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Arctic, Montane and Steppe birds as Glacial relicts in the West Palearctic

By **Tommy Tyrberg**

1. Introduction

The theory that speciation of forest birds has taken place in isolated forest refugia during glacial periods is well established both in the Palearctic and elsewhere (e. g. HAFFER 1974, HARRISON 1982, MOREAU 1966). While this concept is very likely correct in its essentials it is not verifiable by fossil evidence even in the West Palearctic (which has by far the richest Pleistocene avian fossil record in the World), due to the virtual absence of Pleistocene avifaunas from the putative refuge areas, especially southern Spain, the southern Balkans and Asia Minor.

It is however not generally appreciated that a similar process of range fragmentation and creation of relict populations by the glacial/interglacial climatic cycle also affects arctic, montane and steppe birds, and that at least in the West Palearctic the fossil record of this process is fairly good.

2. The "Mammoth steppe" avifauna

It has long been known that steppe conditions have prevailed over large parts of Europe during glacial periods. This steppe which at times extended essentially unbroken from the Atlantic to the Mackenzie Basin of northwestern Canada was characterized by a cold, dry continental climate, a vegetation usually dominated by *Artemisia* and a spectacular mammalian megafauna. This biome which has no exact counterpart today is known by a variety of names: "steppe tundra", "arctic steppe", "periglacial steppe", "loess steppe", "arctic grassland" and "mammoth steppe"

The avifauna of the mammoth steppe has received much less attention than the mammals but at least in Europe it is quite well known from several hundred sites.

It has often been noted that glacial mammalian faunas are "disharmonious" i. e. they contain forms which today are found in quite different habitats (an extreme example is Muskox *Ovibos moschatus* occuring together with Lion *Felis leo*). This also applies to the avifauna. Thus among the gallinaceous birds (which were apparently abundant on the mammoth steppe) the normally dominant Ptarmigan *Lagopus mutus* and Willow Grouse *Lagopus lagopus* are regularily found together with Partridge *Perdix perdix*, Quail *Coturnix coturnix* and Black Grouse *Tetrao tetrix*.

Other characteristic members of the mammoth steppe avifauna are raptors (especially Golden Eagle *Aquila chrysaetos*, Kestrel *Falco tinnunculus*, and Snowy Owl *Nyctea scandiaca*), Larks (usually Skylark *Alauda arvensis* though other species also occur) and corvids (particularily Raven *Corvus corax*, Red-billed Chough *Pyrrho-*

corax pyrrhocorax and Alpine Chough *Pyrrhocorax graculus*). In addition to these largely arctic-alpine forms a number of "steppe" and "mediterranean" species are also regularily found, examples being Long-legged Buzzard *Buteo rufinus,* Pallid Harrier *Circus macrourus,* Red-footed Falcon *Falco vespertinus, Alectoris* partridges, *Melanocorypha* and *Calandrella* larks and Rosy Starling *Sturnus roseus.*

There is a clear climatic gradient in the composition of the faunas, the "mediterranean" species being more common in southern Europe, but there is an extensive overlap of northern and southern forms with birds like Snowy Owl and *Alectoris* sp. being regularily found in the same deposits.

3. Relict Distribution Patterns

Among the biogeographically significant characteristics of the mammoth steppe avifauna is the considerable fossil evidence that the present discontinuous ranges of a number of bird species in the West Palearctic may plausibly be regarded as relicts of a continuous range during the last (Würmian) glacial period. These birds can be divided into three groups based on their present distribution:

1. Predominantly arctic birds with isolated southern montane populations: Ptarmigan *Lagopus mutus,* Willow Grouse *Lagopus lagopus,* Dotterel *Eudromias morinellus* and Shore Lark *Eremophila alpestris.*

2. Montane species with a number of isolated populations in different mountain ranges and in some cases also a coastal population along the Atlantic coast: Rock/Water Pipit *Anthus spinoletta/petrosus,* Alpine Accentor *Prunella collaris,* Citril finch *Serinus citrinella,* Snow Finch *Montifringilla nivalis,* Red-billed Chough *Pyrrhocorax pyrrhocorax* and Alpine Chough *Pyrrhocorax graculus.*

The Ring Ouzel *Turdus torquatus* also belongs to this group but the fossil record of this species is too questionable to warrant analysis since the european *Turdus* species are hardly osteologically distinguishable except by size.

3. Eastern steppe species with an isolated population in the Iberian peninsula and/or Maghreb: Long-legged Buzzard *Buteo rufinus,* Imperial Eagle *Aquila heliaca,* Demoiselle crane *Anthropoides virgo,* Pintailed Sandgrouse *Pterocles alchata,* and Black-bellied Sandgrouse *Pterocles orientalis.*

4. The Würmian fossil record

There is some confusion about the terms used to designate the last glacial period and the period to which they apply. In the context of this paper "Würmian" is regarded as a synonym to "Weichselian", "Devensian" and "Valdai" and is considered to begin with Isotope Stage 5d about 115 000 BP and end with the Younger Dryas stadial c. 10 000 BP.

The fossil records in fig. 1–14 are based on data from some 850 sites with Würmian avifaunas. The quality of the fossil record is very uneven geographically, in particular with regard to Passerines. The best-studied area by far is southern France, other areas with fairly good fossil records include Switzerland, Italy, Hungary and parts of Yugoslavia, Poland and Romania. Many rich Pleistocene avifaunas are also known from Great Britain, Germany and Czechoslova-

kia but these were mostly studied long ago and badly need restudy. In the Soviet Union the Pleistocene avifaunas of Caucasus, Crimea and parts of Ukraine are reasonably well known while there are few records from other areas. Pleistocene avifaunas are also scarce or unknown from Scandinavia, most of the North European Plain, Portugal and southern Spain, the southern Balkans, Asia Minor, North Africa and the Near East.

It must be emphasized that the Würmian lasted for approximately 100 000 years and encompassed several colder and milder climatic phases and that the maps include records spanning the whole of this time interval. The records therefore indicate the "envelope" of a species' Würmian range rather than the range at any one time. Most of the avifaunas are however late glacial (c. 15 000–10 000 BP).

5. Arctic/Alpine Species

5.1 Ptarmigan

The Ptarmigan *Lagopus mutus* is the classic example of an arctic species with isolated southern montane populations. There is at present seven populations in the West Palearctic; in the Pyrenees, the Alps, the Scottish Highlands, the Scandinavian mountains, the northern Urals, Iceland and Spitzbergen. These populations, with the possible exception of the last two, are completely isolated and have presumably been

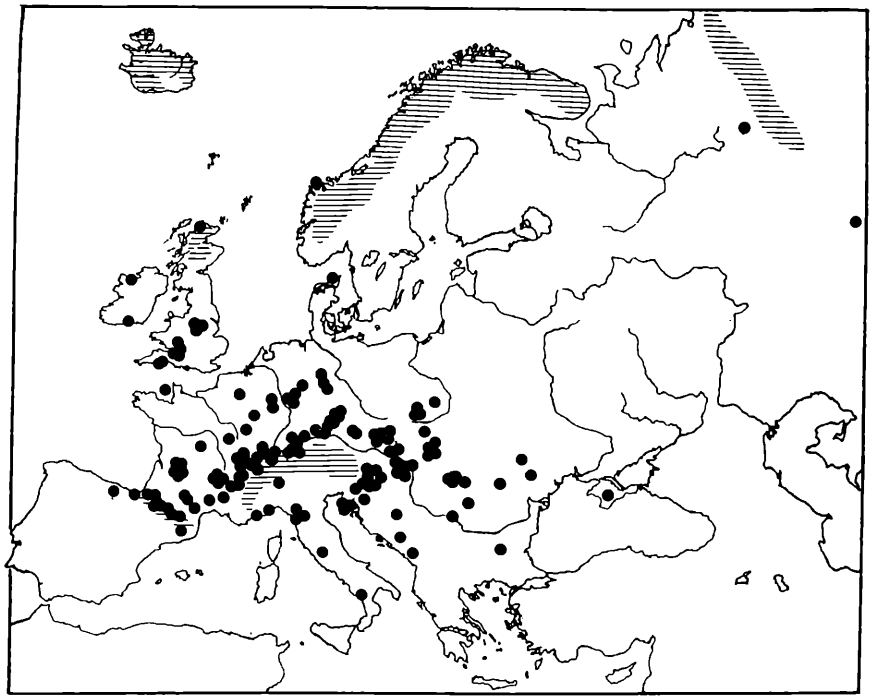

Figure 1:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Ptarmigan. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) des Alpenschneehuhns.*

so since the end of the Würmian. Each population is usually regarded as a separate subspecies.

The map (Fig. 1) shows that Ptarmigan were quite common throughout the uplands of central and southern Europe during the Würmian. In the southernmost part of the glacial range it was apparently restricted to the highest mountain ranges (the Pyrenees, the Cantabrian mountains, the Appennines and the Stara Planina). The species seems to have avoided plains. The Ptarmigan was apparently quite scarce in the plain of Aquitaine in southwest France in contrast ot the Willow Grouse (Mourer–Chauviré 1979). In Russia it is only found in the foothills of the Carpathians, in the mountains of Crimea and in the Urals and there is virtually no records from the North European plain. Despite the general scarcity of fossil birds from these areas the absence of Ptarmigan is probably real since there are several records of Willow Grouse (Fig. 2) and Black Grouse from both the Russian and the North European plains. This probably means that the European Ptarmigan were more or less isolated from the populations in the Urals and further east even at the glacial maximum. This accords well with the fact that the Pyrenean, Alpine, Scottish and Scandinavian Ptarmigan form the greyish "mutus" group of subspecies while the birds in the Urals, Spitzbergen and Iceland belong to the browner "rupestris" group. Iceland has presumably been colonized from Greenland, and Spitzbergen either from Greenland or from Siberia by way of Franz Josefs' Land (Ptarmigan from Greenland appa-

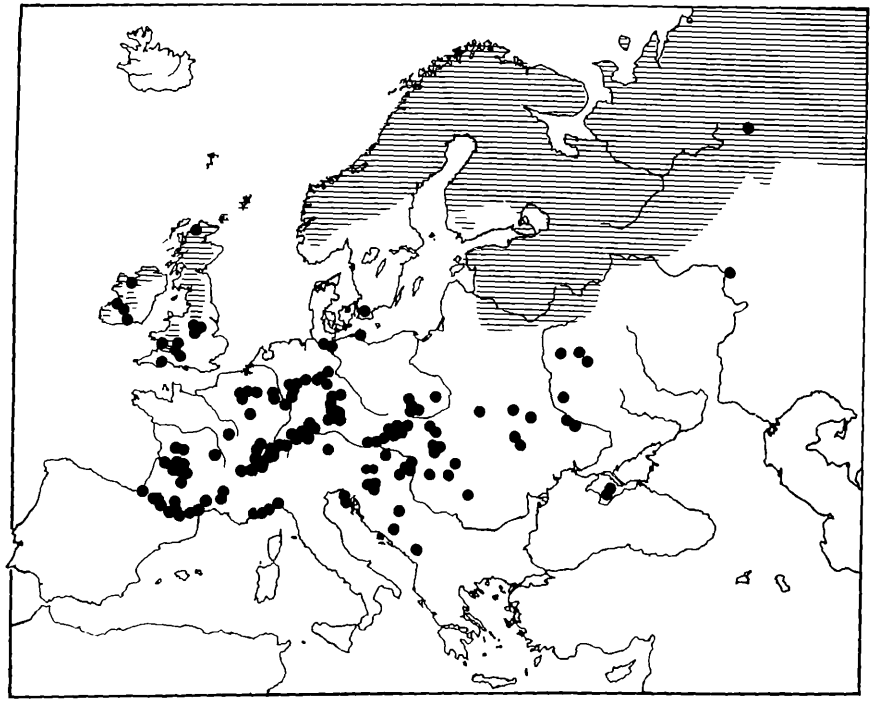

Figure 2:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Willow Grouse. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) des Moorschneehuhns.*

rently still occasionally reach Iceland (GUDMUNDSSON 1972)). Whether the Ptarmigan colonized the Scandinavian mountains at the end of the Würmian from central Europe across the North European plain or from Britain across the North Sea is uncertain. The distance across the then partly dry North Sea from Scotland to Norway is no longer than from Greenland to Iceland and the North Sea was then presumably at least as icebound as the Denmark Strait today. Ptarmigan have recently been found in deposits of Mid-Würmian interstadial age (c. 30 000 BP) in Skjonghelleren Cave in western Norway (LARSEN et al. 1987) and the possibility that the species might have survived the glacial maximum on some unglaciated refugium on the Norwegian coast should perhaps not be entirely discounted.

5.2 Willow Grouse

The Willow Grouse *Lagopus lagopus* has only one isolated population in the West Palearctic, the *scoticus* subspecies in the British Isles. This subspecies occurs in several separate areas but these are probably not isolated with the possible exception of the Shetland birds.

The fossil record (Fig. 2) shows that the Willow Grouse was quite common in central Europe during the Würmian. The Willow Grouse apparently did not range quite as far south as the Ptarmigan, since there are no records south of the Pyrenees or the Alps. On the other hand the species is found at several sites in the Russian and North European plains. Both these differences in the Würmian range compared to the Ptarmigan is presumably due to the Willow Grouse not being dependent on upland habitat. It is notable that neither the Willow Grouse, the Ptarmigan or the Black Grouse seem to have reached the Caucasus though all three species occurred in Crimea. Possibly they were excluded by the Caucasian Black Grouse *Tetrao mlokosiewiczi* and the Caucasian Snowcock *Tetraogallus caucasicus* which have been present in the Caucasus at least since the Middle Pleistocene (BARYSHNIKOV & CHEREPANOV 1985, BURCHAK-ABRAMOVICH 1975).

The end of the Würmian apparently caused a straightforward withdrawal of the Willow Grouse northward across the North European plain where (in contrast to the Ptarmigan) there are a few late glacial records from northern Germany, Denmark and southern Sweden. During this process the population on the British Isles was cut off by the North Sea and adapted to the maritime conditions on the heather moorlands of Great Britain and Ireland. That no relict Willow Grouse survived on the European mainland is presumably due to the absence of suitable lowland moor and scrub habitat.

5.3 Dotterel

The southern European populations of the Dotterel *Eudromias morinellus* are only doubtfully glacial relicts. They are all small (Fig. 3) and subspecifically identical to the main North Eurasian population, and since dotterels spend the winter in the subdesert zone of North Africa and the Middle East the montane population may have been established during the Holocene by shortened migration. Such a process would be facilitated by the fact that Dotterels seems to have relatively little ortstreue.

The fossil record however indicates that the Dotterel was widespread on the glacial steppes of central Europe (Fig. 3) and it is perhaps equally likely that at least some of the southern populations have persisted since the Würmian. This at least seems to be the most likely origin of the rather larger populations in the mountains of Central Asia.

The two late glacial records from Apulia are probably of wintering birds. This part of Italy was apparently very dry steppe or

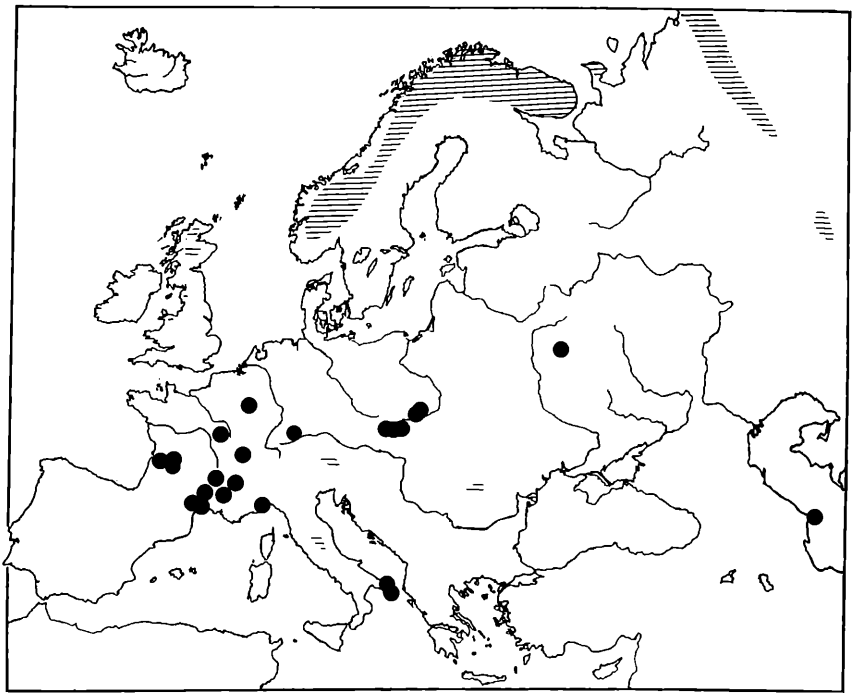

Figure 3:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Dotterel. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) des Mornells.*

semi-desert during at least part of the last glaciation as indicated by the presence of e. g. sandgrouse (Cassoli et al. 1979) and it would presumably have been suitable winter habitat for Dotterels. The record from Binagady near Baku (Burchak-Abramovich 1975) is of broadly last interglacial date and probably from a migrating bird.

5.4 Shore Lark

All the West Palearctic populations of the Shore Larks *Eremophila alpestris* are subspecifically distinct with ssp. *flava* in the north, *balcanica* in SE Europe, *atlas* in Morocco, *albigula* east of the Caspian, *penicillata* in parts of Anatolia and Iran and *bicornis* in southern Anatolia and Lebanon. Some 35 other subspecies occur in Asia and North and South America. This strong tendency to form subspecies presumably indicates a high degree of isolation between populations.

The Shore Lark is not very common as a fossil but there are enough records to show that it was widely distributed in central Europe during the Würmian (Fig. 4). Considering the wide glacial distribution it is not immediately obvious why there are no relict populations in western Europe. Possibly the montane habitats there are too wet for Shore Larks. In the Scandinavian mountains it is normally confined to the drier montane heath and the same seems to be true in the Atlas Mountains (pers. obs.)

The only other member of the genus, Temminck's Horned Lark *Eremophila bilopha,* occurs in desert habitat from Morocco to Kuwait. It is tempting to speculate that this form is derived from a population isolated either in Maghreb or the Near East during some earlier interglacial.

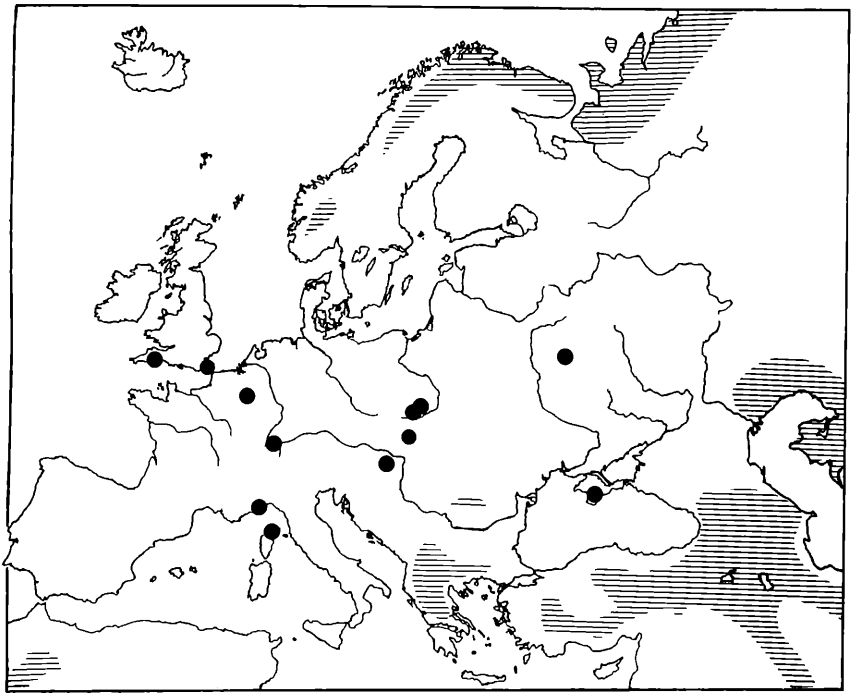

Figure 4:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Shore Lark. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) der Ohrenlerche.*

6. Montane Species

6.1 Rock / Water Pipit

The Rock/Water Pipit complex has recently been split into two species, the coastal Rock Pipit and the montane Water Pipit (RISBERG in press).

The Rock Pipits of NW Europe are usually subdivided into three subspecies: *petrosus* on the British Isles, *kleinschmidtii* on the Faeroes and *littoralis* in Scandinavia while the Water Pipits in the mountains of southern Europe all belong to the nominate *Anthus s. spinoletta*.

The fossil record of *Anthus spinoletta* sensu lato is rather exiguous, consisting of half a dozen records in France, three in England and one in Czechoslovakia (Fig. 5). These however mostly lie well outside the present breeding range of the species and probably indicate that the ranges of the Rock and Water Pipits were contiguous during the Würmian.

6.2 Citril Finch

The Citril Finch *Serinus citrinella* has a very limited range in the mountains of southwestern Europe (Fig. 6). The populations on Corsica and Sardinia belong to a separate subspecies, *corsicana*.

The few Würmian records (Fig. 6) neatly link the existing populations in Massif Central and the Pyrenees. There is also two Middle Pleistocene records from southern France (MOURER-CHAUVIRÉ 1975) but neither these nor the younger finds give any clue to the origin of the uniquely circumscribed range of this species.

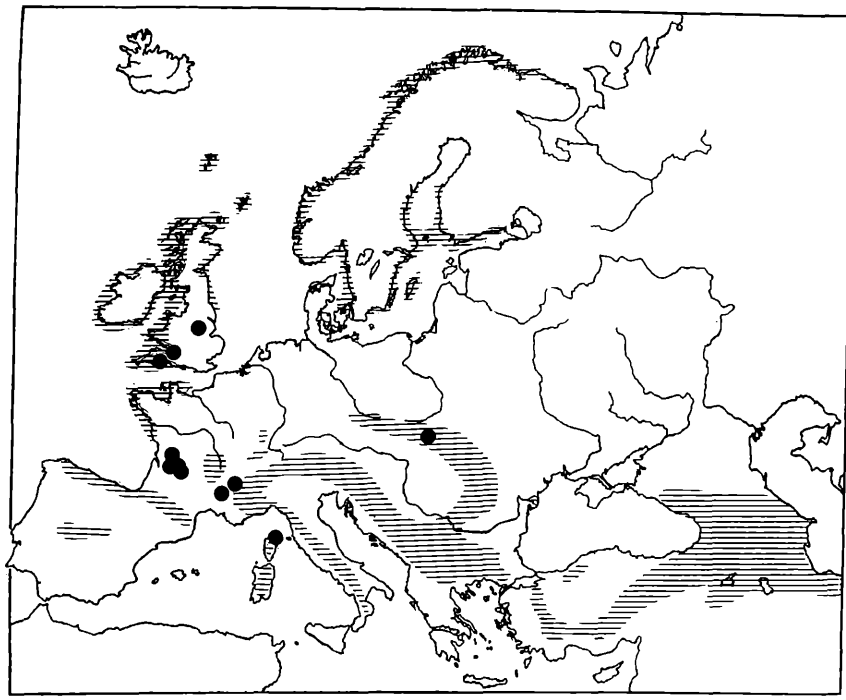

Figure 5:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Rock/Water Pipit. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) von Strand/Wasserpieper.*

6.3 Snow Finch

The Snow Finch *Montifringilla nivalis* occurs in a number of isolated montane populations from the Cantabrian Mountains to Tibet. The European populations belong to *Montifringilla nivalis nivalis* while the birds in Caucasus – Armenia belong to the subspecies *alpicola*. The Snow Finch is quite common in Würmian avifaunas of southern France and the Alpine countries (Fig. 7). The French sites link the extant populations in the Pyrenees and the Alps. During the late Glacial the species apparently ranged farther north in central Europe than today (the northernmost finds are from Oberfranken (Brunner 1939, 1959)). The scarcity of finds in eastern Europe – there is none between Austria and Crimea – is puzzling since there is a fair number of well-studied avifaunas from Hungary, Yugoslavia and Romania where the species might be expected to occur. The subspecific separation between the european populations and the Snow Finches in Caucasia – Armenia may however indicate a discontinuous distribution in southeastern Europe even under glacial conditions.

6.4 Choughs

Next to the Ptarmigan and the Willow Grouse the two *Pyrrhocorax* species are among the commonest and most characteristic birds in european Pleistocene avifaunas. Unfortunately the nomenclature of these two species is extremely confused in

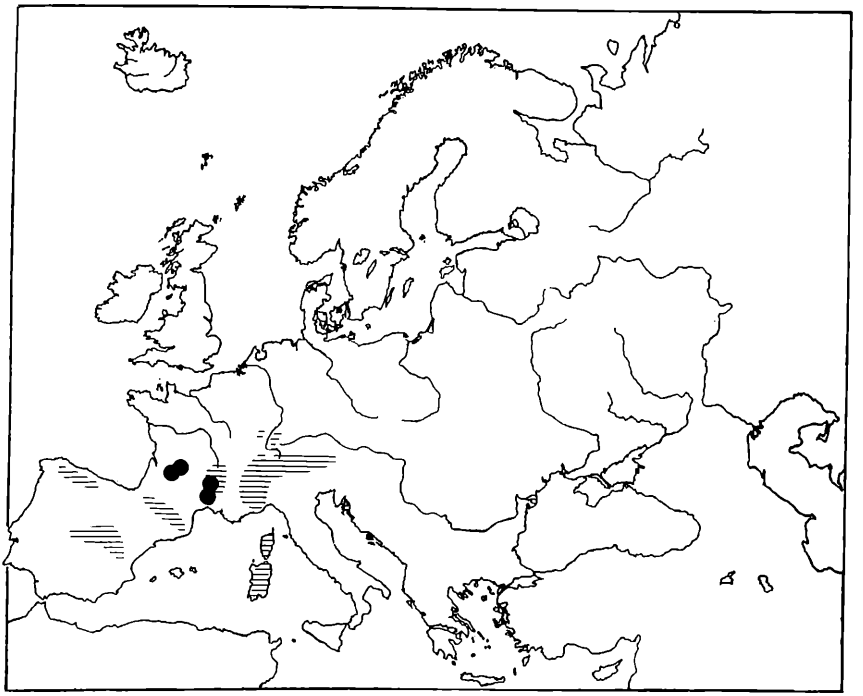

Figure 6:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Citril Finch. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) des Zitronengirlitz.*

the older literature and in some cases it is virtually impossible to decide which species the records refer to (for some details on the nomenclatural problems see JÁNOSSY 1954).

6.4.1 Red-billed Chough

Four subspecies of Red-billed Chough *Pyrrhocorax pyrrhocorax* occur in the west Palearctic, *pyrrhocorax* in Great Britain and Ireland, *erythrorhamphus* in western Europe, *barbarus* in Maghreb and *docilis* in eastern Europe and the Near East.

During the Würmian the Red-billed Chough occurred throughout southern Europe (Fig. 8). The northern limit of the distribution was apparently the foothills of Massif Central, the Alps and the Balkan mountains south of the Danube. The Würmian records link virtually all extant West Palearctic populations and the Red-billed Chough then also occurred in several areas where it is no longer found e. g. the Balearics, northern Yugoslavia and the Crimea. However in most areas the Red-billed Chough is rather less common as a fossil than the Alpine Chough and this is particularily true of the Balkans.

The three records from Great Britain (Fig. 8) are well separated from the other Würmian records. One record (Kirkdale Cave in Yorkshire [HARRISON 1980, LYDEKKER 1891]) may in fact be from the Eemian (Ipswichian) Interglacial and in that case the presence of this typically montane bird in the British Isles would be a very interesting parallel to the species' range during the present interglacial though the species does not occur in Yorkshire today.

The other two sites (Chudleigh and Paviland Cave [BELL 1915, 1922, HARRISON 1980]) are either of late Glacial or (more likely) Ho-

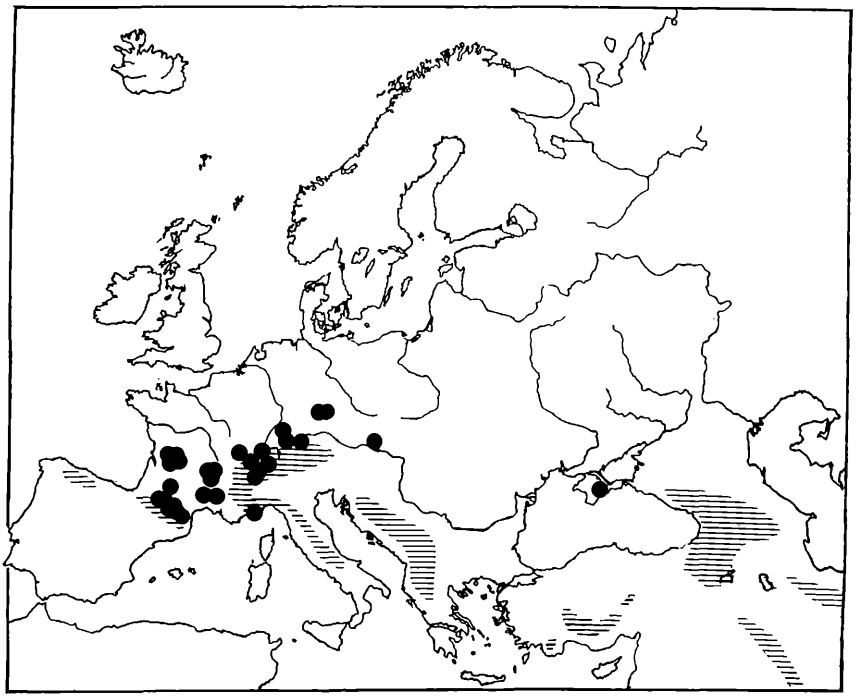

Figure 7:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Snow Finch. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) des Schneefinks.*

locene age. The Red-billed Chough presumably recolonized the British Isles during the Late Glacial by following the Atlantic coast north from Spain and southern France since it seems unlikely that the species could have survived the Glacial maximum in the British Isles. It was definitely present in Wales by the early Holocene when it is recorded from Port Eynon Point Cave (Harrison 1987).

6.4.2 Alpine Chough

All european populations of the Alpine Chough *Pyrrhocorax graculus* belong to the nominate subspecies. The Alpine Chough is even more common than the Red-billed Chough in Würmian avifaunas (Fig 9). However, in contrast to the latter species the Alpine Chough was also common in hilly areas in the Pannonian Basin and in the Carpathians. Also in contrast to *Pyrrhocorax pyrrhocorax* the Alpine Chough expanded northwards to the edge of the North European plain during the late Glacial (the northernmost sites are in Luxemburg, Thuringia and the Ojcow region of southern Poland (Bocheński 1974, Ferrant & Friant 1940, Musil 1980). The differences in the Würmian ranges of the two *Pyrrhocorax* species may be due to a greater tolerance for cold continental climates by the Alpine Chough.

6.5 Alpine Accentor

Three subspecies of The Alpine Accentor *Prunella collaris* occur in the West Palearctic. The nominate subspecies occurs in SW Europe and Maghreb, *subalpina* in SE Europe, Crete and W Anatolia and *montana* in Caucasus and Iran.

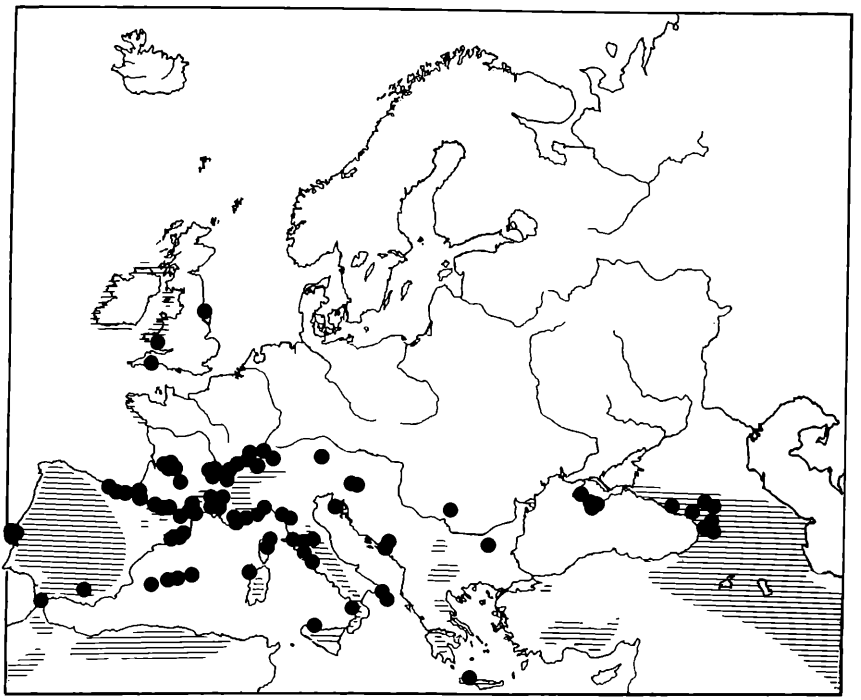

Figure 8:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Red-billed Chough. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) der Alpenkrähe.*

Most Würmian records are from SW Europe and link the populations in the Pyrenees, Massif Central and The Alps (Fig. 10). There is only two records from SE Europe, on Crete and Karpathos (WEESIE 1984, 1987). The find from Karpathos (where the species no longer occurs) suggests that the Alpine Accentor colonized Crete from Anatolia.

6.6 Other species

In addition to the species mentioned above some other species which lack a fossil record have similar distribution patterns: The Wallcreeper *Tichodroma muraria* and the Twite *Acanthis flavirostris* clearly belong to the species with "type 2" discontinuous montane ranges, though the Twite is unusual in lacking any montane populations between eastern Anatolia and the largely coastal subspecies in NW Europe and also in having a lowland subspecies on the Transcaspian steppes.

The Crimson-winged Finch *Rhodopechys sanguinea* is a somewhat anomalous case. It occurs in the mountains of Eastern Anatolia and reappears in the Atlas mountains. As pointed out by MOREAU (1966) it is unlikely that this strictly montane bird could ever have crossed the lowland deserts of Egypt and Libya and it must thus be presumed to have colonized the Atlas around the north side of the Mediterranean, though it has left no trace either in the form of fossils or relict populations. The Rock Pigeon *Columba livia* may also originally have been a "type 2" species, but in this case the original range has been blurred by the presence of feral populations.

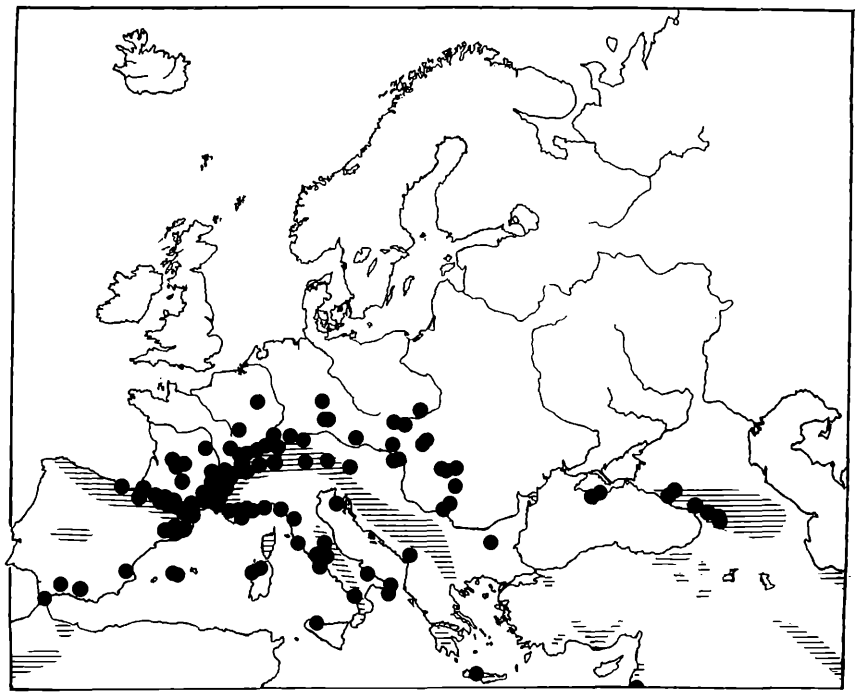

Figure 9:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Alpine Chough. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) der Alpendohle.*

7. Steppe Birds

7.1 Long-legged Buzzard

Two subspecies of the Long-legged Buzzard occur in the West Palearctic, *Buteo rufinus cirtensis* in Maghreb and Libya and the nominate subspecies from the Balkans eastward. The Long-legged Buzzard is not common as a Würmian fossil (Fig. 11). There are single records from Azerbaijan, Hungary and Luxemburg and a group of six sites in southwestern France.

This distribution of finds probably indicates that the Long-legged Buzzard occured on the mammoth steppe across Europe, perhaps with a concentration in SW France.

The concentration of sites in the plain of Aquitaine is parallelled in another steppe species, the Saiga antelope *Saiga tatarica* which is also found at scattered Würmian sites across Europe but was apparently quite common in southwestern France during part of the late Würmian (Delpech 1975, 1983).

7.2 Imperial Eagle

The spanish population of the Imperial Eagle forms a well defined subspecies *Aquila heliaca adalberti* which may qualify as a separate species while the birds in the rest of the species range from Eastern Europe to Lake Baikal belong to the nominate subspecies.

There are a few Würmian records of Imperial Eagle well west of its present range in

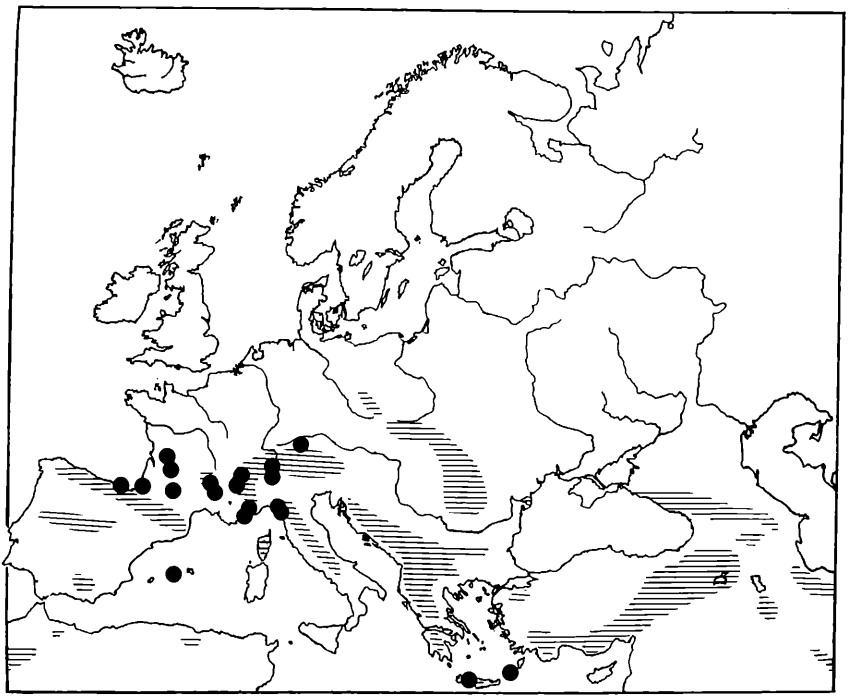

Figure 10:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Alpine Accentor. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) der Alpenbraunelle.*

the Balkans. The westernmost are Saccopastore near Rome (CASSOLI 1978) and Cotencher in Switzerland (JÁNOSSY 1980) (Fig. 12).

It is interesting to note that of the six Würmian records four (Saccopastore, Cotencher, Kálmán Lambrecht Cave in Hungary and Ripa in Romania) are of early Würmian age (>60 000 years BP), one (Grotta Romanelli in Apulia) is from the late Glacial (10 000–12 000 BP) while one (Teufelslukken in Austria) cannot be closely dated. Admittedly the evidence is slight, but it seems likely from these dates that the main Würmian expansion of the Imperial Eagles' range took place early during the glacial cycle. This fits in well with the considerable differentiation of the *adalberti* subspecies which argues that this population has been isolated for a long time.

7.3 Demoiselle Crane

The Demoiselle Crane *Anthropoides virgo* breeds mainly in the Eurasian steppe zone from the Ukraine to Manchuria. There is also a small population in Eastern Anatolia and another, very isolated and now almost extinct, in Maghreb. No subspecies have been recorded.

There are only four Würmian records of this species: Binagady near Baku, Karmalki on the Upper Volga, Pin Hole Cave in northern England and Gorham's Cave in Gibraltar (BURCHAK-ABRAMOVICH 1975, COWLES 1981, EASTHAM 1968). Unfortunately none of the finds are well dated, but the one from Pin Hole Cave may be of Mid-Würmian age (COWLES 1981) and that from Gibraltar is probably rather older (EASTHAM 1968, GAMBLE 1986). Despite the sparseness of the fossil record a wide Würmian range linking

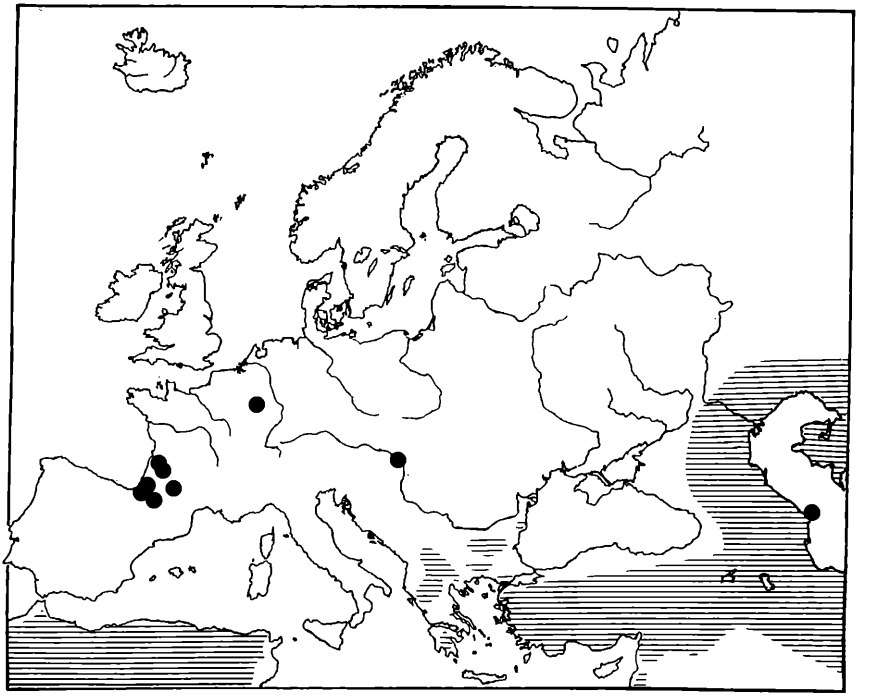

Figure 11:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Long-legged Buzzard. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) des Adlerbussards.*

the isolated population in Maghreb with the main range of the species on the Eurasian steppe seems likely.

7.4 Black-bellied Sandgrouse

The nominate subspecies *Pterocles o. orientalis* occurs in the Iberian Peninsula, Maghreb, Cyprus and Anatolia and is replaced by ssp. *arenarius* from Iran and the Caspian eastwards. There are four Würmian records of this species (Fig. 13). Of these the three finds from southern Italy are the most significant from a biogeographic viewpoint since they are approximately halfway between the extant populations in Anatolia and Tunisia. Of these three finds one, Torre a Nave in Calabria, is of early Würmian age while the other two, Grotta della Madonna near Torre a Nave and Grotta Romanelli in Apulia, are from the late Glacial.

7.5 Pin-Tailed Sandgrouse

The subspeciation pattern in this species is different from that in the Black-bellied Sandgrouse. The nominate *Pterocles a. alchata* occurs in southern France and the Iberian penninsula while ssp. *caudacutus* is found in Maghreb, Libya and south-west Asia.

There is only one Würmian record of this species, from the late Glacial of Grotta Romanelli in Apulia (Cassoli 1972).

The palaeoecology of the Grotta Romanelli avifauna form Dryas 3, the final "cold

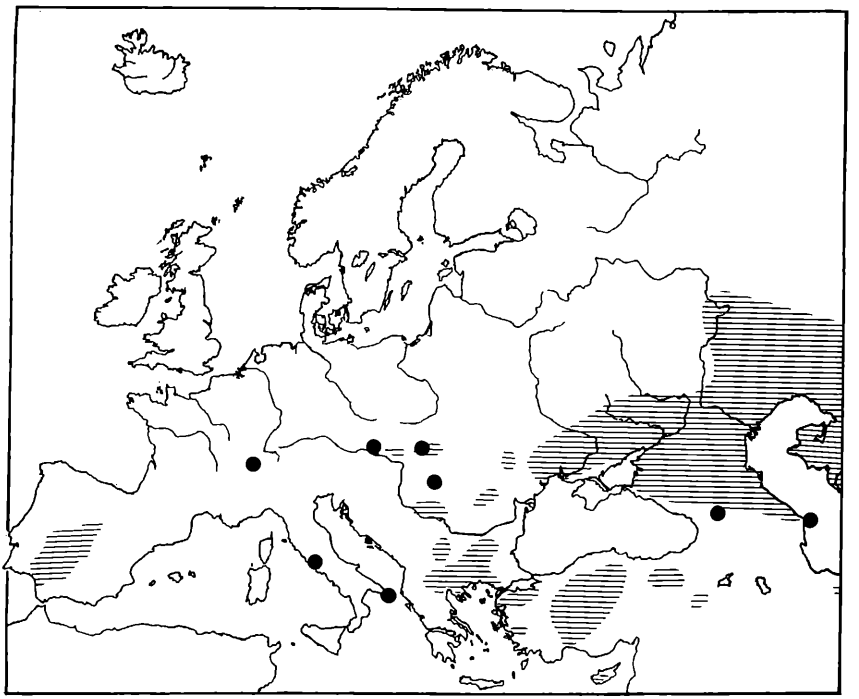

Figure 12:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Imperial Eagle. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise (Punkte) des Kaiseradlers.*

snap" of the Würmian has been studied by CASSOLI (CASSOLI et al. 1979). The sandgrouse apparently lived on the semi-desert littoral sandplains uncovered by the low glacial sea-level. The existance of this habitat may have been important in facilitating the spread of sandgrouse in the central Mediterranean area, both by narrowing water-gaps and by providing suitable habitat since both Black-bellied and Pin-tailed Sandgrouse generally avoid rocky and broken country.

8. Discussion

8.1 Dispersal

It is notable that most arctic or steppe species which had a glacial range extending over much of Europe have left no relict populations. Some such species are e. g. Gyrfalcon *Falco rusticolus,* Pallid Harrier *Circus macrourus,* Snowy Owl *Nyctea scandiaca* and Snow Bunting *Plectrophenax nivalis.*

On the other hand there are no fossil records of any montane species which occured in Europe during the Würmian and which has failed to survive to the present. The only possible exception would be *Melanocorypha maxima* which is only found on the Tibetan high plateau today, but has been reported from a site in Liguria by CASSOLI (1980), but the identification is uncertain. It would seem – not surprisingly – that the

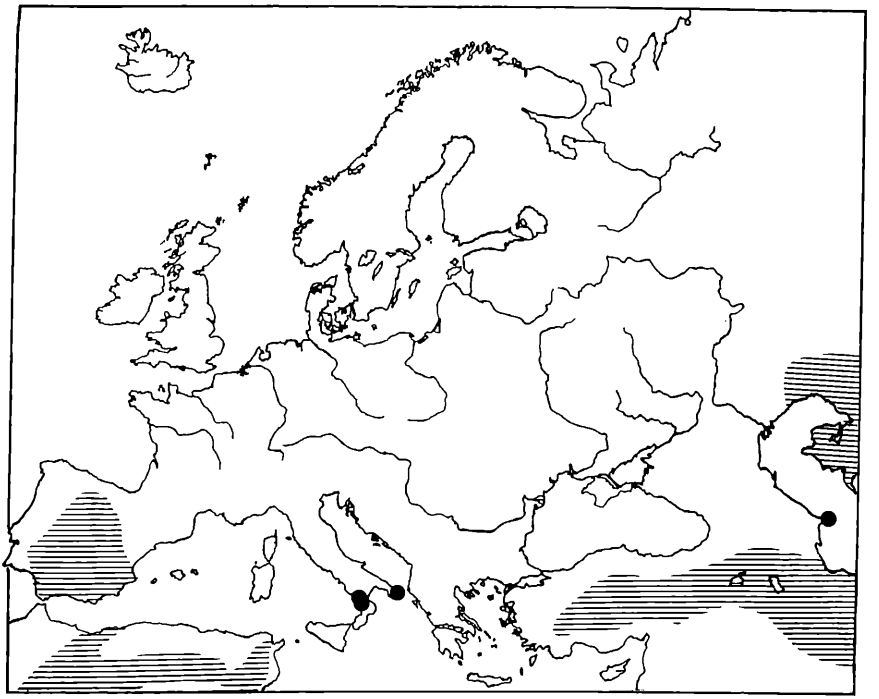

Figure 13:
Present breeding range (horizontal hatching) and Würmian records (black dots) of Black-bellied Sandgrouse. – *Gegenwärtiges Vorkommen (Schraffur) und würmeiszeitliche Nachweise des Sandflughuhns.*

montane species are better adapted to survive for long periods in isolated montane "islands" than the arctic or steppe birds.

The only real barrier to dispersal of the "type 2" montane birds between Himalaya and the Atlantic Ocean seems to have been between Asia Minor and Balkan. Several montane birds have ranges that extend from Central Asia to the mountains of Asia Minor or Caucasus (Snowcocks *Tetraogallus* sp., White-throated Robin *Irania gutturalis*, Güldenstedts Redstart *Phoenicurus erythrogaster*, Red-fronted Serin *Serinus pusillus*, Raddes Dunnock *Prunella ocularis* and Great Rosefinch *Carpodacus rubicilla*) while every montane bird species which occurs on both sides of the Aegean-Black Sea barrier has a range that extends all the way to the Atlantic.

The "type 3" birds could have colonized Maghreb and the Pyrenean Peninsula either by way of the glacial steppes north of the Mediterranean or along the North African littoral. The northern route would have been open during most of the Würmian while the hyperarid desert of Egypt and Libya would have been most easily traversed during periods of increased precipitation either during the mid Würmian interstadial complex or during the early Holocene climatic optimum.

A third alternative is a "diagonal" route from the Balkan to Tunisia by way of southern Italy-Sicily. Under glacial conditions dispersal by this route would have been facilitated by greatly narrowed water-gaps and the emergent areas would probably have been suitable habitat for steppe birds.

The virtual absence of Pleistocene avifaunas from North Africa makes it impossible

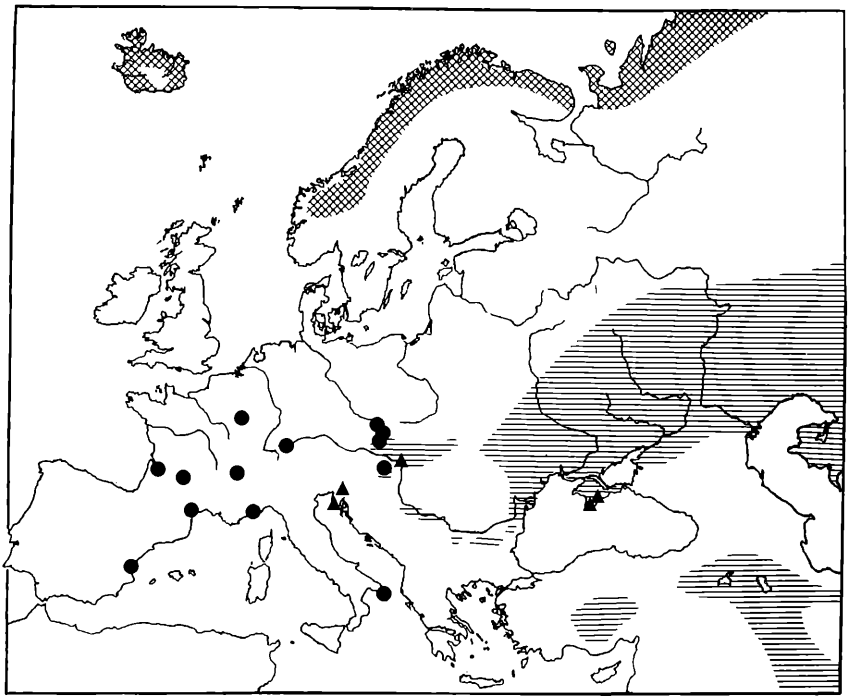

Figure 14:
Present breeding ranges and Würmian records of Gyrfalcon (cross-hatching/black dots) and Saker (horizontal hatching/triangles). – *Gegenwärtiges Vorkommen und würmeiszeitliche Nachweise von Gerfalke (Kreuzschraffur/Punkte) und Würgfalke (Horizontalschraffur/Dreiecke).*

to decide the issue one way or the other but at least in the cases of the Imperial Eagle and the Demoiselle Crane the northern route would seem to be more likely.

It is possible that several more species had "type 3" ranges during the early Holocene but that the distribution patterns have been blurred through adaption to the artificial "steppe" habitat created in Europe by agricultural activities from the Mid-Holocene onwards. This in particular applies to the White Stork *Ciconia ciconia*, Great Bustard *Otis tarda* and Little Bustard *Tetrax tetrax*. These three species were fairly common on the Glacial steppe and today have strongholds in the Eurasian steppe zone and in the Iberian peninsula, though they also occur more or less widely on farmland in central Europe.

8.2 Speciation

It would seem that the approximately 10 000 years since the Würmian have in general been insufficient for speciation to occur though *Anthus spinoletta/petrosus* is certainly a borderline case and some other subspecies e. g. *Lagopus lagopus scoticus* and *Serinus citrinella corsicana* may also be close to species status.

On the whole the diversity is low among arctic and steppe birds which argues that speciation due to interglacial isolation is not a common event in these groups. This is probably due to the relative shortness (10 000–20 000 years) and low frequency (about every 100 000 years) of interglacials.

There is however a few likely cases of such speciation in addition to *Eremophila alpe-*

stris/bilopha mentioned earlier. One is Ptarmigan/Willow Grouse. The Willow Grouse has occured in Europe since the beginning of the Pleistocene (JANOSSY 1974) while the Ptarmigan shows up only towards the end of the Middle Pleistocene (JANOSSY 1976, 1980, 1984, MOURER-CHAUVIRÉ 1975). It seems reasonable that the "new" species evolved from some isolated population, but there is of course no indication where this happened.

Another possible case ist the Gyrfalcon *Falco rusticolus* and the Saker *Falco cherrug*. A probable ancestor of these closely related species *Falco antiquus* is known from deposits of probably penultimate glacial age in France and Hungary (JANOSSY 1977, MOURER-CHAUVIRÉ 1975) while during the Würmian both the Gyrfalcon and the Saker occurred in Europe and apparently behaved as parapatric species (Fig. 14). This makes it likely the speciation occurred during the Eemian interglacial, probably with the ancestral Gyrfalcons in the Arctic and the ancestral Sakers in the Eurasian steppe zone and the two populations isolated from each other by the taiga belt.

Among montane birds there is a distinct center of diversity in the mountains of Central Asia with e. g. some ten species each of *Prunella, Montifringilla* and *Carpodacus*. Exactly why there has been so much speciation in this area is unclear, but the large and geographically complex mountain system and the frequently extreme aridity of the intermontane basins have probably facilitated isolation. The montane avifauna of the West Palearctic on the other hand seems to consist largely of "immigrant" species which have evolved in Central Asia. Only the Citril Finch seems likely to have evolved in Europe. Interestingly speciation has apparently been rather more common in the Middle East where two montane endemics with Palearctic affiliations occur; Syrian Serin *Serinus syriacus* and Arabian Accentor *Prunella fagani*.

An intriguing parallell to the Willow Grouse/Ptarmigan species pair is found among the montane birds in the two *Pyrrhocorax* species. In the *Pyrrhocorax* case it is *Pyrrhocorax graculus* which has occurred in the West Palearctic from the Early Pleistocene while *Pyrrhocorax pyrrhocorax* only shows up towards the end of the Middle Pleistocene. However in this case too, there is no clue where speciation took place.

Summary

Arctic, Montane and Steppe birds as Glacial relicts in the West Palearctic

A number of birds with predominantly arctic, alpine or steppe distributions have discontinuous ranges in the West Palearctic.

Fossil evidence shows that in several cases the modern range is relict and a remnant of a continuous range on the periglacial steppes of the latest (Würmian) glaciation.

Among arctic species this is definitely so in the cases of Ptarmigan and Willow Grouse (Fig. 1–2) and probable for Shore Lark and Dotterel (Fig. 3–4).

Among montane birds with more or less isolated populations in the mountains of Central and Southern Europe there is extensive fossil evidence for a continuous lowland distribution during the Würmian for Snow Finch, Red-billed Chough, Alpine Chough and Alpine Accentor (Fig. 7–10) and some data indicating the same for Rock/Water Pipit and Citril Finch (Fig. 5–6). A similar history is likely for a number of other species with similar ranges but with no fossil record, e. g. Wallcreeper, Twite and Crimson-winged Finch.

There is also a number of steppe birds with isolated populations in SW Europe and/or Maghreb i. e. Long-legged Buzzard, Imperial Eagle, Demoiselle Crane, Black-bellied Sandgrouse and Pintailed Sandgrouse. For these species there is also

some fossil data indicating a continuous Würmian range (Fig. 11–14) though the evidence is weaker than for most of the arctic or montane birds.

A similar pattern of range fragmentation and isolation has presumably occurred during previous interglacials. Despite this the diversity of the affected groups is low in the West Palearctic, indicating that such isolation has only exceptionally led to speciation. This is probably due to the relative shortness (10000–20000 years) and low frequency of interglacials.

There is however a few species-pairs in the West Palearctic where speciation due to interglacial isolation seems likely, i. e. Ptarmigan/Willow Grouse, Gyrfalcon/Saker, Shore Lark/Temminck's Horned Lark and Red-billed Chough/Alpine Chough, though in most of these cases speciation may have occurred outside the West Palearctic. There is also two borderline cases of "incipient speciation" among the taxa treated in this paper (*Auila heliaca/adalberti* and *Anthus spinoletta/petrosus*).

Zusammenfassung

Arktische, montane und Steppenvogelarten als Eiszeitrelikte in der Westpaläarktis

In der Westpaläarktis weist eine Anzahl Vogelarten mit vorwiegend arktischer, alpiner oder Steppenverbreitung unzusammenhängende Areale auf. Die Fossilfunde beweisen, daß in einer Reihe von Fällen das gegenwärtige Areal ein Reliktvorkommen darstellt, welches ursprünglich die Eisrandsteppen der letzten Vereisungsperiode (Würm-Eiszeit) umfaßte. Für Arten mit arktischem Verbreitungstyp trifft dies sicher bei Alpen- und Moorschneehuhn, wahrscheinlich auch bei Ohrenlerche und Mornell zu.

Für montane Arten gibt es umfassendes fossiles Belegmaterial für ein zusammenhängendes Tieflandsverbreitungsgebiet im Falle von Schneefink, Alpenkrähe und Alpendohle sowie für die Alpenbraunelle. Diese Arten haben gegenwärtig ein diskontinuierliches, montanes Areal in den Gebirgen von Mittel- und Südeuropa. Auch für Strand/Wasserpieper und für den Zitronengirlitz zeichnen sich derartige Verhältnisse ab. Für Arten ohne fossile Belege, wie Mauerläufer, Berghänfling und Rotflügelgimpel, dürfte dieselbe Erklärung zutreffen.

Auch für eine Reihe von Steppenvogelarten mit isolierten Populationen in Südwesteuropa und/oder im Maghreb, wie beispielsweise für den Adlerbussard, den Kaiseradler, den Jungfernkranich, das Sandflughuhn und das Spießflughuhn, belegen die Fossilfunde ein kontinuierliches würmeiszeitliches Verbreitungsgebiet, wenngleich die Evidenz schwächer als im Fall der montanen Vogelarten ist.

Ähnliche Muster zwischeneiszeitlicher Arealzersplitterungen verbunden mit Isolation der Populationen, dürften während der früheren Vereisungsperioden und Zwischeneiszeiten entstanden sein. Aber trotz der Unterschiedlichkeit der betroffenen Vogelgruppen ist die davon abzuleitende Artaufspaltung und Diversitätszunahme nur vergleichsweise geringfügig ausgefallen. Möglicherweise hängt das mit der kurzen Dauer der Zwischeneiszeiten von nur 10000–20000 Jahren und ihrer geringen Frequenz des Auftretens zusammen. Für einige Artenpaare, wie Alpen- und Moorschneehuhn, Ger- und Würgfalke, Ohren- und Hornlerche sowie für Alpenkrähe und Alpendohle, läßt sich die zwischeneiszeitliche Arealaufspaltung mit Arttrennung annehmen, obgleich in diesen Fällen auch Einflüsse von außerhalb der Westpaläarktis in Betracht zu ziehen sind. Die Zwillingsarten Kaiseradler und Spanischer Kaiseradler sowie Strand-(Fels-) und Wasserpieper befinden sich gerade im Prozeß der Arttrennung.

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