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Local extinction, colonisation and turnover rates of breeding birds in fragmented landscapes: differences between migratory guilds

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Several features of habitat fragmentation, including habitat area, isolation from other suitable habitats and habitat-edge phenomena, have been associated with negative effects on animal populations. Most studies on birds have concerned forest islands. In this paper I tested a hypothesis of different sensitivity of birds to fragmentation. In selected heterogeneous habitat fragments in southern Poland I analysed differences in local extinction, colonisation and turnover rates between groups of species of different migration status. Some disparities are expected because of the differences in the mobility of birds, as reflected in species dispersal distances. Only for resident species does the number of species lost between two breeding seasons significantly differ from the number of species gained. No significant differences in turnover rates were evident between the guilds. However, the extinction rate of tropical migrants was higher than that of European migrants and the colonisation rate of resident species was lower than that of tropical migrants. Changes in the breeding species composition were not of the island–mainland type. The variables important for explaining year-to-year changes were: "number of habitats" per fragment, fragment size, perimeter, distance to other fragments, vegetation density, number of connectedness and surrounding features. However, there were differences in the importance of these variables to the migratory guilds. The results indicate that the populations of many species of each of the guilds continue to occupy those fragmented landscapes where their long-term persistence will depend on continued dispersal. However, it is difficult to discern for each group whether the changes are caused by dispersal due to alterations in habitat structure and configuration or by stochastic processes.

1. Introduction

Heterogeneous habitats will, in contrast to homogeneous ones, allow co-occurrence of species both because species-specific habitat requirements are met and because species may be spatially segregated, which reduces competition opportunities (Blake & Karr 1987). Many changes in the distribution and abundance of species are natural processes, but natural changes are slow and inconspicuous when compared with the dramatic changes due to human impact. There is an optimum level at which human activity results in the maximum gain of species, just as natural disturbance events that are a starting point for ecological successions and regulate species diversities in forest ecosystems (Blondel 1997). Nowadays, human impact on landscapes is far beyond the optimal level, particularly in the countries with quickly developing economies. In Poland, the process of habitat fragmentation is not yet so advanced as, for example, in Britain, but it still is increasing, partly because of the traditionally fragmented structure of agriculture. In the dynamically changing environment it is important to determine directions of changes in plant and animal populations in the fragmented landscape because they usually are the first signals of the subsequent steady trends.

Many fragmentation studies on birds have concentrated on forest patches surrounded by cuttings (e.g. Cieślak 1994, Haila *et al.* 1994, Jokimäki *et al.* 2000), agricultural areas (e.g. Tryjanowski 1999, Kujawa & Tryjanowski 2000, Dombrowski & Goławski 2002) or urban areas (e.g. Natuhara & Imai 1999, Jokimäki 2001, Fernández-Juricic & Jokimäki 2001). Selection of variables serving to describe habitat patches may considerably influence the results of measured parameters of bird communities (Robbins 1988, Opdam 1991, Merriam & Weger 1992). Several features of habitat fragmentation have been associated with negative effects on animal populations, including habitat area, isolation from other suitable habitats and habitat-edge phenomena (Hagan *et al.* 1996). Nowadays it is obvious that in a mosaic landscape, the habitats are subject to great pressures from the surroundings, manifested in the biocoenotic relationships. The habitat fragments are open to influences from the surrounding landscape to the extent that these phenomena can be more important than the processes occurring within these habitats (Hobbs 1993). What happens within the fragments is also often dependent on the phenomena of a wider, landscape-related context. The high mobility of birds makes it difficult to discern some effects of the habitat fragmentation. The dispersal of individuals is a key process (Wiens 1994).

Turnover of breeding bird species has already been investigated in forest fragments (Haila *et al.* 1993a, Hinsley *et al.* 1995, Jokimäki *et al.* 2000, Mason 2001). However, the fragmented landscapes in many countries in Europe consist of not only forests but also patches of meadow, brushwood or rush vegetation, which make them much more heterogeneous. These fragments differ from each other in many characteristics such as size, spatial structure and degree of isolation. Additionally, many empirical studies demonstrate a wide variety of direct and indirect effects, sometimes with mutually opposing implications (Haila 2002).

In this paper, I searched for factors affecting some temporal parameters in the dynamics of avian breeding communities, in a heterogeneous landscape typical of southern Poland. The relatively high mobility of birds, reflected, for example, in habitat selection, should counteract some of the effects of habitat fragmentation. This is one of the reasons for deeming resident species to be much more vulnerable to habitat changes than migratory species (Bierregaard *et al.* 1992). To test a hypothesis of different vulnerability of birds to greater fragmentation, I looked at differences in the local rates of extinction, colonisation and species turnover between groups of species of different migration status, and if any such differences appeared, I looked at the relationships affecting them.

2. Methods

2.1. Study area

The study area was situated in southern Poland in the northwestern part of the province of Małopolska, mostly in the Rów Krzeszowicki lowland. The size of the study area was about 6 km × 15 km and was roughly centred in the town of Zabierzów (50°07′N, 19°49′E). The location of the area at the border of different geobotanical units resulted in a great natural variability of habitats and vegetation. The dominating land uses were intensive arable farming and pasturing (approximately 53%). Urban habitats form about 10% of the study area. Two main types of cultivation were predominant, depending on the soil fertility: communities on fertile soils, occurring predominantly on loess soils and in river valleys where the main crops were rape and maize, and communities on poorer soils where older sediments were covered by sands and loams and cultivation was more diversified with cereals and crops. In addition to arable land, a large area was covered by fresh pastures and meadows that owing to intense drainage and fertilisation replaced the former fertile wet meadows.

Within this area, habitat fragments (remnants of natural and/or seminatural habitats within arable fields), ranging in size from 0.2 ha to 40 ha, were investigated (n = 131, mean ± SD = 12.7 ± 12.43). The fragments consisted of a wide range of woody vegetation types: broadleaved, alder, riparian, but also osiers, shrubby fens, reed beds and sedges. They contained habitats that differed from the surrounding environment, comprising mainly arable fields, grassland and urban areas. As a result their borders were mostly natural and easy to identify.

2.2. Habitat and landscape variables

The particular fragments, their position in the landscape and the surrounding land uses were described using the variables listed in Table 1. Site area and perimeter were measured directly in the field for the small fragments and from 1:10 000 maps for the larger ones. The shape of each fragment was determined following Hinsley *et al.* (1995), using the Pm/Pc index, where "Pm" was the measured perimeter, and "Pc" was the perimeter of a circular plot of the same area. The identification of "habitats" and the estimation of their number present within each fragment were based on 16 categories: deciduous forest; coniferous forest; mixed forest; dense brushwood; thin brushwood; old undergrowth; young undergrowth; alley of trees; orchard; meadow; reed bed; fen; cultivated area; pond, stream or drainage ditch; building(s); waste land. In general, the number of habitats increased with increasing plot area ($y = 5.54 + 0.67 \log \text{area}$; $n = 131$; $R^2 = 0.340$; $P < 0.001$).

For forest habitats within each fragment, the age of stand was determined using the tree age index. Four categories of stands were distinguished: 0 = no stand (lack of trees), 1 = 1–20-year-old stand, 2 = 21–50-year-old stand, 3 = over 50-year-old stand. By marking them on maps, I determined the proportion of a given stand category in the whole area. The age index was calculated using the formula:

$$\text{Index} = \sum (\text{category} \times \text{proportion}) \qquad (1)$$

Table 1. Variables describing fragments used in multiple regression analyses: area and structure, degree of isolation and surrounding features.

Variable	Abbreviation
AREA and STRUCTURE	
1. Size (ha)	SIZE
2. Perimeter (m)	PERIMET
3. Shape	SHAPE
4. Age of tree stand	TREEAGE
5. Percentage cover of tree stand older than 50 years (%)	OLDTREES
6. Density of canopy layer	CANOPY
7. Density of shrub layer	SHRUB
8. Density of herb layer	HERB
9. Percentage cover of wetland (%)	WATER
10. Number of habitats	HABITATS
ISOLATION and SURROUNDING FEATURES	
11. Distance to the nearest fragment (km)	NEAREST
12. Distance to the nearest similar fragment (km)	SIMILAR
13. Distance to the nearest larger similar fragment (km)	LARGER
14. Number of connectedness	CONNECT
15. Percent of perimeter adjoined by grass (%)	S-GRASS
16. Percent of perimeter adjoined by crops (%)	S-CROPS
17. Percent of perimeter adjoined by buildings and yards (%)	S-FARMS

Because this variable estimates only the limited scope of the importance of older forest stands (some fragments could be in part free of any trees while other parts could be covered by an old forest stand), another variable was used to describe the proportion of the over 50-year-old stand in the whole of the stand in a given fragment. The remaining proportion variable — the percentage cover of wetland (including rivers, streams, small ponds and other water bodies) — was calculated in relation to the whole area of a particular fragment.

Once per year in June, during the period of full vegetation growth, canopy, shrub and herb layer covers were determined. For each fragment the cover was scored on an arbitrary scale of 0–2, where 0 = lack of vegetation in a given layer, 1 = partial cover (sparse vegetation) and 2 = full cover (closed tree canopy or dense vegetation in the shrub or herb layers). Then, the proportion of the area in a given category, which could be classified as one of the three available categories of the whole area, was marked on the maps. The cover index was then calculated using the same formula as for the age stand index. The minimum and maximum values for each layer were 0 and 2, respectively.

Three variables were used as a measure of isolation, one was a determinant of connectedness and three more characterized the features of the surrounding areas. Distances from the border of the fragment to the nearest fragment of any size, to the nearest similar fragment and to the nearest similar fragment larger than the investigated one, were measured directly in the field or from maps scaled 1:10 000 or 1:25 000. To ascertain plot similarity, I compared the proportions of main habitats between plots based on the 16 habitat categories distinguished and then each plot was classified into "woody", "scrubby", "mixed" and "field-meadow" categories (Tworek 2001). The plots belonging to one category were considered to be similar. The total number of linear connections (ditches, hedges, dirt roads) connected to each fragment was used as a measure of connectedness. These were counted directly in the field. Surrounding land use was assessed annually and was expressed as the percentage of the perimeter of each fragment adjoining the three most frequent categories of land use: meadows, arable fields and buildings (yards). As in the case of other variables, estimates for small plots were made directly in the field and for larger sites, maps scaled 1:10 000 were used.

2.3. Bird censuses

Most bird populations vary markedly from year to year. At low densities birds may not occupy all suitable habitats, while at high densities they occupy also poorer habitats (Rotenberry 1985, Jokimäki & Huhta 1996). This may mask differences between preferred and less desirable habitats for birds. As a consequence, a short-term study based on single-year results will be misleading in studying bird–habitat relationships (Wiens 1989). To avoid this problem a five-year study was undertaken. Breeding birds were surveyed using the territory mapping method (Bibby *et al.* 1992) from 1995 to 1999. During each breeding season I conducted 7–11 counts in the selected fragments. The number of counts varied depending on the weather conditions in any given year of the studies. Some of the breeding seasons started earlier, even in mid-March, others began later, even as late as mid-April. Irrespective of their starting date they ended usually in mid-July, and thus the number of counts differed between years. Additionally, in small plots with a simple spatial structure a lower number of counts was sufficient to determine the number of breeding species, as compared with large fragments. I usually started the counts early in the morning (4 am to 6 am) and continued until the evident drop in birds' singing activity (usually between 11 am and 12 noon). Alternatively, I started one or two counts in the afternoon (4 pm to 5 pm) and continued until dusk to count species that are more active at nightfall.

Then I charted all the observations on the prepared plans of fragments where orientation points had already been marked. In recording singing males of the most numerous species, I paid particular attention to simultaneous observations. In small fragments located close to each other, I tried to find as many nests as possible so as to determine more precisely to which plot a given pair–territory belonged. When I found no direct evidence of breeding, I based the determination of a territory on at least three observations of a singing male, pair of birds or other behaviour suggesting the possession of a territory.

2.4. Analyses

Each year I estimated the number of breeding pairs (N) and number of species (S) in particular fragments. On the basis of their migration status I divided the species into resident, European migrants and tropical migrants. Each guild covered a somewhat similar number of species (Table 2). By analysing year-to-year changes in the breeding species composition of each fragment, I arrived at the estimates of extinction (E), colonisation (C) and turnover (T) rates for particular groups of different migration status. Extinction and colonisation rates were expressed by the numbers of species that were lost and gained, respectively, between two consecutive seasons. Following Diamond (1969), I calculated species turnover rate using the formula:

$$T = (E + C) / (S1 + S2) \times 100\% \qquad (2)$$

where *E* and *C* are numbers of species that disappeared from a fragment (extinction) and appeared in a fragment (colonisation) between seasons 1 and 2, and S1 and S2 are numbers of all species of a given migratory guild breeding in a fragment in seasons 1 and 2. With five consecutive annual surveys, extinction, colonisation and species turnover rates between breeding seasons were calculated four times. Differences between three migratory guilds in (1) numbers of species and numbers of breeding pairs per fragment and (2) numbers of extinctions, colonisations and turnover rates were analysed using one-way ANOVA and multiple comparisons with the T-Tukey (HSD) test at P-level = 0.05. Differences between the numbers of extinctions and the numbers of colonisations for particular guilds were analysed using the two-tailed t-test for independent samples.

To evaluate the effects of habitat and landscape components on extinction, colonisation and turnover rates of migratory guilds, I used the stepwise multiple regression (forward). For the independent variables I used the predictor variables listed in Table 1. All statistical analyses were made with the Statistica for Windows (1997) package.

3. Results

The number of breeding species for migratory guilds ranged in fragments from 0 to 18 for resident species (mean ± SD = 5.7 ± 4.55); from 1 to 17 for European migrants (6.4 ± 3.95); and from 0 to 19 for tropical migrants (6.5 ± 4.28). There were no significant differences in the number of species per fragment for the groups of different migration status (ANOVA, $F_{2,131} = 0.89$, $P = 0.410$). However, the number of breeding pairs per fragment of resident species was lower than that of tropical migrants ($F_{2,131} = 9.43$, $P < 0.001$). Species turnover occurred across the whole size range of plots surveyed. The relative rate of species turnover was higher in small plots and — within the studied size ranges — decreased linearly with the log of fragment size (Fig. 1). The mean number of species lost between two years (± SD), calculated per plot, was 1.2 ± 1.21 (range 0–4) for resident species, 1.0 ± 0.89 (range 0–3) for European migrants and 1.4 ± 1.30 (range 0–6) for tropical migrants. The mean number of species gained between two years, calculated per plot, was 0.8 ± 0.89 (range 0–3) for resident species, 1.1 ± 1.07 (range 0–4) for European migrants and 1.3 ± 1.18 (range 0–5) for tropical migrants. The extinction rate of tropical migrants was the highest and it was significantly higher than for European migrants ($F_{2,128} = 4.73$, $P < 0.01$). The colonisation rate of resident species was the lowest; it was significantly lower than for tropical migrants ($F_{2,128} = 5.197$, $P < 0.01$). The comparison of the numbers of species lost and gained for particular guilds showed that the extinction rate of resident species was significantly higher than the colonisation rate ($t = 2.52$, $P < 0.05$). For other guilds, the differences between the extinction and colonisation rates were not significant. The mean rate of species turnover (± SD) was 28.8% ± 32.02 (median = 16.7%) for resident species, 22.4% ± 21.52 (median = 15.8%) for European migrants and 26.0% ± 19.26 (median = 20%) for tropical migrants. No significant differences in turnover rate were evident between the guilds ($F_{2,128} = 2.118$, $P = 0.122$).

Table 2. Species breeding in the study fragments in 1995–1999. * species that did not contribute to species turnover.

Resident	European migrants	Tropical migrants
Sparrowhawk *Accipiter nisus*	Skylark *Alauda arvensis*	Marsh Warbler *Acrocephalus palustris*
Long-eared Owl *Asio otus*	Kingfisher *Alcedo atthis*	Sedge Warbler *Acrocephalus schoenobaenus*
Goldfinch *Carduelis carduelis*	Mallard *Anas platyrhynchos*	Reed Warbler *Acrocephalus scirpaceus*
Greenfinch *Carduelis chloris*	Meadow Pipit *Anthus pratensis*	Tree Pipit *Anthus trivialis*
Short-toed Treecreeper *Certhia brachydactyla*	Buzzard *Buteo buteo*	Scarlet Rosefinch *Carpodacus erythrinus*
Treecreeper* *Certhia familiaris*	Linnet *Carduelis cannabina*	Marsh Harrier *Circus aeruginosus*
Hawfinch *Coccothraustes coccothraustes*	Stock Dove *Columba oenas*	White Stork *Ciconia ciconia*
Raven* *Corvus corax*	Woodpigeon *Columba palumbus*	Quail *Coturnix coturnix*
Carrion Crow *Corvus corone*	Reed Bunting *Emberiza schoeniclus*	Corncrake *Crex crex*
Great Spotted Woodpecker *Dendrocopos major*	Robin *Erithacus rubecula*	Cuckoo *Cuculus canorus*
Middle Spotted Woodpecker *Dendrocopos medius*	Kestrel *Falco tinnunculus*	Hobby *Falco subbuteo*
Lesser Spotted Woodpecker *Dendrocopos minor*	Chaffinch *Fringilla coelebs*	Collared Flycatcher* *Ficedula albicollis*
Syrian Woodpecker *Dendrocopos syriacus*	Snipe *Gallinago gallinago*	Pied Flycatcher *Ficedula hypoleuca*
Black Woodpecker *Dryocopus martius*	Moorhen* *Gallinula chloropus*	Icterine Warbler *Hippolais icterina*
Yellowhammer *Emberiza citrinella*	Pied Wagtail *Motacilla alba*	Wryneck *Jynx torquilla*
Jay *Garrulus glandarius*	Black Redstart *Phoenicurus ochruros*	Red-backed Shrike *Lanius collurio*
Great Grey Shrike *Lanius excubitor*	Chiffchaff *Phylloscopus collybita*	River Warbler *Locustella fluviatilis*
Coal Tit* *Parus ater*	Dunnock *Prunella modularis*	Grasshopper Warbler *Locustella naevia*
Blue Tit *Parus caeruleus*	Bullfinch *Pyrrhula pyrrhula*	Thrush Nightingale *Luscinia luscinia*
Great Tit *Parus major*	Goldcrest* *Regulus regulus*	Nightingale *Luscinia megarhynchos*
Willow Tit *Parus montanus*	Penduline Tit *Remiz pendulinus*	Yellow Wagtail *Motacilla flava*
Marsh Tit *Parus palustris*	Stonechat *Saxicola torquata*	Spotted Flycatcher *Muscicapa striata*
House Sparrow *Passer domesticus*	Woodcock *Scolopax rusticola*	Wheatear *Oenanthe oenanthe*
Tree Sparrow *Passer montanus*	Serin *Serinus serinus*	Golden Oriole *Oriolus oriolus*
Grey Partridge *Perdix perdix*	Starling *Sturnus vulgaris*	Wood Warbler *Phylloscopus sibilatrix*
Pheasant *Phasianus colchicus*	Blackcap *Sylvia atricapilla*	Willow Warbler *Phylloscopus trochilus*
Magpie *Pica pica*	Redshank *Tringa totanus*	Redstart *Phoenicurus phoenicurus*
Grey-headed Woodpecker *Picus canus*	Wren *Troglodytes troglodytes*	Spotted Crake *Porzana porzana*
Green Woodpecker *Picus viridis*	Song Thrush *Turdus philomelos*	Whinchat *Saxicola rubetra*
Nuthatch* *Sitta europaea*	Fieldfare *Turdus pilaris*	Turtle Dove *Streptopelia turtur*
Collared Dove *Streptopelia decaocto*	Lapwing *Vanellus vanellus*	Garden Warbler *Sylvia borin*
Tawny Owl *Strix aluco*		Whitethroat *Sylvia communis*
Blackbird *Turdus merula*		Lesser Whitethroat *Sylvia curruca*
		Barred Warbler *Sylvia nisoria*

Out of 98 species observed to be breeding within the surveyed period, 91 were included in estimating the species turnover (Table 2). The species that were not included in the total turnover were found every year only in one or two fragments throughout the study period. Among these, the resident species predominated (4 species). The species with the highest numbers in the total turnover of particular guilds were: Pheasant (12.5%), Greenfinch (10.7%) and Blue Tit (9.1%) for resident species; Mallard (11.4%), Reed Bunting (10.5%) and Woodpigeon (9.6%) for European migrants and Red-backed Shrike (9.7%), Garden Warbler (8.1%) and Whitethroat (7.2%) for tropical migrants (in brackets: percent of contribution to the total turnover).

In general, all the variables, that is, those associated with the size of the fragments and their structure, as well as with isolation from other fragments, connectedness and features of the surrounding areas, seem to be important for explaining the year-to-year changes in breeding species composition. Depending on the guild, the variables analysed explain 15%–18% of the variability in the extinction rate (Table 3), 17%–25% of the variability in the colonisation rate (Table 4) and 29%–50% of the variability in the species turnover rate (Table 5). Although the percentages of the explained variability for the guilds distinguished in the study are similar, the variables responsible for the explanations are different and sometimes differ in their importance for different groups, such as the distance to the nearest similar plot (SIMILAR) and the connectedness measure (CONNECT) in the turnover rate model for European and tropical migrants (Table 5).

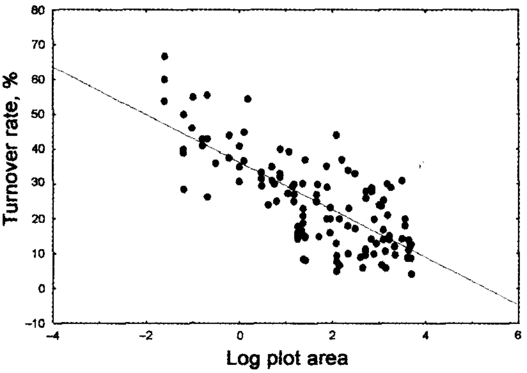

Fig. 1. Relationship between turnover rate of breeding bird species and plot area for habitat fragments in 1995–1999. $y = 36.255 - 6.826 \times \log \text{Area}$, $n = 131$, $R^2 = -0.75$, $P < 0.001$.

4. Discussion

4.1. Validity and level of turnover rate in terrestrial conditions

Diamond (1984) argues that 1%–30% of bird species on ocean islands and in fragmented tropical

Table 3. Stepwise multiple regression analysis of extinction rates for breeding species of three migratory guilds in relation to area, structure, isolation and surrounding land use of habitat fragments. For variable abbreviations, see Table 1.

	Step	Variables entered	Additional percent of variance explained	Statistical significance (P)
Resident	1	CANOPY	11.3	<0.001
	2	CONNECT	6.1	<0.05
	Total		17.4	
European migrants	1	HERB (–)	5.9	<0.01
	2	NEAREST (–)	5.2	<0.01
	3	PERIMET	3.9	<0.05
	Total		15.0	
Tropical migrants	1	SIMILAR (–)	8.3	<0.001
	2	S-CROPS	5.0	<0.01
	3	PERIMET	4.8	<0.05
	Total		18.1	

(–) after variables denotes a negative relationship forests disappear from year to year or are replaced by a similar number of newly appearing species. Does this phenomenon occur in terrestrial situations on a similar scale? The year-to-year changes in breeding species composition manifesting in local extinctions and colonisations result in calculating relatively high rates of turnover for particular migratory guilds in the surveyed areas. Other authors also point out the occurrence of the turnover of avian species in habitat islands (Hinsley *et al.* 1995, Boulinier *et al.* 2001, Mason 2001). As the validity and level of the species turnover rate on habitat fragments may vary with organisms, habitat types, and geographic regions

Table 4. Stepwise multiple regression analysis of colonisation rates for breeding species of three migratory guilds in relation to area, structure, isolation and surrounding land use of habitat fragments. For variable abbreviations, see Table 1.

	Step	Variables entered	Additional percent of variance explained	Statistical significance (P)
Resident	1	TREEAGE	13.9	<0.001
	2	WATER (–)	11.3	<0.001
	Total		25.2	
European migrants	1	CONNECT	9.4	<0.001
	2	HERB (–)	5.1	<0.01
	3	LARGER	3.8	<0.05
	Total		18.3	
Tropical migrants	1	LARGER	12.8	<0.001
	2	CONNECT (–)	4.1	<0.05
	Total		16.9	

(–) after variables denotes a negative relationship

Table 5. Stepwise multiple regression analysis of turnover rates for breeding species of three migratory guilds in relation to area, structure, isolation and surrounding land use of habitat fragments. For variable abbreviations, see Table 1.

	Step	Variables entered	Additional percent of variance explained	Statistical significance (P)
Resident	1	HABITATS (–)	17.0	<0.001
	2	S-GRASS	6.7	<0.05
	3	SIMILAR (–)	5.5	<0.05
	Total		29.2	
European migrants	1	SIZE (–)	17.8	<0.001
	2	S-CROPS (–)	11.3	<0.001
	3	SIMILAR	7.9	<0.01
	4	HERB (–)	7.0	<0.01
	5	CONNECT	6.4	<0.01
	Total		50.4	
Tropical migrants	1	HABITATS (–)	12.4	<0.001
	2	CONNECT (–)	9.6	<0.01
	3	SIMILAR (–)	6.3	<0.01
	4	PERIMET	5.5	<0.01
	5	LARGER	3.7	<0.05
	Total		37.5	

(–) after variables denotes a negative relationship

(Haila 2002), the potential sources of errors in the estimates are worth attention because they have sometimes been questioned (e.g. McCoy 1982, Williamson 1989).

The error in counts may either raise or lower the estimation of the species turnover rate. The studies were conducted in five consecutive breeding seasons. If a species was not found in any of the middle seasons (even though it was a breeding species), this resulted in the recording of a spurious extinction followed by a false record of colonisation in the following year. Such errors contribute to a higher estimated rate of species turnover in both years. On the other hand, when a colonisation event is not recorded, the estimated turnover rate is lower. However, of the species that stay in the area, finding one in the next year will provide a false colonisation result. In this case, the calculation of the species turnover rate cancels both errors. Because of this, the higher estimates occur probably more often. The number of local extinctions and colonisations for particular guilds did not reach the level of six cases even in the largest fragments with a great number of species. The mapping method of bird censuses, when somewhat similar intervals between counts are presumed, should provide relatively credible results, although with a larger plot size, the risk of error increases, because of a higher probability of assessing a non-breeding species as breeding (Hinsley *et al.* 1995). If this observation holds for the study, it can be expected that the relationship between the turnover rate and the area size is even stronger than suggested in Fig. 1: the larger the area, the lower the relative rate of species turnover.

The size of territory can be another factor of significance for the level of turnover rate in a fragmented landscape. For species with large territories, the turnover may be apparent because two nearby fragments can indeed be in one large territory and a breeding pair may occupy either one. This may be a reason for the relatively high turnover rate in species whose territory sizes, delimited according to the mapping method, were usually comparatively large (e.g. Woodpigeon, Red-backed Shrike, Garden Warbler, Blue Tit). Nevertheless, we should remember that territory sizes and areas covered for foraging may vary considerably within the species (Schifferli 2001). In addition, breeding individuals of some species may range more widely than is apparent from territory size, determined by song post location (Hanski & Haila 1988, Zając & Solarz in prep.). Such transfers are, however, associated with a correspondingly higher energy expenditure and greater exposure to predation, already high in a fragmented landscape (Rolstad 1991, Paton 1994); hence, these movements are not likely to occur often in the study area.

4.2. Changes in breeding species composition

The set of variables of substantial importance in explaining the variability in particular models is different in each group. The connectedness measure is similar in significance for the increasing rate of extinction of resident species as for the increasing rate of colonisation of the European migrants. On the other hand, for tropical migrants the significance of this variable for the rate of colonisation is just the opposite to that found in the European migrants. As the remnants of natural habitats in altered surroundings in terrestrial conditions may not be treated as islands (Haila *et al.* 1993b, Norton *et al.* 2000), it is worth considering what factors determine the differences. Are the differences found between migratory guilds a true representation of actual and different reactions of species of different migratory statuses, or do they derive from some other relationships?

The importance of the density of the canopy to the rate of extinction of resident species does not support the suggestion of greater vulnerability to increased fragmentation in this group as suggested by Wiens (1994). Because they are forest species, above all, one would expect a reverse relationship. Again, the significance for the turnover rate of the distance from the smallest similar fragment does not support a negative impact of isolation often suggested with respect to usually resident old-growth specialist bird species (Kouki & Väänänen 2000). At the same time, the importance of the age of tree stand for the rate of colonisation, and of the habitat diversity in a fragment for the rate of species turnover could be linked with a biotope preferred by most species of the group in a fragmented landscape: homogeneous woodland islands with a high proportion of old stands. Density of the herb layer (HERB) is a variable that contributes much to explaining variability in each of the regression models for European migrants. The importance of this variable may be connected directly to the location of nests by birds of this group of species as well as the available ways to conceal nests. In general, the results of regression analyses show that changes in the species composition of resident and tropical migrant species are connected above all with the heterogeneity of habitats (variable HABITATS). Then for the European migrants, the most important factors are the fragment size and features of the surrounding area.

The capability of dispersion in species of the groups of different migration status used in this study can be an indicator of the scale in which their turnover should be considered. However, the difficulties in studying dispersal and thus the estimation of its scale, result in major obstacles to find the reasons for differences in turnover between migratory guilds. Generally, the relations found between turnover rates and predictor variables, especially isolation measures, point to the importance of the source-sink dynamics (Amarasekare & Nisbet 2001). In a fragmented landscape, the patches of habitats available to a given species are scattered amidst areas either unsuitable or barely suitable for colonisation. Populations living under conditions conducive to their survival may reach high numbers, being subject to density-dependent regulation mechanisms. The individuals unable to secure a territory will emigrate, providing a permanent source supporting local populations living in less-suitable sites. The results show that the mosaic pattern of a landscape and habitats, which is a condition for the existence of metapopulations, may be of similar importance for all three groups distinguished in this study.

The changes in the breeding species composition in the studied fragments are not of the island-mainland type, as in the MacArthur and Wilson (1967) model. The rate of extinction, expressed as the number of species lost, was not connected to the size of fragment (island) in any of the migratory guilds. Also, the rate of colonisation, expressed by the number of species gained, did not increase along with the greater degree of isolation from other fragments. Even more, for both groups of migrants (European and tropical) the rate of colonisation did rise significantly as the distance to the nearest larger similar fragment than that studied got longer. These results are not surprising given the fact that water, which isolates ocean islands, is not an accessible habitat to most terrestrial organisms and thus provides an extremely effective barrier to their movements. In the case of habitat fragments, (treated as terrestrial islands), the surroundings isolating them are inhospitable or even hostile as a possible site for reproduction or longer residence, but are not an impenetrable barrier. Birds are extremely mobile animals, and thus it is difficult to estimate the significance of isolation in a fragmented landscape, and the changes in species composition can be caused by either dispersion or stochastic events, being directly reflected in the extinction, colonisation or species turnover rates.

4.3. Significance of area size

Small populations are exposed to a high risk of extinction (Wilcox & Murphy 1985, Fahrig & Merriam 1994). In line with the principle that large areas can support more individuals than small ones, the larger the population, the lower the risk of extinction should be. Therefore, the rate of extinction should depend on the size of the area. This was confirmed both by studies on the bird fauna of islands (Diamond 1984), and on habitat fragments in an agricultural landscape (Opdam 1991). However, in this study, using regression analysis, I did not find any support for such a relationship. The lack of support could result from the great habitat diversity of the surveyed plots, but not only from this feature. Hinsley *et al.* (1995) have also failed to find a significant relationship between the extinction rate depending on the size of the plot, even though they limited their studies to forests. They stress that different species may have different requirements for the minimum size of habitat. The larger the size of an area, the less likely it is that the populations of some species will drop to such levels that extinction — caused by stochastic events — will occur. But there are also other species, which maintain low numbers and are still vulnerable to extinction. Because of this, the low rates of extinction among the most numerous species are masked by the high levels among rarer species. This results in a non-significant relationship between the extinction rate and area size. A similar process may pertain to the rate of species turnover, and the whole process continues until the size of the area is not large enough to support all populations in the community on a level allowing them to avoid extinction caused by stochastic events.

In the study area where the particular fragments were of a maximum size of tens of hectares, the effect of area size was found only for European migrants. One should remember, though, that the assumptions referred to above pertain to fairly homogeneous forest fragments. A species may be absent from a suitable biotope due to some specific habitat requirements. As indicated by the results, the plot size and habitat diversity may be significantly correlated, which makes a separation of their effects difficult. Thus, in some cases, a mechanism similar to the effect of size can operate through the habitat-related limitations, not directly linked with the plot size. As the variables which determine the degree of isolation did significantly affect the rate of colonisation, as opposed to the McArthur and Wilson model, the relationship between the species turnover rate and the size of plot could be disturbed by the interactions between the variables pertaining to the quality of habitats, and the species-specific requirements connected with the landscape heterogeneity.

4.4. Management implications

The results suggest that landscape structure and fragment "quality" may influence bird communities in a mosaic landscape through their effects on the temporal rates of changes in species composition. Generally, the variables responsible for explaining most of the variation in extinction, colonisation and/or turnover rates are similar to those from other studies of bird-habitat relationships in agricultural landscapes (e.g. Kujawa & Tryjanowski 2000, Miller & Cale 2000, Mason 2001). In other landscapes the results obtained for habitat patches may be different. In forest fragments the area size and degree of isolation have, generally, a greater effect on species composition (e.g. Opdam 1991, Bellamy *et al.* 1998). In urban areas, human activity is an additional, important factor (Jokimäki 1999, Natuhara & Imai 1999, Fernández-Juricic & Jokimäki 2001,). However, some differences may be rather the effect of different qualities of investigated habitats, the specificity of the methods and the use of different variables than the result of objectively existing dependences (Storch & Kotecky 1999).

Species differ in dispersal distances, and a landscape that is fragmented for one species may be connected to a significant extent for another one. Several studies have also shown that the individual responses of bird species to fragmentation can be different (Berg 1997, Edenius & Sjöberg 1997, Tworek 2002). The results of an analysis of changes in species composition among groups of different migration status also indicate that populations of many species of each of the guilds continue to be present in fragmented landscapes where their numbers are likely to be small enough to show appreciable turnover and where the long-term persistence of species will depend on continued and effective dispersal.

The explanatory power of the regression models is not high because changes in species composition can be caused by either dispersal of individuals due to alterations in habitat structure and configuration or casual changes (stochasticity), and these are difficult to discern. Other factors, which in these conditions could explain the residual variation, could be found probably among variables connected with habitat quality. For example, it would be advisable to analyse how the structure of vegetation, characterized in detail, influence species composition. Should the comparisons of results between particular breeding seasons lack any consistency altogether, then each year's results yielding a completely different set of variables explaining the variability and the importance of stochastic processes must be still suspect. Presently, there is still a lack of quantitative information on how individuals move through a mosaic environment, and there is a need to analyse, at least on the landscape level, changes in species composition in "the classical" way of fragmentation: from single breaks in a homogeneous habitat leading to the emergence of progressively smaller and more isolated fragments, and to learn more about the differences in turnover between resident and migrant species.

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Selostus: **Paikallisella tasolla tapahtuvat pesimälajien katoamiset, kolonisaatiot sekä lajiston vaihtuvuus pirstoutuneessa elinympäristössä**

Monien elinympäristön pirstoutumista kuvaavien muuttujien, kuten habitaattilaikun pinta-alan, isolaation sekä reunavaikutuksen, on todettu vaikuttavan haitallisesti eläinpopulaatioihin. Useimmat elinympäristön pirstoutumiseen liittyvistä lintututkimuksista on tehty metsäsaarekkeissa. Artikkelin kirjoittaja tutki, kuinka lintulajien muuttotapa vaikutti lajien katoamiseen, kolonisaatioon sekä lajiston vaihtuvuuteen heterogeenisissä habitaattilaikuissa Etelä-Puolassa. Lintulaskentamenetelmänä käytettiin pesimälinnuston kartoitusmenetelmää. Laskennat tehtiin vuosina 1995–1999 ja jokaisella laikulla vierailtiin 7–11 kertaa vuodessa. Kaikkiaan habitaattilaikkuja oli tutkimuksessa mukana 131. Habitaattilaikkua kuvaavia taustamuuttujia oli kaikkiaan 10 ja laikun isolaatiota ja ympäristöä kuvaavia muuttujia oli kaikkiaan 7 (ks. taulukko 1). Pesivien paikkalintujen lajimäärän keskiarvo oli laikussa 5,7. Euroopassa talvehtivien lintulajien lajimäärän keskiarvo oli 6,4 ja tropiikissa talvehtivien lintulajien määrän keskiarvo oli 6,5. Ryhmien laikkukohtaiset lajimäärät eivät eronneet toisistaan. Sen sijaan paikkalintulajien parimäärät olivat laikuissa alhaisempia kuin tropiikin muuttolintulajien parimäärät. Lajiston vaihtuvuus kasvoi laikkukoon pienentyessä. Laikkua kohden laskettuna paikkalintulajeja katosi tutkimusvuosien välillä keskimäärin 1,2. Euroopassa talvehtivilla lajeilla ja tropiikissa talvehtivilla lajeilla vastaavat luvut olivat 1,0 ja 1,4. Tropiikissa talvehtivien lajien katoaminen laikusta oli yleisempää kuin Euroopassa talvehtivien lajien katoaminen. Uusia paikkalintulajeja habitaattilaikulle ilmestyi keskimäärin 0,8. Euroopassa talvehtivilla lajeilla ja tropiikissa talvehtivilla lajeilla vastaavat luvut olivat 1,1 ja 1,3. Paikkalintulajien kolonisaatiota tapahtui harvemmin kuin tropiikissa talvehtivien lajien kolonisaatiota. Paikkalintulajien kohdalla katoamisia tapahtui useammin kuin kolonisaatiota. Muiden ryhmien kohdalla vastaavaa eroa ei havaittu. Lajiston vuosien välinen vaihtuvuus oli paikkalintulajeilla 29%, Euroopassa talvehtivilla lajeilla 22% ja tropiikissa talvehtivilla lajeilla 26%. Havaitut erot eivät olleet tilastollisesti merkitseviä. Paikkalintulajiston vaihtuvuutta laikussa aiheuttivat lähinnä fasaani, viherpeippo ja sinitiainen. Euroopassa talvehtivien lajien osalta lajiston vaihtuvuuteen vaikuttivat eniten sinisorsa, pajusirkku ja sepelkyyhky sekä vastaavasti tropiikissa talvehtivien osalta pikkulepinkäinen, lehtokerttu ja pensastasku. Linnuston koostumuksen vuosien väliseen vaihteluun vaikuttivat laikussa olevien habitaattityyppien määrä, laikkukoko, laikun ympärysmitta, habitaattilaikun etäisyys toisiin laikkuihin, kasvillisuuden tiheys, laikkujen yhteys toisiinsa sekä ympäröivien alueiden laatu. Tulokset osoittavat, että monien lajien populaatiot voivat esiintyä pirstoutuneessa elinympäristössä, mutta lajien pitkäaikainen esiintyminen laikussa riippuu lajien jatkuvasta levittäytymisestä alueelta toiselle. On kuitenkin vaikea erottaa, johtuuko lajiston vaihtuvuus laikussa elinympäristön rakenteessa tapahtuvista muutoksista vai satunnaisista prosesseista.

References

Amarasekare, P. & Nisbet, R. M. 2001: Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. — Am. Nat. 158: 572–584.

Bellamy, P. E., Brown, N. J., Enoksson, B., Firbank, L. G., Fuller, R. J., Hinsley, S. A. & Schotman A. G. M. 1998: The influences of habitat, landscape structure and climate on local distribution patterns of the nuthatch (*Sitta europaea* L.). — Oecologia 115: 127–136.

Bellamy, P. E., Hinsley, S. A. & Newton, I. 1996: Factors influencing bird species numbers in small woods in south-east England. — J. Appl. Ecol. 33: 249–262.

Berg, A. 1997: Diversity and abundance of birds in relation to forest fragmentation, habitat quality and heterogeneity. — Bird Study 44: 355–366.

Bibby, C. J., Burgess, N. D. & Hill, D. A. 1992: Bird census techniques. — Academic Press, London. 257 pp.

Bierregaard, R. O., Jr., Lovejoy, T. E., Kapos, V., dos Santos, A. A. & Hutchings, R. W. 1992. The biological dynamics of tropical rainforest fragments. — Bioscience 42: 859–866.

Blake, J. G. & Karr, J. R. 1987: Breeding birds of isolated woodlots: area and habitat relationships. — Ecology 68: 1724–1734.

Blondel, J. 1997: Evolution and history of the European bird fauna. — In: Hagemeijer, W. J. M. & Blair, M. J. (eds.), The EBCC Atlas of European Breeding Birds: cxxiii-cxxvi. T & A D Poyser, London. 903 pp.

Boulinier, T., Nichols, J. D., Hines, J. E., Sauer, J. R., Flather, C. H. & Pollock, K. H. 2001: Forest fragmentation and bird community dynamics: inference at regional scales. - Ecology 82: 1159 — 1169.

Cieślak, M. 1994: The vulnerability of breeding birds to forest fragmentation. — Acta Orn. 29: 29–38.

Diamond, J. M. 1969: Avifaunal equilibria and species turnover rates on the Channel Islands of California. — Proc. Nat. Acad. Sci. USA 69: 3199–3203.

Diamond, J. M. 1984: "Normal" extinctions of isolated populations. — In: Nitecki M. H. (ed.), Extinctions: 191–246. University of Chicago Press, Chicago. 354 pp.

Dombrowski, A. & Goławski, A. 2002. Changes in numbers of breeding birds in an agricultural landscape of east-central Poland. — Vogelwelt 123: 79–87.

Edenius, L. & Sjöberg, K. 1997: Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. — Ecography 20: 425–431.

Fahrig, L. & Merriam, G. 1994: Conservation of fragmented populations. — Cons. Biol. 8: 50–59.

Fernández-Juricic, E., Jokimäki, J. 2001: A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. — Biodiver. Conserv. 10: 2023–2043.

Hagan, J. M., Van der Haegen, W. M. & McKinley, P. S. 1996: The early development of forest fragmentation effects on birds. — Conserv. Biol. 10: 188–202.

Haila, Y. 2002: A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. — Ecol. Appl. 12: 321–334.

Haila, Y., Hanski, I. K., Niemela, J., Puntilla, P., Raivio, S. & Tukia, H. 1994: Forestry and the boreal fauna: matching management with natural forest dynamic. — Ann. Zool. Fenn. 31: 187–202.

Haila, Y., Hanski, I. K. & Raivio, S. 1993a: Turnover of breeding birds in small forest fragments: the "sampling" colonization hypothesis corroborated. — Ecology 74: 714–725.

Haila, Y., Saunders, D. A. & Hobbs, R. J. 1993b: What do we presently understand about ecosystem fragmentation? — In: Hobbs, R. J., Ehrlich, P. R., & Saunders, D. A. (eds.), Nature Conservation 3: Reconstruction of fragmented ecosystems: 45–55. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia. 326 pp.

Hanski, I. K. & Haila, Y. 1988: Singing territories and home ranges of breeding chaffinches: visual observation vs. radiotracking. — Ornis Fenn. 65: 97–103.

Hinsley, S. A., Bellamy, P. E. & Newton, I. 1995: Bird species turnover and stochastic extinction in woodland fragments. — Ecography 18: 41–50.

Hobbs, R. J. 1993: Effects of landscape fragmentation on ecosystem processes in the Western Australian wheatbelt. — Biol. Conserv. 64: 193–201.

Jokimäki, J. 1999: Occurrence of breeding bird species in urban parks: Effects of park structure and broad-scale variables. — Urban Ecosystems 3: 21–34.

Jokimäki, J. & Huhta, E. 1996: Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. — Ornis Fenn. 73: 97–113.

Jokimäki, J., Huhta, E., Monkkonen, M. & Nikula, A. 2000: Temporal variation of bird assemblages in moderately fragmented and less-fragmented boreal forest landscapes: a multi-scale approach. — EcoScience 7: 256–266.

Kouki, J. & Väänänen, A. 2000: Impoverishment of resident old-growth forest bird assemblages along an isolation gradient of protected areas in eastern Finland. — Ornis Fenn. 77: 145–154.

Kujawa, K. & Tryjanowski, P. 2000. Relationships between the abundance of breeding birds in Western Poland and the structure of agricultural landscape. — Acta zool. Hung. 46: 103–114.

MacArthur, R. H. & Wilson, E. O. 1967: The theory of island biogeography. — Princeton University Press, Princeton, New Jersey, USA.

Mason, C. F. 2001: Woodland area, species turnover and the conservation of bird assemblages in lowland England. — Biodiver. Conserv. 10: 495–510.

McCoy, E. D. 1982: The application of island biogeographic theory to forest tracts: problems in the determination of turnover rates. — Biol. Conserv. 22: 217–227.

Merriam, G. & Weger, J. 1992: Local extinctions, habitat fragmentation and ecotones. — In: di Castri, F. & Hansen, A. J. (eds.), Landscape boundaries. Consequences for biotic diversity and ecological flows: 150–169. Springer-Verlag, New York. 451 pp.

Miller, J. R. & Cale P. 2000: Behavioral mechanisms and habitat use by birds in a fragmented agricultural landscape. — Ecol. Appl. 10: 1732–1748.

Natuhara, Y. & Imai, C. 1999: Prediction of species richness of breeding birds by landscape-level factors of urban woods in Osaka Prefecture, Japan. — Biodiver. Conserv. 8: 239–253.

Norton, M. R., Hannon, S. J. & Schmiegelow, F. K. A. 2000: Fragments are not islands: patch vs. landscape perspectives on songbird presence and abundance in a harvested boreal forest. — Ecography 23: 209–223.

Opdam, P. 1991: Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. — Landscape Ecol. 5: 93–106.

Paton, P. W. C. 1994: The effect of edge on avian nest success: how strong is the evidence? — Conserv. Biol. 8: 17–26.

Robbins, C. S. 1988: Forest fragmentation and its effects on birds. — In: Johnson, J. E. (ed.), Managing north central forests for non-timber values: 61–65. Soc. Am. Foresters, Bethesda.

Rolstad, J. 1991: Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. — Biol. J. Linn. Soc. 42: 149–163.

Rotenberry, J. T. 1985: The role of habitat in avian community composition: physiognomy or floristics? — Oecologia 67: 213–217.

Schifferli, L. 2001: Birds breeding in a changing farmland. — Acta Orn. 36: 35–51.

Statistica for Windows, 1997: StatSoft Inc. Tulsa OK. Polish Edition by StatSoft Polska Sp. z o.o. Kraków, Poland.

Storch, D. & Kotecky, V. 1999: Structure of bird communities in the Czech Republic: the effect of area, census technique and habitat type. — Folia Zool. 48: 265–277.

Tryjanowski, P. 1999. Effect of habitat diversity on breeding birds: comparison of farmland bird community in the region of Wielkopolska (W Poland) with relevant data from other European studies. — Pol. J. Ecol. 47: 153–174.

Tworek, S. 2001: Breeding bird communities in relation to different habitat islands. — Nature Conserv. 58: 117–128.

Tworek, S. 2002: Different bird strategies and their responses to habitat changes in an agricultural landscape. — Ecol. Res. 17: 339–359.

Wiens, J. A. 1989: Spatial scaling in ecology. — Funct. Ecol. 3: 385–397.

Wiens, J. A. 1994: Habitat fragmentation: island *vs* landscape perspectives on bird conservation. — Ibis 137: 97–104.

Wilcox, B. A. & Murphy, D. O. 1985: Conservation strategy: the effects of fragmentation on extinction. — Am. Nat. 125: 879–887.

Williamson, M. 1989: The MacArthur and Wilson theory today: true but trivial. — J. Biogeogr. 16: 3–4.