Changes in bird distribution in a Central European country between 1985-1989 and 2001-2003

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Abstract European birds have been significantly affected by dramatic environmental changes during the last decades. The effects of these changes on species richness and distribution in particular countries remain poorly understood due to a lack of high-quality, large-scale data standardized over time. This is especially true in Central and Eastern Europe. On a model group of birds in the Czech Republic (countrywide atlas mapping data), we examined whether long-term changes of species richness and distribution between 1985–1989 and 2001–2003 differed among groups of species defined by their habitat requirements, type of distribution in Europe, migratory strategy, and the degree of national legal protection. Further, we investigated the effects of colonizers and local extinctions on these changes. Whereas the number of species in the whole country remained the same in both periods (208 species), species composition had changed. Increasing occupancy (i.e., number of occupied mapping squares) was observed in species of forest and wetland habitats, in short-distance migrants and in non-protected species. Southern species also positively changed their occupancy but this pattern disappeared after the inclusion of six species dependent on extensively cultivated farmland that went extinct between mappings. The overall occupancy of all species together showed positive changes after excluding colonizers and extinct species. We suggest that the improvement of environmental conditions after 1990 caused the stability of or increased the distribution of common birds in the Czech Republic and it was the disappearance of specific farmland practices that might cause the loss of several species.

Keywords bird community, species richness, distribution, central Europe, global change, land use

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Introduction

Biodiversity conservation is one of the fundamental objectives of current initiatives for nature protection (Primack 2006). Although most attention is paid to the ongoing decline of global species richness (Swanson 1998), we should bear in mind that management measures are most frequently implemented at local or regional levels, usually within individual states (Lenzen et al. 2008; Yamamura 2008; Orłowski and Ławniczak 2009). Local change in species richness is determined by the number of species which colonize the area and the number of species that disappear. Local colonization and extinction rates are related to the sensitivity of particular species to current changes in the landscape (Donald et al. 2007; Lenzen et al. 2008). For effective conservation management it is, therefore, important to see whether species undergoing range retraction have different ecological traits from species with expanding ranges. For this purpose, we can examine the mean change in regional distribution of groups of species with defined ecological characteristics (Gregory et al. 2005, Jiguet et al. 2007, Van Turnhout et al. 2010).

Such an ”ecological-group” approach has been used successfully for the examination of temporal changes in regional breeding bird distribution in several Western European countries (Gregory et al. 2004, Julliard et al. 2004, Lemoine et al. 2007, Van Turnhout et al. 2007, Bauer et al. 2008). These studies have found prominent effects of various environmental changes on European birds such as the intensification of farming practices, urbanization and global climate change or habitat degradation on stop-over and wintering sites in the Mediterranean region and Sahel zone (Feranec et al. 2000; Jongman 2002, Opdam and Wascher 2004; Moreno-Rueda and Pizarro 2008; Schaefer et al. 2008).

Despite this large body of evidence, our information about factors affecting changes in bird distribution is incomplete due to an apparent regional bias in these studies. Findings from former communist Central and Eastern European countries are based only on a few local scale results (e.g., Tryjanowski 2000, Verhulst et al. 2004, Goławski 2006, Orłowski and Ławniczak 2009) and their generalisation is thus problematic. At the same time, factors affecting bird distribution might differ between Western and Eastern European countries: agriculture was less intensive in the East (Donald et al. 2001), implementation of conservation legislation was delayed (Donald et al. 2007) and many migratory species use different flyways and wintering grounds (Busse 2001, Cepák et al. 2008). The examination of whether the patterns found in Western parts of the European continent also hold true in former communist Central and Eastern European countries is thus of high conservation importance. In this respect, birds of the Czech Republic represent an ideal opportunity to fill this knowledge gap. Their breeding distribution was mapped using a standardized technique in two mapping sessions during the last decades: in 1985–1989 and 2001–2003. Moreover, their ecological requirements are well known and documented (Hudec 1983, 1994; Hudec and Šťastný 2005; Cepák et al. 2008) enabling the sorting of particular species into various ecological groups.

Based on the results of studies of European bird communities, we can formulate the following predictions about recent changes in distribution of particular ecological groups of Czech birds. First, landscape changes, such as the loss of extensively cultivated farmland due to agricultural intensification or land abandonment followed by forest spread, should reduce the distribution of farmland birds and increase the distribution of forest species (Lenzen et al. 2008; Reif et al. 2008a; Orłowski and Ławniczak 2009). Second, the increase in the average annual temperature should have a positive effect on the distribution of south-European species and a negative impact on the north-European ones (Bauer et al. 2008; Reif et al. 2008b). Third, global warming, along with the degradation of wintering habitats, should lead to an increase in the distribution of resident species and to a decrease of migrants (Schaefer et al.

2008). Fourth, legal protection should have a positive impact on protected species compared to unprotected ones (Donald et al. 2007).

The aim of the study was to examine these predictions comparing particular ecological groups of Czech birds between the two mapping periods. For each species group, we have focused on changes in breeding distribution. We have paid special attention to the species that colonized the country or went extinct between the mappings and how these species influenced the observed patterns.

Methods

Bird distribution data

We used data from the two atlases of breeding bird distribution (hereafter Atlases) in the Czech Republic covering the period 1985–1989 (Šťastný et al. 1996) and 2001–2003 (Šťastný et al. 2006). Data was collected in a unified network of 628 squares of 10´ longitude and 6´ latitude (roughly 12 by 11.1 km) evenly covering the entire territory of the country. The method of fieldwork was based on the contributions of a high number of volunteers (750 and 532 in the first and second mapping periods, respectively) and was the same in both Atlases. Each volunteer was requested to survey all habitats in a selected square. It was recommended they start with the most frequent habitats (fields, meadows, forests, towns, villages, etc.) and then move onto rarer ones (water bodies, wetlands, streams, etc.). Finally, a targeted search was carried out for individual species in appropriate environments or at appropriate times – e.g., at dusk in case of the owls, crakes, nightingales etc. Field observations of each bird species in the particular mapping squares were recorded using 17 numerical breeding codes with respect to the probability of its breeding occurence, according to the standards used in Europe (Hagemeijer and Blair 1997).

The distribution of each species (hereafter occupancy) was expressed as the number of occupied squares with categories of ”probable” or ”confirmed breeding” (breeding codes 3–16 in Hagemeijer and Blair 1997) in respective mapping periods. There were 215 species conforming to these criteria.

Definition of explanatory variables

We have recognized the following species groups (Appendix 1) differing in (i) habitat requirements, i.e., forest species (78 species in the first and 80 in the second mapping), wetland species (61 / 65), farmland species (50 / 44) and urban species (19 / 19), (ii) migration strategy, i.e., resident species (45 / 44), partial migrants (22 / 23), short-distance migrants (71 / 74) and long-distance migrants (70 / 67), (iii) breeding distribution in Europe, i.e., northern species (68 / 69), southern species (53 / 51), central species (22 / 22) and widespread species (65 / 66), and (iv) legal protection in the Czech Republic, i.e., critically endangered (30 / 28), highly endangered (56 / 55), endangered (28 / 28) and species without any special legal protection (94 / 97). The terms like ”endangered” do not describe the real level of threat but they are the title of the official categories of legal protection listed in Czech conservation law (Anonymus 2008). Therefore, a ”critically endangered” species is under the highest conservation concern according to Czech conservation law but in reality it may not be more threatened than other species. The real levels of threat to a particular bird species in the Czech Republic are currently unknown as no one has performed any formal analysis (Voříšek et al. 2008).

Most of the species used for further analyses were already sorted into these categories in Reif et al. (2006, 2008b) and Voříšek et al. (2008). For the categorization of the remaining species, we used the following literature sources: Hudec (1983, 1994) and Hudec and Šťastný (2005) for the habitat requirements, Anonymus (2008) for legal protection status and Hagemeijer and Blair (1997) for the breeding distribution in Europe.

Determination of particular groups defined by different breeding distributions in Europe followed the two-step assessment procedure described in Reif et al. (2008b). First, we divided Europe into three large regions with respect to the location of the Czech Republic: the northern region had its southern boundary five geographical degrees north of the latitudinal midpoint of the Czech Republic, the southern region had its northern boundary five degrees south of the midpoint of the Czech Republic and the central region laid between the northern and southern regions. These regions broadly correspond to the biogeographical divisions of Europe. The Mediterranean region is in the south, the boreal region is in the north and the continental region is in the central part (European Environmental Agency 2006). In the second step, we measured the area of the breeding range of each species in each region and calculated the proportion of a region covered by the range of the focal species. Based on these proportions, we defined four species groups differing in the latitudinal distributions of their breeding ranges in Europe. As nearly all species occurring in the Czech Republic have relatively large European breeding ranges distributed in all three regions, we could not use strict criteria such as ”northern species are those confined solely to northern region”. Instead, we used a criteria focused on the avoidance of a region in which a species has the lowest proportion of its range. We thus recognized: (i) northern species whose ranges cover < 30% of the southern region (e.g., *Turdus pilaris*); (ii) southern species whose ranges cover < 30% of the northern region (e.g., *Luscinia megarhynchos*); (iii) central species whose ranges cover < 30% of southern and northern regions (e.g., *Parus palustris*); (iv) widespread species whose ranges cover more than 30% of the area of each region (e.g., *Passer domesticus*). Although such species sorting is arbitrary to some extent, and indeed 30% has no biological meaning, we trust that it mirrors the real latitudinal preferences of a particular species.

Migratory strategy of each particular species were excerpted from the new Czech and Slovak bird migration atlas (Cepák et al. 2008) which is based on all known ringing recoveries of Czech birds up to 2002.

Statistical analysis

We calculated the change in occupancy (C) of each particular species between the two mapping periods using the formula introduced by Lemoine et al. (2007):

$$C = (N_2 - N_1)/((N_2+N_1)/2)$$

$N_{1,2}$ is the occupancy of a given species in the first and second mapping period, respectively. Positive values of C indicate increasing occupancy, negative values decreasing occupancy and where C = 0 there is an indication of no change (Lemoine et al. 2007).

To test whether mean occupancy of particular species groups increased or declined, we performed the one-sample t-tests. Each test tested the null hypothesis that the mean change in occupancy of a given group is zero. Performance of 16 repeated tests using the same dataset would result in an elevated risk of a Type I error (Zar 1996). To account for this factor, we have applied the Bonferroni correction, adjusting the 0.05 level of significance (α) to 0.0031.

To test whether mean changes in occupancy differ among the focal species groups, we have applied analysis of variance (ANOVA). First, we have performed one-way ANOVAs for each factor (i.e., habitat, European distribution, migratory strategy and protection status) separately. Tukey's HSD post hoc test was used to compare means where significant differences were found with the ANOVA. Second, we have examined the effects of each factor, controlling the influence of the others, using main-effects ANOVA.

Finally, we were interested in the influence of colonization/extinction processes on changes in the distribution of birds in the Czech Republic. For this purpose, we have excluded all species (n = 14) present only in one of the mapping periods and then repeated all the tests described above. Comparison of the outcome of the tests with and without such species revealed their possible influence.

Results

The number of species in the Czech Republic remained the same in both periods – 208 species. Seven species went extinct in the Czech Republic during the time between the mappings (*Falco vespertinus, Otis tarda, Burhinus oedicnemus, Charadrius hiaticula, Coracias garrulus, Lanius minor* and *L. senator*) and, at the same time, seven species colonized the country (*Egretta alba, Anas penelope, Tadorna tadorna, Pandion haliaetus, Aquila heliaca, Chlidonias hybridus* and *Otus scops*). The prevailing characteristics of the species which were not registered in the second mapping period were: farmland habitat (six species), long-distance migratory strategy (six species), southern distribution (five species) and critically endangered protection status (four species). The colonizers were characterized by wetland habitat (five species), long-distance (three species) or short-distance migratory strategy (three species), southern distribution (three species) and no legal protection (four species).

The overall mean change in occupancy between both mappings was not significantly different from zero (Table 1a). Regarding particular species groups, we found a positive change in occupancy in forest and wetland species, short-distance migrants and non-protected species. After application of the Bonferroni correction, the result remained significant in the wetland species only (Table 1a). No group showed a significantly negative change in mean occupancy, although the result in farmland birds approached the 0.05 significance level (Table 1a).

We applied analysis of variance to test whether some ecological characteristics would predict differences among the species groups in their mean changes in occupancy. We have found that habitat requirements were the only significant predictor of these changes, as shown by both one-way and main effects ANOVAs (Table 2a, b, Fig. 1). Post hoc comparisons using Tukey's HSD tests showed that both forest (P = 0.0138) and wetland (P = 0.0001) species extended their distribution more than farmland species.

After exclusion of the 14 species present only in one of the two mappings, we found that the overall mean change in occupancy between the mappings was positive (Table 1b). Further, the results showed increasing occupancy in southern species (Table 1b). Excluding colonizers and extinct species did not qualitatively change the results for forest, wetland and non-protected species (Table 1b). In contrast, change in short-distance migrants was no longer significant (Table 1b). After the Bonferroni correction, the overall average change in occupancy and change in southern and non-protected species remained significant (Table 1b).

Exclusion of the 14 species, present only in one of both mappings, did not reveal any significant results in both one-way and main effects ANOVAs (Table 2c, d).

Discussion

Our results based on the analysis of the large-scale mapping data showed four striking patterns of changes in breeding bird distribution in the Czech Republic between 1985–1989 and 2001–2003: (i) dominant effect of habitat over all other factors, (ii) weaker but significant effects of European distribution, migratory strategy and protection status in some tests, (iii) influence of rare species on most of the observed patterns, (iv) prevalence of positive changes in bird distribution over the negative ones. The effects of habitat and European distribution were in congruence with our initial predictions, but the legal protection status showed the opposite pattern to what we had expected. The effect of migratory strategy did not support our prediction of decline in long-distance migrants and increase of residents.

The effect of habitat was caused by expansion of forest and wetland species in contrast to farmland birds. Since this contrast was not significant after excluding species detected in one mapping only, the marked difference between these habitat-defined species groups is probably caused by the extinction of six farmland species between the mapping periods: *Falco vespertinus, Otis tarda, Burhinus oedicnemus, Coracias garrulus, Lanius minor* and *L. senator*. Their disappearance from the Czech Republic indicates a possible adverse impact of the recent land use practices on these species. This result is somewhat surprising as the decrease in agricultural intensity after the fall of communism probably reduced the rate of population decline of common farmland birds in the Czech Republic (Reif et al. 2008a), Poland (Goławski 2006) and Hungary (Verhulst et al. 2004). This land use change obviously did not prevent more sensitive farmland species from extinction. The exact causes of the loss of these species remains unexplored. We can only speculate about the switch from an extensively cultivated agricultural landscape providing a heterogenous mosaic of habitats to either highly intensive agriculture or the complete abandonment of arable land in the key areas for populations of these species (Konvička et al. 2006, 2008, Ludwig et al. 2009; see also Šťastný et al. 1996). The disappearance of these highly specialized species is consistent with Kerbiriou's et al. (2009) findings on the spread of tolerant species with a broad ecological niche leading to biotic homogenization of bird communities in France (Devictor et al. 2008) and the Netherlands (Van Turnhout et al. 2007).

The increasing occupancy of forest and wetland birds was found even if the species detected in only one mapping were excluded (although with lower significance). Therefore, we suggest that these patterns were caused mainly by extending distribution of common species already breeding in the Czech Republic and the colonization of the country by new species has only strenghtened this effect. In the case of forest birds, this result is in accordance with studies based on annual monitoring of populations of common species in the Czech Republic (Reif et al. 2007) and other parts of Europe (Gregory et al. 2007, Van Turnhout et al. 2007). It might be attributed to forest expansion, the alteration of forest age class composition towards older classes and/or by the impact of forest recovery after the reduction of imissions in the 1990s (Reif et al. 2007, 2008c). The increase of wetland birds was also confirmed in local bird communities in central and western Europe (Lemoine et al. 2007, Van Turnhout et al. 2010, Orłowski and Ławniczak 2009) and was probably caused by lower hunting pressure and the fact that many newly established nature reserves in the country protected wetland habitats (Málková & Lacina 2002).

Southern species that bred in the Czech Republic in both mapping periods extended their occupancy, corresponding with findings of an earlier study focused on annual changes in abundance of common birds in the Czech Republic (Reif et al. 2008b). This result is consistent with the observations of climate change impact on bird species (Julliard et al. 2004, Jiguet et al. 2007, Bauer et al. 2008). It also corroborates predictions of future breeding bird distribution patterns modelled under various scenarios of climatic warming (Huntley et al.

2007). Increasing occupancy of southern species, however, vanished after the inclusion of the species which became extinct between the mappings. A more detailed focus on particular species uncovered the fact that decrease was caused by the extinction of the farmland species which were probably more affected by unfavourable land use practices than by the climate. This result implies that global warming itself is not a sufficient impetus for range expansion of the southern species, if their habitat is destroyed.

Regarding changes of distribution of birds with different migratory strategies, we have found two unexpected results: increased occupancy in short-distance migrants and no change in occupancy in long-distance migrants. The first pattern was driven by the expansion of several colonizers of wetland birds (*Egretta alba, Anas penelope* and *Tadorna tadorna*) and it was probably caused by habitat effects. The second pattern contrasts with observations of population decline of long-distance migrants in several western European countries (e.g., Lemoine et al. 2007, Heldbjerg and Fox 2008) and might be attributable to the use of different migratory routes and/or wintering sites by the Czech populations (Busse 2001, Cepák et al. 2008).

Increasing occupancy was found in non-protected species and the same result was found in all species grouped together after the exclusion of species detected in one mapping only. These results imply that common birds probably benefited from changes in the Czech landscape after 1990. In fact, components of the environment, including water, air, forests and farmland were heavily affected by human activity within all of Europe in the late 1980s (Moldan 1990). During the 1990s, the water quality and air pollution greatly improved and there was also a sharp decrease in agricultural intensity. These positive changes were also documented in Poland (Goławski 2006) and Hungary (Verhulst et al. 2004). Moreover, forests, defoliated in extensive areas due to air pollution, started to recover (Anonymus 1996; Reif et al. 2007, 2008a). At the same time, we have failed to find any significant positive effect of legal protection on the occupancy of species. The reason may lie in the low effectiveness of direct conservation actions (Kumstátová et al. 2005). Czech nature conservation is probably not able to take care of problematic bird species (Voříšek et al. 2008). Further studies are needed to ensure that existing protected areas create suitable conditions for endangered birds' existence (e.g., Kollar and Wurm 1996).

To our knowledge, our study is the first attempt to examine the patterns of changes in breeding bird distribution on a country-wide level within the former Eastern block. Compared to the previous studies based on population trends from annual monitoring schemes (e.g., Gregory et al. 2007, Reif et al. 2008a, b, c), our breeding distribution mapping data involve information about uncommon species (Van Turnhout et al. 2007). They are, therefore, less biased and the observed patterns are more general. Our results imply that the major drivers of changes (agricultural intensification, forest expansion, global climate change, biotic homogenization) are probably similar across European regions, although local specificities of several aspects emerged (e.g., poor performance of legal protection). Future studies should focus in more detail on the investigation of particular drivers.

Zusammnefassung

Veränderungen in der Vogelverbreitung in einem mitteleuropäischen Land zwischen 1985-1989 und 2001-2003

Europäische Vögel sind in den letzten Jahrzehnten signifikant von dramatischen Umweltveränderungen betroffen worden. Die Effekte dieser Veränderungen auf den Artenreichtum und die Verbreitung in bestimmten Ländern sind nach wie vor schlecht verstanden, da hochwertige, großräumige Daten fehlen, die über die Zeit standardisiert sind.

Dies trifft besonders auf Mittel- und Osteuropa zu. Anhand einer Modellgruppe von Vögeln in Tschechien (landesweite Atlaskartierungsdaten) haben wir untersucht, ob sich Langzeitveränderungen in Artenreichtum und Verbreitung zwischen 1985-1989 und 2001-2003 zwischen Artengruppen unterschieden, die anhand ihrer Habitatansprüche, ihrem Verbreitungstyp in Europa, ihrer Zugstrategie und ihrem nationalen Schutzstatus voneinander abgegrenzt sind. Außerdem haben wir die Effekte von Erstbesiedlungen und lokalen Ausrottungen auf diese Veränderungen untersucht. Während die Artenzahl im gesamten Land in beiden Zeiträumen gleich blieb (208 Arten), hat sich die Artenzusammensetzung verändert. Zunehmende Besiedlung (d.h. Zahl besetzter Kartenquadrate) wurde für in Wald- und Feuchtlandhabitaten vorkommende Arten, Kurzstreckenzieher und nicht geschützte Arten beobachtet. Im Süden vorkommende Arten veränderten ihre Besiedlung ebenfalls zum Positiven, doch dieses Muster verschwand nach der Einbeziehung von sechs Arten, die auf extensiv bewirtschaftetes Ackerland angewiesen sind und zwischen den Kartierungen ausstarben. Die gesamte Besiedlung aller Arten zusammengenommen zeigte positive Veränderungen, nachdem Erstbesiedler und ausgestorbene Arten ausgeschlossen worden waren. Wir schlagen vor, dass die Verbesserung der Umweltbedingungen nach 1990 die Verbreitung von häufigen Vögeln in Tschechien stabilisierte oder ansteigen ließ, und der Verlust mehrerer Arten könnte durch das Verschwinden spezifischer Ackerbautechniken verursacht worden sein.

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Table 1 Changes in species richness (total number of species in the country) and occupancy (number of occupied mapping squares) of birds in the Czech Republic between 1985–1989 and 2001–2003 as revealed by the country-wide breeding distribution altas mapping. Species were sorted into groups defined by their habitat requirements, migratory strategy, European distribution and legal protection status in the Czech Republic. Statistics refer to single sample t-tests that tested the significance of change in occupancy of each group between the mapping periods. Significant differences ($P < 0.05$) are in bold type and those significant after the Bonferroni correction ($P < 0.0031$) are underlined. Tests were performed with (a) and without (b) 14 species that colonized the country or went extinct between the mapping periods. See Methods section for a detailed description of the calculation of change in occupancy and for more details on the sorting of species into the ecological groups

	Species richness		a) Change in occupancy (± SE)	*N*	*t*	*P*	b) Change in occupancy (± SE)	*N*	*t*	*P*
	1985–9	2001–3								
Habitat requirements										
Farmland	50	44	-0.21 (± 0.11)	50	-1.92	0.0614	0.04 (± 0.06)	44	0.58	0.5626
Forest	78	80	**0.14 (± 0.05)**	80	**2.74**	**0.0076**	**0.09 (± 0.04)**	78	**2.33**	**0.0220**
Urban	19	19	-0.09 (± 0.06)	19	-1.42	0.1742	-0.09 (± 0.06)	19	-1.41	0.1742
Wetland	61	65	**0.28 (± 0.96)**	66	**3.10**	**0.0029**	**0.19 (± 0.07)**	60	**2.63**	**0.0107**
Migratory strategy										
Resident	45	44	0.02 (± 0.08)	45	0.24	0.8127	0.06 (± 0.06)	44	1.03	0.3096
Partial migrants	22	23	0.14 (± 0.10)	23	1.34	0.1934	0.05 (± 0.06)	22	0.87	0.3934
Short-distance migrants	71	74	**0.19 (± 0.07)**	74	**2.64**	**0.0102**	0.11 (± 0.06)	71	1.90	0.0619
Long-distance migrants	70	67	0.01 (± 0.10)	73	0.08	0.9328	0.10 (± 0.05)	64	1.94	0.0571
European distribution										
Central	22	22	0.02 (± 0.17)	23	0.09	0.9271	0.02 (± 0.13)	21	0.13	0.8947
Northern	68	69	0.13 (± 0.08)	70	1.70	0.0930	0.11 (± 0.06)	67	1.70	0.0882
Southern	53	51	0.10 (± 0.12)	56	0.86	0.3951	**0.20 (± 0.06)**	48	**3.14**	**0.0029**
Widespread	65	66	0.05 (± 0.04)	66	1.23	0.2239	0.02 (± 0.03)	65	0.73	0.4708
Protection status										
Non-protected	94	97	**0.12 (± 0.05)**	98	**2.43**	**0.0168**	**0.06 (± 0.02)**	93	**3.29**	**0.0014**
Endangered	28	28	0.03 (± 0.06)	28	0.43	0.6692	0.03 (± 0.06)	28	0.43	0.6692
Highly endangered	56	55	0.10 (± 0.09)	57	1.02	0.3137	0.14 (± 0.07)	54	1.86	0.0679
Critically endangered	30	28	0.03 (± 0.20)	32	0.16	0.8769	0.19 (± 0.16)	26	1.21	0.2344
Total	208	208	0.09 (± 0.05)	215	1.91	0.0576	**0.09 (± 0.03)**	201	**3.00**	**0.0030**

Table 2 The effects of ecological characteristics of bird species expressed as four factors on changes in their mean occupancy between 1985–1989 and 2001–2003 tested by one-way ANOVAs (seperate tests for each factor) with (a) and without (c) 14 species present in only one of the mappings, and by main effects ANOVAs (all factors included into one model) with (b) and without (d) 14 species present in only one of the mappings. See Table 1 for identification of the levels of each factor

Factor	a)		b)		c)		d)	
	$F_{3,211}$	P	$F_{3,202}$	P	$F_{3,197}$	P	$F_{3,188}$	P
Habitat requirements	**6.6040**	**0.0003**	**5.7691**	**0.0008**	2.4741	0.0628	2.1731	0.0926
Migratory strategy	1.1359	0.3355	0.2256	0.8785	1.1795	0.9102	0.1149	0.9512
European distribution	0.2533	0.8589	0.3632	0.7796	1.8702	0.1471	1.6522	0.1789
Protection status	0.2152	0.8858	0.3402	0.7963	1.0695	0.3631	0.2533	0.8589

Fig. 1 Mean changes in the occupancy of Czech birds between 1985–1989 and 2001–2003 according to their habitat requirements. The vertical bars denote 0.95 confidence intervals. In one-way ANOVA, $F_{3,211} = 6.6040$ and $P = 0.0003$. Pairwise comparisons of means by the Tukey test gave the following results: Forest different from Farmland ($P = 0.0138$) and Wetland different from Farmland ($P = 0.0001$)

Appendix 1 List of species and their habitat requirements (habitat: A – farmland, F – forest, U – urban, W –

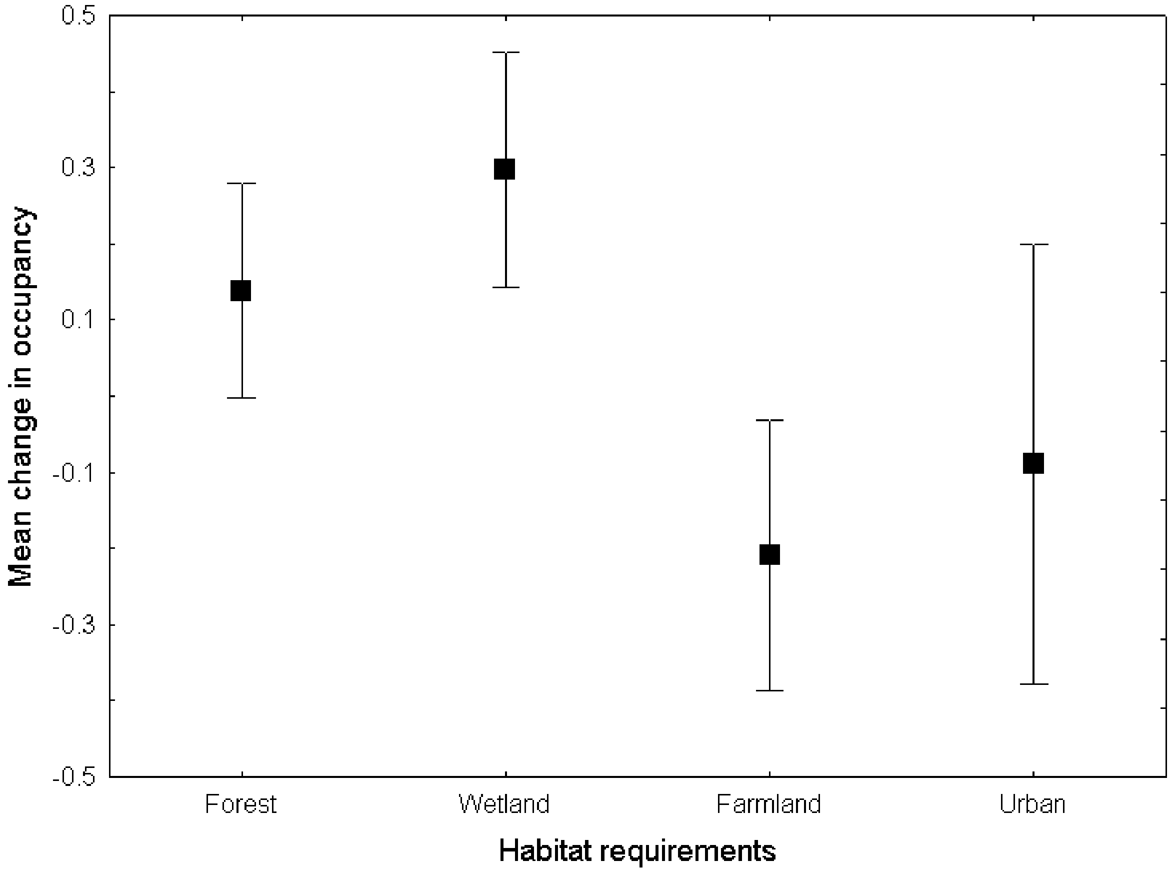
wetland), migratory strategy (migration: R – resident, P – partial migrants, S – short-distance migrants, L – long-distance migrants), European distribution (distribution: C – central, N – northern, S – southern, W – widespread) and legal protection status (protection: N – non-protected, E – endangered, H – highly endangered, C – critically endangered) in the Czech Republic

Species	Habitat	Migration	Distribution	Protection
Accipiter gentilis	F	R	W	E
Accipiter nisus	F	P	W	H
Acrocephalus arundinaceus	W	L	S	H
Acrocephalus palustris	A	L	N	N
Acrocephalus scirpaceus	W	L	W	N
Acrocephalus schoenobaenus	W	L	N	N
Actitis hypoleucos	W	L	W	H
Aegithalos caudatus	F	R	W	N
Aegolius funereus	F	R	N	H
Alauda arvensis	A	S	W	N
Alcedo atthis	W	P	S	H
Anas acuta	W	S	N	C
Anas clypeata	W	S	N	H
Anas crecca	W	S	N	E
Anas penelope	W	S	N	N
Anas platyrhynchos	W	P	W	N
Anas querquedula	W	L	N	H
Anas strepera	W	S	C	E
Anser anser	W	S	N	N
Anthus campestris	A	L	S	H
Anthus pratensis	A	S	N	N
Anthus spinoletta	A	S	S	H
Anthus trivialis	F	L	W	N
Apus apus	U	L	W	E
Aquila heliaca	F	P	C	N
Aquila pomarina	F	L	C	C
Ardea cinerea	W	S	W	N
Ardea purpurea	W	L	S	C
Asio flammeus	A	S	N	H
Asio otus	A	P	W	N
Athene noctua	U	R	S	H
Aythya ferina	W	S	N	N
Aythya fuligula	W	S	N	N
Aythya nyroca	W	S	C	C
Bonasa bonasia	F	R	N	H
Botaurus stellaris	W	S	C	C
Bubo bubo	F	R	W	E
Bucephala clangula	W	S	N	H
Burhinus oedicnemus	A	L	S	C
Buteo buteo	F	P	W	N
Caprimulgus europaeus	F	L	W	H
Carduelis cannabina	U	S	W	N
Carduelis carduelis	U	P	S	N
Carduelis flammea	F	R	N	N
Carduelis chloris	U	P	W	N
Carduelis spinus	F	S	N	N
Carpodacus erythrinus	A	L	N	E
Certhia brachydactyla	F	R	S	N
Certhia familiaris	F	R	N	N
Ciconia ciconia	U	L	S	E
Ciconia nigra	F	L	S	H
Cinclus cinclus	W	R	W	N
Circus aeruginosus	W	L	C	E
Circus cyaneus	F	S	N	H

791	*Circus pygargus*	A	L	S	H
792	*Coccothraustes coccothraustes*	F	S	S	N
793	*Columba livia* f. *domestica*	U	R	W	N
794	*Columba oenas*	F	S	W	H
795	*Columba palumbus*	F	S	W	N
796	*Coracias garrulus*	A	L	S	C
797	*Corvus corax*	F	R	W	E
798	*Corvus cornix*	A	R	W	N
799	*Corvus corone*	A	R	S	N
800	*Corvus frugilegus*	U	P	C	N
801	*Corvus monedula*	U	P	W	H
802	*Coturnix coturnix*	A	L	S	H
803	*Crex crex*	A	L	N	H
804	*Cuculus canorus*	A	L	W	N
805	*Cygnus olor*	W	P	C	N
806	*Delichon urbica*	U	L	W	N
807	*Dendrocopos leucotos*	F	R	W	H
808	*Dendrocopos major*	F	R	W	N
809	*Dendrocopos medius*	F	R	C	E
810	*Dendrocopos minor*	F	R	N	N
811	*Dendrocopos syriacus*	F	R	S	H
812	*Dryocopus martius*	F	R	N	N
813	*Egretta alba*	W	S	S	H
814	*Egretta garzetta*	W	L	S	H
815	*Emberiza citrinella*	A	R	W	N
816	*Emberiza hortulana*	A	L	W	C
817	*Emberiza schoeniclus*	W	S	N	N
818	*Erithacus rubecula*	F	S	W	N
819	*Falco cherrug*	F	P	C	C
820	*Falco peregrinus*	A	P	W	C
821	*Falco subbuteo*	F	L	W	H
822	*Falco tinnunculus*	U	P	W	N
823	*Falco vespertinus*	A	L	C	C
824	*Ficedula albicollis*	F	L	C	N
825	*Ficedula hypoleuca*	F	L	N	N
826	*Ficedula parva*	F	L	N	H
827	*Fringilla coelebs*	F	S	W	N
828	*Fulica atra*	W	S	W	N
829	*Galerida cristata*	A	R	S	E
830	*Gallinago gallinago*	W	S	N	H
831	*Gallinula chloropus*	W	S	W	N
832	*Garrulus glandarius*	F	P	W	N
833	*Glaucidium passerinum*	F	R	N	H
834	*Grus grus*	W	S	N	C
835	*Haliaeetus albicilla*	W	R	N	C
836	*Himantopus himantopus*	W	L	S	N
837	*Hippolais icterina*	F	L	N	N
838	*Hirundo rustica*	U	L	W	E
839	*Charadrius dubius*	W	L	W	N
840	*Charadrius hiaticula*	W	L	N	N
841	*Charadrius morinellus*	A	S	N	C
842	*Chlidonias hybridus*	W	L	S	N
843	*Chlidonias niger*	W	L	C	C
844	*Ixobrychus minutus*	W	L	S	C
845	*Jynx torquilla*	A	L	W	H
846	*Lanius collurio*	A	L	N	E
847	*Lanius excubitor*	A	P	W	E
848	*Lanius minor*	A	L	S	H
849	*Lanius senator*	A	L	S	H
850	*Larus cachinnans*	W	S	S	N

851	*Larus canus*	W	S	N	N
852	*Larus melanocephalus*	W	S	C	H
853	*Larus ridibundus*	W	S	N	N
854	*Limosa limosa*	W	L	C	C
855	*Locustella fluviatilis*	A	L	C	N
856	*Locustella luscinioides*	W	L	C	E
857	*Locustella naevia*	A	L	N	N
858	*Loxia curvirostra*	F	P	N	N
859	*Lullula arborea*	F	S	S	H
860	*Luscinia luscinia*	A	L	N	H
861	*Luscinia megarhynchos*	A	L	S	E
862	*Luscinia svecica cyanecula*	W	S	S	H
863	*Luscinia svecica svecica*	W	S	N	C
864	*Mergus merganser*	W	S	N	C
865	*Merops apiaster*	A	L	S	H
866	*Miliaria calandra*	A	P	S	C
867	*Milvus migrans*	F	L	S	C
868	*Milvus milvus*	F	S	S	C
869	*Motacilla alba*	U	S	W	N
870	*Motacilla cinerea*	W	S	S	N
871	*Motacilla flava*	A	L	W	H
872	*Muscicapa striata*	F	L	W	E
873	*Netta rufina*	W	S	S	H
874	*Nucifraga caryocatactes*	F	R	N	E
875	*Numenius arquata*	W	S	N	C
876	*Nycticorax nycticorax*	W	L	S	H
877	*Oenanthe oenanthe*	A	L	W	H
878	*Oriolus oriolus*	F	L	S	H
879	*Otis tarda*	A	R	S	C
880	*Otus scops*	F	L	S	C
881	*Pandion haliaetus*	W	L	N	C
882	*Panurus biarmicus*	W	P	S	H
883	*Parus ater*	F	R	W	N
884	*Parus caeruleus*	F	P	W	N
885	*Parus cristatus*	F	R	W	N
886	*Parus major*	F	P	W	N
887	*Parus montanus*	F	R	N	N
888	*Parus palustris*	F	R	C	N
889	*Passer domesticus*	U	R	W	N
890	*Passer montanus*	A	R	S	N
891	*Perdix perdix*	A	R	C	E
892	*Pernis apivorus*	F	L	N	H
893	*Phalacrocorax carbo*	W	S	N	E
894	*Phasianus colchicus*	A	R	C	N
895	*Phoenicurus ochruros*	U	S	S	N
896	*Phoenicurus phoenicurus*	F	L	W	N
897	*Phylloscopus collybita*	F	S	W	N
898	*Phylloscopus sibilatrix*	F	L	N	N
899	*Phylloscopus trochiloides*	F	L	N	N
900	*Phylloscopus trochilus*	F	L	N	N
901	*Pica pica*	A	R	W	N
902	*Picoides tridactylus*	F	R	N	H
903	*Picus canus*	F	R	N	N
904	*Picus viridis*	F	R	S	N
905	*Platalea leucorodia*	W	S	S	C
906	*Podiceps cristatus*	W	S	N	E
907	*Podiceps grisegena*	W	S	N	H
908	*Podiceps nigricollis*	W	S	C	E
909	*Porzana parva*	W	L	C	C
910	*Porzana porzana*	W	L	N	H

Prunella collaris	A	S	S	H
Prunella modularis	F	S	W	N
Pyrrhula pyrrhula	F	P	N	N
Rallus aquaticus	W	S	S	H
Recurvirostra avosetta	W	S	S	C
Regulus ignicapillus	F	S	S	N
Regulus regulus	F	S	N	N
Remiz pendulinus	W	S	S	E
Riparia riparia	A	L	W	E
Saxicola rubetra	A	L	N	E
Saxicola torquata	A	S	S	E
Scolopax rusticola	F	S	N	E
Serinus serinus	U	S	S	N
Sitta europaea	F	R	W	N
Sterna hirundo	W	L	N	H
Streptopelia decaocto	U	R	S	N
Streptopelia turtur	A	L	S	N
Strix aluco	F	R	W	N
Strix uralensis	F	R	N	C
Sturnus vulgaris	F	S	W	N
Sylvia atricapilla	F	S	W	N
Sylvia borin	F	L	W	N
Sylvia communis	A	L	W	N
Sylvia curruca	U	L	N	N
Sylvia nisoria	A	L	C	H
Tadorna tadorna	W	S	W	N
Tachybaptus ruficollis	W	S	S	E
Tetrao tetrix	A	R	N	H
Tetrao urogallus	F	R	N	C
Tringa ochropus	F	S	N	H
Tringa totanus	W	S	N	C
Troglodytes troglodytes	F	S	W	N
Turdus iliacus	F	S	N	H
Turdus merula	F	P	W	N
Turdus philomelos	F	S	W	N
Turdus pilaris	F	S	N	N
Turdus torquatus	F	S	N	H
Turdus viscivorus	F	S	W	N
Tyto alba	U	R	S	H
Upupa epops	A	L	S	H
Vanellus vanellus	A	S	N	N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0.3
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Mean change in occupancy
Forest
Wetland
Farmland
Urban
Habitat requirements