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The effect of the habitat on wintering birds in Central Europe

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Abstract. The aim of this work was to analyse assemblages of wintering birds in three areas of central Europe, that differ in climate: eastern Poland, northern Poland and western Germany in winter in 2003-2009. The severity of winter moderates distinctly from eastern Poland to Germany, so there ought to be more species and larger numbers of birds in Germany. 5445 birds from 73 species were recorded on the 491 transects with a length 500 m. Generalized linear models of the influence of habitat types and localities on the species richness reflected the significant effect of three habitat types and study area location. The species richness was positively affected by the surface area of towns and villages, and negatively by that of grassland areas. The most species were recorded in W Germany, in E Poland, and the fewest in N Poland. While, numbers of birds increased with increasing areas of hedgerows, villages and towns. Most birds wintered in eastern Poland, and reached higher value compared to N Poland; mostly because of large numbers of a few of the most abundant species: yellowhammer, fieldfare, great tit. We can expect that, with warming climate, the wintering areas in central Europe will host increasingly significant bird numbers.

Key words: Germany, Poland, species richness, weather, winter

Introduction

Winter in the temperate zone may be a crucial period for regulating population dynamics, mainly of resident or semi-migratory birds (Newton 2008). Generally, birds may avoid harsh winter conditions since the winter distribution and abundance patterns of several avian species are directly linked with their physiological demands, and also with their metabolic rates, which are higher near the northern boundary of that distribution (Rott 1988, Canterbury 2002). Not only physiological constraints but also food availability is critical for the winter survival of birds (Newton 1980, Peach et al. 1999). It has been demonstrated many times that as winter conditions deteriorate, especially when temperatures fall and there is snow cover, the species richness declines (Stapanian et al. 1999, Galarza 2000, Goławski & Kasprzykowski 2010). This dependence has also been shown by the geographical gradient of declining numbers of species from the southern parts of Europe and North America to their northern parts, where climatic conditions are different (Jokimäki et al. 2002, Whittaker et al. 2007), and even at a more local scale (Lennon et al. 2000, Carrascal et al. 2002). In Europe, where the weather in the west is decidedly milder than in the east (Bednorz 2004), the same principle can be applied. However, this east-west gradient may be perturbed as a result of human activities, e.g. birds overwintering in built-up areas where food is more readily accessible or are deliberately provided with it (Robb et al. 2008a, Zuckerberg et al. 2011). Species richness should be linked with numbers of birds (Carnicer et al. 2012, Carrascal et al. 2012a, Seoane et al. 2017), since studies have demonstrated a correlation between species numbers and the numbers of overwintering birds (Gillings et al. 2005, Siriwardena et al. 2007).

However, changes in the global climate over the past few decades have already had a major impact on biodiversity (Hughes 2000), and that includes wintering birds. Species that forty or fifty years ago used to spend the winter in southern Europe or northern Africa now do so much farther to the north or east (Onrubia & Tellería 2012, Tellería et al. 2015). The winter distribution ranges of many North American species have also changed (La Sorte & Thompson 2007). Blackcap (*Sylvia atricapilla*) is a spectacular example of a species that has changed its wintering areas and shortened its migration distances (Bearhop

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et al. 2005). The fact that wintering grounds are now closer to breeding areas means lower mortality and energy savings and thus improved breeding success, which in turn is reflected in population trends (Robb et al. 2008b, Grande et al. 2009).

The aim of this work was to analyse assemblages of wintering birds in three areas of central Europe: eastern Poland, northern Poland and western Germany. Our hypothesis was that these study areas, up to 1100 km distant from each other, would differ with respect to the species composition and numbers of birds as a consequence of the different weather conditions prevailing in each area. Such relationships are common, and the deviations from them very rarely quoted (Jokimäki et al. 2002). The severity of winter moderates distinctly from eastern Poland to western Germany, so there ought to be more species of birds and larger numbers of them in Germany. The data can therefore be taken as representative of larger areas. Apart from demonstrating the relationships between the numbers of birds in these three locations, we also analysed the influence of the various habitats on the overwintering birds.

Material and Methods

Study area

The research was carried out in two regions of Poland and one of Germany. In Poland, one study site was located in the east-central part of the country near the town of Siedlce (52°09′ N, 22°17′ E) and included 149 transects (henceforth E Poland). The other was in the north of the country near Koszalin (54°11′ N, 16°10′ E) and covered 191 transects (henceforth N Poland). The study area in Germany was in North Rhine-Westphalia, near the city of Cologne (50°55′ N, 06°59′ E), and covered 151 transects. The distance between Cologne and Koszalin is about 740 km, between Cologne and Siedlce it is 1100 km, and between Koszalin and Siedlce it is 470 km. The dominant landscape type in all the regions was agricultural, but other habitats were also present. We distinguished seven habitat types: 1) villages, 2) towns, 3) crop fields, 4) grasslands, 5) coniferous woodland, 6) deciduous woodland, 7) hedgerows. Villages were small linear settlements, whereas the towns were larger places with the compact area of buildings criss-crossed by numerous streets. Crop fields covered all types of arable land, which at this time of year were ploughed up, sown with winter corn or an intercrop, or were left as stubble fields. Grasslands were meadows and pastureland along with small watercourses or water bodies. Woodlands were either exclusively coniferous or deciduous, or else they were mixed. To which category – coniferous or deciduous – they were allocated depended on which tree type was dominant; this was assessed during the fieldwork. Hedgerows were rows or clumps of trees covering an area of no more than 1 ha; if the area exceeded 1 ha, they were classified as woodlands.

Bird census

Birds were counted on one occasion on each transect. The count took place in December – early February in 2003-2009. Birds were counted between 07:45 and 15:50 hours using the line-transect method. The beginning of the transect was chosen at random. Before the survey we had planned a route to be covered by car. Along this route we stopped every 10 km and this halt was the start of a transect. From there, using GPS, we walked a 500 m long transect perpendicular to the road, recording the bird species and the extent of all the habitats in the vicinity. The width of the strip of land to be censused depended on the type of habitat. In open habitats, that is, where the visibility was good, the strips were 200 m wide, so that an area of up to 100 m wide on either side of the transect was censused. The open habitats were crop fields and grasslands. In the other habitats, where visibility was limited (apart from coniferous woodlands), the census strip was 100 m wide, i.e. 50 m on either side of the transect path. In coniferous woodlands the strip width was established at 80 m. The width of the census strips was chosen by measuring the distances from which birds were detected. Ten such measurements were made in each habitat. The habitat areas are listed in Table 1. Each transect ran in a straight line; only exceptionally, in built-up areas, did it follow the line of the streets, but always running as nearly as possible at right angles to the road where the transect started. Each transect was walked slowly and all the birds were recorded. No counts were done in bad weather, i.e. in rain or snow, strong wind or poor visibility.

Statistical methods

The statistical analysis addressed two problems. First, using generalized linear models (GLZ) with a log-link function and Poisson error distribution, we tested the impact of habitat types on the number of species and bird numbers (dependent variables). The continuous predictors were the areas of the habitats, described above. Collinearity of the selected variables in the models was studied by variance inflation factor (VIF), which is the inverse of tolerance (Quinn & Keough 2002). VIF values greater than ten suggest strong

Table 1. Mean ± 1 SE area (ha, n = number of transects) of seven habitats and Shannon-Weiner index of diversity. Significance levels were tested by ANOVA with sequential Bonferroni corrections.

	Germany n = 151	N Poland n = 191	E Poland n = 149	Mean n = 491	ANOVA n = 491 transects
villages	0.20 ± 0.07	0.20 ± 0.06	0.37 ± 0.10	0.25 ± 0.04	F = 1.72, *P* = NS
towns	0.74 ± 0.14	0.39 ± 0.09	0.14 ± 0.07	0.42 ± 0.06	F = 7.61, *P* = 0.003
crop fields	3.87 ± 0.40	4.03 ± 0.30	5.48 ± 0.35	4.42 ± 0.19	F = 6.71, *P* = 0.004
grasslands	1.12 ± 0.19	0.90 ± 0.15	1.18 ± 0.21	1.05 ± 0.11	F = 0.71, *P* = NS
coniferous forest	0.49 ± 0.09	1.13 ± 0.12	0.54 ± 0.10	0.76 ± 0.06	F = 11.24, *P* < 0.001
deciduous forest	0.77 ± 0.12	0.35 ± 0.08	0.27 ± 0.07	0.46 ± 0.05	F = 8.23, *P* < 0.001
hedgerows	0.18 ± 0.05	0.18 ± 0.04	0.20 ± 0.07	0.19 ± 0.03	F = 0.15, *P* = NS
Shannon-Weiner index of diversity	0.63	0.60	0.50	0.59	-

collinearity. This was in fact one parameter, the area of coniferous woodland; the analysis thus embraced the other six habitats. Because species richness strongly depended on the number of individuals (Seoane et al. 2017) we included the number of birds as a covariate in the GLZ model of species richness. In addition, the analysis took into account two categorical predictors, namely, the study area: E Poland, N Poland and W Germany, and year of study (2003-2009).

Since one of the assumptions of this work was to analyse the overwintering of birds in three geographical regions, the second problem to be tested statistically concerned the number of species and density of birds in the various habitats in those regions. To calculate this we used ANOVA with Tukey's post-hoc test. Seven separate analyses were performed for each habitat. We calculated the density of birds in each habitat on a particular transect using the data on where exactly the birds were observed. A sequential Bonferroni adjustment was used for between-group comparisons, and only results with a probability of $\alpha \leq 0.05$ were assumed statistically significant. The calculations were performed using Statistica 10.0 (StatSoft 2012).

Results

Bird assemblages

A total of 5445 birds from 73 species were recorded (Appendix 1). The most numerous species were yellowhammer (*Emberiza citrinella*) (10.7 % of all individuals), fieldfare (*Turdus pilaris*) (9.4 %), great tit (*Parus major*) (6.3 %), house sparrow (*Passer domesticus*) (5.5 %) and Eurasian siskin (*Carduelis spinus*) (5.1 %). The numbers of these five species made up 37.1 % of the entire bird assemblage. They were recorded on 83.9 % of the transects overall: on 86.6 % of transects in E Poland, on 75.9 % in N Poland and on 91.4 % in Germany. The largest numbers of birds were recorded on crop fields (25.4 % of all individuals) and grasslands (15.0 %), in towns (14.0 %), along hedgerows (13.0 %); fewer birds were observed in villages (11.7 %), and in coniferous (11.0 %) and deciduous woodlands (10.0 %).

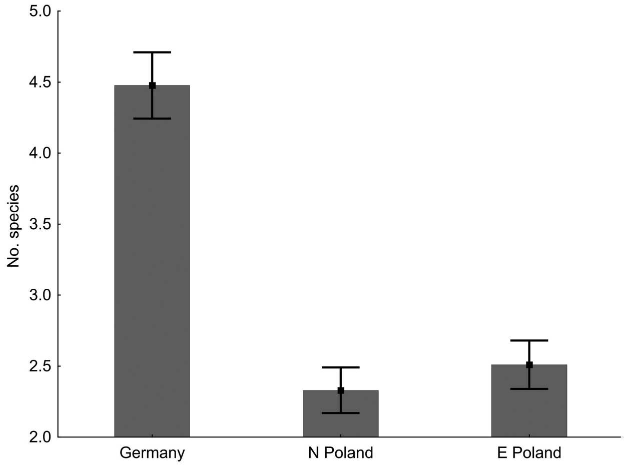

Fig. 1. Species richness per transect in the three study areas.

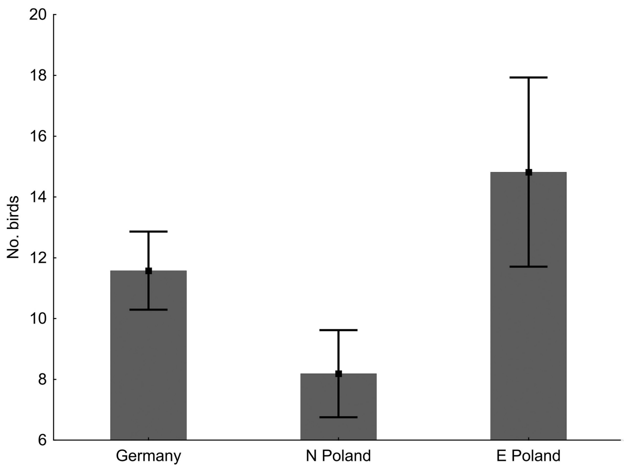

Fig. 2. Abundance of birds per transect in the three study areas.

Table 2. Results of GLZ analyses of species richness and the total numbers of birds in relation to habitat type, year and study area location (and number of birds for species richness analysis).

	Number of species			Number of birds		
	Estimate (SE)	Wald Stat.	*P*-value	Estimate (SE)	Wald Stat.	*P*-value
villages	0.074 (0.026)	7.93	0.005	0.120 (0.034)	12.30	< 0.001
towns	0.059 (0.021)	8.13	0.004	0.102 (0.028)	12.83	< 0.001
crop fields	–0.014 (0.013)	1.11	0.293	–0.015 (0.012)	1.64	0.200
grasslands	–0.039 (0.009)	19.47	< 0.001	0.034 (0.054)	0.41	0.523
deciduous forest	0.040 (0.014)	1.27	0.235	0.133 (0.068)	3.58	0.055
hedgerows	0.050 (0.392)	1.63	0.201	0.142 (0.031)	14.14	< 0.001
study area location	0.309 (0.039)	88.72	< 0.001	0.133 (0.068)	4.02	0.045
year	0.334 (0.095)	25.57	< 0.001	0.035 (0.097)	3.81	0.702
number of birds	0.007 (0.001)	117.42	< 0.001	-	-	-

Table 3. Densities of five bird species (individuals/1 ha) found along transects in Germany, N Poland and E Poland. Mean values ± 1 SE (sample size) are given.

	Germany	N Poland	E Poland
Parus major	2.3 ± 0.2 (n = 63)	1.9 ± 0.2 (n = 53)	3.0 ± 0.5 (n = 34)
Emberiza citrinella	2.0 ± 0.7 (n = 13)	3.4 ± 0.9 (n = 37)	11.1 ± 3.1 (n = 39)
Passer domesticus	3.9 ± 0.7 (n = 16)	13.9 ± 3.8 (n = 14)	3.3 ± 0.6 (n = 13)
Turdus pilaris	1.3 ± 0.3 (n = 3)	1.8 ± 0.4 (n = 13)	61.0 ± 29.6 (n = 8)
Carduelis spinus	3.0 ± 1.0 (n = 7)	1.8 ± 0.6 (n = 6)	17.7 ± 5.0 (n = 14)

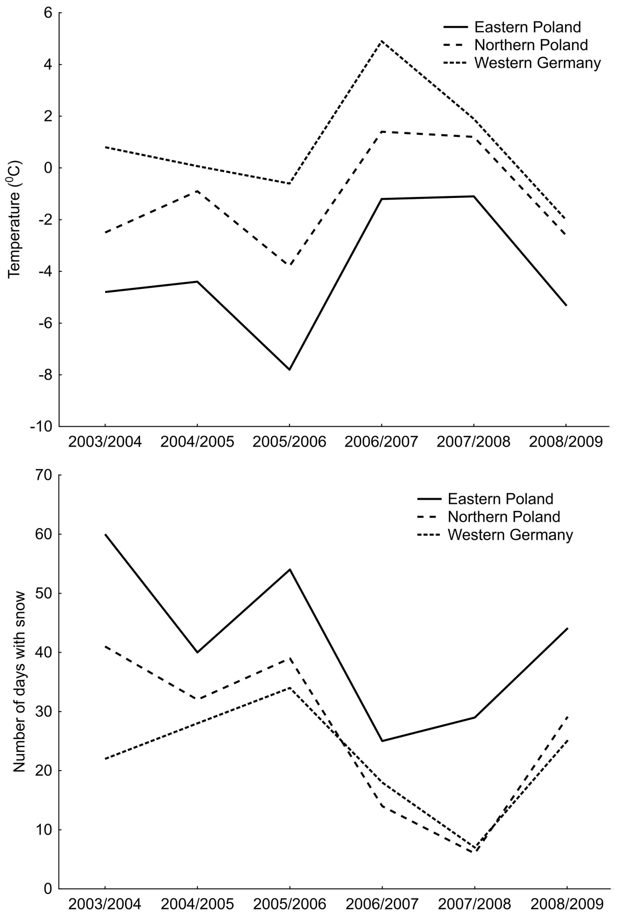

Fig. 3. Minimal daily temperature and the number of days with snow during the overwintering period of birds (December-February) in three study areas in successive seasons. The meteorological data were obtained for the nearest weather stations: E Poland – Siedlce, N Poland – Koszalin, W Germany – Maastricht (no reliable data was available from a German weather station; and the nearest weather station was at Maastricht in the Netherlands). Weather data were obtained from the website http://www.tutiempo.net.

Effect of habitat and study area position on species numbers and numbers of birds

GLZ analysis of the influence of habitat types, number of birds, year of study and localities on the number of species reflected the significant effect of six variables; three habitat types, number of birds, year of study and study area location (Table 2). The number of species was most strongly and positively affected by the surface area of towns and villages, and negatively by that of grassland areas. The most species were recorded in W Germany and the fewest in N Poland (Fig. 1). Statistically significant differences were found between the numbers of species in Germany and the two Polish localities (post-hoc Tukey test, $P < 0.001$ in both cases), whereas the numbers of species in the two Polish localities did not differ significantly (post-hoc Tukey test, $P = 0.766$). The GLZ analysis also showed the influence of habitat types and localities on the total number of birds to be statistically significant (Table 2). Numbers of birds increased with increasing areas of hedgerows, villages and towns. These numbers were also dependent on the location of the study area. On average, the largest numbers of birds were recorded in E Poland, a statistically significant higher value compared to N Poland (post-hoc Tukey

Table 4. Bird species richness along transects in seven habitats in Germany, N Poland and E Poland. Mean values ± 1 SE (sample size) are given. Significance levels were tested by ANOVA (with sequential Bonferroni corrections) with post-hoc contrasting used where appropriate.

Habitat	Germany	N Poland	E Poland	Significance	Post-hoc contrasting
villages	2.9 ± 0.6 (n =19)	2.4 ± 0.5 (n = 22)	2.7 ± 0.4 (n = 18)	$F_{2,56}$ = 0.30; *P* = NS	-
towns	4.8 ± 0.5 (n = 28)	3.9 ± 0.6 (n = 18)	3.7 ± 1.4 (n = 6)	$F_{2,49}$ = 0.76; *P* = NS	-
crop fields	1.4 ± 0.2 (n = 72)	0.6 ± 0.1 (n = 105)	1.2 ± 0.2 (n = 105)	$F_{2,279}$ = 8.45; *P* < 0.001	*P* < 0.004 Germany/ N Poland E Poland/N Poland
grasslands	0.6 ± 0.2 (n = 38)	0.5 ± 0.1 (n = 44)	0.9 ± 0.2 (n = 32)	$F_{2,111}$ = 1.18; *P* = NS	-
coniferous forest	3.1 ± 0.5 (n = 29)	1.9 ± 0.2 (n = 71)	2.0 ± 0.4 (n = 36)	$F_{2,133}$ = 3.38; *P* = NS	-
deciduous forest	3.9 ± 0.5 (n = 46)	1.4 ± 0.3 (n = 30)	2.2 ± 0.4 (n = 20)	$F_{2,93}$ = 9.90; *P* < 0.001	*P* = 0.001 Germany/ N Poland
hedgerows	2.4 ± 0.3 (n = 48)	1.1 ± 0.2 (n = 63)	1.3 ± 0.3 (n = 19)	$F_{2,127}$ = 7.98; *P* = 0.003	*P* = 0.001 Germany/ N Poland

Table 5. Densities of birds (individuals/1 ha) found along transects in seven habitats in Germany, N Poland and E Poland. Mean values ± 1 SE, (sample size) are given. Significance levels were tested by ANOVA (with sequential Bonferroni corrections) with post-hoc contrasting used where appropriate.

Habitat	Germany	N Poland	E Poland	Significance	Post-hoc contrasting
villages	9.1 ± 3.1 (n = 19)	9.1 ± 3.7 (n = 22)	5.5 ± 1.4 (n = 18)	$F_{2,56}$ = 3.30; *P* = NS	-
towns	3.7 ± 0.8 (n = 28)	4.5 ± 1.1 (n = 18)	5.5 ± 2.6 (n = 6)	$F_{2,49}$ = 0.44; *P* = NS	-
crop fields	0.6 ± 0.2 (n = 72)	0.4 ± 0.2 (n = 105)	1.0 ± 0.3 (n = 105)	$F_{2,279}$ = 1.36; *P* = NS	-
grasslands	0.2 ± 0.1 (n = 38)	0.8 ± 0.4 (n = 44)	2.8 ± 1.8 (n = 32)	$F_{2,111}$ = 4.32; *P* = 0.032	*P* = 0.044 Germany/ E Poland
coniferous forest	3.5 ± 1.3 (n = 29)	1.3 ± 0.2 (n = 71)	4.5 ± 2.2 (n = 36)	$F_{2,133}$ = 3.76; *P* = NS	-
deciduous forest	3.7 ± 0.6 (n = 46)	1.4 ± 0.4 (n = 30)	3.6 ± 1.1 (n = 20)	$F_{2,93}$ = 3.33; *P* = NS	-
hedgerows	26.6 ± 8.3 (n = 48)	9.7 ± 3.1 (n = 63)	34.9 ± 19.8 (n = 19)	$F_{2,127}$ = 8.91; *P* < 0.001	*P* < 0.037 Germany/N Poland N Poland/E Poland

test, *P* = 0.050), whereas no such relationships were found in the numbers of birds between N Poland and Germany or between Germany and E Poland (post-hoc Tukey test, *P* > 0.490 in both cases, Fig. 2). As many as four of five species dominating the assemblages were highest in E Poland. Only the densities of house sparrow were the largest in N Poland (Table 3).

Number of species and densities of birds in the various habitats in the three study areas

There were statistically significant differences in the numbers of species between the three study areas for three habitats (Table 4). In the case of crop fields these differences related to species numbers in Germany and N Poland as well as in E and N Poland. On the other hand, in deciduous woodland and in hedgerows the differences between the abundance of species were significant only in Germany and N Poland. The same pattern always emerged from the above: the number of species was the largest in Germany, the next largest in E Poland, and the smallest in N Poland.

Comparison of bird densities in the seven habitat types and the three study areas revealed statistically significant differences for two of them (Table 5). Bird densities in hedgerows differed between Germany (where they were higher) and N Poland. Densities in E Poland were higher than in N Poland in the case of hedgerows. Moreover, there were differences in bird densities between E Poland and Germany with respect to grasslands (Table 5).

Discussion

Effect of habitat on numbers of species and numbers of birds

This work has shown that both the numbers of species and the numbers of birds increased with growing areas of land occupied by towns and villages. The importance of built-up areas to overwintering birds has been substantiated in previous studies (e.g. Goławski & Dombrowski 2011, Jokimäki & Kaisanlahti-Jokimäki 2012a, Tryjanowski et al. 2015a). Such environments provide more stable and predictable food supplies (McCafferty et al. 2001, Fuller et al. 2012), and moreover, supplementary feeding may reduce starvation and thus enhance winter survival in birds (Newton 1980, Brittingham & Temple 1988). In the whole of Poland, too, studies of the effect of bird tables, feeders etc. on the numbers of overwintering birds and species richness have overwhelmingly demonstrated a positive effect (Tryjanowski et al. 2015b). The positive impact of bird feeding on their numbers is more widely known, also from other habitats than built-up areas; it is even suggested that supplementary feeding affects birds no less than habitats (Carrascal et al. 2012b). In addition, in the built-up areas, especially in cities, the air temperature may be up to several degrees higher than in areas around the building. Therefore, the bird physiological mechanism does not have to invest much in keeping body temperature and night survival is easier than in lower temperature locations (Brodin 2000, Gosler 2002). In addition, birds can easily find safe roosts in buildings (Walsberg 1986), where the temperature is higher than outdoors; this, in turn, affects metabolic rate and energy conservation, and ultimately, mortality (McCafferty et al. 2001). In consequence, survival in built-up areas may be easier than in other habitats, and numbers of birds may exceed those in other habitats (Suhonen et al. 2009, Goławski & Dombrowski 2011, Jokimäki & Kaisanlahti-Jokimäki 2012b). Even though we did not monitor the numbers of bird tables in the present study, there will have been a sufficient number of them, as the data collected in the study area on other occasions testify (Goławski et al. 2015, Tryjanowski et al. 2015b). The importance of built-up areas to wintering birds increases when the weather deteriorates, especially when the show cover is thick, which restricts access to food elsewhere and causes the birds to move into towns and villages (Goławski & Kasprzykowski 2010, Goławski & Dombrowski 2011).

It was rather surprising to discover that hedgerows had a positive effect only on the numbers of birds: previous studies had suggested that species richness above all should increase in this habitat (Tryjanowski 1995). Hedgerows, in addition to providing foraging sites, offer cover for birds, increasing the safety with which they can exploit nearby resources and allowing them access to locations which might otherwise be too risky to use at all (Carrascal & Tellería 1990, Hinsley & Bellamy 2000).

Grasslands were the only habitat acting negatively on species richness. Bird species inhabiting open terrain usually prefer stubble fields in winter because of the rich abundance of food there (Moorcroft et al. 2002, Bellebaum 2008, Perkins et al. 2008, Chamberlain et al. 2010). These habitats have plentiful weeds, on the seeds of which seed-eaters can feed. In Poland this significance of stubbles is explained by the preferences of buntings and tree sparrows (*Passer montanus*), which are the dominant species in wintering assemblages of birds (Kasprzykowski & Goławski 2012, Goławski et al. 2013). On the other hand, grassy areas, richer in invertebrates, are important to wintering invertebrate-feeding species (Atkinson et al. 2004, Perkins et al. 2008), but only small numbers of these species were found in our study areas (Appendix 1). The grasslands are also important for raptors, especially for the most common species – common buzzard (*Buteo buteo*) (Skibbe 2009, Skibbe et al. 2009).

In the case of species richness, the variable that significantly influenced this factor was the survey season. The number of wintering bird species in a given area in the following seasons may vary considerably (Jokimäki & Kaisanlahti-Jokimäki 2012b), and the main factor influencing the conditions of central Europe is the presence of snow cover (Goławski & Kasprzykowski 2010). The number of species was also influenced by the overall abundance of birds, which is well described by other authors (Seoane et al. 2017).

Species richness and abundance of birds in the three study areas

We had anticipated that numbers of birds would be the highest in Germany and the lowest in E Poland, in accordance with the general pattern described in the literature emerging from the milder climate in western Europe (e.g. Carrascal et al. 2002, Carnicer et al. 2012). Our expectation was not fulfilled, as the most were found in E Poland and the least (only half as many) in N Poland. There were only slightly fewer birds in Germany than in E Poland. To some extent, however, these results may simply be due to the large numbers of a few of the most abundant species in the three areas. Yellowhammer was recorded in the largest numbers: an average of 11 was recorded on transects in E Poland, though only two in Germany and three in N Poland. The differences were even greater for the second-most abundant species – fieldfare: in E Poland there were an average of 61 per transect, but less than two in both Germany and N Poland. These two of the 73 species recorded in all made up as much as 20 % of the total number of birds. They may have found particularly propitious foraging conditions in E Poland, which in the other two areas did not exist. It was the heaps of dung which farmers piled up in their fields that proved so attractive to yellowhammers (Goławski & Kasprzykowski 2011, Orłowski et al. 2014). Fieldfares, on the other hand, being a frugivorous species, tend to remain in areas with harsher winter weather, but where fruit are readily available (Tellería et al. 2015); E Poland, with its numerous orchards and chokeberry cultivations, are just such a region. Nevertheless, we should not lose sight of the fact that each transect was walked just once, and that the average between-winter variation (CV%) in bird species richness was half that of bird abundance (Jokimäki & Kaisanlahti-Jokimäki 2012b). While, the species richness on an average transect in Germany was more than twice than in either of the study areas in Poland. This remains in line with the pattern of species richness dependent on energy availability, which is associated, among others, with air temperature (Carrascal et al. 2002, Jokimäki et al. 2002).

If we now look at the habitats in the three study areas, we find that the number of species usually differed only between Germany and N Poland, the number always being higher in Germany. This pattern was discernible for three out of the seven habitats examined. In contrast, the differences in bird densities between the three regions were less distinct. Be that as it may, the smallest densities were usually recorded in N Poland and differed statistically from the densities recorded in Germany and/or E Poland. Wintering bird assemblages in N Poland are thus numerically the smallest and the least diverse, an inference drawn earlier from analyses of such assemblages in a number of habitats in a farming landscape (Goławski et al. 2013).

The large number of species recorded in Germany compared with the two study areas in Poland was probably due to the milder weather during the wintering period, since the Shannon's diversity indices of habitats for all three areas were similar in value. Such dependences have been demonstrated earlier (Jarvinen & Vaisanen 1980, Goławski & Kasprzykowski 2010, Zuckerberg et al. 2011). The results of those papers indicate that not only species richness but also the abundance of birds dropped with decreasing air temperatures, and especially after falls of snow. The weather conditions during the birds' overwintering period, as measured by the minimal daily temperature and the number of days with snow, are the mildest in Germany and the harshest in E Poland (Fig. 3). In view of this, it seems surprising that the largest numbers of birds were reported from E Poland, the coldest of the three areas and the one with the longest period of snow cover. Temperature determines the metabolic expenditure of birds below the thermoneutral zone, the lower limit being around 20 °C for many winter acclimated species in temperate areas (Kendeigh et al. 1977). The temperatures in our study areas were lower than the critical temperature, ranging from –7.8 to + 4.9 °C (especially in eastern Poland), so overwintering in these areas is energetically demanding in terms of thermoregulatory metabolic costs (Carrascal et al. 2012a). It is known also that many species prefer the warmest areas to overwinter, but some species are wintering in locations colder than their thermal preferences, probably reflecting the interaction between habitat and thermal requirements (Carrascal et al. 2016). As mentioned earlier, the difference in bird abundances was largely due to the much larger numbers of the dominant species (four of the five species) in E Poland. These species must have found good overwintering conditions in E Poland (Kasprzykowski & Goławski 2012, Goławski et al. 2013), especially yellowhammer, which is sedentary there with a numerous breeding population (Goławski & Dombrowski 2002).

Summarizing, species richness and bird numbers rose with increasing sizes of built-up areas, which tallies with the overall pattern found in Europe. Species richness fell with increasing areas of grassland, which is in agreement with the birds' preference for open habitats, where stubble fields play a key role. Bird numbers increased in hedgerows, which supply not only food but also shelter; but whether this habitat affects species richness remains uncertain. This is probably because hedgerows are important to just a few species, like yellowhammer, which was the most abundant species that we found. The geographical locations of the study areas exerted a significant influence on both species richness and bird abundance. Whereas species richness was the highest in Germany, where the mildest winter weather prevailed, bird abundances were the highest in E Poland, where the winter conditions were the harshest. This is a big surprise, because generally milder climate allow for occurrence of the greater numbers of birds (Jokimäki et al. 2002). In all probability, such a result is largely due to the large numbers of overwintering birds from a few of the most numerous species in E Poland; these species made up as many as 30 % of the entire bird assemblage. Comparison of the wintering bird associations in seven habitat types in the three study areas showed that species richness is significantly higher in three habitats between Germany and N Poland and in one habitat between E Poland and N Poland, whereas bird abundance is higher in one habitat between E Poland and Germany, in one habitat between Germany and N Poland and also in one habitat between E Poland and N Poland. In almost every case the assemblage of birds spending the winter in N Poland was the poorest. This result concurs with data comparing the wintering bird assemblages of N Poland with those of other, more central areas of Poland (Goławski et al. 2013). These results may also be indicative of climate-change related processes taking place in the wintering grounds of some species (Maclean et al. 2008). It turns out that the numbers of some species traditionally wintering in the Mediterranean region, such as robin, chaffinch and white wagtail, have fallen in recent years: since the climate is warming up, they are spending the winter farther north than hitherto (Tellería et al. 2015). The same phenomenon has been observed in North America (Zuckerberg et al. 2011). We can expect that, with warming climate, the wintering areas in central Europe will host increasingly significant bird numbers. Reducing of the bird migration distance to wintering areas can contribute to improve survival and, as a consequence, increase breeding populations of species (Visser et al. 2009).

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Appendix 1. Numbers of species in seven habitats.

Species	villages	towns	crop fields	grasslands	coniferous forest	deciduous forest	hedgerows	Total
Accipiter gentilis	0	0	0	1	1	0	1	3
Accipiter nisus	0	1	1	0	0	1	1	4
Aegithalos caudatus	0	5	0	0	12	16	10	43
Alauda arvensis	0	0	114	0	0	0	0	114
Anas platyrhynchos	0	0	0	80	0	0	0	80
Anthus pratensis	0	0	7	4	0	0	0	11
Ardea cinerea	0	0	2	2	0	0	0	4
Bombycilla garrulus	43	11	0	0	3	0	20	77
Buteo buteo	0	1	34	4	2	8	12	61
Buteo lagopus	0	0	2	0	0	0	1	3
Carduelis carduelis	7	2	3	2	0	5	23	42
Certhia brachydactyla	2	1	0	0	0	0	0	3
Certhia familiaris	0	0	1	0	20	17	4	42
Chloris chloris	6	21	113	0	1	0	10	151
Chroicocephalus ridibundus	0	4	6	2	0	0	0	12
Circus cyaneus	0	0	1	0	0	0	0	1
Coccothraustes coccothraustes	0	3	0	0	0	29	3	35
Columba oenas	0	0	0	3	0	0	0	3
Columba palumbus	2	7	52	2	10	4	108	185
Columbia livia	1	97	0	0	0	0	0	98
Corvus corax	3	0	29	3	8	6	3	52
Corvus cornix	0	0	27	1	0	0	2	30
Corvus corone	10	11	74	21	2	4	10	132
Corvus frugillegus	14	0	0	0	0	0	0	14
Corvus monedula	86	78	26	1	0	0	33	224
Cyanistes caeruleus	37	27	14	1	80	67	28	254
Cygnus olor	0	0	1	12	0	0	0	13
Dendrocopos major	2	0	0	0	32	22	3	59

Dendrocopos minor	0	0	1	0	0	0	0	1
Dryocopus martius	0	0	0	0	2	1	0	3
Emberiza citrinella	27	38	431	39	8	3	39	585
Emberiza calandra	12	0	39	4	0	0	4	59
Eremophila alpestris	0	0	45	0	0	0	0	45
Erithacus rubecula	0	5	0	0	1	15	11	32
Falco tinnunculus	0	0	8	0	0	1	2	11
Fringilla coelebs	11	30	52	0	2	29	28	152
Fringilla montifringilla	0	0	50	0	0	20	0	70
Garrulus glandarius	2	1	7	3	24	17	7	61
Lanius excubitor	0	0	6	2	0	0	2	10
Larus argentatus	0	14	3	1	0	0	0	18
Larus canus	0	1	0	0	0	0	0	1
Linaria cannabina	0	0	30	8	0	0	0	38
Linaria flammea	0	0	0	0	1	2	0	3
Lophophanes cristatus	1	0	0	0	50	6	0	57
Loxia curvirostra	0	5	0	0	2	1	0	8
Lullula arborea	0	0	6	0	0	0	0	6
Mergus merganser	0	0	0	2	0	0	0	2
Parus major	63	59	37	0	53	80	50	342
Passer domesticus	180	113	7	0	0	0	0	300
Passer montanus	19	72	63	0	0	0	15	169
Perdix perdix	0	0	0	9	0	0	4	13
Periparus ater	0	0	0	0	19	0	1	20
Phalacrocorax carbo	0	0	0	1	0	0	0	1
Phasianus colchicus	0	0	1	0	0	0	1	2
Pica pica	17	30	17	10	1	5	16	96
Picus viridis	0	0	0	2	0	0	0	2
Plectrophenax nivalis	0	0	1	1	0	0	0	2
Poecile montanus	0	0	2	0	15	8	2	27
Poecille palustris	0	0	0	0	11	5	12	28
Prunella modularis	0	4	0	0	1	3	5	13
Pyrrhula pyrrhula	1	2	13		5	15	12	48
Regullus regullus	1	2	0	0	178	8	0	189
Serinus serinus	7	0	0	0	0	0	0	7
Sitta europaea	0	0	1	0	18	25	0	44
Spinus spinus	0	25	23	35	22	40	135	280
Streptopelia decaocto	32	6	0	0	0	0	0	38
Sturnus vulgaris	29	26	1	81	1	9	17	164
Troglodytes troglodytes	0	4	3	0	2	12	10	31
Turdus iliacus	0	0	0	1	0	6	0	7
Turdus merula	18	50	9	0	10	52	54	193
Turdus philomelos	0	0	0	0	0	0	2	2
Turdus pilaris	6	4	18	480	0	1	5	514
Vanellus vanellus	0	0	1	0	0	0	0	1
Total	639	760	1382	818	597	543	706	5445