

## An East–West gradient in the breeding distribution and species richness of the European woodland avifauna

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**Abstract.** In spite of environmental uniformity of the European Plains, a conspicuous east-west gradient in the woodland avifauna and breeding bird community composition has been revealed. The species richness in the western woodland avifauna is lower by 32–36% than in the respective eastern samples ( $n = 120$ – $127$  species). Apart from being poorer in species, western communities tend to contain a higher proportion of species which develop dense populations. These features may result from past — mostly postglacial — natural events, from a secondary gradient in the intensity of human impact or from both of them. The data at hand provide evidence for a strong prevalence of the second factor. In view of the mostly anthropogenic character of the differences described, many west-European data can hardly be used as models of the natural patterns in studies of breeding bird ecology. New continent-wide comparative research is necessary to better control for anthropogenic bias in field data. For valid future pan-continental comparisons of bird communities a few large patches of near-pristine woodland should be preserved in the East, as well as restored in the West. Bird ecology studies need also a better co-operation with the archaeozoological and historical research to take into consideration past conditions which could also have influenced the present-day life patterns of European birds.

**Key words:** bird distribution, species richness, anthropogenic changes, E–W gradient

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### INTRODUCTION

The three main longitudinal biogeographical zones (mediterranean, nemoral and boreal) in Europe are internally fairly uniform. The east-west extension of the boreal and nemoral zones (“nemoral” — non-mediterranean, mainly lowland, part of the temperate zone) is not disrupted by any north-south running mountain barrier so typical of Americas. In spite of this, and apart from the well known south-north gradient in the nature and intensity of human post-glacial colonization, also a longitudinally oriented gradient in species richness seems to occur in the avifauna.

In this paper, which develops the line of reasoning briefly expressed earlier (Alerstam 1985, Blondel & Farré 1988, Tomiałojć & Wesolowski 1990, Fuller 1995, Angelstam et al. 1997, Mikusiński 1997), the focus will be on the E–W (precisely: NEE–SWW) gradient in the present-day patterns of forest bird richness and bird community composition across Europe. The presence of this gradient has never been documented and explained satisfactorily. Two kinds of questions will be addressed here:

- 1) Is the E–W gradient in the European bird species richness a real phenomenon?
- 2) What kind of factors were responsible for such a pattern: natural (and which) or anthropogenic ones,

or both of them in a combination? In what proportion did they contribute to producing the present-day pattern?

## METHODS AND RESULTS OF ANALYSIS

Before comparing the avifauna of the western and eastern part of Europe it should be made sure that it is methodologically justified. Considering the common history of bird fauna in the Western Palearctic (Blondel & Mourer-Chauviré 1998) this is indeed the case. Strong evidence for general uniformity of the European Lowland from England to the Ural Mts. can also be found in environmental measures: the topographically, edaphically and climatically comparable conditions extend along the E–W (precisely: NEE–SWW) axis almost unbroken (Stanners & Bourdeau 1995). Moreover, the comparable western and eastern climatic conditions — e.g. a uniform pattern in the summer temperatures and in climatic precipitation deficit (see maps in Jahn 1991 and Stanners & Bourdeau 1995), have produced a remarkable uniformity in plant species richness (Barthlott et al. 1996), in the identity or close-relatedness of forest-forming tree species (oaks, lime, hornbeam, pine, alder, elms, birches, beeches), as well as in the similarity of the main forest associations within the whole or large parts of each of the three European longitudinal subregional zones (Jahn 1991, Hansson 1992, Latham & Ricklefs 1993, Ellenberg 1996). It can be assumed that in broad ecological categories the East differs from the West much less than it was intuitively imagined, except for a difference in winter climate, which has, however, probably little or no influence on breeding of migratory birds.

### Measuring the gradient in bird species richness

For the first time a geographic pattern in the European breeding species richness was visualized by Mönkkönen (1994) in his insightful paper comparing bird diversity in the Western Palearctic (its western part only) and eastern Nearctic forests. His paper failed, however, to reveal a full degree of the east-west gradient in the European bird species richness because of some methodological weaknesses. They resulted from: a) restricting the analysis to the western part of

the continent (up to 35° E, instead of up to the foothills of Ural Mts., c. 58° E); b) restricting woodland avifauna to passerines, which are less sensitive to anthropogenic pressures than other birds, and c) calculating bird distribution from outdated maps in the field guide by Bruun et al. (1986), incorrect mainly for Central and Eastern Europe. Mönkkönen's (1994) data (from his map 1) on the number of woodland passerine species in each of the 200 × 200 km squares have here been recalculated into a graph (Fig. 1). A slight W–E increase in his species richness was real, while a decline in the areas east of central Poland was an artefact resulting from outdated information on eastern breeding ranges. To compensate for this shortcoming, I repeated Mönkkönen's calculation using most recent distribution accounts from Poland and Belarus and have included the result as a correction into Fig. 1.

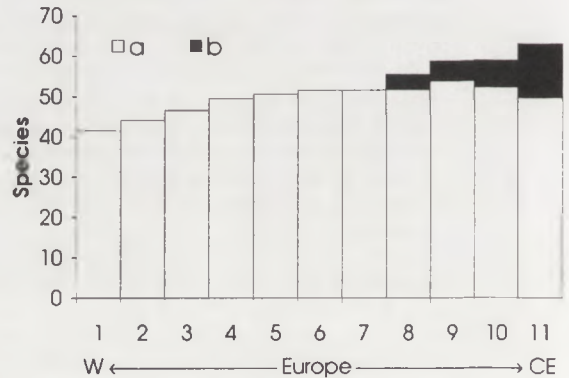


Fig. 1. The average number of woodland passerines breeding in 200 × 200 km squares across the western and central European Lowland (a — data by Mönkkönen 1994, b — corrected data from Belarus, Poland, part of Lithuania). Values are averages from (two) four squares forming a latitudinal belt: 1 — Wales, Devon, Somerset and Bretagne, 2 — England and N. France, 3 — E. Anglia, Belgium, NE France, 4 — Holland and Germany, etc... up to 10 — E. Poland and fringe of W. Belarus, 11 — W. Belarus and Lithuania.

To obtain a more rigorous analysis, my other calculations have been: a) restricted to the topographically and climatically uniform nemoral belt — the European Lowland — roughly between 45° N and 57° N, b) extended to cover all breeding land birds and only afterwards the woodland avifauna alone, c) cleared of variation introduced by two confusing factors: the presence of feral species, and then, the presence of non-woodland



birds, as strongly dependent on the local variation in the inland water-body distribution. The well-established feral species abound only in the West: c. 13 species versus only one — *Columba livia f. domestica* in the East (Hagemeijer & Blair 1997). Subtracting them gives a net measure for the remaining avifauna equivalent to the native species richness. The calculations made for Central Europe by Bezzel (1982), when he attempted to compare the number of species breeding within  $300 \times 300$  km squares ( $90\,000$  km<sup>2</sup>), have here been taken as a starting point. Having excluded feral species, I have extended the analysis geographically to incorporate the data for similar-sized squares covering central England, eastern Poland and Belarus (Fig. 2A). Within the Russian territory two regions relatively well studied during 20th century have been chosen: the Moscow Province and the Tatarstan Autonomous Republic. In the Moscow Province ( $48\,000$  km<sup>2</sup>, that is more than a half of the standard square) at least 197 species have been breeding during that century (Ptushenko & Inozemtsev 1968, updated after Ilyichev et al. 1987 and notes from "Ornitologiya" journal). This regional avifauna has probably been somewhat impoverished by the impact of the large urban agglomeration. For Tatarstan and the neighbouring territories, c.  $70\,000$  km<sup>2</sup>, at least 198 breeding plus 3 probably breeding species have been listed; this figure should probably be corrected upwards to compensate for a shorter period of intensive research (Askeyev & Askeyev 1999).

The next step was to compare only the woodland and woodland-edge avifauna, with birds of small woodland marshes and peatbogs included. Scrub species (e.g. *Sylvia communis*, *S. undata*) or open-land species only sporadically nesting in young tree-plantations (*Circus cyaneus*, *Asio flammeus*) have been dropped from this category. Seven samples of woodland avifauna well studied during the 20th century were at disposal here (Fig. 2B):

- English woodland within the standard size ( $90\,000$  km<sup>2</sup>) square (the numbers of breeding species after Gibbons et al. 1993 and Fuller 1995) — 81 species;
- east Germany woodland within a standard square embracing Mecklenburg, part of Brandenburg and a small part of the Polish territory (after Klafs & Stübs 1977, Rutschke 1983, Tomiałojć 1990), 103 species;
- two standard size squares for western and eastern (with the western half of the Białowieża Forest) Poland

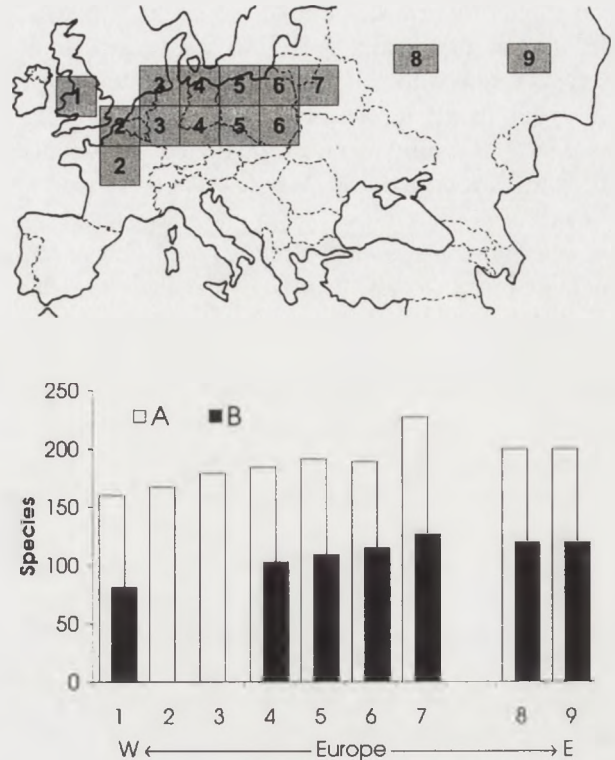


Fig. 2. An east-west gradient of the declining numbers of the European breeding bird species (after Bezzel 1982, extended geographically and recalculated). A — All land birds, but feral species. The geographic samples ( $90\,000$  km<sup>2</sup> each) come from: 1 — England, 2 — Belgium, N France, 3 — Holland, W Germany, 4 — E Germany, 5 — W Poland and the Czech Rep., 6 — E Poland, 7 — W Belarus, 8 — Moscow Province (smaller area), 9 — Tatarstan Rep., Russia (smaller area). B — Woodland and woodland-edge species alone, data from seven of the above listed samples.

(Tomiałojć 1990, 1995) — 109 and 115 species respectively;

— the western Belarus, a standard size square (Nikiforov et al. 1997) — 127 species;

— the central Russian region — the Moscow province ( $48\,000$  km<sup>2</sup>), at least 122 species;

— the Tatarstan Republic and neighbouring territories (c.  $70\,000$  km<sup>2</sup>) — c. 120 species.

#### Interpretation of the breeding ranges of woodland birds

Another methodological problem faced during pan-continental or intercontinental comparisons stems from the fact that such comparisons are usually based

on maps of exclusively recent distribution of the species, thus ignoring the human confusing impact. In this paper an attempt has been made to visualize some dynamics in the historical versus the present European distribution of some bird species (Fig. 3–6). Evidence that human factor might be the strongest force in shifting breeding ranges has been searched for in the ornithological and archaeozoological data, as well as in the knowledge of the past forms of forest management. Palaeo-ornithological studies have proved that the Pleistocene and early Holocene European avifauna differed considerably from the present one (Harrison 1982, Bocheński 1993, Mourer-Chauviré 1993, Blondel 1990, 1997, Blondel & Mourer-Chauviré 1998). For the purpose of this paper, however, a shorter time-span of the past few centuries is considered, during which the extant bird species have also been changing their distribution. This is best known for big birds, such as raptors, forest grouse species, storks or cranes. Below, a pristine — or a hypothetically pristine — distribution of four species and its subsequent transformation under anthropogenic stress have been briefly outlined.

**1. Capercaillie** *Tetrao urogallus*. Subfossil and early historical data confirm its pan-continental distribution between the Middle Ages and the 17th century (Glutz et al. 1973–93, Cramp & Simmons 1980, Bocheński 1993, Wyrost 1994). The Capercaillie may serve as an example of a species that has retreated from much of Europe (Fig. 3) undoubtedly under the pressure of anthropogenic factors: habitat loss, forest management and hunting. There is equally strong evidence (Glutz et al. 1973–93, Cramp & Simmons 1980, 1983, Cramp 1985–92, Blondel & Vigne 1993) that also other species once retreated from a part of Western Europe, either under the pressure of persecution or as a result of anthropogenically-induced habitat loss. These were the following among woodland and woodland-edge birds: *Ciconia nigra*, *C. ciconia*, *Grus grus*, *Tetrao tetrix*, *Bonasa bonasia*, *Haliaeetus albicilla*, *Aquila chrysaetos*, *A. pomarina*, *Circaetus gallicus*, *Milvus milvus*, *M. migrans*, *Pandion haliaetus*, *Falco peregrinus*, *Bubo bubo*, *Dryocopus martius*, *Corvus corax*. Some of them have later recovered or been just recently recovering from their low numbers.

**2. Lesser Grey Shrike** *Lanius minor*. The species occurring in open landscape and along woodland edges had apparently to colonize deforested parts of central

and western Europe during earlier centuries. Then, during the last hundred years it experienced a strong decline and marked range contraction. Data at hand indicate that once it was much more widespread (Fig. 4 drawn independently of a remarkably similar map by Kristin 1998) than it is shown in traditional handbooks. For Central and part of Western Europe this is a well documented fact while for the remaining part of Western Europe a working hypothesis to be checked by future archaeozoological research. The species withdrawal from the north-western part of its range is thought to have been triggered by man-caused habitat deterioration, including a decline in big insect fauna (Hagemeyer & Blair 1997). Again, it is partly documented, partly suspected, that some other species, like *Aquila adalberti*, *Aquila clanga*, *Hieraaetus pennatus*, *Falco vespertinus* (?), *Otus scops*, *Coracias garrulus*, *Upupa epops*, *Lanius excubitor*, *Luscinia svecica*, have also once retreated from the West because of several forms of human pressure, large scale drainage of marshy forest edges and/or deterioration of their food supplies among them.

**3. White-backed Woodpecker** *Dendrocopos leucotos*. Its distribution map (Fig. 5) addresses the following questions, which go even more ahead than Mikusiński's (1997) very true conclusion on a general decline in western populations of European woodpeckers: a) was this species once breeding across most of France, Low Countries and in the British Isles (which is again a hypothesis testable by archaeozoological research) and b) what was the cause of its retreat? Being the most dependent on decaying deciduous timber of all woodpeckers (Wesołowski & Tomiałojć 1986, Aulén 1988, Mikusiński 1997), this species has probably failed to survive the consequences of western-European woodland management, which from the mediaeval times until the mid-20th century was depriving those woods of decaying timber (Rackham 1980). Recent isolated breeding sites or ephemeral findings of this species, alongside some vague records from old German literature, all suggest that once it must have occurred not only in the Oder/Odra and Warta valleys but also along the German section of the Baltic coast (Klafs & Stübs 1979, Glutz & Bauer 1980, Rutschke 1983, Tomiałojć 1990). Some arguments suggest its possible former distribution across the European Lowland, down to the Pyrenees (where this species still occurs)



and Corsica (where it formerly occurred — J. Blondel, in lit.), including the once extensive ancient beech, oak-beech, oak-hornbeam and riparian western woodland. There seems to be no alternative limiting factor but forest management which could have prevented western distribution of this quite versatile species that in the East populates all deciduous and mixed deciduous-coniferous old woodland types, southern and boreal, in both the lowlands and in the mountains. Like most other woodpeckers, and first of all like the Three-toed Woodpecker *Picoides tridactylus* (Mikusiński 1997), the species has survived only in less managed mountain or eastern swampy forests. Judging from the newest policy, if some forest patches were left unmanaged and once intensively cultivated stands renaturalized, also this species would predictably recover even in the lowlands, like this is the case with the Black Woodpecker (Mikusiński 1997).

**4. Collared Flycatcher *Ficedula albicollis*.** The *Ficedula* flycatchers are another victim group of the past forms of forest management (Fuller 1995), or at least the Collared Flycatcher is. Its recent distribution (Fig. 6) and habitat requirements suggest that in the past the species occurrence in north-western and central Europe was much wider. This suggestion finds support in the 19th century records on its local breeding in Brandenburg, Mecklemburg and Pommern/Pomerania (Klafs & Stübs 1979, Rutschke 1983, Tomiałojć 1990), hints once doubted or long ignored in the recent literature. The species is a typical and numerous breeder in very old oak-hornbeam and ash-alder stands in the lowlands, as well as in various types of old beech and oak forests in the upland and mountain elevations (Glutz & Bauer 1993). In view of its being not very selective about forest association type, the absence of the Collared Flycatcher from the West is surprising. On the other hand, the species depends strongly on dense-canopied, shadowy old-growth treestands abundant with tree-holes, which are necessary for widely scattered but very dense "source" populations to be built. Contrarily, its small isolated relict or "satellite" populations, have no chance to persist even in otherwise suitable, but too small for a viable population, patches of a proper habitat. And thus, the reason for its absence from NW Europe lies in woodland management, which for centuries have kept those woods poor in natural holes (coppice) or with the main canopy too

open, as in the case of wood-pasture and coppice-with-standards techniques (cf. Rackham 1980, Fuller 1990, 1995, Peterken 1996). On the mainland, quite similarly, the mediaeval "Niederwald" or later "Mittelwald" management, which once prevailed across the German Lowland (Thomasius 1978, Ellenberg 1996), also caused that well into the 20th century in most of western Central Europe the deciduous woodland was too young for this species. Hard-timber trees, oaks, beeches and hornbeams, are known to develop natural cavities only at a very old age (Sandström 1992, Scherzinger 1996). For centuries such an age was only exceptionally and locally allowed to be reached under the wood pasture or shelterwood management regime (Ferry & Frochet 1970, 1990), yet those stands were probably too open for the species. Only since the middle 20th century some patches of dense high-forest, old enough to contain numerous cavities, have started to re-appear in the western- and central-European lowlands as nature reserves or national parks. Such isolated "islands" have apparently failed so far to be colonized by Collared Flycatchers originating from their distant eastern or mountain refuges. In addition to that the main autumn migratory route of the Collared Flycatcher is to the SSE (Cramp & Perrins 1993), thus the species never passes through the deserted NW region. Flycatchers were suspected to avoid the cool maritime climate of the British Isles, although the Collared Flycatcher's abundant breeding in the middle of the very cool Baltic Sea (on the Oland and Gotland islands) undermines such a supposition and points out to the British forest management as the main cause.

The White-backed Woodpecker and Collared Flycatcher, both populate the forests composed of the commonest and most widespread trees: beeches, hornbeam, oaks, birches and lindens. For at least three-four millennia these trees have been the main forest-forming species also in the West (Rackham 1980, Jahn 1991, Ellenberg 1996, Peterken 1996). Therefore, it would be risky to assume that these bird species, so well adapted to those tree stands, have always avoided their apparently ideal western habitats just for an unknown reason; there is a strong argument at hand that human impact has for centuries made west-European forests unsuitable for them.

The anthropogenic deterioration of woodland could also have caused the very probable, though barely



Fig. 3. The Capercaillie *Tetrao urogallus* — its older and recent distribution in Europe. XVII–XX centuries of regional extinction.



Fig. 4. The Lesser Grey Shrike *Lanius minor* — its past (+) and recent distribution, as well as a hypothetical suggestion on former occurrence in the West.



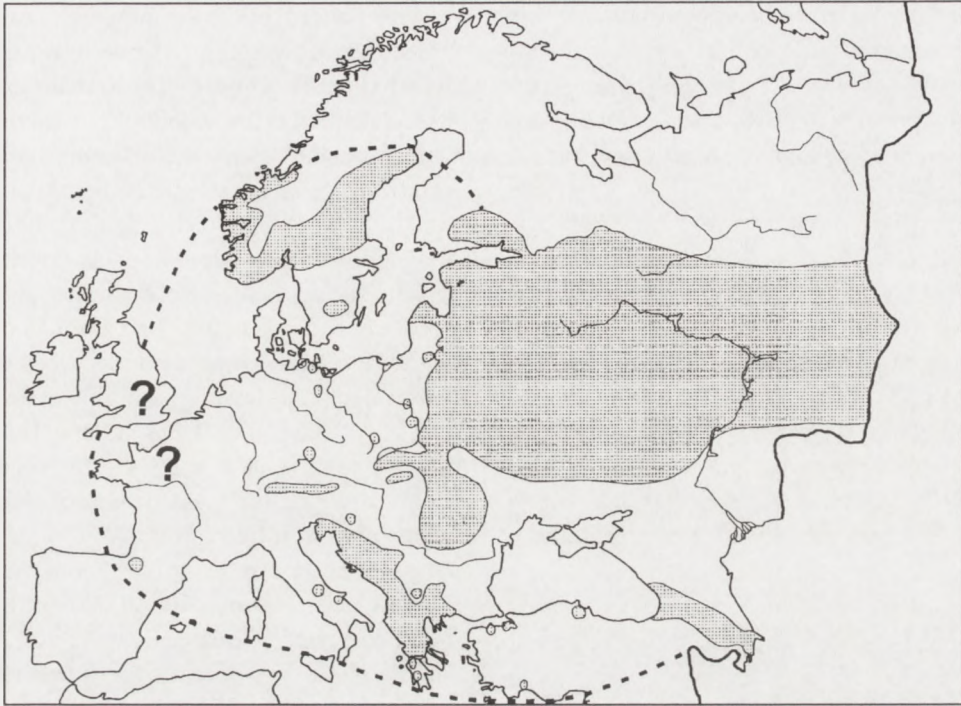


Fig.5. The White-backed Woodpecker *Dendrocopos leucotos* — the present-day and hypothetical past distribution.

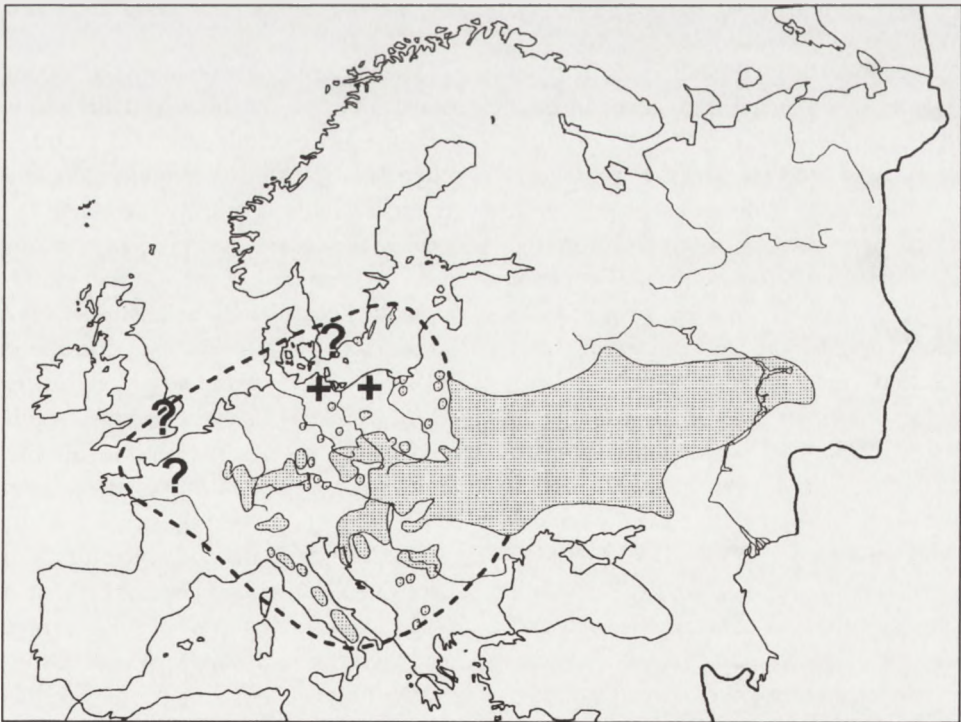


Fig. 6. The Collared Flycatcher *Ficedula albicollis* — the present-day and hypothetical past distribution.

documented, retreat from some regions of Western Europe of other old-growth or marshy-forest breeders. Such as: *Bucephala clangula*, *Mergus merganser*, *Tringa ochropus*, *Strix uralensis* (?), *Aegolius funereus*, *Picus canus* (withdrawal from the lowlands), *Dendrocopos medius*, *Picoides tridactylus* (retreat to mountains), *Dryocopus martius* (probable past retreat from the Atlantic fringe of Europe, including Low Countries and Great Britain), *Apus apus* (extinction of its western forest form), *Ficedula hypoleuca* (retreat from some strongly deforested regions). Some recent colonizations, having apparently resulted from secondarily increasing mature woodland coverage in some parts of western Europe, by the following species: *Pernis apivorus*, *Bubo bubo*, *Dryocopus martius*, *Ficedula hypoleuca*, *Regulus ignicapillus* (Hagemeijer & Blair 1997), may actually be re-colonizations.

#### BIRD SPECIES RICHNESS ALONG THE E-W AXIS

Most European lowland bird species have the trans-Palaearctic or the Holarctic distribution type because of virtually the same Pliocene-Pleistocene history throughout the continent (Voous 1961). Therefore, mostly the same species formed the bulk of western- and eastern-European avifaunas originally. A few pairs of closely-related species replacing each other in both parts of Europe (like *Picus viridis/canus*, *Corvus corone/cornix*, *Phylloscopus bonelli/sibilatrix*, *Regulus ignicapillus/regulus* etc.) failed to differentiate the overall species richness. This aspect has been omitted from the paper as it does not help with explaining the gradient pattern.

In spite of such, generally true, generalization, it has long been realised that in recent times the western avifaunas and bird communities of Europe have been tending to be less species-rich than the eastern ones. Geographical differences could be traced in maps showing the species richness of either the woodland passerine group (Mönkkönen 1994) or of all breeding land birds (Fig. 5 in Hagemeijer & Blair 1997). In both cases, however, the picture was obscure: the S-N and the E-W gradients were barely conspicuous. Instead, the maps documented a slightly lower species richness at the margins of the continent: along its Mediterranean, Atlantic (including British Isles) and North-Sea coastal regions.

The pattern becomes more noticeable when corrected data from central and eastern Europe are introduced (Fig. 1). They reveal a clear gradient: higher species numbers of woodland passerines in eastern than in western areas, the difference being statistically significant ( $r_s = 0.67$ ,  $p = 0.024$ , Spearman rank correlation) in the case of corrected eastern values while it was non-significant for Mönkkönen's (1994) original data ( $p = 0.56$ ). Independent comparison of recent data on distribution of all native land birds confirms that the overall breeding bird richness does increase eastwards (Fig. 2A), forming a highly statistically significant ( $r_s = 0.93$ ,  $p = 0.0003$ ) gradient. The highest number of breeding land species (218) occurs within the square covering the western half of Belarus, but high values may also be typical of the central and eastern parts of European Russia. In both regions, around Moscow and Kazan, almost 200 bird species were found to breed in this century, c. 120 of them being woodland or woodland-edge birds (Ptushenko & Inozemtsev 1968, Ilyichev et al. 1987, Askeyev & Askeyev 1999), though even these figures, very high as for Europe, may still be incomplete, being obscured by an impact of Moscow agglomeration and smaller sample size.

The next step in the analysis, a comparison of the species richness for the woodland and woodland-edge avifauna alone, offers a similar picture (Fig. 2B), with differences statistically significant ( $r_s = 0.67$ ,  $p = 0.21$ ). Again, the highest values of woodland species richness occur in the central and probably (incomplete samples) in the eastern part of the continent. Still more detailed approach was that by Mikusiński (1997) and Mikusiński & Angelstam (1997), who documented a decline in woodpecker species richness alongside E-W gradient.

All comparisons, have revealed a conspicuous E-W decrease of species richness in all the categories of European birds taken into analysis: land birds, woodland birds, woodland passerines, and the woodpecker guild. Considering woodland birds alone, the results surpass Fuller's (1995) conclusion that there are some 30 species occurring in woods of central Europe but not in Britain (nor in the western part of the mainland, e.g. northern France, Fig. 2A). Moreover, there is not a single species that is confined to British nemoral woodland. As one reaching farther to the East, my analysis shows that the west-European woodland avifauna



is actually poorer by 39–46 species (Fig. 2B), or by 32–36%, than that of the areas eastwards of Belarus (120–127 species assumed as a total).

#### WHY FEWER WOODLAND BIRD SPECIES IN WESTERN EUROPE?

Two groups of historical factors might be involved in producing the pattern:

1) natural factors (e.g. a biogeographical effect of a smaller size of western versus eastern part of Europe), already originally resulting in a more diverse eastern avifauna which either better managed to evolve and survive the glaciations or to adapt to a more diverse eastern woodland: coniferous + deciduous + mixed (Monkkönen 1994);

2) secondary (anthropogenic) factors, resulting in more frequent recent regional extinctions of woodland species in the West and South than in the East. Part of this process might have taken place centuries or millennia ago, with no written record available.

Even in pristine times westernmost Europe might have had fewer bird species, owing to palaeohistorical events and/or smaller and more uniform area of the western glacial refuge (a possible “peninsula effect” — cf. Taylor & Regal 1978) than the eastern one (Harrison 1982, Blondel & Mourer-Chauviré 1998, Monkkönen 1994). An indication of such a possibility can be seen in a slightly higher numbers of woodland-inhabiting small representatives of the following genera: *Falco* (4 western vs. 5 eastern species), *Acrocephalus* (1 vs. 3 sp., if including the *caligata* form) and *Phylloscopus* (3–4 vs. 5) warblers, *Ficedula* (1–2 vs. 3), *Parus* (6 vs. 7), *Emberiza* (4 vs. 4–6 ?). Such a regularity cannot be a result of the anthropogenic extirpation of those small passerines from the West because they, except for *Ficedula albicollis*, easily adapt to secondary conditions. So, even if some natural factor had contributed to western woodland avifauna impoverishment, it would have produced a reduction by no more than a dozen or so species, which is c. 10% less than in the East (Fig. 7).

Of recent natural climatic factors, only winter severity shows a distinct east-west gradient. The difference in climatic parameters — winter temperatures milder in the West than in the East and/or snow cover absent in the West while deep in the East — fails, how-

ever, to explain why bird species richness is higher in the East. A negative relationship could rather be expected because: 1) other severe climate zones (boreal or alpine) have fewer, not more, bird species; 2) most birds of the nemoral zone are summer visitors, which makes them hardly exposed to the winter climate of breeding grounds. If so, why, in spite of a uniform climatic and ecological background, does the European woodland avifauna differ geographically? Originally slight East-West differentiation in species richness must have later been strengthened by a secondary factor — human impact. Europe has experienced the pressure of one of the longest-lasting and most intensive human pressures, chiefly in the Mediterranean region (Goudie

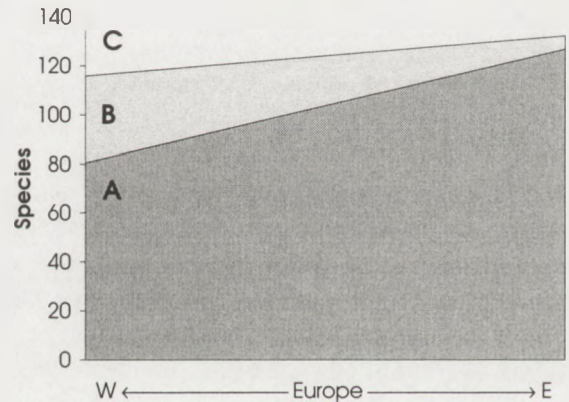


Fig. 7. Breeding species richness of European woodland birds alongside E–W gradient (a model). A — present-day species numbers, B — human-caused loss of species, C — near-pristine number of breeding species.

1986, Blondel 1990, Blondel & Aronson 1999). Deep transformation of European woodland was caused already by ancient civilizations (Thirgood 1981), owing to burning and felling, timber and forest litter collecting, grazing and browsing by domestic animals (Goudie 1986, Ralska-Jasiewiczowa 1991, Blondel & Vigne 1993). In the nemoral zone this impact, though also traced from the Neolithic, was more recent than in the Mediterranean region and more diversified geographically in timing and intensity (Thirgood 1981). It reached its culmination locally in the North-West during the 18th century (Jahn 1991), in central Europe in the 19th century (Ellenberg 1996), while in the East still more recently. This resulted in regional differences in ad-

vances of deforestation, woodland fragmentation, rejuvenation and in a large-scale replacement of deciduous tree stands with recently prevailing coniferous ones or vice versa (Jahn 1971). Though anthropogenic impact was once superimposed on the changes triggered by natural climatic fluctuations (Huntley 1993), yet during the last two millennia of warmer (Scandinavian and Neotropical) climate, and mostly during the last 900 years of its cooler Pacific phase, the European climatic conditions fluctuated less than before. Though anthropogenic factor became gradually the predominant changing force, two categories of factors — natural and anthropogenic — acted intermittently or in a cumulative way.

The presented earlier four detailed examples of past changes in bird species distribution, as well as the cases of other (c. 30) species, strongly suggest that the human impact must have reduced considerably the local or regional bird species richness in the west-European woodland while not so much in the East. A similar argument, though from a narrower perspective, was expressed by Wilson (1977), who suggested that the impoverishment of the Irish woodland avifauna resulted largely from anthropogenic deforestation and transformation of those woods, while only to a lesser degree from Ireland's insularity. Interpretation of this kind was applied to account for the distinctiveness of some British data when confronted with the Białowieża Forest results (Tomiałojć & Wesolowski 1990, Wesolowski & Tomiałojć 1995), with some detailed reservations based on climatic basis (unequal level of humidity) expressed by Fuller (1995).

The broad pattern in the age and intensity of human impact, even if irregular and patchy, appears to be negative to that in the bird species richness. To check this, the data on land bird species richness increasing eastwards (Fig. 2A) were compared with the human population density declining eastwards (or to NEE). The latter values have been calculated (as weighed averages) from the map by Stanners & Bourdeau (1995) for the same nine 300 × 300 km squares. Both factors appear strongly negatively correlated ( $r_s = -0.91$ ,  $p = 0.005$ , Spearman rank correlation). When replacing rural human density of c. 90 persons/km<sup>2</sup> in the Moscow Province alone with the averaged value of c. 270 pers./km<sup>2</sup> for the Province plus Moscow agglomeration, then still  $r_s = -0.79$ ,  $p = 0.01$ .

Most would agree that of the 39–46 bird species missing from western woodland the bulk have retreated under the pressure of humans. Though both factors, natural and anthropogenic, have undoubtedly been involved (Fig. 7), yet, the human impact was responsible for 2/3 to 3/4 of the regional extinction cases, which means that mainly "artificial" impoverishment of the western bird species richness prevailed (cf. Wilson 1977, Blondel & Farré 1988, Tomiałojć & Wesolowski 1990, Mikusiński 1997, Mikusiński & Angelstam 1997). The situation in a part of Europe appears, thus, similar to that one found in oceanic insular avifaunas, once also thought to remain in a natural state until white-men colonization (Olson & James 1984). Consequences of this finding may be quite serious: the west-European sophisticated analyses of bird distribution and species richness may deal largely with the secondary state of avifauna, which deviates considerably from the pristine state. Generalisations of western patterns to the continent-wide scale may thus be groundless.

#### BREEDING BIRD COMMUNITY COMPOSITION

Not only whole avifaunas, but also many west-European local woodland bird communities no longer contain their original set of species. Such groups like storks, crane, big raptors and owls, several species of wood grouse, woodpeckers, some flycatchers, etc., are secondarily lacking in the West. Therefore the present-day western communities should only cautiously be regarded as models of the natural ecological patterns, or results of evolutionary processes, silently assumed as little disturbed. The warning expressed by Lack (1965) and Elton (1966) as concerns the limited "naturalness" of British woods, later strengthened by Fuller (1995), Peterken (1996) and Perrins (1998), should be kept in mind when attempting analyses of the west-European bird communities and avifaunas. The more so that the notion of "naturalness" is relative: what seems natural for the British or Dutch conditions, like e.g. the Wytham Wood near Oxford once was for D. Lack (1965), it may still be far from natural state in the pan-European context. The differences seem to be especially deep between younger successional stages (more human disturbed) while the rarely preserved



avifauna of mature forest (less disturbed) is almost identical across most of the south-western and central Europe (Blondel & Farré 1988).

Detailed comparisons of the bird community composition from the Białowieża Forest or southern Sweden, assumed to represent a near-pristine state, with the British woodland bird assemblages (Tomiałojć et al. 1984, Alerstam 1985, Tomiałojć & Wesolowski 1990, Fuller 1995), have documented that western communities are not only less species-rich, being poorer in big and shy forms, but also composed in higher proportion of the species which have developed (secondarily?) dense or very dense breeding populations. Prolonged absence of some core species may have serious consequences for the rest of community. If some important community members were regionally absent for many bird generations, then this partial release from competitors or predators might influence the abundance of the remaining species (e.g. Perrins 1998). The latter apparently include birds such as the Blackcap *Sylvia atricapilla*, Robin *Erithacus rubecula*, Blackbird *Turdus merula*, Song Thrush *T. philomelos*, Mistle Thrush *T. viscivorus*, Dunnock *Prunella modularis*, Wren *Troglodytes troglodytes* or Woodpigeon *Columba palumbus*. In western Europe, mainly in the British Isles, part of northern France and in Low Countries, these species hold remarkably dense populations, often incomparable with the eastern ones (Simms 1971, Tomiałojć 1980, Wesolowski 1983, Cramp 1988, 1992, Cramp & Perrins 1993, Tomiałojć et al. 1984, Tomiałojć & Wesolowski 1990, Fuller 1995).

The community composition pattern of the type: less breeding species but higher abundance of the remaining ones is widespread among the plant and animal assemblages which have undergone the process of synanthropisation (Sukopp 1969, Tomiałojć & Profus 1977, Tischler 1980, Bezzel 1982, Kornaś 1983). Such pattern may be consistent, however, also with alternative assumption about the natural character of differences. Theoretically, the latter might result either from:

- British insularity, although the bird communities from the western mainland woods seem to be similar to the British ones (this should be proved beyond doubt in France, Belgium or the Netherlands),
- milder oceanic climate of the West, allowing for resident life which in turn may allow to built-up high densities, or

— from different forest structure shaped under (natural) conditions of a more humid climate and devoid of snowy winters, but equally well it may result from human-caused absence of big herbivores.

Woodland structural modifications harmful to hole-nesters, may by themselves be directly beneficial to crown-, bush- or lower-canopy-dwellers (Fuller 1995). This alternative should be analysed in detail and tested by field experiments. Also in this case it would be important to find out to what extent the present structure of western bird communities is a near-pristine feature resulting from oceanic climate or from its consequences for the composition and structure of local vegetation, and to what degree it is a secondary feature due to either making use of favourable man-made changes in the structure and character of the breeding or wintering habitat, or via filling empty ecological niches after human removal of important predators and competitors. More evidence, collected across the continent, is needed on these points.

#### THE FUTURE PAN-CONTINENTAL RESEARCH

The adjective "natural", so abused with reference to woodland avifauna, may be misleading, as the major part of European nature is no longer pristine. Though in theory everybody acknowledges this danger, yet, in the everyday research activity most students tend to ignore anthropogenic disturbance. The ecological patterns described on the example of the west-European bird communities are too often considered to represent the whole European continent, or assumed to be natural (near-pristine). In fact, many results reflect only the situation typical of deeply transformed Atlantic region, with its secondary state of avifauna. Contrarily, little is known about the pristine or near-pristine state of the European woodland avifauna, its remnants preserved in the remote East, South-East or North. Ancient forests, as situated far from academic centres, are too rarely chosen for studies, only occasionally offer a reference point for research conducted in secondary habitats. Even in the East and North such near-pristine sites are far from academic centres, which makes intensive field work hardly possible. The results from the West strongly exceed qualitatively and quantitatively the amount of

data from the East. Consequently, intercontinental studies (North America vs. Europe), though methodologically valuable (Monkkonen 1994, Martin & Clobert 1996), suffer from overlooking the fact that the knowledge of even the mere bird distribution is in different parts of Europe hardly comparable directly. The geographical lack of balance between the amount and quality of data available causes a widespread bias in the knowledge of the European bird ecology. It causes that conclusions of some wide syntheses cannot be true unless as Europe one will unjustifiably understand its atypical westernmost fringe.

From this evaluation a recommendation for future studies can be derived. Only pan-continental studies would help to replace the western-biased knowledge with a balanced all-European synthesis (cf. Angelstam et al. 1997). A hypothesis on the anthropogenic impact, on its timing, intensity and extent, as the crucial factor for the European bird communities and species life histories, should be taken as a starting point for pan-continental studies of forest bird ecology. Comparable sets of data should be collected from a spectrum of habitats, but later carefully allocated into at least three main degrees of habitat transformation: near-pristine extensive forests — fragmented secondary woods — human-shaped rural and urban green areas.

Very urgent is an internationally supported research concentrated on the attempts to define the factors still acting in last remnants of the ancient European forests, because:

1) Identification of what is *primaeval* and what *secondary* in bird life becomes a priority; with the progress of time the difference between these two states will be less and less clear.

2) Contrarily, the *secondary* (*synanthropic*) set of conditions will be spreading and strengthening, hence studying it just now is *less urgent*, even if undoubtedly useful.

#### PRESERVATION/RESTORATION OF LITTLE-DISTURBED WOODLAND SITES

For pan-European studies of woodland ecology regional co-occurrence of both types of conditions, the near-pristine and the *secondary* (*synanthropic*) ones, in

all the main biogeographical subdivisions of the continent is fundamental. While there are equivalent urban zones in the West and in the East, there are no patches of a near-pristine woodland in the West comparable to the eastern ones. Preservation of a few big (c. 500 km<sup>2</sup>) forest complexes, located on fertile lowland soils, sufficiently protected to serve as “zero models” for research and nature-mimicking forest management (Nilsson 1992, Scherzinger 1996), is of critical importance for further advances in European woodland ecology. In western and south-western Europe, where no undisturbed woodland is left, some programmes of “ancient woodland” restoration should be launched. After a few human generations such patches would become important research laboratories. The Dutch endeavours to restore the Hoge Veluwe national forest (on poor and much polluted soils, unfortunately) or the efforts to create some municipal forests in England demonstrate that woodland restoration/renaturalization is a realistic task. The “ancient woodland” models should be restored/renaturalized at least in — after Jahn’s (1991) terminology: — the Atlantic type of broad-leaved deciduous lowland forest,

— the Mediterranean (west, middle and east) lowland forests,

— the European (west-central) lowland forest

— the Boreoatlantic (Scottish) Caledonian pine forest.

The ever growing impact, on the European woodland, of human activity and of the resultant climate change urges for far-sighted, generous and quick nature conservation decisions.

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## STRESZCZENIE

**[Gradient wschód-zachód w rozmieszczeniu i różnorodności gatunkowej leśnych ptaków Europy]**

W obrębie Niżu Europejskiego, mimo znacznej jednorodności warunków edaficznych, klimatycznych, botanicznych i leśnych, uwidacznia się wyraźny gradient wschód–zachód w składzie awifauny. W kierunku zachodnim maleje bogactwo gatunkowe ptaków (Fig. 1 i 2), w tym zwłaszcza leśnych, a wzrasta liczba gatunków o wysokiej gęstości populacji. Zróznicowanie to może być wynikiem działania czynników naturalnych, wpływu człowieka, albo też oddziaływań obu kategorii czynników równocześnie. Na dokładniej przeanalizowanych przykładach czterech gatunków (głuszca, dzierzby czarnoczelnej, dzięcioła białogrzbiatego i muchołówki białoszyjej, Fig. 3–6) wykazano, że wiedza o dawnym i obecnym rozmieszczeniu poszczególnych gatunków zawiera wskazówki sugerujące zaistnienie w przeszłości poważnych zmian w ich zasięgach lęgowych. Całkowite wycofanie się pewnych gatunków lub silne zredukowanie zasięgu lęgowego w zachodniej części kontynentu innych zwykle miało antropogeniczną przyczynę. Zubożona awifauna lęgowa lasów (z gatunkami obrzeży lasów i leśnych błot) zachodu Europy, nie tylko Wysp Brytyjskich, lecz także północnej Francji, z Belgią i Holandią, liczy dziś zaledwie ok. 81 gatunków, wobec 127 gniazdujących w zachodniej Białorusi, i co najmniej 120 gatunków w regionie moskiewskim oraz wokół Kazania w Tatarstanie. Spośród brakujących lub prawie nieobecnych dziś na Zachodzie 39–46 gatunków tylko ok. 12–14 zapewne nigdy tam nie występowało w czasach polodowco-



wych, i to z przyczyn najprawdopodobniej naturalnych. Są to głównie drobne gatunki ptaków wróblowych, znanych ze swej plastyczności w wybiórczości siedliskowej. Dla pozostałych istnieją dowody lub pośrednie poszlaki sugerujące, że formy reprezentujące głównie ptaki większe i bardziej płochliwe, jak bociany, żurawie, ptaki drapieżne i duże sowy, kuraki leśne, dzięcioły oraz muchołówki, niegdyś na Zachodzie także były znacznie szerzej rozprzestrzenione. Wycofały się stamtąd pod wpływem człowieka: wskutek wytopienia, bądź wskutek antropogenicznych zmian w rozmieszczeniu i w charakterze ich biotopów lęgowych. Zmiany te w znacznym stopniu mogły zajść jeszcze zanim rozpoczęto najwcześniejsze badania ornitologiczne. Fauna leśnych ptaków Zachodniej Europy jest więc daleko silniej zubożona przez oddziaływanie człowieka (Fig. 7), niż to dotąd sobie wyobrażaliśmy. Dlatego opisywane na przykładzie zachodnioeuropejskich zespołów ptaków prawidłowości ekologiczne

mogą się okazać mocno zniekształconymi zjawiskami wtórnymi, a skład ilościowy tych zbiorowisk może mieć proporcje liczbowe poważnie odbiegające od stanu naturalnego.

Dzisiejsze warunki polityczne po raz pierwszy stwarzają możliwość realizowania ogólnoeuropejskich programów badawczych, które mogłyby sprawdzić słuszność powyższych wniosków. Badania te powinny być skoncentrowane zwłaszcza na opisywaniu zanikających pierwotnych leśnych ekosystemów i ich słabo jeszcze zmienionych zespołów i populacji ptasich na wschodzie Europy. Dokładniejsze trans-kontynentalne porównania składu i struktury odległych geograficznie zespołów i populacji ptasich wymagać będą odtworzenia kilku wielkich fragmentów dawnych lasów Zachodniej Europy, doprowadzenia ich, jako przyszłych terenowych laboratoriów dla badań ekologicznych, do stanu bliskiego pierwotnemu i porównywalnemu z niektórymi lasami wschodnimi.

XXIII INTERNATIONAL ORNITHOLOGICAL CONGRESS  
BEIJING, CHINA, AUGUST 2002

The XXIII International Ornithological Congress will be held in Beijing, China on 11-17 August 2002. The following officers were selected:

Honorary President: Prof. Ernst Sutter (Switzerland),

President: Prof. Walter Bock (USA) [Department of Biological Sciences, Columbia University, 1200 Amsterdam Avenue, Mail Box 5521, New York, NY 10027, phone: 1-212-854-4487, fax (o): 1-212-865-8246, (h): 1-212-568-7026, e-mail: wb4@columbia.edu].

The Scientific Program Committee for the XXIII International Ornithological Congress has been appointed under the chairmanship of Dr Fernando Spina [Istituto Nazionale per la Fauna Selvatica, Via Ca' Fornacetta 9, I-40064 Ozzano Emilia (BO), Italy, phone: +39-051-65-12-111, fax: +39-051-79-66-28, e-mail: infsioc@iperbole.bologna.it].

General information on the Congress can be obtained via e-mail: [infocenter@ioc.org.cn](mailto:infocenter@ioc.org.cn), or via the internet at <http://www.ioc.org.cn>. Information about the IOC can also be obtained from new home page at <http://www.nmnh.si.edu/BIRDNET/IOC/>

All inquiries about the scientific program of the XXIII Congress, as well as comments and suggestions for the general program, plenary lectures and symposia should be sent to Dr Fernando Spina.

Symposia contributions at the Congress are intended for the general ornithologist rather than the specialist and should offer updated review papers on recent developments in a research field. Contributed papers provide a means for individual ornithologist to present their most recent findings and ideas to the Congress. Round table discussions are workshops, discussion groups, etc. designed for exchange of ideas among specialists in a field. Round table discussions should not be used to present a longer lecture by the organizer of the discussion group or a series of symposium-type papers.

The Scientific Program Committee is especially interested to solicit high standard proposals concerned with the contribution of ornithology to biological conservation and wildlife management. All proposals should reach the Chair of the committee within the end of April 2000 at latest.