

The effect of scale-dependent habitat gradients on the structure of bird assemblages in the Czech Republic

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Reif J., Storch D., Šímová I. 2008. The effect of scale-dependent habitat gradients on the structure of bird assemblages in the Czech Republic. *Acta Ornithol.* 43: 197–206. DOI 10.3161/000164508X395315

Abstract. Spatial patterns in bird community structure are closely related to changes in habitat composition at small spatial scales, but the explanatory power of habitat declines towards larger scales, where dispersal limitations and historical factors becoming more important. To disentangle these effects, we performed a large-scale bird census using a small-scale field approach in the Czech Republic. Using canonical correspondence analysis, we found that the strongest scale-independent gradient in bird community composition goes from higher-altitude forest assemblages to lower-altitude farmland and human settlement assemblages. The other gradients were also scale-dependent, probably due to the different distributional patterns of particular habitats at the respective scales. Closer examination of bird occurrence in particular habitats revealed that water bodies host the most distinct bird assemblage compared to the assemblages of other habitats. Interestingly, although the census tracked the most important east-west biogeographical gradient within the Czech bird fauna, we did not find longitude to be a significant predictor of changes in bird community structure along the transect at any resolution. We suggest that the biogeographical gradient is actually related to the habitat-based distinction between the coniferous-forested higher-altitude West and the deciduous-forested lower-altitude agricultural East. Fine-scale bird-habitat associations are thus responsible for the patterns of community structure at all spatial scales.

Key words: bird community, spatial structure, habitat gradients, biogeographical gradients, scaling, habitat requirements, multivariate statistics

Received — Oct. 2007, accepted — Sept. 2008

INTRODUCTION

Spatial patterns in bird community structure emerge as a result of interspecific variability in spatial distribution of individuals (Wiens 1989). Within small scales, spatial changes in habitat composition account for the largest part of such a variability (James & Warmer 1982, Sanders & Edge 1998, Laiolo et al. 2004, Lee & Rottenberry 2005, Matlock & Edwards 2006). Habitat composition affects structure of communities through the differential adaptations of species to particular habitats (Wiens 1989). When moving towards larger scales, distribution of individual species seems to be less affected by habitat (Tomiałojć 2000, Rodewald & Yahner 2001, MacFaden & Capen

2002, Johnson et al. 2007). In that case, dispersal limitations underlie the effects of historical factors or physical barriers on distribution (Holt & Keitt 2000) and abundance of species irrespective to changes in small scale habitat composition (Robinson et al. 2000). The failure of habitat composition in explaining large scale patterns in bird community structure has been attributed to the greater influence of factors which are more closely connected to geography and history than to habitat (Jokimäki & Huhta 1996, Storch et al. 2003).

However, the decline in the explanatory power of habitat composition at larger spatial scale can partly be an artefact. Inaccurate description of habitat composition at large scales can mask fine scale habitat changes which can drive some pat-

terns in bird community structure regardless of the role of the rough habitat variables entering the analyses (Böhning-Gaese et al. 1994, Miller et al. 2004, Titeux et al. 2004). Therefore, to reveal the role of these fine habitat changes in large-scale community patterns, it is necessary to map fine scale habitat composition over a large area with the accuracy used in small scale studies, which is apparently difficult (McGarigal & McComb 1995, Heikkinen et al. 2004). Moreover, results of spatial analysis are inevitably affected by the size of spatial units used in data (Šizling & Storch 2004). We could expect that large grain size will probably accentuate the effect of geography, as fine-scale habitat variability is averaged out, whereas analysis based on smaller grain will be more sensitive to fine scale habitat variation. Therefore, it is crucial to perform the analyses simultaneously for various grain sizes. To our knowledge, such an approach has never been adopted in any attempt to describe major gradients in the structure of bird communities.

There is a large number of studies focusing on the description of species habitat requirements within central European local bird communities (e.g. Štátný & Bejček 1985, Storch 1998, Kujawa & Tryjanowski 2000, Laiolo 2002, Kocian et al. 2003, Wesołowski et al. 2006). However, there are only two comprehensive studies whose findings imply general conclusions about major trends in bird-habitat associations in this region. First, Storch & Kotecký (1999) performed an analysis based on results of 133 small-scale studies comprising species abundances within local bird communities in the Czech Republic. They found that communities of reedbeds were most different from the communities of all other habitats. Moreover, communities of different forest types did not differ from each other substantially but they were markedly separated from communities of open habitats. Second, Storch et al. (2003) analysed maps of species distributions in the Atlas of Breeding Bird Distribution in the Czech Republic (Štátný et al. 1996). They found that the most important factors structuring bird communities at this scale were not strictly bond to habitat cover. Instead, climate, altitude and the west-east gradient were the most important variables in the multivariate analysis. The authors attributed this finding to the position of the Czech Republic at the biogeographical boundary between hercynian and pannonian domains, representing the transition from Atlantic to continental Europe (Culek et al. 1996), and to the history of bird populations

spreading from respective domains (Taberlet et al. 1998).

Here we focus on the effects of fine-scale habitat variation and differences in spatial grain sizes on large-scale patterns in the structure of bird assemblages in the Czech Republic. We used a hybrid approach combining methods from both small scale and large scale ecology. We performed a bird census at the 400 km long transect intersecting the whole territory of the Czech Republic from the west to the east. We used the same census method as the majority of the local studies and constrained the number of observers to two persons to avoid the observer effect. Moreover, we performed precise habitat mapping along the whole transect. Using these data, 1) we describe the most important gradients in the bird community structure at two different scales of spatial resolution with particular emphasis on the scale-dependency of performance of particular environmental variables; 2) we test whether findings of Storch & Kotecký (1999) and Storch et al. (2003) hold true if more accurate methods of bird sampling and habitat mapping are used and we explain differences between theirs and our results.

STUDY AREA AND METHODS

We used data from a 400 km long linear transect of 768 census points going across the southern part of the Czech Republic, from the Šumava Mountains in the west to the Bílé Karpaty Mountains in the east (Fig. 1). The transect followed minor roads accessible by bicycle. It was as straight as possible to sample representatively all components of the Czech landscape, avoiding centres of large cities where the bird counts would be biased due to traffic noise. Census points were located regularly along the transect and separated by the distance ca. 500 m. All birds were counted by J.R. and D.S. using the point count method (Bibby et al. 2000) within the distance limited by 150 m around each point. Birds were counted during five early morning visits in the breeding season (April–June), with five minutes-long count at a census point in one visit. The total time of bird counts at a census point in a breeding season was thus longer than suggest Sorace et al. (2000) for good description of its bird community. One person visited about 30 points during one morning count. Only maximum recorded numbers of individuals of every species from the five visits were then taken for every point to improve accuracy

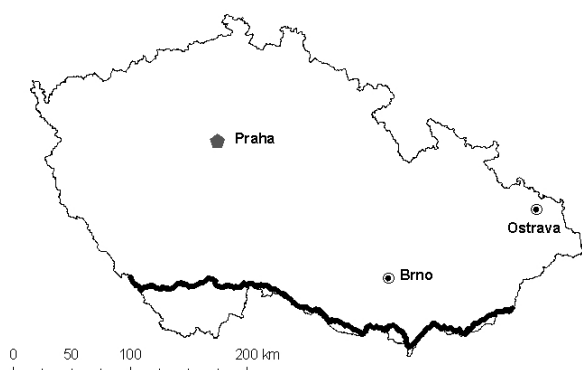


Fig. 1. Location of the 400 km long west-east transect (black line) across the southern part of the Czech Republic consisting of 768 census points.

(see Storch et al. 2002). We highlighted the breeding activity of recorded individuals in point abundance calculation by treating an individual with breeding activity (a singing male in most cases) as one breeding pair and an individual without breeding activity as a half of a breeding pair (Janda & Řepa 1986). Abundance of a species at a census point was thus expressed as a sum of breeding pairs rounded to integer.

We recognized 14 habitat types along the transect (i.e. field, meadow, scrubland, vineyard, town, village, montane deciduous forest, mixed forest, coniferous forest, lowland broad-leaved forest, forest clearing, wetland, water and bare ground) and their relative coverage was mapped within the distance of 150 m around each census point. Both bird and habitat data were collected in 2004 at points 1–512 and in 2005 at points 513–768. Each census point was further characterized by its altitude (i.e. elevation above sea level in metres) and longitude (i.e. distance from the Greenwich meridian in geographical degrees), both measured in the field using GPS, and average annual rainfall and temperature, both extracted from Vesecký et al. (1958). Therefore, we had 18 explanatory variables for further analysis. Most of them were the same as those used by Storch et al. (2003).

We recalculated our data for two scales of spatial resolution. First, 0.5-km resolution was the original one, as census points were 500 m apart in the field. Second, we calculated 8-km resolution from the original one by summing up bird abundances for each 16 adjacent points. For habitat areas and climatic and geographic variables we used arithmetic averages. We thus obtained datasets for two different grain sizes: 0.5 km containing 768 spatial units, and 8 km containing

48 spatial units. Grain size of 8 km was selected for a better comparison with the results of Storch et al. (2003), whose grids were 11.2 × 12 km. Larger grain size (e.g. 16 km) would not be appropriate for this purpose, as the small number of spatial units (24) would too much reduce the number of degrees of freedom in the analyses (note we had 18 explanatory variables).

In addition to the data on bird abundances and habitat composition at particular census points we obtained a different data set on bird-habitat associations as follows. During all bird counts each bird individual recorded at a census point was located into one of 11 habitats (field, meadow, vineyard, human settlement, coniferous forest, mixed forest, deciduous forest, forest clearing, scrubland, wetland, water body). These 11 habitats were recognized independently of the 14 habitat types mentioned above, which were mapped after breeding season when bird counts were finished. Field matching of bird individuals into 11 habitats provided more direct information about habitat use by particular species than the post-hoc habitat mapping because it respected interspecific differences in habitat selection within individual points. However, habitats recognized during bird counts were in some cases expressed in broader categories than habitats from independent habitat mapping because finer distinction between habitat types was not possible during bird counting. We summed all individual records of a species from all visits at all census points for each habitat, obtaining the habitat-species matrix, with total numbers of observations of given species in each habitat.

Statistical analyses

We used canonical correspondence analysis (CCA) to relate the data on abundances of 146 bird species detected at the transect to 18 explanatory variables. CCA is a multivariate direct gradient analysis technique able to detect the patterns of variation in community composition that can be explained by the set of environmental variables. CCA ordines samples (census points) and variables (species and environmental variables) along axes such that the differences among species and samples, respectively, are maximized. Each ordination axis represents an environmental gradient along which the centroids of individual variables and samples are distributed so as to maximize differences between them (Reif et al. 2006). CCA is based on the assumption that species distribution is unimodal along environmental gradients. The

species score is proportional to the mean of sample scores weighted by the abundance of respective species in the samples, and indicates the centre of distribution of the species along the gradients. The analysis was performed with downweighting of rare species (Lepš & Šmilauer 2003), separately for 0.5 km and 8 km resolutions.

Significance of each ordination axis was tested by Monte Carlo tests (499 permutations) controlling for the effect of spatial autocorrelation in data (Lepš & Šmilauer 2003). We also used Monte Carlo permutations for testing the significance of particular environmental variables (i.e. areas of 14 habitat types, average annual temperature, average annual rainfall, altitude and longitude) which account for the structure of the bird community. This procedure randomly permutes values of the variable in question, keeping the values of all other variables that have been included in the model. The ordering of variables that are subsequently included in the model is important, however, as including a variable that is strongly correlated to some other variable precludes revealing any significant effect of this other variable, because of low residual variability of it. Thus, we used manual forward selection that allowed subsequent inclusion of individual variables. We first included variables, whose importance was revealed by the CCA, i.e. rainfall, altitude (elevation above sea level), field and village. Although the variable temperature was not very important according to CCA it was included at the beginning for better comparability of results with Storch et al. (2003). Then we added other variables whose effect was expected, followed by the rarer habitat types whose effect was not expected, and finally, after controlling for all other factors, we tested the effect of longitude (in geographical degrees). Such an approach ensured that eventual significance of less obvious factors was not because of their correlation with the obvious ones. Moreover, final inclusion of longitude warranted testing of its pure geographical effect unaffected by habitat factors. We also performed the same tests with reversed ordering of explanatory variables, to check whether the significance of the most obvious variables was not only due to their correlation with those that had appeared less obvious.

We used the principal component analysis (PCA) to explore major trends in the fine-scale bird-habitat associations based on the locations of bird individuals during bird counts (the habitat-species matrix, see above). PCA is based on the

assumption that species distribution is linear along environmental gradients. We confirmed reliability of this assumption by a test using correspondence analysis detrended by segments. The length of the gradient provided by the first axis was less than 4.0 and thus our use of PCA for further analysis was satisfied (Lepš & Šmilauer 2003). PCA was based on the rectangular matrix where individual bird species were treated as "samples" and individual habitats were treated as "species" in the CANOCO terminology (Lepš & Šmilauer 2003). The analysis was performed for standardized log-transformed data centered by "species" focused on interspecies correlations. PCA produced four most important independent habitat axes expressed as four principal components.

RESULTS

Habitat gradients at 0.5-km resolution

All four canonical axes together explained 24.8% of variability in bird data ($p < 0.05$). First axis (12.3% of variability, $p < 0.05$) depicted the gradient from bird assemblages of open areas and human settlements to bird assemblages of coniferous and mixed forests (Fig. 2a). This gradient was also correlated with altitude and rainfall (Fig. 2a). Second axis (6.4% of variability, $p < 0.05$) put the distinction between assemblages of open areas (mainly fields, scrublands and meadows) and human settlement (towns and villages) (Fig. 2a). Third axis (4.1% of variability, $p < 0.05$) separated birds of lowland broad-leaved forests, associated with low rainfall, from the rest of bird assemblages (Fig. 2b). Fourth axis (2% of variability, $p < 0.05$) separated birds of meadows, wetlands and water bodies (Fig. 2b).

Habitat gradients at 8-km resolution

All four canonical axes together explained 50.4% of variability in bird data ($p < 0.05$). Gradient along the first axis (26.7% of variability, $p < 0.05$) expressed the difference between forest bird assemblages, also associated with higher altitude and higher rainfall, and bird assemblages of fields, villages and scrubland (Fig. 2c). The birds of meadows were placed among bird assemblages of montane forests (montane deciduous forest, coniferous forest and mixed forest, Fig. 2c), because meadows are mostly located in higher altitudes. Second axis (11.4% of variability, $p < 0.05$) separated bird assemblages of lowland broad-leaved forests and forest clearings from

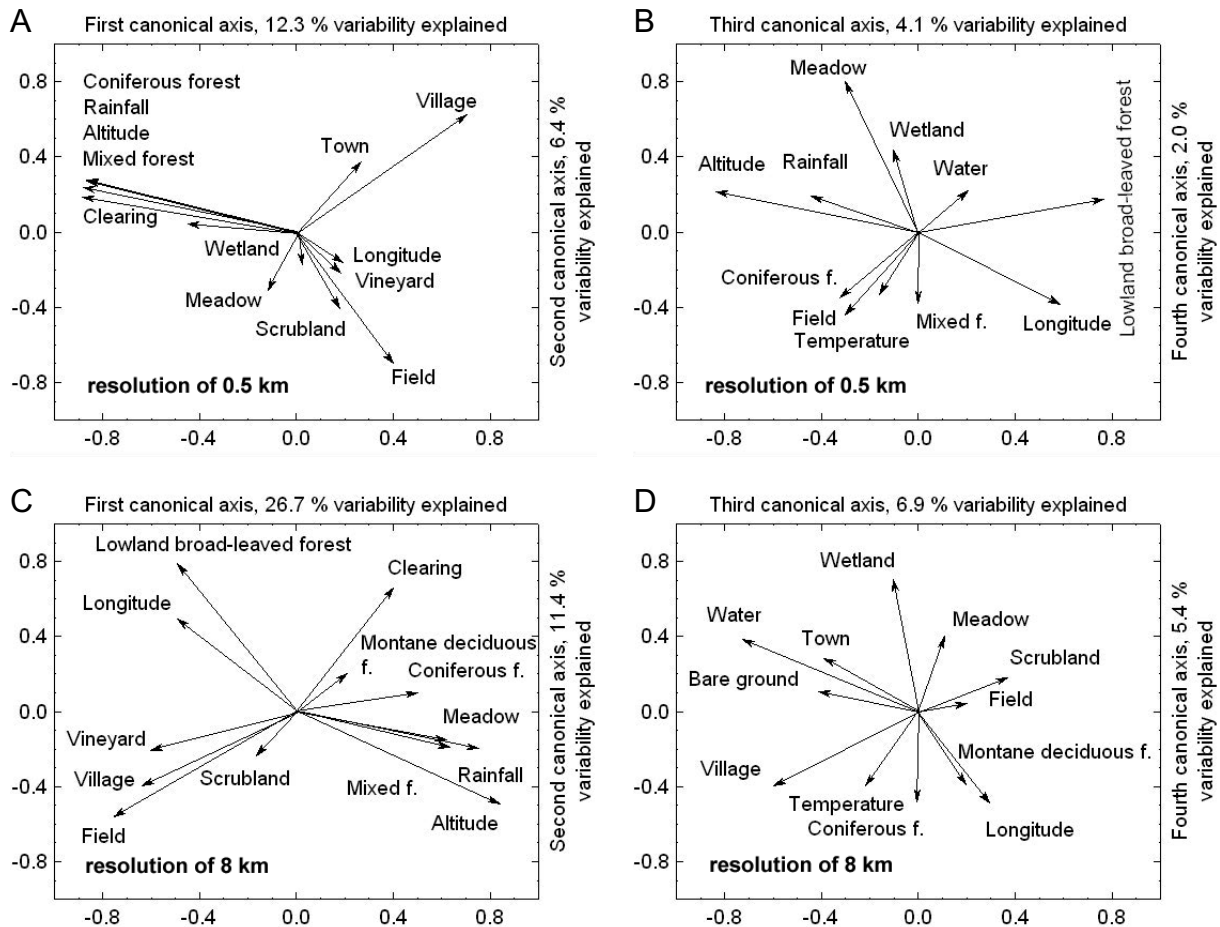


Fig. 2. The most important gradients in bird community structure in the Czech Republic expressed by four canonical axes from canonical correspondence analysis for two levels of spatial resolution: first and second axes at resolution of 0.5 km (A), third and fourth axes at resolution of 0.5 km (B), first and second axes at resolution of 8 km (C), third and fourth axes at resolution of 8 km (D). Variables which were uncorrelated with respective axes and their positions were situated in the centre of the graph are not depicted. Note that positions of particular variables are indicated by arrows and their text labels could have been moved for better readability.

assemblages of other habitats (Fig. 2c). Third (6.9% of variability, $p < 0.05$) and fourth (5.4% of variability, $p < 0.05$) axes separated birds of water bodies and wetland bird species, respectively, from the other bird assemblages (Fig. 2d).

Forward selection of environmental variables

All but four environmental variables revealed a significant independent contribution to the variance explained in bird data at 0.5-km resolution (Table 1). Both temperature and longitude were insignificant when included into the model among first variables (Table 1). Only seven environmental variables remained significant at 8-km resolution (Table 1): altitude, fields,

meadows, villages, towns, water bodies and forest clearings.

Examination of habitat-species matrix

First four PCA axes explained 84.6% of the variability in data. The first axis in the PCA, accounting for most variability (57%), separated water bird communities from the rest of the bird fauna (Fig. 3a). The forest-open landscape distinction was expressed by the second axis (Fig. 3a). The third axis opposed bird assemblages of human settlements to bird assemblages of fields and meadows and wetlands (Fig. 3b). The gradient along the fourth axis separated bird assemblages of deciduous forests from birds of coniferous forests (Fig. 3b).

Table 1. Results of forward selection analysis of environmental variables explaining patterns in bird community structure in the Czech Republic for two levels of spatial resolution (0.5 km and 8 km). The analysis was performed using Monte Carlo tests with 499 permutations. Variables are ordered according to their stepwise inclusion into the model. Columns marked with * indicate analysis where the reversed order of variables inclusion was applied. Results, that were significant in both orderings, are underlined.

Variable	Resolution 0.5 km				Resolution 8 km			
	F	p	F*	p*	F	p	F*	p*
Temperature	5.83	0.398	5.23	0.006	1.99	0.368	2.24	0.034
Rainfall	<u>34.02</u>	<u>0.034</u>	3.09	<u>0.010</u>	9.21	0.070	1.08	0.298
Altitude	<u>21.22</u>	<u>0.004</u>	<u>14.27</u>	<u>0.002</u>	<u>5.89</u>	<u>0.024</u>	<u>2.59</u>	<u>0.004</u>
Field	<u>37.53</u>	<u>0.002</u>	<u>2.82</u>	<u>0.002</u>	<u>7.29</u>	<u>0.008</u>	<u>1.82</u>	<u>0.022</u>
Village	<u>72.16</u>	<u>0.002</u>	<u>48.71</u>	<u>0.002</u>	<u>5.73</u>	<u>0.012</u>	<u>4.09</u>	<u>0.004</u>
Lowland broad-leaved f.	<u>90.09</u>	<u>0.004</u>	<u>41.52</u>	<u>0.002</u>	1.64	0.108	4.80	0.016
Meadow	<u>27.13</u>	<u>0.002</u>	<u>17.53</u>	<u>0.004</u>	<u>2.44</u>	<u>0.012</u>	<u>2.98</u>	<u>0.012</u>
Coniferous f.	<u>7.28</u>	<u>0.002</u>	<u>28.78</u>	<u>0.002</u>	1.41	0.180	3.93	0.012
Town	<u>20.79</u>	<u>0.002</u>	<u>12.66</u>	<u>0.002</u>	<u>2.74</u>	<u>0.008</u>	<u>1.44</u>	<u>0.034</u>
Mixed f.	9.52	<u>0.002</u>	<u>27.35</u>	<u>0.002</u>	1.54	0.080	3.21	0.008
Water	<u>8.54</u>	<u>0.002</u>	<u>7.82</u>	<u>0.002</u>	<u>3.88</u>	<u>0.018</u>	<u>3.11</u>	<u>0.028</u>
Wetland	<u>6.81</u>	<u>0.002</u>	<u>7.90</u>	<u>0.002</u>	1.32	0.218	1.29	0.258
Clearing	<u>4.42</u>	<u>0.002</u>	<u>19.04</u>	<u>0.002</u>	<u>1.91</u>	<u>0.026</u>	<u>3.28</u>	<u>0.030</u>
Scrubland	<u>4.03</u>	<u>0.004</u>	<u>12.93</u>	<u>0.004</u>	1.07	0.364	1.86	0.048
Montane deciduous f.	<u>4.29</u>	<u>0.002</u>	<u>5.56</u>	<u>0.006</u>	1.42	0.116	3.60	0.016
Vineyard	1.59	0.054	5.46	0.004	1.34	0.088	3.45	0.072
Bare ground	2.86	0.002	1.64	0.056	1.69	0.034	0.96	0.286
Longitude	4.58	0.002	16.45	0.388	1.48	0.118	4.57	0.348

DISCUSSION

We found two major habitat gradients in the structure of the Czech bird fauna which are worth mentioning. The strongest gradient was defined by the difference between bird assemblages characteristic to open areas with human settlements on one side and montane and coniferous forest

bird communities on the other side at both 0.5 km and 8 km resolutions. Altitude and rainfall also corresponded to this gradient: larger areas of forests are located in higher altitudes with higher rainfall and larger areas of open landscape are connected with lowlands, which are also characterised by lower rainfall. Because we did not adjust the results for unequal detectability of

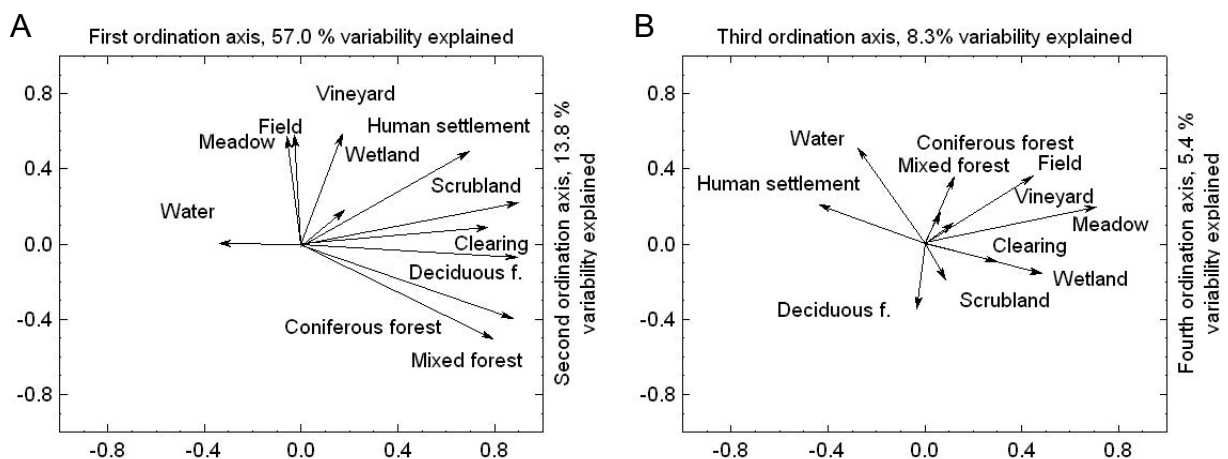


Fig. 3. The most important gradients in bird community structure in the Czech Republic revealed by the principal component analysis on the habitat-species matrix and expressed by first and second ordination axes (A), and third and fourth ordination axes (B). The habitat-species matrix is based on the number of direct observations of each species in each of 11 habitats at all census points together. Note that positions of particular variables are indicated by arrows and their text labels could have been moved for better readability.

particular species in different habitats, detected pattern in bird assemblage composition could be partially affected by the distribution of species which actually breed in both forest and open landscape habitats. Lower detectability of those species in forest could reinforce the differences between these habitats. However, we suggest that this bias is relatively small as different sets of species occupy these habitats (Skórka et al. 2006). Moreover, the gradient "from forest to farmland (or steppe)" is probably the strongest gradient in the bird community structure worldwide (Fuller et al. 1997, Brawn et al. 2001, Pasinelli et al. 2001, Berg 2002, Waltert et al. 2005, Reif et al. 2007) and reflects deep differences in selection pressures that take place in these habitats (Wiens 1989).

The other important habitat hosting specific bird assemblage was lowland broad-leaved forest (third axis at 0.5-km resolution and second axis at 8 km resolution). Preferential separation of lowland broad-leaved forest bird assemblage from all other forest types indicates that this habitat is more important for structuring of bird assemblages than the widely cited coniferous-deciduous distinction (Welsh & Loughheed 1996, Donald et al. 1998, Storch & Kotecký 1999). Indeed, we found that montane forest bird assemblages are quite similar to each other irrespective whether the forest consists from deciduous or coniferous trees. We can speculate that the distribution of species which are able to live in higher altitudes is probably more influenced by climatic conditions than by habitat features. Alternatively, even pure deciduous (or coniferous) montane forest plots could contain some coniferous (or deciduous) trees, which were not mapped in our field sampling, generating mixed bird assemblages. This is not the case of lowland broad-leaved forests which consist entirely from deciduous trees (Chytrý et al. 2001).

In accord with other studies (Allen & O'Connor 2000, Gutzwiller & Barrow 2002, MacFaden & Capen 2002), it seems that the differences in bird community structure revealed by the CCA at the two spatial resolutions can be attributed to differential distributional patterns of different habitats at different scales. For example, whereas villages and fields were placed at opposite sites of the second axis at the 0.5 km resolution, they were placed together in the biplot at 8-km resolution. Farmland and urban birds thus seem to be syntopic in larger areas of landscape (see also Devictor & Jiguet 2007) but they form different bird communities at particular census points.

Generally, habitats that strongly affected fine-scale structure of bird communities (e.g. scrubland, mixed forest or wetlands) failed to explain significant amount of variability in distribution of bird species at 8 km resolution if the area of these habitats did not vary among larger parts of landscape. The opposite pattern was found in the case of habitats which are only marginally represented at the particular census points but whose distribution, at the same time, is spatially clustered at the landscape scale (e.g. water bodies). Different spatial clustering of habitats at different scales thus leads to different ordination of habitats and species at these scales.

The birds of wetlands and water bodies form an assemblage with strong habitat association, as found also by Skórka et al. (2006). However, separation of wetland and waterbird species from the rest of the bird community differed between gradients detected by CCA and the results of the PCA on habitat-species matrix. Whereas wetlands and water bodies contributed only marginally (although significantly) to explained variability in bird data in CCA, water was far most important habitat in PCA, explaining more than half of all variability in data. These contrasting results can be explained by the fact that any analysis of community structure based on spatial data necessarily reflects two sorts of patterns: 1) patterns of co-occurrence of habitats and 2) patterns of co-occurrence of species within individual habitats. At the broad scale (large grain size), many habitats co-occur within each of the spatial units, and correlations between habitats drive the observed patterns. Therefore, even if some birds are strongly associated with water bodies, this association is masked by the local co-occurrence of water bodies with other habitat types. On the other hand, PCA on habitat-species matrix factors out the effect of habitat co-occurrence. PCA results are thus determined by species turnover of bird assemblages between individual habitat types. Water bodies (i.e. the habitat with the most distinct bird assemblage from all other habitats according to the PCA) obviously demand the most specific adaptations (Gill 1995) and thus water birds do not enter other habitats and, at the same time, species of other habitats cannot occur in water. This result is similar to that of Storch & Kotecký (1999), who found that bird communities of reedbeds are the most different from all other habitats in the Czech Republic (although this has been attributed rather to historical factors, as reedbeds themselves do not require too different adaptations from other

land environments). The agreement between these results is apparently due to the same way of comparison, i.e. comparison of bird communities of single habitat types.

The results of the forward selection of environmental variables in the CCA showed that habitat variables *sensu stricto* (i.e. vegetation) explained more variability in bird community composition than climate and longitude (Table 1). Interestingly, longitude (a surrogate for the effects of geography) was not significant even at the 8-km resolution. This result differs from that of Storch et al. (2003) although sample units and the region of interest were similar. How could these differences emerge? We offer two explanations, not mutually exclusive. First, Storch et al. (2003) analysed data from a distribution atlas (Št'astný et al. 1996) based on presence/absence of bird species in 624 grid cells covering the whole territory of the Czech Republic. Storch et al. (2003) thus gathered information about the distribution of 197 bird species comparing to 146 species counted at our transect. Our census did not capture the occurrence of ca. 50 species, mostly those with spatially restricted distribution, which could have had the largest impact on the major gradients related to geographical position, i.e. latitude and longitude, revealed by Storch et al. (2003). Indeed, typical eastern European species like Roller *Coracias garrulus*, European Bee-eater *Merops apiaster* or White-backed Woodpecker *Dendrocopos leucotos* were mapped during the atlas work in the south-eastern part of the Czech Republic (Št'astný et al. 1996) and their distribution could therefore produce a strong east-west gradient in the bird community structure described by Storch et al. (2003). These species were not detected at our transect as their occurrence within the landscape is extremely patchy (Št'astný et al. 2006) and the transect did not sample any of these patches. Some other species which are typical of the south-eastern part of the Czech Republic according to their distribution in the Atlas (e.g. Northern Wheatear *Oenanthe oenanthe* or Crested Lark *Galerida cristata*) occurred so rarely along the transect that they could not influence results of our statistical analysis.

Second (and perhaps more importantly), our transect habitat mapping determined fine scale habitat composition which could not be captured in Storch et al. (2003) analysis of atlas mapping squares. Our high-accuracy examination of bird-habitat associations showed that several species which have apparent geographic trends in distribution and abundance are simply confined to

habitats that are scarce in areas where these species are absent. This explanation could be valid also for similar results reported by other studies performed in different regions, where the accurate descriptors of habitat composition were used and landscape-scale variables failed to account for remaining variability in changes in bird community composition (Allen & O'Connor 2000, Miller et al. 2004, Lee & Rotenberry 2005, Johnson et al. 2007, Veech & Crist 2007). Both open habitat species (e.g. Stonechat *Saxicola torquata*, Barred Warbler *Sylvia nisoria* or Corn Bunting *Miliaria calandra*) and broad-leaved forest species (e.g. Wryneck *Jynx torquilla*, Nightingale *Luscinia megarhynchos* or Collared Flycatcher *Ficedula albicollis*) were more abundant in the eastern part than in the western part of the transect. Our data indicate that the emergence of the geographic gradient in Czech bird fauna can simply be attributable to the habitat-based distinction between western higher altitude plateaux with dominance of coniferous forests on one side and eastern lowlands covered by fields and broad-leaved forests on the other side. This result does not dispute the existence of biogeographical boundary between pannonian and hercynian domains in the Czech bird fauna (Culek et al. 1996), but suggests that this boundary is characterized by significant habitat gradient which could be actually responsible for patterns in bird distribution and community structure.

ACKNOWLEDGEMENTS

We thank J. Mourková and J. Cepák for their help with the fieldwork. We are grateful to an anonymous reviewer for her/his valuable comments to earlier versions of the manuscript. The project was supported by grants No. LC06073 and MSM0021620845 from the Czech Ministry of Education, and IAA601970801 from the Grant Agency of the Academy of Sciences of the Czech Republic.

REFERENCES

- Allen A. P., O'Connor R. J. 2000. Hierarchical correlates of bird assemblage structure on northeastern USA lakes. *Environ. Monit. Assess.* 62: 15–35.
- Berg A. 2002. Composition and diversity of bird communities in Swedish farmland-forest mosaic landscapes. *Bird Study* 49: 153–165.
- Bibby C. J., Burgess N. D., Hill D. A., Mustoe S. H. 2000. *Bird census techniques*. 2nd ed. Academic Press, London.

- Böhning-Gaese K., Taper M. L., Brown J. H. 1994. Avian community dynamics are discordant in space and time. *Oikos* 70: 121–126.
- Brawn J. D., Robinson S. K., Thompson F. R. 2001. The role of disturbance in the ecology and conservation of birds. *Annu. Rev. Ecol. Sys.* 32: 251–276.
- Chytrý M., Kučera T., Kočí M. (eds). 2001. [Catalogue of habitats in the Czech Republic]. Agency for Nature Conservation, Praha.
- Culek M., Grulich V., Pokorný D. (eds). 1996. [Biogeographic division of the Czech Republic]. Enigma, Praha.
- Devictor V., Jiguet F. 2007. Community richness and stability in agricultural landscapes: the importance of surrounding habitats. *Agr. Ecosyst. Environ.* 120: 179–184.
- Donald P. F., Fuller R. J., Evans A. D., Gough S. J. 1998. Effects of forest management and grazing on breeding bird communities in plantations of broadleaved and coniferous trees in western England. *Biol. Conserv.* 85: 183–197.
- Fuller R. J., Trevelyan R. J., Hudson R. W. 1997. Landscape composition models for breeding birds populations in lowland English farmland over a 20 year period. *Ecography* 20: 295–307.
- Gill F. B. 1995. *Ornithology*. 2nd ed. W. H. Freeman, New York.
- Gutzwiller K. J., Barrow W. C. Jr. 2002. Does bird community structure vary with landscape patchiness? A Chihuahuan Desert perspective. *Oikos* 98: 284–298.
- Heikkinen R. K., Luoto M., Virkkala R., Rainio K. 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *J. Appl. Ecol.* 41: 824–835.
- Holt R. D., Keitt T. H. 2000. Alternative causes of range limits: a metapopulation perspective. *Ecol. Lett.* 3: 41–47.
- James F. C., Warmer N. O. 1982. Relationships between temperate forest bird communities and vegetation structure. *Ecology* 63: 159–171.
- Janda J., Repa P. 1986. [Quantitative methods in ornithological research]. Státní Zemědělské Nakladatelství, Praha.
- Johnson M., Reich P., MacNally R. 2007. Bird assemblages of a fragmented agricultural landscape and the relative importance of vegetation structure and landscape pattern. *Wildlife Res.* 34: 185–193.
- Jokimäki J., Huhta E. 1996. Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. *Ornis Fennica* 73: 97–113.
- Kocian L., Némethová D., Melicherová D., Matušková A. 2003. Breeding bird communities in three cemeteries in the City of Bratislava (Slovakia). *Folia Zool.* 52: 177–188.
- Kujawa K., Tryjanowski P. 2000. Relationships between the abundance of breeding birds in Western Poland and the structure of agricultural landscape. *Acta Zool. Acad. Sci. Hung.* 46: 103–114.
- Laiolo P. 2002. Effects of habitat structure, floral composition and diversity on a forest bird community in north-western Italy. *Folia Zool.* 51: 121–128.
- Laiolo P., Dondero F., Ciliento E., Rolando A. 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J. Appl. Ecol.* 41: 294–304.
- Lee P.-Y., Rotenberry J. T. 2005. Relationships between bird species and tree species assemblages in forested habitats of eastern North America. *J. Biogeogr.* 32: 1139–1150.
- Lepš J., Šmilauer P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge.
- MacFaden S. W., Capen D. E. 2002. Avian habitat relationships at multiple scales in a New England forest. *Forest Sci.* 48: 243–253.
- Matlock R. B., Edwards P. J. 2006. The influence of habitat variables on bird communities in forest remnants in Costa Rica. *Biodivers. Conserv.* 15: 2987–3016.
- McGarigal K., McComb W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecol. Monogr.* 65: 235–260.
- Miller J. R., Dixon M. D., Turner M. G. 2004. Response of avian communities in large-river floodplains to environmental variation at multiple scales. *Ecol. Appl.* 14: 1394–1410.
- Pasinelli G., Naef-Daenzer B., Schmid H., Keller V., Holzgang O., Graf R., Zbinden N. 2001. An avifaunal zonation of Switzerland and its relation to environmental conditions. *Global Ecol. Biogeogr.* 10: 261–274.
- Reif J., Sedláček O., Hořák D., Riegert J., Pešata M., Hrázský Z., Janeček Š. 2007. Habitat preferences of birds in a montane forest mosaic in the Bamenda Highlands, Cameroon. *Ostrich* 78: 31–36.
- Reif J., Sedláček O., Hořák D., Riegert J., Pešata M., Hrázský Z., Janeček Š., Storch D. 2006. Unusual abundance-range size relationship in an Afrotropical bird community: the effect of geographical isolation? *J. Biogeogr.* 33: 1959–1968.
- Robinson W. D., Brawn J. D., Robinson S. K. 2000. Forest bird community in central Panama: influence of spatial scale and biogeography. *Ecol. Monogr.* 70: 209–235.
- Rodewald A. D., Yahner R. H. 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82: 3493–3504.
- Sanders T. A., Edge W. D. 1998. Breeding bird community composition in relation to riparian vegetation structure in the western United States. *J. Wildl. Manage.* 62: 461–473.
- Šizling A. L., Storch D. 2004. Power-law species-area relationships and self-similar species distributions within finite areas. *Ecol. Lett.* 7: 60–68.
- Skórka P., Martyka R., Wójcik J. D. 2006. Species richness of breeding birds at a landscape scale: which habitat type is the most important? *Acta Ornithol.* 41: 49–54.
- Sorace A., Gustin M., Calvario E., Ianniello L., Sarrocco S., Carere C. 2000. Assessing bird communities by point counts: repeated sessions and their duration. *Acta Ornithol.* 35: 197–202.
- Šťastný K., Bejček V. 1985. Bird communities in spruce forests affected by industrial emissions in the Krušné Hory (Ore Mountains). In: Taylor K., Fuller R. J., Lack P. C. (eds). *Bird Census and Atlas Studies. Proc. VIIIth Int. Conf. on Bird Census and Atlas Work. Tring*, pp. 243–253.
- Šťastný K., Bejček V., Hudec K. 1996. [Atlas of the breeding bird distribution in the Czech Republic 1985–1989]. Nakladatelství H & H, Jinočany.
- Šťastný K., Bejček V., Hudec K. 2006. [Atlas of the breeding bird distribution in the Czech Republic 2001–2003]. Aventinum, Praha.
- Storch D. 1998. Densities and territory sizes of birds in two different lowland communities in eastern Bohemia. *Folia Zool.* 47: 181–188.
- Storch D., Gaston K. J., Cepák J. 2002. Pink landscapes: 1/f spectra of spatial environmental variability and bird community composition. *Proc. R. Soc. B* 269: 1791–1796.
- Storch D., Konvička M., Beneš J., Martinková J., Gaston K. J. 2003. Distribution patterns of butterflies and birds in the Czech Republic: separating effects of habitat and geographical position. *J. Biogeogr.* 30: 1195–1205.
- Storch D., Kotecký V. 1999. Structure of bird communities in the Czech Republic: the effect of area, census technique and habitat type. *Folia Zool.* 48: 265–277.
- Taberlet P., Furnagalli L., Wust-Saucy A. G., Cosson J. F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Mol. Ecol.* 7: 453–464.
- Titeux N., Dufrene M., Jacob J.-P., Paquay M., Defourny P. 2004. Multivariate analysis of a fine-scale breeding bird atlas

- using geographical information system and partial canonical correspondence analysis: environmental and spatial effects. *J. Biogeogr.* 31: 1841–1856.
- Tomiałojć L. 2000. An East-West gradient in the breeding distribution and species richness of the European woodland avifauna. *Acta Ornithol.* 35: 3–17.
- Veech J. A., Crist T. O. 2007. Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within regions. *Global Ecol. Biogeogr.* 16: 650–656.
- Vesecký A., Petrovic S., Briedon V., Káráský V. (eds). 1958. [Climatic atlas of the Czech Republic]. Academia, Praha.
- Waltert M., Bobo K. S., Sainge N. M., Fermon H., Muhlenberg M. 2005. From forest to farmland: habitat effects on afro-tropical forest bird diversity. *Ecol. Appl.* 15: 1351–1366.
- Welsh D. A., Loughheed S. C. 1996. Relationships of bird community structure and species distributions to two gradients in northern boreal forest. *Ecography* 19: 194–208.
- Wesołowski T., Rowiński P., Mitrus C., Czeszczewik D. 2006. Breeding bird community of a primeval temperate forest (Białowieża National Park, Poland) at the beginning of the 21st century. *Acta Ornithol.* 41: 55–70.
- Wiens J. A. 1989. *Ecology of bird communities*. Cambridge Univ. Press, Cambridge.

STRESZCZENIE

[Związek środowisk i struktury zespołów ptaków w Czechach w różnych skalach przestrzennych]

Czynniki biogeograficzne wpływające na strukturę zespołów ptaków silnie zależą od skali, w jakiej są one rozpatrywane. W mikroskali do najważniejszych należy układ i udział środowisk, w skali makro zmienne środowiskowe wydają się tracić na znaczeniu, gdyż ważniejsze stają się ograniczenia w dyspersji oraz czynniki historyczne. Z drugiej strony taka interpretacja może być związana ze sposobem prowadzenia badań i opisywaniem środowisk. Celem badań było określenie czynników wpływających na zespoły ptaków, przy analizach prowadzonych w różnej skali przestrzennej.

Opis zespołów ptaków prowadzono w latach 2004–2005 przy użyciu metody punktowej. Wyznaczono 768 punktów położonych wzdłuż transektu (400 km) przebiegającego przez całe południowe Czechy (Fig. 1). Punkty były oddalone od siebie o 500 m. Aby zminimalizować efekt obserwatora, liczenia — 5 w ciągu sezonu, trwające 5 minut, dokonywane były tylko przez dwie osoby. Ptaki zapisywano w promieniu do 150 m od wyznaczonego punktu. W analizach brano pod

uwagę maksymalną liczbę osobników danego gatunku z 5 wizyt, a biorąc pod uwagę zachowanie ptaków przeliczano je na liczbę par lęgowych/punkt.

W wyznaczonym promieniu 150 m opisano udział wyróżnionych 14 środowisk (pola, łąki, zakrzaczenia, winnice, miasta, wsie, górskie lasy liściaste, mieszane i iglaste, nizinne lasy liściaste, zręby i polany, tereny podmokłe, wody oraz odsłonięty grunt). Prócz tego każdy punkt został scharakteryzowany przez szerokość i długość geograficzną, wysokość n. p. m., oraz średnią temperaturę i opady.

Zmienne te analizowano w dwóch skalach przestrzennych — 0.5 (dane z każdego punktu analizowanego pojedynczo) i 8 km (uśrednione dane z 16 punktów). Do analiz zastosowano kanoniczną analizę zgodności (CCA), oraz analizę składowych głównych. Aby wyselekcjonować zmienne, które najbardziej wpływają na zespoły ptaków do modelu wprowadzono zmienne w kolejności, w jakiej pojawiały się istotne w analizach CCA — najpierw opady, wysokość nad poziomem morza, udział pól, następnie temperatura, potem pozostałe zmienne środowiskowe, zaś na koniec szerokość geograficzna. Następnie przeprowadzono ponowne analizy włączając zmienne w odwrotnej kolejności, aby uniknąć ewentualnego wzajemnego skorelowania zmiennych.

Stwierdzono, że dla analiz w skali 0.5 km wszystkie cztery osie wyjaśniały 24.8% zmienności, zaś w skali 8 km wszystkie osie wyjaśniały 50.4% zmienności struktury zespołów ptaków. (Fig. 2). W analizach tych wyróżniały się zespoły ptaków leśnych, oraz terenów otwartych (pól, łąk), oraz terenów podmokłych i związanych z wodami. Analizy składowych głównych wyraźnie wskazywały, że zespoły ptaków środowisk wodnych i podmokłych najbardziej różniły się od zespołów innych środowisk (Fig. 3). Średnia temperatura oraz szerokość geograficzna nie różnicowały badanych zespołów ptaków dla obu skal przestrzennych (Tab. 1). Wydaje się więc, że czynniki środowiskowe (np. roślinność) znacznie lepiej opisują zmienność struktury zespołów ptaków niż czynniki klimatyczne czy geograficzne.