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Landscape and patch characteristics affecting the assemblages of birds in reedbeds in terrestrial matrix

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We conducted an analysis of relationships between results of survey on breeding community of birds, including species richness, abundance of individual species and ecological groups of birds, and habitat features of 91 isolated reed patches in southwestern Poland. The approach to the reedbed habitat involves environmental differentiation at the patch level, landscape context and isolation, including the impact of man-made structures as potential constraints to the occurrence of birds. Generalized linear models have shown that 12 out of 14 analyzed environmental predictors had a statistically significant effect on birds. The results from individual species (sedge warbler, great reed warbler, bluethroat, Savi's warbler, water rail, moorhen and coot) models revealed that the number of territories was affected from two to four predictors. The number of reedbed specialists was affected positively by reed edge, water area and proportion of reed habitat within a 100-m radius, and negatively by railway. The number of water birds was affected positively by reedbed area, internal reed edge, treebelt, distance to reedbed > 1 ha and a proportion of reed habitat within a 100-m radius, and negatively by external reed edge. The proportion of reed habitat within a 100-m radius and internal reed edge were the predictors which positively affected richness of bird species. Our results showed that, apart from the habitat features measured within a reedbed, i.e. area of a reed patch, length of external edge or presence of trees, some other factors measured in larger landscape context, i.e. isolation (expressed mainly as the proportion of reed habitat within a 100-m radius) and the presence of man-made structures are important predictors in explaining the abundance of birds. The area sensitivity of birds nesting in reedbeds in terrestrial habitat was considerably lower than in reed islands located in lakes and wetlands of southern Europe.

Introduction

Reedbeds are broadly recognized as an important habitat for some birds, including endangered and declining species. In Europe, within reedbeds a specific fauna of birds and other groups of animals (mainly invertebrates) has evolved (Bibby & Lunn 1982, Tscharntke 1992, Heath &

Evans 2000, Hoi 2001, Valkama *et al*. 2008). In a narrow sense, reedbeds are formed by monospecific stands of the common reed *Phragmites australis*, although in some habitat conditions reed may occur simultaneously with other plants, including woody species, which depends mainly on the presence of water and height its level. Hereafter, we use the term 'reedbed' referring to habitats dominated by the common reed. The reed has a very broad habitat tolerance and may occur in different habitats, from dry, agricultural land to marshland habitats. The reed may therefore displace other, more valuable associations of marshland vegetation, i.e. sedges *Carex* spp. or peat mosses (e.g. in primeval conditions of Biebrza National Park), hence in some regions of the World (e.g. North America) and in newly colonized areas, it is recognized as an invasive plant species (reviews in Boszke *et al*. 2005, Valkama *et al*. 2008). Nowadays, in many human-transformed landscapes of Europe reedbeds are often the only remnants of marshland habitats within large agricultural or other anthropogenic areas; therefore, they play an important role as remnant habitats for birds and other animal species (Tscharntke 1992, Foppen *et al*. 2000, Fouque *et al*. 2002).

From the perspective of landscape ecology, isolated wetlands distributed over large areas of human-dominated landscapes, including agricultural or built-up areas, provide suitable material for exploration of bird–habitat relationships, including factors affecting distribution patterns of species with narrow ecological requirements (Foppen *et al*. 2000, Verboom *et al*. 2001). The presence of birds in reedbeds may be affected by both the internal (within-patch) and external features of a reed patch. Within-patch environmental variables affecting the presence and abundance of birds include: reed patch area, length of a reedbed edge, proportion of the waterlogged reeds, structure of reed stand and presence of other vegetation, including emerged water plants (Foppen *et al*. 2000, Poulin *et al*. 2002, 2005, Martínez-Vilalta *et al*. 2002, Baldi 2006). Although many papers have underlined the great importance of the reedbed size for some species, mainly for birds with large body size (Baldi & Kisbenedek 1998), this variable is not the main predictor of the presence of birds in a reed patch. External factors include the landscape context of a reed patch, i.e. its isolation (e.g. connectivity) and habitat composition surrounding it (Foppen *et al*. 2000, Verboom *et al*. 2001, Baldi 2006). The disappearance of differentiated structure of reed stands, including waterlogged parts of reedbeds, is quoted as the main reason for the decline of the great reed warbler (*Acrocephalus arundinaceus*) in western Europe (Graveland 1998). Similarly, in France and Great Britain, the bittern (*Botaurus stellaris*) occurs in wet reedbeds and avoids areas colonized by willows (Gilbert *et al*. 2005, Poulin *et al*. 2005).

The numbers of some small reedbed passerines are affected more by the length of a reedbed edge than by its size (Baldi & Kisbenedek 1999, Foppen *et al*. 2000), which is largely due to the fact that these birds use the adjacent habitats (Surmacki 2005). Therefore, for an effective management and conservation of reedbed avifauna, especially in terrestrial environments, recognition of all environmental requirements of birds is essential. On the other hand, the distinction between the area and the habitat quality effects causes difficulties, and there is still a shortage of studies on how these two groups of variables affect the reed birds (Baldi & Kisbenedek 2000). Additionally, communities of birds inhabiting isolated wetlands may be affected by the surrounding matrix and man-made structures, i.e. roads, as well as by the form of adjacent land-use (Whited *et al*. 2000). Moreover, it seems that nowadays, during rapid development of transportation infrastructure, roads and growing traffic intensity as well as noise associated with it can negatively affect the richness and abundance of birds directly and indirectly, through traffic mortality and alternation of habitat quality, respectively (Forman *et al*. 2002, Holm & Laursen 2011, Summers *et al*. 2011). Therefore, there is an urgent need to identify key anthropogenic factors shaping the avian community in various landscapes or habitat types.

The aim of the present study was to carry out an analysis of relationships between breeding bird community, including avian diversity, number of individual species and ecological groups of birds, and habitat features of reedbeds located in a terrestrial environment; some of these reedbeds serve as natural waste-water treatment plants. The approach to the reedbed habitat involves the environmental differentiation both at the patch and landscape levels, including the potential impact of man-made structures on the occurrence of birds. Our study differs from others mostly with regard to the habitat modelling and requirements of reedbed birds. First, although many studies on bird–habitat relationships and requirements of reed birds during the breeding season have recently been conducted in Europe, most of them were carried out in areas with permanent water presence, i.e. river estuaries, lakes or near sea coasts (e.g. Bibby & Lunn 1982, Baldi & Kisbenedek 2000, Poulin *et al*. 2002, Baldi 2006, Paracuellos 2006). Second, papers dealing with habitat requirements of bird communities in reedbeds located in human-dominated landscapes are scarce and, additionally, many of these publications are restricted only to the individual species (e.g. Foppen *et al*. 2000). Furthermore, whereas other studies analysing bird–habitat relationships involved just the isolation and general land-use characteristics (water, reed and land) around a patch as the main landscape variables, we measured other impacts on bird abundance linked with human activity, such the presence of railways, built-up areas and roads. Moreover, the results of our studies may prove to be very useful for the designation and creation of artificial wetlands for reedbed avifauna, especially today, when large financial means are invested in marshland restoration projects (Hawke & Jose 1996, White & Gilbert 2003). In time of the global disappearance of wetland habitats (Fouque *et al*. 2002, Nivet & Frazler 2004) this study also underlines the essential role of reedbeds growing at wastewater treatment sites as habitats for many declining bird species and the importance of their incorporation into the areas with high conservation status. The present paper is based on a survey conducted in the area recognized as one of the Important Bird Areas in Europe (Wilk *et al*. 2010). The main criterion for its approval as IBA was the remarkable proportion of the bluethroat (*Luscinia svecica*) population, accounting for about 4% of its total number in Poland (Orłowski & Sęk 2005, Orłowski *et al*. 2008).

Material and methods

Study area and reedbed characteristics

The research was conducted on a sewage farm (51°08´23´´–51°12´22´´N, 16°56´14´´–17°00´19´´E) located in the northern, peripheral part of the City of Wrocław (640 000 inhabitants), southwestern Poland. The surveyed area (ca. 1400 ha) was shaped entirely by the human activity in the second half of the 19th century, as a natural sewage treatment facility, by levelling the remaining parts of natural river-beds of two rivers, Odra and Widawa (J. Paluch unpubl. data). The research focused on extensively used (partly disused) sedimentation basins and reserve fields overgrown by reed. Locally, some reedbeds with permanent water (with small depth up to only several cm) presence had some other emergent vegetation [i.e. reedmace (*Typha platyphyllos*) and sweet flag (*Acorus calamus*)] growing along the border between the reed and water. The reedbeds were located in the open terrain, surrounded by meadows (that covered ca. 90% of the total study area); only a small proportion of reedbeds was partially surrounded by bushes or trees. Larger suburban woods border the area in the north, west and south. The area is not inhabited; some small settlements lie outside (Fig. 1). Apart from two cobbled roads, one major thoroughfare and a busy railway run along the eastern border of the surveyed area. In recent years, a gradual drying of many reedbeds has been taking place, due to the opening of a new sewage-treatment plant in another location that cut by more than a half the amount of sewage delivered to the area (150 000 m^3 per day^{-1} in the 1980s, 50 000–70 000 m^3 day^{-1} now) (J. Paluch pers. comm.).

In total, 91 reedbeds were selected (all in this area), situated in small, walled, regular-shaped sedimentation basins or in some semi-natural depressions, partly filled with sewage water, with an irregular and varied shorelines. All reedbeds were isolated and homogenous reed patches with distinct borders that, in some cases, run along roads or railway embankment. Using aerial photos and ordnance survey maps (1:25 000 and 1:50 000), we measured 14 habitat, landscape and isolation variables describing

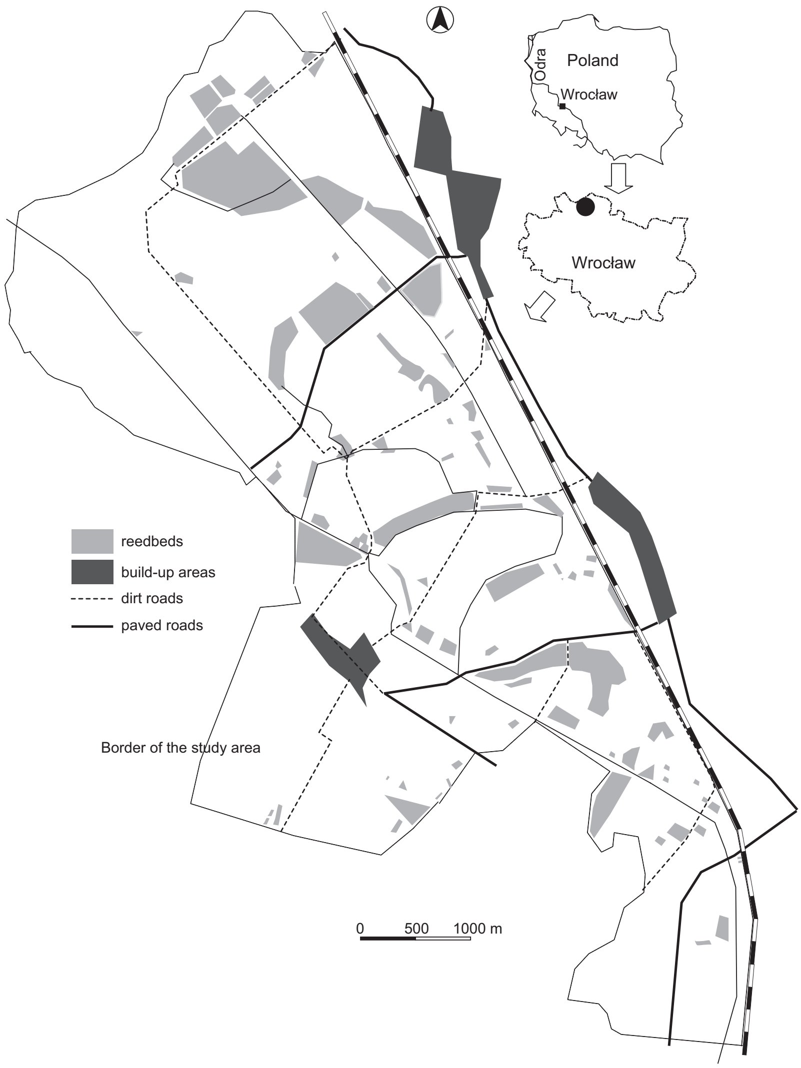

Fig. 1. Spatial distribution of 91 reedbeds on the sewage farm in Wrocław, southwestern Poland.

the surveyed reedbeds; these were: (1) reedbed area, (2) length of external (outer) reed edge (hereafter 'reed edge'), (3) shape, (4) length of internal (inner) reed edge ('internal reed edge'), (5) water area, (6) length of adjacent treebelt ('treebelt'), (7) length of adjacent dirt road ('dirt road'), (8) length of adjacent paved road ('paved road'), (9) distance to railway ('railway'), (10) distance to built-up area ('built-up area'), (11) distance to nearest reedbed, (12) distance to reedbed > 1 ha, (13) proportion of reed habitat within a 100-m radius, (14) proportion of reed habitat within a 300-m radius (Table 1).

Reedbed area varied widely (Table 1), and the distribution of this variable was clearly left-skewed (Kolmogorov-Smirnoff test: $D = 0.32$, $p < 0.01$). Eighty two (90%) reedbeds did not exceed 5 ha (*see* Results). The total area of reedbeds was 162.73 ha. Over the last years, the areas of some reed patches have increased as a result of spontaneous development of reed stands.

Shape (after Baldi 2006) was calculated as the ratio of the edge length of a reed patch to the length of the edge of a circle with the same area. The value of this index was the smallest for the narrow and elongated reed patches, and the highest for the round or almost circular ones. Internal reed edge was found in 47 (52%) reedbeds. This variable was measured within compact, monospecific reed stands, along the border with open water.

Water area (presence of permanent water) was found for 37 (41%) reedbeds, which were regularly flooded by sewage; only one reservoir contained water after the purification process. In most reedbeds, the open water was bordered with reed stands. In a few wet reedbeds it was not possible to measure the extension of open water; therefore, water area for these patches was assumed to be 0.01 ha.

Length of adjacent treebelt, dirt and paved roads was measured along the reedbed border. Treebelts grew around 60 (66%) reedbeds. They comprised broad-leaved species, mainly old specimens of the pedunculate oak (*Quercus robur*), white willow (*Salix alba*), crack willow (*Salix fragilis*), poplar (*Populus* spp.), domestic apple (*Malus domestica*), common pear (*Pyrus communis*) and sweet cherry (*Prunus avium*). Dirt and paved roads were found in 62 (68%) and 13 (14%) reedbeds, respectively; both these types of the roads run along the borders of reedbeds, hence we accepted that their lengths are a better measure of impact of roads than the distance between the road and the centre of the reedbed. Traffic on the dirt roads was either very limited or non-existent. Paved roads were characterized by the stone (cobbled) surface and periodically high traffic, mainly during the day between 06:00 and 18:00 (up to several hundred of cars per day), despite the fact that these roads are very narrow (6 m) and not adapted to such a high traffic flow. Paved roads have been intensively used in the last few years, which reflects the intensive urbanization of the surrounding settlements.

For the rest of the variables, including two variables explaining isolation of reedbed (distance to nearest reedbed and distance to reedbed > 1 ha), the edge of a reed patch was accepted as a starting point for measuring the shortest distance between reedbeds and other habitats, i.e. railway and built-up area.

Isolation was expressed also as the proportion of the total cover of reed within the radii of 100 m and 300 m (herafter, proportion of reed habitat) around each reed patch. These two variables may be treated also as landscape variables (Baldi 2006), however, considering the presence of many other non-reed habitats (e.g. trees or roads) and a large number of very small reed patches (53% of reedbeds did not exceed 0.5 ha) distributed mainly around large reedbeds (Fig. 1), we accepted that they could be suitable for explaining spatial isolation of a reedbed. Furthermore, values of these variables are useful for the comparison of the total extent of reedbeds with the territory size and home range of different species of reed birds.

Table 1. Descriptive statistics of habitat and landscape variables of 91 reedbeds used in modeling of the number of breeding birds on the sewage farm in Wrocław.

Variable (unit)	Median	Mean ± SE	95%CL	Min	Max
Habitat variables					
Reedbed area (ha)	0.50	1.79 ± 0.39	1.01–2.57	0.016	29.30
Reed edge (m)	328	493.6 ± 47.9	398.5–588.7	40	2301
Shape	0.81	0.81 ± 0.01	0.79–0.84	0.39	1.27
Internal reed edge (m)	5	147.6 ± 26.6	94.72–200.51	0	1152
Water area (ha)	0	0.18 ± 0.06	0.06–0.29	0	4.25
Landscape variables					
Treebelt (m)	19	87.18 ± 17.09	53.23–121.13	0	897
Dirt road (m)	60	116.96 ± 18.21	80.78–153.13	0	1024
Paved road (m)	0	20.96 ± 10.14	0.82–41.09	0	768
Distance to railways (m)	623	781.08 ± 61.50	658.90–903.25	10	2108
Distance to built-up area (m)	570	626.90 ± 35.35	556.67–697.14	76	1650
Isolation					
Distance to nearest reedbed (m)	28	63.77 ± 9.38	45.18–82.35	4	505
Distance to reedbed > 1 ha (m)	90	167.01 ± 18.49	130.27–203.75	4	748
Percentage of reed habitat within a 100-m radius	61.1	51.22 ± 3.30	44.67–57.77	0.95	95.93
Percentage of reed habitat within a 300-m radius	12.3	19.44 ± 17.95	15.70–23.18	0.53	81.38

Bird data

The distribution and abundance of territories, and breeding pairs of birds (hereafter, 'bird territories') in reedbeds were evaluated in the field from the beginning of April until the second half of June 2008 using the territory mapping method (Bibby *et al*. 1992). The census results were plotted on the 1:12 500 maps. Each reed patch was visited at least four times, including one night census in June (to detect vocal activity of rails and crakes). Three censuses started at dawn and lasted until around 10:00. For detection of evidence of breeding of shy and secretive water birds, namely rails and ducks (i.e. presence of their nests, fledglings and families) nesting within large reedbeds, the censuses on open water were carried out 5–8 times during the breeding period with the use of a spotting scope. Additionally, a census of reed warbler (*Acrocephalus scirpaceus*) territorries was carried out at the turn of June and July, by visiting small reed patches which grew only in late spring.

The field-visit duration in one reedbed varied with its size and lasted from a few minutes to three hours. Small reed patches were surveyed along their external edges. In larger reedbeds, over 100 m wide, the counts were conducted also inside a reedbed along parallel lines about 100 m apart. During censuses special attention was paid to the simultaneous records of singing males and to their movements during (or immediately after) display flights, mainly in the case of the bluethroat and sedge warbler (*Acrocephalus schoenobaenus*). The abundance of most small passerines [*Acrocephalus* and *Locustella* warblers; reed bunting (*Emberiza schoeniclus*), bluethroat, yellow wagtail (*Motacilla flava*), whinchat (*Saxicola rubetra*) and stonechat (*S. torquata*), rails and corncrake (*Crex crex*)] was mainly based on a minimum of two records (registrations) of a singing male at least 14 days apart. The number of territories of the other species (and in some cases also the ones mentioned above) was assessed based on other evidence of breeding, i.e. presence of occupied nests [little grebe (*Tachybaptus ruficollis*), mute swan (*Cygnus olor*), penduline tit (*Remiz pendulinus*)], presence of fledglings [ducks, moorhen (*Gallinula chloropus*), coot (*Fulica atra*)], presence of adult birds with food and nesting material [crane (*Grus grus*) and marsh harrier (*Circus aeruginosus*)] or upset birds. Due to the small detectability and high density of reed warbler, associated with the hardly audible song and singing activity in females (Borowiec & Ranoszek 1984, Cramp 1998), we did not obtain a reliable data on the abundance of this species, hence in the Results only frequencies of its distribution in reedbeds were provided. The Results include the data on the size of the smallest occupied reedbed and the number of reedbeds with a given bird species. Bearing in mind the small number of field visits (classic mapping method recommends eight censuses in a breeding season; e.g. Moskat & Baldi 1999), our results should be treated only as an index of bird abundance, which still can be useful in modelling bird-habitat relationships in reed habitats (*sensu* Foppen *et al*. 2000).

All bird species recorded in the surveyed reedbeds were divided into three ecological groups: reedbed specialists, waterbirds and habitat generalists. This division corresponds to the habitat requirements of particular species in central Europe and Poland (according to Cramp 1998, Tomiałojć & Stawarczyk 2003). Due to the lack of reliable data on the number of small reed warblers, it was not possible to calculate the proportions of three ecological groups of birds in the total community, and thus their further use in the statistical analysis.

Statistical analyses

The associations between the number of the bird territories (i.e. the eight most numerous species, including five reedbed specialists: sedge warbler, great reed warbler, reed bunting, bluethroat, Savi's warbler (*Locustella luscinioides*) and three species of water birds: water rail, moorhen and coot), three specified ecological groups of birds (reedbed specialists, waterbirds and habitat generalists), the whole community of birds and the number of species and 14 environmental variables of reedbeds (Table 1) were analyzed using a Generalized Linear Model's (GLZ) multivariate analysis in Statistica ver. 7.1 (Hosmer and Lemeshow 1989, StatSoft 2006). This approach identifies the relative importance

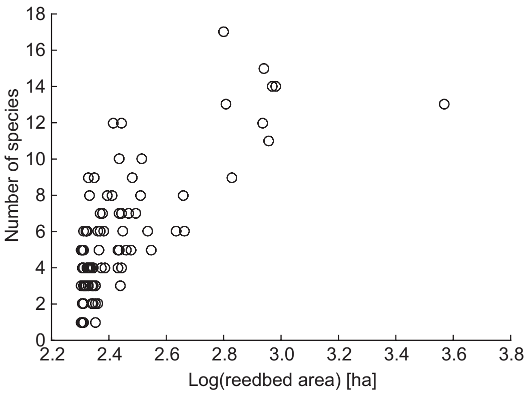

Fig. 2. The relationship between the number of bird species and area of 91 reedbeds on the sewage farm in Wrocław, southwestern Poland; Number of species = –24.69 + 12.44 × log(reedbed area).

of all distinguished variables as potential constraints of avian species occurrence. In GLZ models, a normal distribution with logarithmic link function was applied (McCullagh & Nelder 1989). To validate the proposed models, the Wald (χ^2) statistics was used to check the significance of the regression coefficient for each parameter. A goodnes-of-fit of the whole model was assessed using the ratio of the residual deviance to the residual degrees of freedom (res. dev./res. df). Despite the fact that in our study the two variables indicating the size of a reed patch — area and length of external reed edge (after Foppen *et al*. 2000) — were highly correlated (Spearman's correlation: $r_s = 0.965, p < 0.0001$), we decided to retain these variables in GLZ models simultaneously. Such approach resulted from different sensitivity (preference or avoidance) of individual species and groups of birds to edge and/or interior of a reed stand (Baldi & Kisbenedek 1999).

The marsh warbler (*Acrocephalus palustris*) was excluded from the modelling of bird–habitat relationships because this species is a habitat generalist, and in our study occurred only in the narrow external belts of reedbeds and in other non-reed vegetation (i.e. herbaceous).

Due to the lack of satisfactory quantitative data on the abundance of the reed warbler, we applied a general linear model (GLM) with the use of presence–absence data for this bird species in surveyed reedbeds, and 14 environmental variables. These GLM results are presented separately in the Results and they show only the predictor variables which significantly affected the presence of this species.

Statistical analyses were performed using Statistica 7.1 (StatSoft 2006) and MSExcel.

Results

In total, 27 bird species were recorded. Between 1 and 17 species (average = 5.7, median = 5 species) were found in a single reedbed (Fig. 2). The most numerous group of birds were the reedbed specialists, whose total abundance (excluding reed warbler) amounted to 634 territories (68.3% of the whole community). The proportions of habitat generalists (n = 168) and water birds (n = 126) were 18.1% and 13.6%, respectively. The greatest area requirements among all reed passerines had Savi's warbler (Table 2).

Presence of the breeding territories (pairs) was recorded in all surveyed reedbeds (range = 1–65). The average number of all territories per one reedbed amounted to 10.2 (95%CL = 7.4–12.9) with median = 5 (interquartile range, 3–11). The average density of the territories was the highest in the case of sedge warbler (Table 2).

The number of territories of all birds was not proportionally distributed in different size classes of reedbeds (Fig. 3). Large reedbeds (> 2 ha), comprising 74% of the total area, held 53% of all birds. An inverse relation was found in the case of reedbeds smaller than 2 ha, where in 26% of the total reedbed area, 47% of all birds were recorded (Fig. 3).

Results of GLZ showed that 12 out of 14 analyzed predictors (paved road and proportion of reed habitat within a 300-m radius excluded) had a significant influence on the number of bird territories, but their impact varied across individual species, three specified groups and the whole community of birds. In most cases, the direction of relationships of particular predictors was consistent across all presented models; only four predictors (reedbed area, external reed edge, built-up area and proportion of reed habitat within a 100-m radius) gave both, negative and positive results. The results presented in Table 3 revealed that in terms of the number of

Table 2. Number of territories and occurrence of birds in 91 reedbeds located on the sewage farm in Wrocław, southwestern Poland.

Species (ecological group[1])	Occupied reedbeds		Total number of territories	Mean (± SE) density[2] (territories 10 ha^{-1})	Maximum number of territories in one reedbed	Smallest occupied reedbed (ha)
	Number	Percentage				
Acrocephalus scirpaceus (R)	82	90.1	n.d.	n.d.	n.d.	0.03
Acrocephalus schoenobaenus (R)	64	70.3	267	44.1 ± 7.8	19	0.02
Emberiza schoeniclus (R)	78	85.7	149	40.9 ± 7.5	11	0.02
Acrocephalus arundinaceus (R)	49	53.8	107	20.0 ± 3.7	9	0.05
Acrocephalus palustris (H)	52	57.1	105	36.4 ± 8.1	10	0.02
Luscinia svecica (R)	34	37.4	64	7.3 ± 1.8	7	0.10
Locustella luscinioides (R)	18	19.8	40	1.5 ± 0.4	5	0.36
Rallus aquaticus (W)	20	22.0	39	3.5 ± 1.2	6	0.31
Locustella naevia (H)	32	35.2	37	20.8 ± 8.2	2	0.02
Gallinula chloropus (W)	17	18.7	27	1.9 ± 0.7	6	0.29
Fulica atra (W)	12	13.2	26	1.4 ± 0.6	4	0.28
Anas platyrhynchos (W)	11	12.1	17	1.7 ± 0.8	4	0.31
Tachybaptus ruficollis (W)	8	8.8	10	–	2	0.27
Motacilla flava (H)	7	7.7	9	–	2	0.05
Crex crex (H)	4	4.4	5	–	2	4.36
Saxicola rubetra (H)	2	2.2	4	–	3	4.33
Circus aeruginosus (R)	4	4.4	4	–	1	6.46
Panurus biarmicus (R)	2	2.2	3	–	2	6.46
Anas crecca (W)	3	3.3	3	–	1	2.33
Locustella fluviatilis (H)	3	3.3	3	–	1	1.01
Grus grus (H)	2	2.2	2	–	1	9.69
Porzana porzana (W)	2	2.2	2	–	1	6.46
Cygnus olor (W)	2	2.2	2	–	1	1.69
Remiz pendulinus (H)	2	2.2	2	–	1	0.36
Saxicola torquata (H)	1	1.1	1	–	1	3.58
All birds	91		928[3]	234.6 ± 29.4	65	0.02

[1] Ecological groups of birds: R = reedbed specialists; W = waterbirds; H = habitat generalists, including species nesting in grassland and riparian woodland; [2] densities calculated for species that occurred in at least 10 reedbeds; [3] without *Acrocephalus scirpaceus*; nd = not determined.

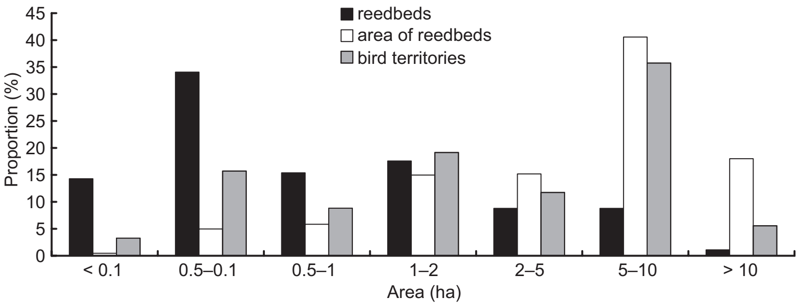

Fig. 3. Percentages of bird territories and 91 reedbed patches and their surface area on the sewage farm in Wrocław in various size classes of reedbeds.

significant effects the analyzed predictors can be ranked as follows: proportion of reed habitat within a 100-m radius (12), external reed edge and internal reed edge (5), water area (4), reedbed area and railway (3), treebelt and built-up area (2) and shape and dirt road (1).

The results from individual-species models revealed that the number of sedge warbler territories was affected by four predictors, including three positive (reed edge, water area and proportion of reed habitat within a 100-m radius) and one negative (railway) interaction. The number of great reed warbler territories was positively affected by reed edge, distance to reedbed > 1 ha and proportion of reed habitat within a 100-m radius, and negatively by reedbed area. Only in the case of the reed bunting we did not find any significant effect. The number of bluethroat territories was positively affected by water area and proportion of reed habitat within a 100-m radius. The number of territories of Savi's warbler was positively affected by proportion of reed habitat within a 100-m radius and negatively by distance to built-up area. Internal reed edge and proportion of reed habitat within a 100-m radius were factors positively affecting the number of the water rail. The abundance of moorhen was positively affected by five variables, i.e. internal reed edge, treebelt, dirt road, distance to reedbed > 1 ha and proportion of reed habitat within a 100-m radius. The abundance of coot was associated with two variables explaining isolation of reedbeds, i.e. distance to reedbed > 1 ha and proportion of reed habitat within a 100-m radius.

The number of reedbed-specialist territories was associated positively with four predictors (reed edge, water area, distance to reedbed > 1 ha and proportion of reed habitat within a 100-m radius), and negatively with one (railway). The number of water birds was significantly affected by six predictors, five influencing positively (reedbed area, internal reed edge, treebelt, distance to reedbed > 1 ha and the proportion of reed habitat within a 100-m radius), and one negatively (external reed edge). Habitat generalists were positively associated with built-up area, and negatively with shape and proportion of reed habitat within a 100-m radius. The number of all birds was related to five predictors, including four positive effects (external and internal reed edge, water area, distance to reedbed > 1 ha, proportion of reed habitat within a 100-m radius), and one negative (railway).

Species richness (expressed as the number of all species) was positively associated with two factors: internal reed edge and proportion of reed habitat within a 100-m radius.

The presence–absence GLM model for the reed warbler revealed a significant effect of two predictors, namely distance to reedbed > 1 ha ($p = 0.005$) and proportion of reed habitat within a 100-m radius ($p = 0.003$).

Discussion

Our results show that habitat variables describing individual reed patch, landscape features and isolation of reedbeds were factors influencing the number of breeding birds, but among individual species and groups of birds there was a great variation in respect to the analyzed environmental variables. Most of our results concerning variables describing within-patch habitat characteristics, i.e. reedbed area, reed edge, internal reed edge and water area reflect general habitat requirements of individual species or group of birds. Importantly, this study shows that two var-

Table 3. Results (Wald χ^2) of all effects Generalized Linear Models (GLZ) exploring the influence of 14 landscape and habitat variables on the number of territories of particular species, ecological groups and the whole community of birds nesting in 91 reedbeds in southwestern Poland; the negative effect is indicated with ↓. Asterisks denote the significance level: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Species	Wald χ^2														Model goodness-of-fit (res. dev./res. df)
	Area	Reed edge	Shape	Internal reed edge	Water area	Treebelt	Dirt road	Paved road	Railway	Built-up area	Distance to nearest reedbed	Distance to reedbed > 1 ha	% reed within 100-m radius	% reed within 300-m radius	
Acrocephalus schoenobaenus	0.2	11.5***	↓0.5	2.1	10.1**	↓2.1	0.1	0.5	↓9.9**	0.1	↓1.2	↓0.6	3.7*	2.4	1.38
Acrocephalus arundinaceus	↓6.5*	5.0**	0.1	1.1	2.7	0.6	0.9	↓1.8	0.4	0.2	0.8	8.4**	6.0*	0.5	0.94
Emberiza schoeniclus	1.7	0.9	0.4	0.2	0.2	↓2.5	0.1	↓0.3	↓0.9	0.6	↓0.1	0.9	1.7	↓0.7	0.48
Luscinia svecica	4.5*	0.1	0.2	↓0.2	4.0*	↓1.8	0.2	0.3	0.1	0.1	0.1	0.1	3.9*	↓1.8	0.87
Locustella luscinioides	0.1	0.1	↓0.1	0.3	0.4	0.1	↓0.1	0.1	↓0.2	↓4.0*	2.1	1.7	7.7**	0.3	0.86
Rallus aquaticus	↓2.0	↓3.2	↓0.3	8.7*	0.2	1.9	2.1	0.1	0.1	↓0.1	↓0.4	3.0	7.8**	0.1	0.67
Gallinula chloropus	↓0.1	↓2.1	↓0.1	5.4*	0.6	10.3**	4.3*	2.9	0.4	0.1	↓0.1	3.7*	5.8*	↓0.3	0.64
Fulica atra	↓0.1	0.1	0.1	1.0	0.3	0.3	↓0.2	↓0.1	↓1.3	↓3.4	↓0.7	5.6*	4.6*	0.1	3.03
Reedbed specialists	0.3	18.9***	0.1	↓0.1	11.3***	↓3.1	↓0.1	↓1.8	↓5.0*	↓0.4	0.1	3.9*	20.4***	1.2	1.83
Waterbirds	9.5**	↓6.7**	↓0.7	31.4***	0.1	20.1***	2.9	1.2	0.7	↓1.1	↓0.9	20.3***	20.5***	0.4	1.34
Habitat generalists	0.1	2.1	↓3.9*	0.1	1.1	2.7	0.7	0.1	0.1	9.1**	0.1	0.1	↓3.7*	0.1	1.28
All birds	2.5	11.8***	↓1.7	4.5*	12.9***	↓0.4	0.8	↓1.1	↓3.2*	0.1	0.1	10.3*	19.9***	1.6	2.39
Number of species	0.1	0.1	↓0.2	5.5*	↓0.1	0.3	↓0.1	↓0.2	↓2.2	↓0.1	0.1	1.3	9.5**	↓0.3	0.86
No significant effects (positive/negative)	3 (2/1)	5 (4/1)	1 (0/1)	5 (5/0)	4 (4/0)	2 (2/0)	1 (1/0)	0 (0/0)	3 (0/3)	2 (1/1)	0 (0/0)	6 (6/0)	12 (11/1)	0 (0/0)	–

iables describing isolation of reedbeds, namely proportion of reed habitat within a 100-m radius and distance to reedbed > 1 ha, are the key factors explaining the abundance of most species of birds and their diversity in reed patches, which could suggest the birds' attachment to a breeding reed patch or/and some species' ability (mainly small passerines) to move between adjacent reed patches. This explanation is particularly evident for species associated with water, namely great reed warbler, moorhen, coot and all water birds, for which relatively stronger effect of distance to reedbed > 1 ha was revealed; than for other small reed passerines (Table 3), which could move between reed patches or adjacent habitat located within distance of 100 m (Besschieter & Goedhart 2005, Surmacki 2005). Furthermore, a lack of significant effect of reedbed area within a 100-m radius showed that this distance could most likely be recognized as a barrier effect (*sensu* Besschieter & Goedhart 2005). Considering that reedbeds provide nesting sites and/or feeding grounds for a particular species or a group of birds with similar habitat requirments, our results mirror both, a real importance of reedbeds as suitable nesting sites (= where territories are established) and, on the other hand, as feeding grounds only.

The most unexpected result was the negative association between reedbed area and the number of great reed warbler. We believe that a potential explanation of this result may be the structure of surveyed reedbeds, mainly a different proportion of suitable habitats for the great reed warbler, which build their nest in border water-reed and occupy territories in the reed edge (Graveland 1998). However, it should be pointed out that this species often leaves its territory to forage at considerable distances (Dyrcz 1986, Dyrcz & Zdunek 1996, Surmacki 2005), and this relation agree a positive effect of proportion of reed habitat within a 100-m radius (Table 3). In our study, water was present only within 41% of the reedbeds; however, we did not find a significant effect of this variable on the number of territories of the great reed warbler, and this species occurred also in some dry reedbeds (*see* below). Moreover, we found a significant positive effect of reed edge on the number of territories of the great reed warbler (also in univariate approach with the use of Spearman rank correlation: $r_s = 0.572$, $p < 0.001$), which indeed confirms the association of this species with the edge of reedbeds. Additionally, in large reedbeds edge/area ratio is declining, which may increase the probability of occupancy of small reed patches by the great reed warbler.

Positive influence of reed edge and water area on the numbers of the sedge warbler, great reed warbler and reedbed specialists may be explained by the use of the edge of these habitat for nesting sites, feeding grounds or for sites acting as song posts (Król 1984, Pikulski 1986, Dyrcz & Zdunek 1996, Graveland 1998, Baldi & Kisbenedek 1999, Foppen *et al*. 2000). In the case of the water rail, moorhen and water birds and all birds, an additional factor positively associated with the abundance was the length of internal reed edge, which may be related to nesting of these birds in the water–reed boundary. The sedge warbler has a relatively broad niche and establishes its territories within mosaic marshland habitats outside compact reed stands, although reedbeds are key factors for high quality territories (Zając *et al*. 2006). In the sedge warbler, the song propagation is the main factor of sexual selection and singing males often use multiple habitats (Buchanan & Catchpole 1997), therefore it might be assumed that the noise of passing trains (negative effect of railway in our study) acted as a disturbance in song hearing and acoustic communication (Slabbekoorn & Ripmester 2008). Similarly, the negative effect of railway found in the case of reedbed specialists and all birds, supports our initial assumption of this factor being a potential constraint for the occurrence of birds.

The lack of significant negative effect of dirt and/or paved road on individual species or whole community of birds (Table 3) could have resulted from the low level of noise (or totally absent in the case of dirt road), which did not reach the critical environmental threshold affecting the birds. On the other hand, we detected a positive effect of dirt road on the number of the moorhen, which could suggest that such an artificial landscape feature could increase the attractiveness and diversity of a reed patch.

The lack of a significant effect of analyzed variables on the abundance of the reed bunting probably reflected a broad habitat preference or ability of this species to occurr in non-reed habitats, which could favour its expansion onto crop fields (Orłowski 2005).

Treebelts were positively associated with the abundance of the moorhen and water birds, probably because of being used as nesting sites, e.g. by the mallard, which can breed in holes of old trees (Cramp 1998).

The positive effect of built-up areas on the abundance of habitat generalists, and negative effect on the number of territories of Savi's warbler could be explained by the location of the large reedbeds (occupied by Savi's warbler) further from settlements, and the small reedbeds (occupied by habitat generalists with small area requirement, cf. Table 2) near the build-up areas. Furthermore, a recent study from northeastern Poland showed that predation of American mink (*Neovison vison*) on clutches of coots and great crested grebes (*Podiceps cristatus*) is significantly lower near human settlements, which apparently suggest that the proximity of built-up areas could act as an umbrella against some predators (Brzeziński *et al*. 2012).

The positive effect of water area inside the reedbed on the number of the bluethroat may suggests a direct association of this species with food resources and feeding habits, i.e. gathering invertebrates from the muddy ground of drying sewage sediments (S. Rusiecki unpubl. data). In the case of Savi's warbler, the similar effect could be explained by its habitat preferences, which encompasses the presence of water being an important element of an optimal breeding site and nest location (Pikulski 1986).

The key influence of the two variables describing isolation of reedbeds, namely proportion of reed habitat within a 100-m radius and distance to reedbed > 1 ha, on the numbers of most species, including waterbirds and the presence of the reed warbler (GLM model based on presence–absence data) could provide an evidence that large reedbeds are better habitats, and small and more isolated reed patches are occupied less frequently. However, on the landscape scale with increasing proportion of reed habitats undoubtedly both the number and probability of occurrence of birds also increase which suggests sensitivity to breeding-patch isolation. In the case of waterbirds, it might translate into small patches of reeds intermingled with open water areas. In the case of reed passerines, small reed patches located around a large reedbed and surrounded by grassy habitats could be attractive nesting sites (and neighbouring non-reed habitat to provide food). Furthermore, the sedge warbler breed in high density (semi-colonial) in optimal or sub-optimal habitat, and males used several patches of vegetation, which indicates genetically regulated preferences towards structure of habitat (Zając *et al*. 2006).

In a reed archipelago located on Lake Valence (western Hungary), Baldi (2006) did not find any significant effects of distance to the nearest reedbed or distance to large reedbed on small reed passerines (with the exception of the reed bunting). These discrepancies may result from different landscape contexts (water *vs*. land), or considerably larger isolation of the reed patches in our study (distance to nearest reedbed in Hungary (Baldi 2006) and our study: 34.7 and 63.8 m, respectively; and distance to large reedbed: 44.0 and 117.0 m, respectively).

In conclusion, our study was conducted in a relatively small area (1400 ha), hence the effect of isolation on patterns of bird-habitat relationships in wetlands or reedbeds is probably different than that on a large landscape scale (> 100 km^2). Therefore, comparisons with other studies dealing with the effect of the isolation on wetland bird communities are difficult. In general, the data on bird–habitat relationships in wetland habitats from large areas indicate that as isolation increases, the abundance and diversity of birds' decreases (Whited *et al*. 2000, Verboom *et al*. 2001, Paracuellos 2006). However, as revealed in our study, it seems that at a smaller scale isolation of reed patches translates into greater habitat fragmentation which may positively affect some birds.

An interesting finding of this study is the presence of the great reed warbler territories in dry reedbeds — they were recorded in 22 (41%) out of 54 dry reed patches. This contradicts some earlier data on habitat requirements of the great reed warbler, which indicates that water had key importance for the nest location in this species (Graveland 1998). The occurrence of the great reed warbler in dry reeds may be linked to their periodical flooding and to the location of some reed patches in proximity to larger, permanently waterlogged reedbeds.

Implications for management of reedbeds and human created wetlands as important bird conservation areas

It is commonly known that reed passerines are not as strictly territorial as forest songbirds; they defend a small area around the nest but move over relatively long distances to take advantage of locally abundant, ephemeral insect resources, or use multiple patches (Bell *et al*. 1973, Król 1984, Dyrcz & Zdunek 1996, Buchanan and Catchpole 1997, Moskat & Baldi 1999, Besschieter & Goedhart 2005). However, considering these constraints, in order to assess the potential conservation value of surveyed reedbeds we compared the requirement area of some reed passerines based on the results of investigations from a mosaic of reed patches (islands) in southern Europe. In general, sensitivity of reed passerines to area was considerably lesser in our study than in reed islands located in lakes and wetlands of southern Europe. For example in Hungary at Lake Velence, the area of the smallest reed patch occupied by most reed birds was from several to several-dozen times greater than in our study (*see* Baldi 2006): the area of the smallest reed patch at Lake Velence occupied by the bluethroat was 4.14 ha (41.4 times greater than in our study, *see* Table 2); sedge warbler, 0.75 ha (37.5 times greater); reed warbler, 0.03 ha (16 times greater); great reed warbler, 0.11 ha (3.7 times greater) and great reed warbler, 0.17 ha (3.4 times greater). One exception was Savi's warbler, which in Hungary occupied very small reed patches (≥ 0.02 ha) (Baldi 2006); this value being 18 times smaller than in our study. Similarly, in the study of 16 marshland fragments with sizes from 0.09 to 29.54 ha located in central Italy, the occurrences of the reed warbler and great reed warbler were confirmed only in wetland patches larger than 1 ha (Benasi *et al*. 2009).

The smaller area requirements of small passerines in reedbeds surveyed in this study can be also considered in the context of territory size. In the Milicz fish ponds (area rich in water reedbeds), the territory size of the great reed warbler on the border of reed and open water ranged between 0.02 and 0.06 ha, while inside large reed stands it was considerably larger, 0.13–0.22 ha (Dyrcz 1986). In the same ponds, the size of Savi's warbler territories ranged between 0.18 and 0.8 ha (mean = 0.49 ha) (Pikulski 1986). In Europe, in optimal and suboptimal habitat conditions, sizes of the bluethroat territories ranged between 0.13 and 1.5 ha (data compiled by Glutz & Bauer 1988). These comparisons might suggest that another factor decreasing area sensitivity of some species in terrestrial environment (besides the abundant food resources, e.g. Graveland 1998) may be isolation of reedbeds, which allows the birds to set up neighbouring territories in small reed patches. Ultimately, it seems that in the case of homogenous reed patches growing entirely in water, greater area requirements of birds are a consequence of the lack of other potential adjacent habitats.

In the light of the presented comparisons, our results indicate that small reed patches located in a terrestrial environment are attractive as breeding sites for many reed birds, including several species of *Acrocephalus* warblers. Smaller area-sensitivity of birds in our study may have resulted from greater food resources in dry reeds and/or proximity and availability of terrestrial feeding grounds (Graveland 1998). The reed warbler and great reed warbler often feed in a woody vegetation growing near reedbeds (Król 1984, Dyrcz 1986, Dyrcz and Zdunek 1996, Surmacki 2005). Another explanation of smaller area-sensitivity of birds in our study may be high fertility of these habitats resulting from irrigation by sewage sludge. The staple diet of small reed passerines, including *Acrocephalus* and *Locustella* warblers, are *Diptera* (Pikulski 1986, Hoi *et al*. 1995, Cramp 1998), and this group of insects is abundant in sewage-irrigated areas (Learner & Chawner 1998).

From the conservation point of view, it is worth noting that reedbeds located in a terrestrial matrix are a valuable habitat for many reed birds. From the habitat management point of view, it is best to create and maintain patches with sizes providing suitable nesting and foraging sites for birds. As our study revealed, small reedbeds (< 1 ha) boost disproportionately higher numbers of bird territories (mainly of small passerines). This finding might be useful in restoration and creation of new reed habitats for wetland birds, and indicates that in many small reed-patches with different adjacent habitats (open water, trees) more birds can occur than in one large reedbed. However, such small reed patches and presence of wastewater may have some disadvantages linked to suboptimal habitat. Firstly, predation is much higher in the edge (= small reed patches) than in the interior of reed patches (Baldi & Batary 2005 and reference herein). Secondly, species with large body size prefer large reed-patches (Bibby & Lunn 1982, Baldi & Kisbenedek 1998, Gilbert *et al*. 2005, *see* Table 2). Furthermore, small patches are used predominantly for feeding and are only a part of the occupied territory (Besschieter & Goedhart 2005, Surmacki 2005, Zając *et al*. 2006). Hence, it seems that an important implication for bird conservation and restoration projects carried out over large areas is to preserve/create reedbeds with various sizes (both small < 1 ha and larger) or a reed 'archipelago' with one large reedbed and several small adjacent reed patches. Apart from that, we realized that considering a large set of variables, some effects of environmental differentiation of reedbeds on numbers of territories and species diversity of birds revealed in our study could actually occur by chance. Moreover, the current analyses were based on variables measured at a larger-landscape scale, and they did not include some habitat features of a breeding site or territory, such as vegetation characteristic (cover, density, types of plant communities) or water condition (depth, surface area), from which breeding of individual species, especially of water-dependent birds, are dependent (e.g. Pikulski 1986, Graveland 1998, De Kroon 2004, Gilbert *et al*. 2005).

Finally, we should remember that the presence of wastewater and the lack of clean water in studied reedbeds cause a reduction of water fauna diversity, mainly fish and some groups of invertebrates with larval stages that need water-dissolve oxygen (Ogielska *et al*. 2009), which is likely to be the main reason behind the absence of fish-eating species of birds, such as the bittern or little bittern (*Ixobrychus minutus*). Finally, it should be noted that the current EU law on water management (The Council Directive 91/271/EEC entitled 'Urban Waste Water Treatment Directive') does not allow the treatment of wastewater on sewage farms anymore, therefore the maintenance of many such areas, valuable for bird conservation in European cities (e.g. in London, Berlin, Münster), requires special conservation efforts, embracing the introduction of new sources of clear water supply and changes in the present land-use.

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