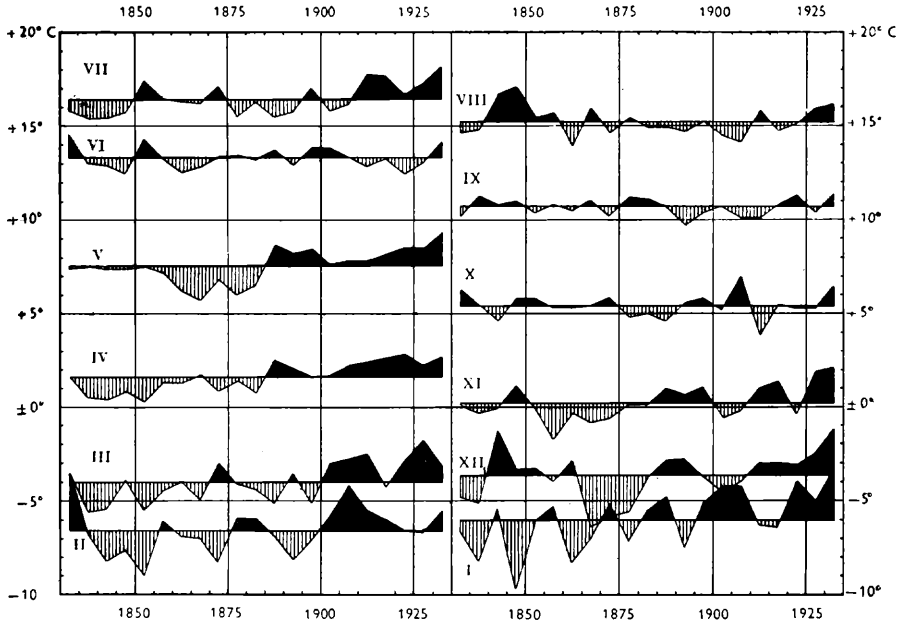

Fig. 5. The monthly mean temperatures for Helsinki 1831-1935, in five-year periods. (From Siivonen & Kalela 1937.)

temperatures has been much less than in northern Europe, and where the cooling of the summer has been of lesser magnitude than that in the parts of central Europe previously. Therefore it seems reasonable that the influence of the changes in temperature on the avifauna of the British Isles and Denmark should have been less pronounced than it has been either in southern Finland or in Germany. However, it appears that phenomena, in many respects corresponding to those in central and northern Europe, can be observed in the avifaunae of the British Isles and Denmark. However, humidity should also be considered as a factor in these changes.

Timmermann (1939) accounts for the spread of several southern birds to Iceland on the basis of the recent changes in temperature.

INFLUENCE OF TEMPERATURE

Increase and decreases in animal populations depend on the equilibrium between the immigration and the birth-rate on the one hand and emigration and mortality rate on the other; this holds, too, for populations at the edges of their range. All the above components may be influenced by climate. In order to penetrate the situation more profoundly, exact population analyses, continued from year to year, such as those of Nice (1933) and Kendeigh and Baldwin (1937), would be absolutely necessary. Since such analyses concerning the species treated here have not been done, we must simply content ourselves with quite general views in understanding the above-mentioned parallelism between faunal and climatic changes from a biologic viewpoint. The following discussion will be confined to three phases in the annual cycle of the birds: the seasons of wintering, spring migration, and breeding.

WINTERING. It has been mentioned above that five of the six receding species of southern Finland, and ten of the fourteen in Germany, are typical "summer birds." In regard to the wintering areas of these 15 "summer birds," marked differences exist between them and the expanding element of southern Finland and Germany. They all winter in the tropical and sub-tropical regions, especially in Africa (Table 1), which are outside of the regions which have recently experienced warmer winters. If indeed their wintering conditions have been influenced at all by recent climatic changes, changes in humidity must be considered to be of prime importance. A deterioration in winter conditions due to increasing aridity might be inferred. Such an explanation for the decline in the northern populations of the species under consideration appears to me to be unnecessary even if it may have been a contributory cause.

With the expanding species the situation is different. They all winter in more northern areas than any of the receding "summer birds." The European populations of *Phoenicurus ochrurus*, *Regulus ignicapillus*, and *Serinus canarius*, withdraw, it is true, in winter, to the Mediterranean regions, where the winter temperatures have shown only a slight change. But in the case of the remaining species, at least a considerable part of their European populations winter in

central Europe, in the British Isles, or even in northern Europe, that is, in the zone of westerly winds. And the recent increase of winter temperatures applies to all of this zone in Europe even though, as we have seen, it is less pronounced in the South, and in the West, than in the North.

The significance of this circumstance can be illustrated by numerous observations related in the ornithological literature about the effect of such hard winters as 1928-1929, 1939-1940, 1940-1941, and 1941-1942. Among the species considered here whose populations were greatly reduced during these winters are primarily the Great Crested Grebe, *Podiceps cristatus* (Linnaeus); Coot, *Fulica atra* Linnaeus; Tawny Owl, *Strix aluco* Linnaeus; Blackbird, *Turdus merula* Linnaeus; *Galerida cristata*; and *Motacilla cinerea* (also the Mute Swan, *Cygnus olor* (Gmelin) and Moorhen, *Gallinula chloropus* (Linnaeus)). The Finnish polecat population was reduced in the years 1940-1942 to one tenth. Also a clear recession of the northern limits of the species was observed. (No definite short-cyclic fluctuations of the polecat population have been observed in Finland.)

So it appears obvious, that the size of the northern populations of many of the advancing species—whether resident or migrant—is largely controlled by the winter mortality and that an amelioration of the winter conditions (increase in temperature and thinning of the snow cover which is largely dependent upon it) is an important factor in their recent expansion.

SPRING MIGRATION. We have seen that the spring migration of most of the expanding migrants occurs during the increasingly warm spring months, whereas in general this is not the case with that of the receding ones. The modifying influence of temperature on spring migration is well known. Thus warmth acts as a stimulus to spring migration and this can induce or further a prolonged northward migration (Lönnberg, 1934). It is obvious that immigration into new area will be favored to a high degree thereby. Among the birds in whose dispersal the prolonged migration plays a greater or smaller part, Lönnberg (1934) mentions, among others, *Phoenicurus ochrurus*, *Motacilla cinerea*, and *Serinus canaria*. Of the northern European species, I might emphasize in this connection the Lapwing, *Vanellus vanellus* (Linnaeus), and the Rook, *Corvus frugilegus* Linnaeus, especially, but prolonged migration would be a much more common means of dispersal.

BREEDING. It is known that the number of broods, the clutch-size, as well as the juvenile mortality can be modified by temperature directly or indirectly and above all through food supply.

According to the data given above, the temperature at the breeding season seems to be of decisive significance in the population dynamics of the decreasing "summer birds." This is very understandable in birds which spend half the year in the tropics or subtropics. It should also be emphasized that the principal breeding range of most of these species lies in the Mediterranean region which is particularly warm in summer.

As to the expanding component, the breeding season of the central European species has not become warmer, but rather the reverse. The situation in northern Europe is different. Here the earlier part of the breeding season of most of the expanding species has displayed a striking rise in temperature, particularly in May. It seems quite possible that the big difference in the relative numbers of expanding species in northern and central Europe depends, to no small degree, on just this circumstance. The important breeding month of June has, it is true, become somewhat cooler also in northern Europe but, however, the change is quite slight in comparison with the marked rise in May temperature.

We are still very far from a satisfactory understanding of the ways in which the recent changes in fauna are associated with temperature. The theory proposed above may have served to emphasize the differ-

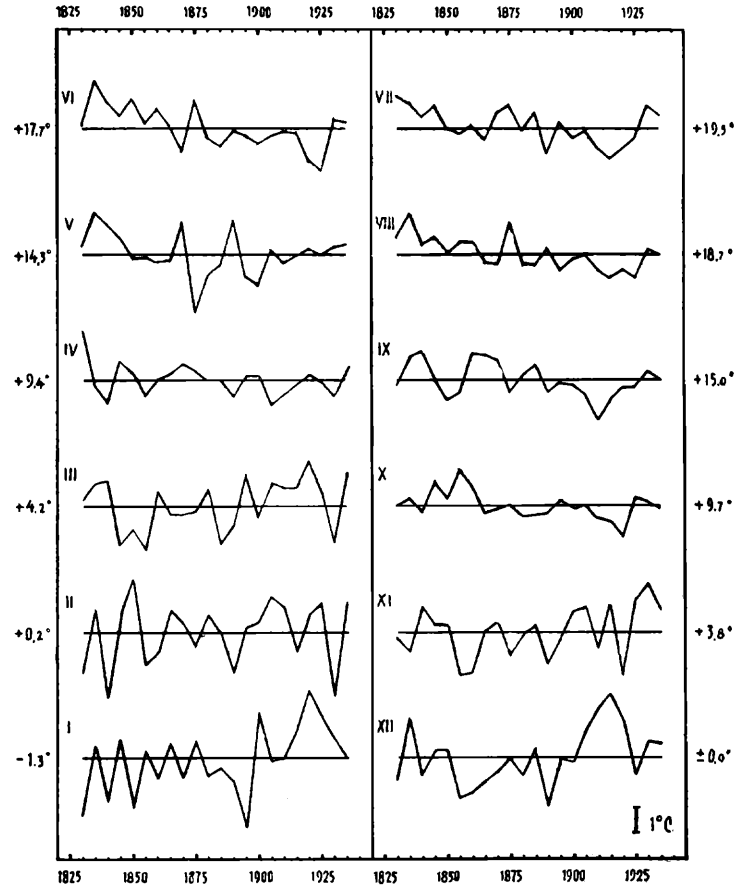

Fig. 6. The monthly mean temperatures for Vienna 1828-1937, in five-year periods. (From Kalela 1946 a.)

ence in the biologic and temperature requirements of the permanent residents and the early arrivals in spring on one hand and the typical "summer birds" on the other. In relation to the winter, spring-migratory, and breeding seasons, it appears that the temperature changes exert their effect, in the former group, in any one, or combination of these seasons. Most of the migrants included in this group are "weather migrants." (See Salomonsen, 1946.) The main part of the species designated here as "summer birds" on the other hand are "instinct migrants." In this group, the changes in temperature seem to exert their influence principally during the breeding season.

THE INFLUENCE OF CHANGES IN THE ATMOSPHERIC HUMIDITY.

THE EXPANDING SPECIES. The fact which first drew the attention of the ornithologists to the recent faunistic changes was the sudden expansion of the southern waterbirds, demonstrable not only in northern Europe but also in the British Isles and in north-central Europe. Even now the best examples of this expansion phenomenon are to be found among the species characteristic of eutrophic lakes. In numbers of species, also, this ecologic element is particularly strongly represented in the expanding component. Among the advancing species in the southern part of northern Europe (not only in southern Finland) are *Podiceps nigricollis*; *Podiceps cristatus*; *Cygnus olor*; the Pochard, *Aythya ferina* (Linnaeus); the Water Rail, *Rallus aquaticus* Linnaeus; *Gallinula chloropus*; *Fulica atra*; the Black-headed Gull, *Larus ridibundus* Linnaeus; the Little Gull, *Larus minutus* Pallas (Kalela, 1946*b*).

A remarkable fact concerning the direction of dispersal of the aquatic species concerned should be mentioned here. The recent changes in temperature signify, as we have seen, in northern and central Europe, and the same applies to the British Isles, a development towards more maritime conditions. In agreement is the fact that the majority of the expanding species, many of the water birds included, have spread towards the north or northeast. In certain water birds, however, a marked northwesterly or even westerly direction of dispersal, that is to say, an expansion from the inner parts of the continent, is to be observed, and this has continued since the latter part of the previous century. The most striking examples are supplied by the Black-necked Grebe, *Podiceps nigricollis nigricollis* C. L. Brehm (See Frieling, 1933.) and *Larus minutus*. Figure 7 illustrates the invasions of Europe by *Podiceps nigricollis nigricollis* in this century. (This map is not correct in all details, but gives a clear picture of the direction and peculiar mode of dispersal of this species.) The facts stressed above suggest that the expansion of the aquatic species themselves is connected not only with changes in temperature but also with other specific factors.

The shallow lakes, which form the typical habitat of the aquatic species under consideration are, of course, exposed to the highest degree of dessication. Consequently one of the first attempts to

explain the expansion of the aquatic species involved the suggestion that the lakes in their former breeding areas had dried up for one reason or another and that this had induced the birds to seek new areas (Baxter and Rintoul, 1922; Lönnberg, 1924). The latter hypothesis has gained new support from the results of modern climatological research (Kalela, 1940*b*; 1946*b*).

As emphasized earlier, the recent changes in the temperature are regarded as a result of increasing atmospheric circulation; the horizontal currents have increased in intensity and therefore an equalization of temperature between the poles and the equator has resulted. With horizontal currents, however, as Wagner (1940) pointed out, the intensity of the vertical component must increase. From this there follows an increased precipitation in the region of rising air currents, that is, in the tropics and above all in the region of the westerly winds, whereas in the region of descending air currents, that

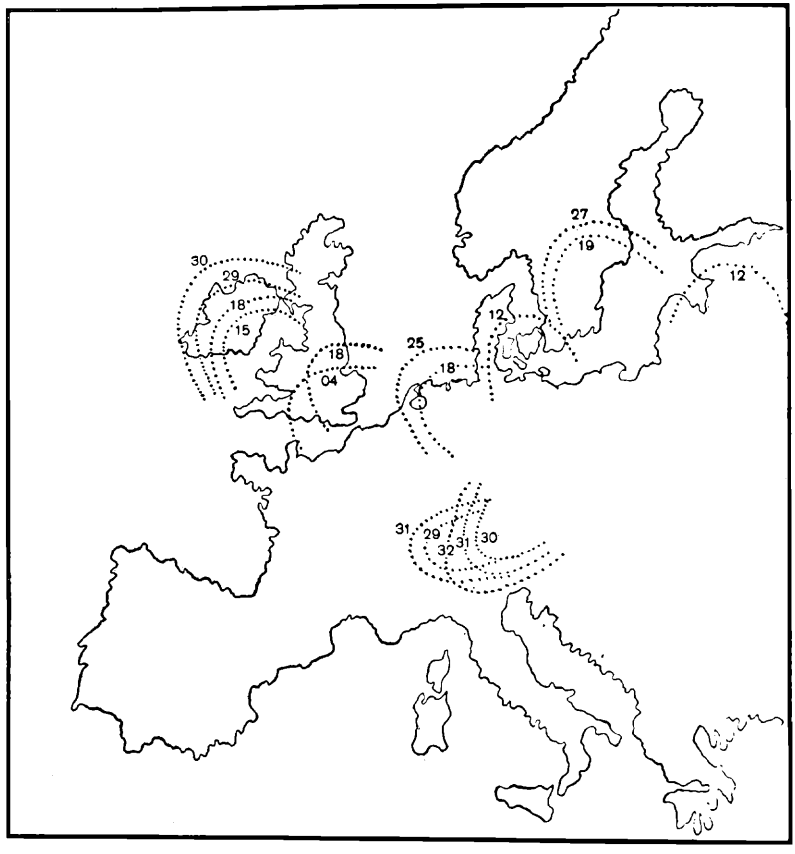

Fig. 7. *Podiceps nigricollis*: Invasions in Europe in the 20th century. (From Frieling 1933.)

is, in the regions of low rainfall in the Horse Latitudes, even less precipitation has occurred. Concerning the latter, it is well known that *the aridity of the dry regions of all of the continents has become more pronounced*. Attempts have been made to link this economically significant phenomenon ("soil erosion") with careless systems of agriculture, but now there can be little doubt that a principal cause is climatic.

The west palaearctic center of distribution of at least the majority of the aquatic species included here lies in the arid Caspian regions and the adjoining parts of Europe (Kalela, 1946*b*). Here the dessication has been very intense. (See, for instance, Jacks and Whyte, 1939.) In the case of the aquatic species of these regions, their rapid reduction as far northwest as Hungary has been well known since the end of the previous century. However, in Hungary the system of cultivation, also, has played an important role in the reduction of the area of water.

The climatically conditioned dessication of the lakes of the steppes is known not to be due to a persistent gradual sinking of the water level but to the fact that, in the sharp annual fluctuations in the water level, the dry years become more and more predominant. But in the dry years, as Formosof (1934) emphasized, whole populations of waterbirds were induced to seek new areas. Such—shorter or longer—invasions into new breeding areas are known to be characteristic for many other steppe animals, too. The mode of expansion of certain waterbirds corresponds largely to this picture. Thus the northwesterly expansion of *Podiceps nigricollis* follows this "invasion type" (Figure 7). These invasions may have several causes, but it appears that they occur particularly frequently during dry years.

It therefore seems to be an acceptable hypothesis that it is this dessication of previous habitats which represents the specific factor responsible for the particularly strong representation of waterbirds among the expanding species, and which makes the somewhat peculiar mode and direction of the expansion of certain species understandable.

THE RECEDING SPECIES. It has just been emphasized that changes in atmospheric humidity have been marked by a heightening of the contrasts in precipitation; simultaneous with the decrease in precipitation in the dry regions, an increase in rainfall is observable in the zone of the westerly winds. The latter is particularly well known in Norway and the British Isles. *Consequently climate in the zone of westerly winds, particularly in the areas especially exposed to the west winds, has become more maritime, not only in temperature but also in humidity*. Has this moisture component exerted any influence on the avifauna?

Durango (1946) has studied the population changes of the Roller, *Coracias garrulus garrulus* Linnaeus, in southern Sweden. This closely resembles in its main distribution the "summer birds" which as we have seen have decreased at their northern limits, especially in central Europe. The marked decrease of the species in Sweden is

shown in Figures 8-9. The food of *Coracias garrulus* consists mainly of flying insects, and the amount of food secured is, as Durango points out, most favored by warm, dry, and sunny summers. Durango associates the decrease of the species with changes in this whole meteorologic complex and not only with the cooling of summer; in fact, he even emphasizes the precipitation factor especially. This explanation seems to be supported by the following facts: (1) The northern limits of *Coracias garrulus* run not only through northern Europe but also through central Europe in a markedly southwest northeast direction fitting in with the rainfall conditions much better than with the contours of the summer isotherms; the species is absent from the coastal countries with high rainfall. (2) The species has only decreased in those westerly parts of its northern range which are particularly exposed to the rain-bearing west wind, whereas farther east, particularly in Russia, on the contrary, it has even displayed some expansion (Timoféeff-Ressovsky, 1939; Durango, 1946).

So if the importance of the precipitation appears particularly probable in the case of the range-changes in *Coracias garrulus*, then this factor (like the intensity of solar radiation) must also be taken

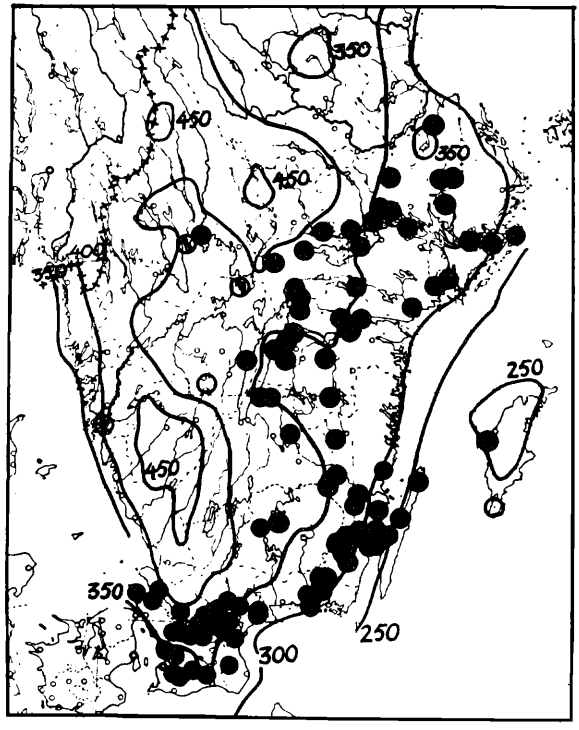

Figure 8

into consideration seriously in the case of the remaining receding "summer birds." Unfortunately, a resolution of the question is difficult because of the fact that the rainfall measurements are beset with much greater sources of error than are the temperature measurements.

CHANGES IN THE AVIFAUNA OF NORTHERN AND CENTRAL EUROPE IN VERY RECENT TIMES

The immediate past occupies such a peculiar position in the changes in fauna in northern and central Europe that it must be treated separately. The most striking feature of changes in range among the southern birds in northern Europe since the end of the last century consists of an expansion of permanent residents and early spring migrants. Since the 1920's, and most especially since the 1930's, however, a new, well-marked and distinctive expansion in range occurred (Leivo, 1946). The following species have undergone an expansion in range in southern Finland or in the Baltic region, especially from the southeast: the Thrush Nightingale, *Luscinia luscinia* (Linnaeus); Grasshopper Warbler, *Locustella naevia naevia* (Boddaert); the Great Reed Warbler, *Acrocephalus arundinaceus*

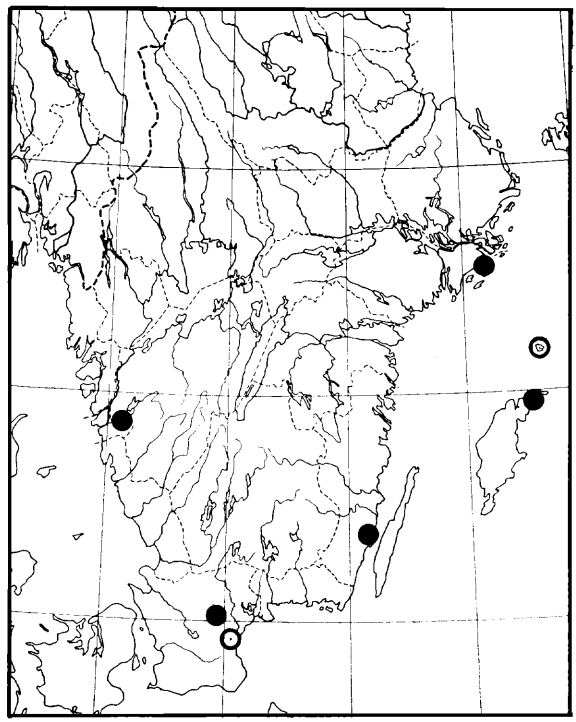

Fig. 8-9. *Coracias garrulus*: Swedish breeding-places (black circles; white circles=breeding probable), occupied before 1925 (Fig. 8) and between 1925-46 (Fig. 9). The curves in Fig. 8 show the average rainfall during May-Oct. in 1880-1909. (After Durango 1946.)

arundinaceus (Linnaeus); the Reed Warbler, *Acrocephalus scirpaceus scirpaceus* (Hermann); Marsh Warbler, *Acrocephalus palustris* (Bechstein); Blyth's Reed Warbler, *Acrocephalus dumetorum* Blyth; Barred Warbler, *Sylvia nisoria nisoria* (Bechstein); the Greenish Warbler, *Phylloscopus trochiloides viridanus* Blyth; the Red-breasted Flycatcher, *Siphia parva parva* (Bechstein); the Scarlet Grosbeak, *Erythrina erythrina erythrina* (Pallas). These are typical late-arriving and late-nesting "instinct migrants" which winter in the tropics or sub-tropics, and thus represent a biological group, which has, as we have seen, in general exhibited a decline since the previous century.

This series of expansion of ranges is, as Leivo has demonstrated, clearly related to climate. Since the 1920's, a marked increase in the summer temperatures has been observed in northern Europe, accompanied by continued change to warmer winters. (The increase in winter temperatures culminated in the latter part of the 1930's; since then there have been several strikingly cold winters.) It is to be noted especially that the June temperatures which have declined somewhat since the turn of the century, have displayed a sharp increase since about 1930. In the following years, June has become warmer on the average than the mean for the entire period of more than a hundred years during which records of Finland's temperatures are available (Figure 10). However, according to Leivo, the range-changes of the above-named species are not correlated with the rise in June temperatures alone, or with the temperature of the summer months in general, but depend primarily on the fact that the temperature *both in May and June* has simultaneously become higher at exactly the time of the range expansion (Figure 10). The increased May temperatures have favored a prolonged northward migration while the nesting success has profited from the warm early summers.

As to the above treated "summer birds" of central Europe which have shown recession in range since the middle of the last century, simultaneously with the climate becoming more oceanic, it must be stressed that, in central Europe, too, there has been an increase in summer temperatures since the 1920's, accompanied by decreased precipitation and increased solar radiation. (As the latest temperature records from Vienna are not available to me, the increase in summer temperatures since the 1920's does not appear with sufficient clarity in Figure 6.)

The matters treated here are of so recent a date that they can be surveyed only in a very unsatisfactory manner. Nevertheless there are unequivocal indications of recovery in the population of certain species. (Durango, 1946; Kalela, 1946*b*). This is the case with *Lanius minor* and *Lanius senator* in Germany. *Monticola saxatilis* seems, at least in southern Russia and in Switzerland, to have displayed a tendency toward range extension. As a further very suitable example, the Hoopoe, *Upupa epops epops* Linnaeus, might be chosen, a species whose northern limits lie between Germany and Finland, and which therefore was not mentioned previously. At least in north-

ern Europe the Icterine Warbler, *Hippolais icterina* (Vieillot), has again become more abundant and the same seems to be true of *Coturnix coturnix* in Sweden and Denmark (Westerskow, 1947). It is interesting to note that, for certain of the above-mentioned species investigated by Leivo, at least a weak temporary expansion seems to have taken place in the last century, so that the difference between them and the "summer birds" already discussed in the present study is hardly a sharp one.

The above-mentioned new climatic phase, which began in the 1920's, and reached its most typical form in the 1930's, marks a peak in the recent climatic changes. Wagner (1940) explains it as the displacement towards the pole of the high pressure belt of the Horse Latitudes as a result of an ever-increasing atmospheric circulation.

This climatic phase is very plainly observable in the dry regions. Dessication has been especially intensive there, and in the southern parts of the zone of the westerly winds as a result of the polar displacement of the high pressure belt of the Horse Latitudes, the dessication has been observed also. This circumstance is well known in the southern part of central Europe just as it is in the prairie and great-plains regions of North America.

Several species of waterfowl characteristic of eutrophic lakes are found among the newest immigrants both in central and in northern Europe, *e. g.* the Gadwell, *Anas strepera* Linnaeus in Sweden (Svärdson, 1943) and the Red-crested Pochard, *Netta rufina* (Pallas), in

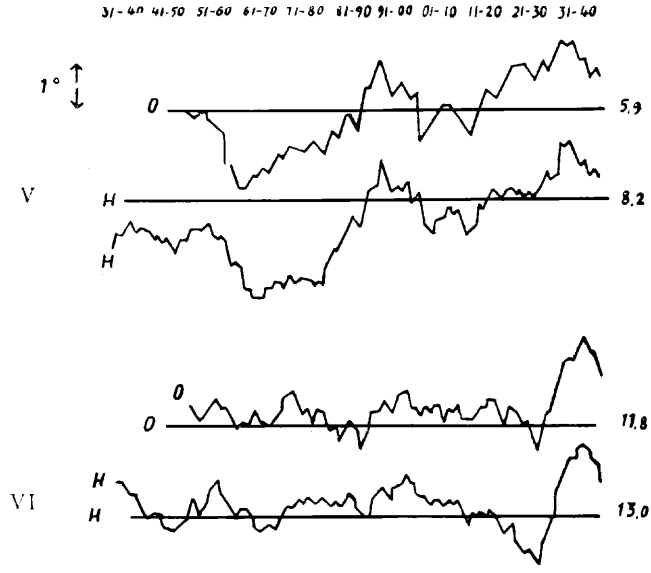

Fig. 10. May and June temperatures for Helsinki (H) and Oulu (O), in ten-yearly averages. The horizontal lines indicate the "normal temperatures", i.e. averages for 1901-30. (According to Keränen, from Leivo 1946.)

certain central European countries (Stresemann, 1943). The expansion of both species seems to be due to typical invasions. The center of their European range clearly lies in the southeast steppe regions. Svärdson assumes in the case of *Anas strepera* that the expansion is connected with the peculiarly intensive dessication of the earlier breeding grounds.

In summary it can be said (1) that an expansion from the inner part of the continent has been very remarkable since the 1920's and especially since the 1930's, and also (2) that apparently changes both in the humidity and in the temperature have been involved.

It has just been mentioned that since the end of the 1930's several very hard winters have occurred, and earlier the devastating effect of the winters 1939-1940, 1940-1941, and 1941-1942 on the populations of several species which winter in the areas of westerly winds was emphasized. It has already been assumed both by climatologists (*e.g.* Keränen, 1944) and by zoologists (*e.g.* Siivonen, 1946) that the period characterized by the rising temperature has reached its culmination in the 1930's and a continental phase is becoming predominant.

THE RHYTHM OF FAUNISTIC CHANGES

Insofar as the recent faunistic changes are climatically conditioned, they are, surely, not to be considered a singular phenomenon but must have occurred (Siivonen and Kalela, 1937) in earlier times. Considering the short time for which data exist, however, it is in general very difficult to produce proof of this. In the case of certain typical "summer birds" (*Lanius minor*, *Lanius senator*, *Upupa epops*, etc.), however, the rhythmic nature of the range-changes is indicated. The same is demonstrably true, too, for certain species which, during "faunistically historical" times seem to have shown a continuous extension toward the north. Thus, historical proof can be adduced that the polecat was widely distributed in southern Finland in the fifteen hundreds (Kalela, 1948). Exactly the same is true of *Galerida cristata* in Germany (Niethammer, 1937-42). After a severe regression of their northern limits which took place apparently in a period marked by particularly hard winters (in the sixteen hundreds?) both species have undergone an intensive expansion again during the previous century and the present century.

A powerful expansion of the southern element, known for a long while, took place in northern Europe during the warm post-glacial period, which reached its maximum in northern Europe about 5000 B.C. Fossil records exist of several of the above-discussed southern species (particularly waterbirds, see Kalela 1946*b*) close to or beyond their present northern limits. The polecat, too, had a more northerly distribution in Scandinavia than it has now.

SUMMARY

1. The present study deals with certain striking changes in the northern limits of species of birds of northern and central Europe since the middle of the 19th century.

2. Of the 25 species which have their northern limits in southwestern Finland, 44 percent have increased in numbers and have displayed an expansion, while 24 percent have grown somewhat rarer. This situation is regarded as characteristic of the southern part of northern Europe. The corresponding figures for central Europe (Germany) are: of a total of 32 southern species, 19 percent have increased and displayed expansion whereas 44 percent have receded. Thus there exists a pronounced difference between the southern part of northern Europe and central Europe in the range dynamics of the southern species.

3. The activities of man are considered not to be a prime cause of the changes described even though they have played an important role in the recession of several species.

4. The most important factor seems to be the present climatic changes which are caused by increased atmospheric circulation. In northern and central Europe, and in general in the European region of the zone of westerly winds, the climate has become more maritime, both in temperature and in humidity. In southern and southeastern Europe, i.e., in parts south and southeast of the regions investigated, the most striking feature of the climatic changes consists, on the contrary, of an increased aridity.

5. The increasing component consists, both in northern and central Europe, partly of permanent residents, partly of such migrants as those whose European populations spend the winter wholly or largely in the zone of the westerly winds and reach their breeding areas early in spring. The expansion is related to the warmer winters and springs, by which the wintering conditions and the spring migration as well as the nesting success could have been influenced.

6. In the expanding component, aquatic species characteristic of eutrophic lakes are strongly represented both in species and in numbers. Their expansion seems to be favored by the dessication of their old breeding areas, especially in the southeastern steppe region in addition to the increase in temperature in the new breeding areas and winter haunts.

7. The decreasing component is comprised, both in northern and in central Europe, chiefly of typical migrants which winter in the tropics and sub-tropics and reach their breeding areas late in spring so that their breeding season falls in the summer months. The decrease in these typical "summer birds"—apart from cultural factors—is related to the decrease in summer temperatures and the increased rainfall, in addition to decreased solar radiation, by which, above all, their nesting success may have been influenced.

8. The differences pointed out in item 2 between northern and central Europe are understandable, at least to an important degree, by the gradual divergence in climatic changes in the two regions.

9. Since the 1920's, but especially since the 1930's, an increase has occurred in a number of typical "summer birds" which had until then been declining. But above all, many new "summer birds,"

especially in northern Europe, have displayed a northwesterly expansion.

10. The last-mentioned period, compared with the previous time, has been characterized principally by strong increase in summer temperature, to which is added, a decrease in rainfall and an increase in solar radiation, especially in central Europe.

11. In relation to certain of the species treated herein, it may be shown with direct evidence that the contemporary changes in range form a part of a rhythmically repeated phenomenon.

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GENERAL NOTES

Laughing Gulls tread out their food.—The mudflats of Long Beach Island 3 miles south of Beach Haven, N. J., have long been a favorite of ornithologists to study birdlife. While the tide is low countless, but rapidly decreasing numbers of many species of shore birds are seen by observers from far and near. There in August 1946 we found Robert W. Storer from California, with his binoculars, while enroute to the A. O. U. meeting in Urbana. The birds seem to appreciate those who come to observe as numerous species permit approach within a few feet. On another day, Mrs. Wood and I watched many birds feeding together in the shallow inch-deep receding waters among which were Dowitchers and Laughing Gulls, quite oblivious of our near presence. The Dowitchers with their long bills easily reached their food in the mud, but the gulls could not reach far enough without immersing their heads. To obviate this each gull rapidly and alternately stamped with his feet until the water became muddy and the little crustaceans or other foods were forced up and easily picked out of the muddy water.-Harold B. Wood, Harrisburg, Pennsylvania.

Recovery of 19-year old Herring Gull.—On June 19, 1948, on a banding trip to Cavalier Island to band gulls and Great Blue Herons, I picked up a dead Herring Gull carrying band No. A-637556. Recently I received word that this band was placed on a Herring Gull, presumably young, by the late Mr. William I. Lyon on July 15, 1929, at Red Bay, Bruce County, Ontario. Red Bay is a small summer resort on the Lake Huron side of the lower part of Bruce Peninsula and Cavalier Island is about three miles out from this shore. This island is one of a group of six small islands, within a radius of one-half mile, on each of which Herring Gulls have been nesting for years. It would seem logical to conclude that Mr. Lyon banded it at one of these islands.

The bird was in good condition when I found it and there were no visible signs of the cause of its death; we estimated that it had been dead for not more than two days. This will make it within a month of being nineteen years old and would appear to be conclusive evidence of an old Herring Gull dying at its birthplace.—Howard H. Krug, Chesley, Ontario.