Factors Affecting Temporal Dynamics of Avian Assemblages in a Heterogeneous Landscape

Author: Tworek, Stanisław

Source: Acta Ornithologica, 39(2) : 155-163

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/068.039.0201

ACTA ORNITHOLOGICA
Vol. 39 (2004) No. 2

Factors affecting temporal dynamics of avian assemblages in a heterogeneous landscape

Stanisław Tworek

Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31–120 Kraków, POLAND, e-mail: tworek@iop.krakow.pl

Tworek S. 2004. Factors affecting temporal dynamics of avian assemblages in a heterogeneous landscape. Acta Ornithol. 39: 155–163.

Abstract. The influence of the characteristics of habitat fragments on the dynamics of avian communities and the effect that fragments of different sizes have on the stability of the breeding species composition, and also on local extinction, colonisation and turnover rates were studied in an agricultural landscape in southern Poland. The fragments included various habitat types that differed from the matrix. Breeding birds were surveyed using the territory mapping method to assess turnover. Species composition depended on both the spatial structure of a fragment and the features of its surroundings. Local declines and appearances of species had a similar influence on the turnover in all size classes of the fragments. Species that contributed most to the total turnover were: *Lanius collurio*, *Phasianus colchicus*, *Anas platyrhynchos*, *Emberiza schoeniclus*, *Columba palumbus* and *Sylvia communis*. However, there were differences among species contributing most to the turnover according to area size classes. Heterogeneous habitats in a mosaic-like, agricultural landscape do not function as islands. The existence of species in an area with such a level of habitat patchiness can be related primarily to habitat quality, mainly because of poor isolation and the high permeability of isolating habitats.

Key words: mosaic landscape, species composition, turnover rate, extinction, colonisation, species-area relationship

Received — Dec. 2003, accepted — Sept. 2004

INTRODUCTION

Habitat fragmentation is the subdivision of a certain habitat into isolated patches (Rolstad 1991). It implies a reduction of the total area of a given habitat, and simultaneously, an increase in the areas of other habitats. It also alters the spatial configuration of habitats, leading to population subdivision which can affect their stability and/or persistence. Despite a sometimes positive effect on the populations of some species (e. g. Hagan et al. 1996, Petersen 1998), habitat fragmentation is nowadays perceived to be one of the greatest threats to biological diversity (Wilcove et al. 1986, Saunders et al. 1991), due to changes it causes at the landscape level.

The researches on the mechanisms explaining species distribution in habitat patches were inspired by the equilibrium theory of island biogeography above all (MacArthur & Wilson 1967), and by metapopulation theory (Gilpin & Hanski 1991). Species turnover is an important indicator of population changes because the persistence of species in habitat patches may depend on efficient dispersal between particular fragments. Many studies on species turnover in fragmented landscapes have concentrated on the year-to-year changes in species composition of birds. Most of these studies concerned forest bird communities (Cieślak 1994, Haila et al. 1994, Mason 2001), but their results do not necessarily apply to more heterogeneous habitats such as remnants of natural and/or seminatural habitats in agricultural landscapes. Species responses to habitat fragmentation may strongly differ in landscapes with different matrix qualities though (Brotons et al. 2003). Since site tenacity and dispersal capacity may be related to the predictability of

habitat suitability over time (Opdam 1991), effects of fragmentation in bird assemblages in woods should be compared to those from less predictable and more changeable environments. In this paper, I studied turnover in breeding bird species composition in habitat fragments of different size classes set within an agricultural landscape in southern Poland. I also examined the influence of the characteristics of the fragments themselves, their degrees of isolation and of the surrounding matrix on the stability of species composition as well as on local extinction and colonisation rates.

STUDY AREA AND METHODS

Study area

The study was carried out in 1995–1999 northwest of Kraków in southern Poland (50°06′–50°08′N, 19°45′–19°55′E). The location of the study area at the borders of different geobotanical units resulted in a great natural variability of habitats and vegetation. The dominating land cover types were intensive arable farming and pasture (Table 1) and the landscape had an agricultural character. Over the whole area (approx. 44 km^2), habitat fragments ranging in size from 0.2 to 40.0 ha were delimited (Table 2). Their borders were usually easy to identify because they included habitats that differed from the matrix. They comprised a wide range of vegetation types: broad-leaved, alder and riparian woodland as well as osiers, shrubby fens, reed beds and sedges.

Table 1. Distribution of land use types on the study area according to PHARE CORINE Land Cover Data.

Land cover types	% of the area occupied
non-irrigated arable land	37.0
complex cultivation patterns	19.9
pastures	16.5
mixed forest	8.5
broad-leaved forest	5.2
coniferous forest	1.5
land principally occupied by agriculture with significant areas of natural character	1.0
green urban areas	0.7
sport and leisure facilities	0.6
water courses	0.5
industrial or commercial units	0.2
discontinuous urban fabric	8.4

Table 2. Size distribution of the fragments studied.

Size class, ha	N	Mean ± SD
0.2–1.0	21	0.51 ± 0.27
1.1–3.9	30	2.71 ± 0.94
4.1–12.0	31	7.47 ± 2.33
13.5–25.0	32	19.34 ± 3.81
26.0–40.0	17	33.71 ± 4.79
Total	131	

Habitat and landscape variables

The particular fragments, their positions in the landscape and the surrounding land-uses were described using 17 variables (Table 3). Site area and perimeter were measured directly in the field for the small fragments and from maps for the larger ones. The shape of each site was determined using the *Pm*/*Pc* index, where *Pm* was the measured perimeter, and *Pc* was the perimeter of a circular plot of the same area (Hinsley et al. 1995). The identification of the "habitats" occurring in each fragment and the estimation of their number present within particular fragments were based on 16 categories: 1) deciduous forest, 2) coniferous forest, 3) mixed forest, 4) dense brushwood, 5) thin brushwood, 6) old undergrowth, 7) young undergrowth, 8) alley of trees, 9) orchard, 10) meadow, 11) reed bed, 12) fen, 13) cultivated area, 14) pond, stream or drainage ditch, 15) building(s), 16) waste land.

A stage of stand development was determined for forest habitats in the fragments using the tree age index. Four categories of stands were distinguished: 0 = no stand, 1 = 1–20 year-old, 2 = 21–50 year-old, 3 = over 50 year-old. Marking them on maps I determined the proportion of a given stand category to the whole area. Another variable was used to describe the proportion of over 50 year-old stand to the whole of the stand in a given plot. Then, the percentage cover of wetlands (including rivers, streams, small ponds and other water bodies), was calculated in relation to the whole area of a given fragment. Once per year in June, during the period of the full development of vegetation, canopy, shrub and herb layer covers were determined. 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). I also noted the proportion of the area in a given category to the whole fragment area.

Table 3. Variables used in multiple regression analysis.

Variable	Abbreviation
1. Plot area (ha)	AREA
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 (%)	WETLAND
10. Number of habitats	HABITATS
11. Distance to the nearest plot (km)	NEAREST
12. Distance to the nearest similar plot (km)	SIMILAR
13. Distance to the nearest larger similar plot (km)	LARGER
14. Number of linear connections	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

Three variables were used as measures of isolation: distances to the nearest fragment no matter which, 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. To ascertain similarity of fragments, I compared the proportions of main habitats between plots and then each fragment was classified into "woody", "scrubby", "mixed" and "field-meadow" categories (Tworek 2001). The fragments belonging to one category were considered to be similar. Additionally, the total number of linear connections to each fragment was used as a measure of connectedness. Surrounding land-use (assessed annually) was expressed as the percentage of the perimeter of each fragment adjoining the three most frequent categories of land use surrounding fragments: meadows, arable fields and buildings.

Bird surveys

Breeding birds were surveyed using the territory mapping method (Bibby et al. 1992). In each year of the study I conducted 7–11 counts in the selected fragments during the breeding season. The number of counts differed between years because the duration of particular breeding seasons was changeble. Surveys were conducted between 25 March and 20 July depending on the weather conditions. I charted all the observations (the identity and activity of all birds) on the prepared plans of fragments where orientation points had been marked. For species with weak signs of territorial behaviour, nest finding was a main method of counting them. For territorial species, when I found no direct evidence of breeding, I based the determination of a territory on at least three records of a singing male, pair of birds or other behaviour suggesting the possession of a territory. For difficult species, especially nocturnal ones, which are considered to have rather few effective visits, two registrations were enough to set up a cluster referring to a pair of breeding birds. The duration of a visit depended on bird activity. I usually started a visit early in the morning (4.00–6.00 a.m.) and continued to about midday through a uniform activity of birds. For some species (mainly thrushes, owls, nightingales, corncrakes) up to 3 evening visits were also helpful.

Parameters measured and analyses

Each year I estimated the following parameters of bird communities in the fragments: number of breeding pairs (N), number of species (S) and extinction (E), colonisation (C) and turnover (TR) rates. Extinction and colonisation are not treated in this paper as directional processes leading to extinction or expansion of the population. They were expressed by the numbers of species that were lost (extinction) and gained (colonisation) respectively between two consecutive seasons. Thus, these phenomena have a local character and can be an indication of fluctuations of unstable communities in a mosaic landscape. I calculated species turnover rate using the formula:

$$TR = (E + C)/(S1 + S2) \times 100\%,$$

where E and C are the numbers of species that disappeared from a plot (extinction) and appeared in a plot (colonisation) between seasons 1 and 2, and S1 and S2 are the numbers of all species breeding in a plot in seasons 1 and 2 respectively (Diamond 1969). The numbers of pairs and proportional occupancy of plots of the individual species responsible for the major contribution to total turnover rate were compared in five size classes of habitat fragments (Table 2). For all the fragments in each class, the number of extinctions and colonisations (E + C) due to each species separately, was calculated as a percentage of the total number of extinctions/colonisations recorded for all the species in all the fragments in each class.

The results for each species were expressed as the mean of the four sets of turnover measurements estimated between 1995 and 1999.

Differences in numbers of extinctions and colonisations for distinguished size classes were analysed using Student t-tests for independent samples. To evaluate the effects of habitat and landscape components on extinction, colonisation and turnover rates I used stepwise multiple regressions using the variables listed in Table 3. All statistical analyses were made with the Statistica package (StatSoft Inc. 1997).

RESULTS

The number of breeding species ranged from no less than four on the smallest fragments to more than 40 on large fragments with diversified habitats (mean ± SD = 18 ± 11.7, n = 131). Species turnover occurred across the whole size range of fragments surveyed. The mean number of species lost between two years, calculated per fragment, was 3.2 ± 1.8 (median = 3, range 0–7). The mean number of species gained between two years, calculated per fragment, was 3.0 ± 1.8 (median = 3, range 0–9). There was no case of a complete turnover of species in any fragment (i.e. totally different species composition between two consecutive breeding seasons) nor a complete lack of species turnover (i.e. identical species composition in two consecutive breeding seasons). The mean rate of species turnover was 23.6 % ± 14.9 % (median = 20 %, range 4.2–66.7 %).

No significant relationship was found between number of extinctions or colonisations and fragment area (Fig. 1). The extinction rate did not also differ significantly from the colonisation rate in any of the size classes of fragments (Student t-tests, all cases $p > 0.25$, Fig. 2). As there were no significant differences in back-to-back years between the total number of species lost and gained and the size of a fragment (ANOVA, $F_{8,234} = 0.90$, $p = 0.15$), the relative rate of species turnover was higher in small than in large fragments.

There are differences, depending on the size range of the fragments surveyed, both in the species composition of the birds which contributed most to the turnover, as well as in the percentage contributions of particular species to the total turnover rate (Table 5). Certain species such as for example Whitethroat *Sylvia communis*, Woodpigeon *Columba palumbus*, Garden Warbler *Sylvia borin* contributed considerably to the species turnover in small fragments (smaller

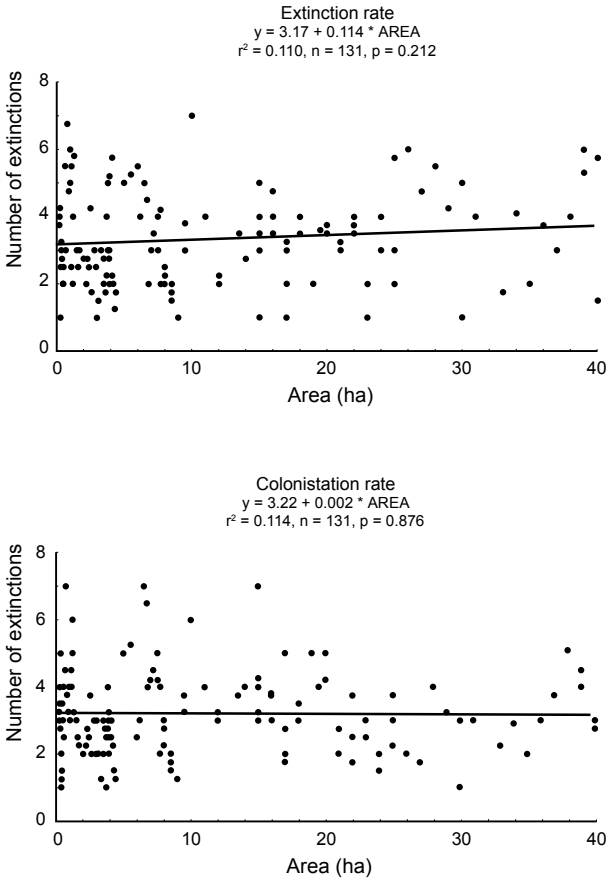

Fig. 1. Relationships between extinction and colonisation rates of breeding species and fragment area (mean values for 1995–1999).

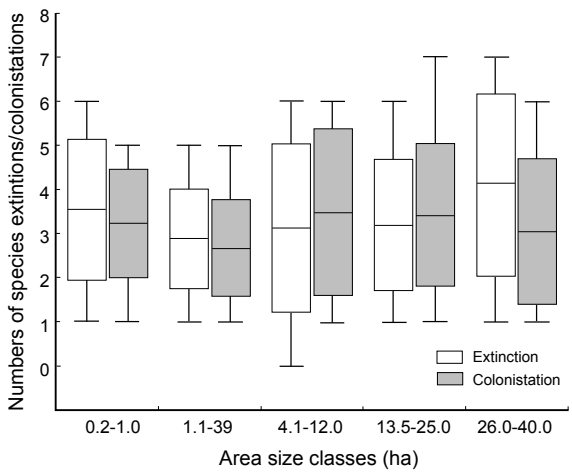

Fig. 2. Extinction and colonisation rates on five size classes of habitat fragments (mean, SD, min–max).

than 4 ha). Others, such as Grasshopper Warbler *Locustella naevia*, Wood Warbler *Phylloscopus sibilatrix* or Corncrake *Crex crex* contributed to the turnover rate mostly in the large fragments, while still others did not show any variation in this participation in relation to the size of the surveyed plot (Hooded Crow *Corvus corone*, Spotted Flycatcher *Muscicapa striata*, Lesser Whitethroat *Sylvia curruca*). On the other hand, two species (Pheasant *Phasianus colchicus*, Mallard *Anas platyrhynchos*) appeared in the groups with the highest participation on both the smallest and the largest fragments. The species, which had the greatest share in the total turnover included the following, in ranking order: Red-backed Shrike *Lanius collurio*, Pheasant, Mallard, Reed Bunting *Emberiza schoeniclus*, Woodpigeon and Whitethroat (Fig. 3).

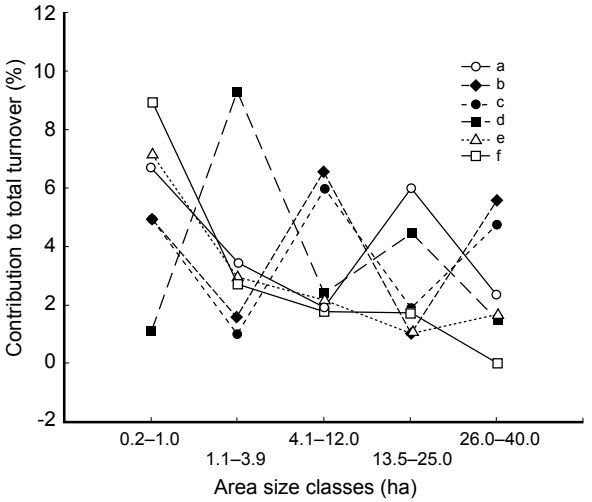

Fig. 3. Turnover results in relation to size classes of habitat fragments for six species contributing most to total turnover rate: a — *Lanius collurio*, b — *Phasianus colchicus*, c — *Anas platyrhynchos*, d — *Emberiza schoeniclus*, e — *Columba palumbus*, f — *Sylvia communis*.

The species that contributed most to turnover in the lowest size fragments were represented by a mere 1 or 2 pairs. This number increases with the size of fragment and drops again in the group of the largest fragments (Table 4). The mean number of pairs of the species participating most in the species turnover was, as a rule, less than one, except for the largest fragments. Although the range of breeding pairs significantly varied in some species, it was only for Marsh Warbler *Acrocephalus palustris* and Whinchat *Saxicola rube-*

Table 4. Contribution of individual species to turnover rate (TR) and mean number of pairs (Np ± SD) of the species contributing most to turnover according to size classes of habitat fragments. % — percentage of sample plots occupied, n — number of fragments, n_a — average number of species ± SD.

Species	TR%	Np ± SD	Range	%
0.2–1.0 ha (n = 21, n_a = 7.3 ± 2.9)				
Sylvia communis	8.9	0.7 ± 0.7	0–2	60
Sylvia borin	7.8	0.2 ± 0.4	0–1	25
Columba palumbus	7.2	0.4 ± 0.5	0–1	40
Lanius collurio	6.7	0.3 ± 0.4	0–1	25
Pica pica	6.1	0.5 ± 0.5	0–1	50
Parus major	5.6	0.3 ± 0.5	0–1	30
Carduelis carduelis	5.6	0.2 ± 0.5	0–2	20
Phasianus colchicus	5.0	0.2 ± 0.4	0–1	20
Anas platyrhynchos	5.0	0.3 ± 0.5	0–1	30
other 24 species	42.1			
1.1–3.9 ha (n = 30, n_a = 14.2 ± 7.1)				
Emberiza schoeniclus	9.3	0.6 ± 0.8	0–3	47
Carduelis cannabina	7.6	1.0 ± 0.9	0–3	67
Hippolais icterina	6.8	0.9 ± 1.4	0–4	33
Streptopelia turtur	5.9	0.2 ± 0.4	0–1	13
Parus caeruleus	5.9	0.6 ± 0.8	0–2	43
Alauda arvensis	5.1	0.2 ± 0.5	0–2	13
Saxicola rubetra	5.1	0.3 ± 0.6	0–2	23
Oenanthe oenanthe	5.1	0.1 ± 0.4	0–1	10
other 30 species	49.2			
4.1–12.0 ha (n = 31, n_a = 19.5 ± 8.8)				
Carduelis chloris	7.7	0.7 ± 1.0	0–4	42
Phasianus colchicus	6.6	0.7 ± 1.5	0–6	68
Anas platyrhynchos	6.0	0.2 ± 0.5	0–2	16
Muscicapa striata	6.0	0.2 ± 0.4	0–1	16
Oriolus oriolus	5.4	0.5 ± 0.6	0–2	48
Phylloscopus trochilus	5.4	0.9 ± 1.2	0–5	48
Luscinia megarhynchos	4.8	1.0 ± 1.2	0–3	35
Parus montanus	4.8	0.2 ± 0.4	0–3	19
Turdus philomelos	4.8	0.1 ± 0.4	0–1	16
other 35 species	48.5			
13.5–25.0 ha (n = 32, n_a = 20.4 ± 12.2)				
Crex crex	6.9	0.8 ± 2.5	0–14	25
Lanius collurio	6.0	0.9 ± 1.1	0–3	56
Acrocephalus palustris	5.0	8.7 ± 8.8	0–34	84
Perdix perdix	5.0	0.4 ± 0.6	0–2	44
Saxicola rubetra	5.0	2.3 ± 2.1	0–7	81
Sylvia borin	5.0	0.3 ± 0.6	0–3	22
Coturnix coturnix	4.5	0.1 ± 0.3	0–1	16
Locustella fluviatilis	4.5	0.9 ± 2.9	0–15	22
Emberiza schoeniclus	4.5	1.8 ± 2.4	0–8	66
Streptopelia turtur	4.5	0.2 ± 0.5	0–2	31
other 42 species	49.1			
26.0–40.0 ha (n = 17, n_a = 26.9 ± 14.5)				
Locustella naevia	7.1	1.1 ± 1.8	0–7	35
Carduelis chloris	6.3	0.8 ± 1.8	0–6	35
Phylloscopus sibilatrix	5.6	1.9 ± 3.8	0–13	29
Dendrocopos minor	5.6	0.4 ± 0.7	0–2	29
Phasianus colchicus	5.6	1.6 ± 2.5	0–7	41
Anas platyrhynchos	4.8	0.5 ± 0.9	0–3	29
Parus caeruleus	4.8	1.7 ± 2.1	0–8	65
Phylloscopus collybita	4.8	1.5 ± 2.5	0–7	41
Sylvia curruca	4.8	0.2 ± 0.5	0–2	18
other 34 species	50.6			

tra in the 13.5–25.0 ha class where the mean number exceeded two pairs.

The variable that contributed most to the explanation of the variability of the extinction and species turnover rates was the number of habitats within the fragment. For the colonisation rate, it was the proportion of old stand within a fragment. No variable, however explained the variability of all three of the measured parameters (Table 5).

Table 5. Stepwise multiple regression analysis of extinction, colonisation and turnover rates of breeding species in relation to area, structure, isolation and surrounding land use of habitat fragments (abbreviations of variables — see Table 3). % — percent of variance explained, (-) after variables indicates a negative relationship.

Parameter	Step	Variables	%	p
Extinction rate	1	HABITATS	15.2	< 0.0001
	2	CANOPY	9.7	0.0002
	3	PERIMET	5.6	0.0089
	Total		30.5	
Colonisation rate	1	OLDTREES	10.9	0.0008
	2	PERIMET	8.0	0.002
	3	S-GRASS	4.6	0.015
	4	S-CROPS	4.1	0.027
	Total		27.6	
Turnover rate	1	HABITATS (-)	22.9	< 0.0001
	2	S-GRASS	19.1	< 0.0001
	3	TREEAGE	8.7	0.0003
	4	CONNECT	4.4	0.002
	Total		55.1	

DISCUSSION

Factors affecting turnover rate

Generally, the variables describing isolation did not have an impact on extinction, colonisation and turnover rates (except for the connectedness measure), whereas the variables describing surrounding matrix impacted on colonisation and turnover rates. In the case of birds, which are extremely mobile animals, in habitat fragments in agricultural environment the probability of individual movements caused by either dispersion or stochastic events, which would be, in turn, directly reflected in the extinction, colonisation or species turnover rates, was very high and did not seem to be related to the variables corresponding with the level of isolation. Water, which isolates oceanic islands, is a habitat not accessible to most terrestrial organisms and thus provides an extremely effective barrier to their movements. In the case of terrestrial island habitats (fragments), the isolating surroundings (arable fields, pastures etc.) are inhospitable or even hostile as a possible site for reproduction or longer residence, but they are not impenetrable barriers. Hence there was no statistically significant effect of the variables characterizing isolation for the parameters studied. At the same time a positive relationship with the variables describing the surroundings (like percent of perimeter adjoined by grass or by crops), that should rather isolate fragments, was found for colonisation and turnover rates (Table 5).

Thus, the effects of the variables describing the number of habitats, isolation and features of the surroundings in the regression models of extinction, colonisation and turnover rates corroborated the hypothesis that heterogeneous habitats in a mosaic landscape cannot be treated as islands (Norton et al. 2000, Haila 2002). The results also showed that for explaining variation in species composition a much more important factor could be variables corresponding with vegetation and its spatial structure. For example, with increasing age of trees and a contribution of old trees in a fragment, new ecological niches emerge and the species colonising them will become permanent elements of a given habitat. The results presented in Table 6 indicated that in a mosaic landscape this process may be reflected in the local rates of colonisation and/or turnover. Under the theory of succession, such rotation of species continues until a certain climax stage is reached in the area (Głowaciński 1981, Baguette et al. 1994). Unexpectedly, the extinction rate increased with the number of habitats in a fragment. This effect could be caused however, by habitat generalists such as Pheasant, Skylark *Alauda arvensis*, Quail *Coturnix coturnix*, Grey Partridge *Perdix perdix* or Corncrake, whose presence was also dependent on the surrounding farmland. As it has already been demonstrated, the domination of species with such a life strategy is negatively correlated with the number of habitats (Tworek 2002). On the other hand, extinction rate may also increase with the number of habitats because as habitat types are added, they may initially be small and hence limit the population size of associated species which in turn makes them vulnerable to stochastic extinction.

Relationships between the rate of species turnover and the variables connected with vegetation are also worth attention because the results obtained may indicate the type of habitats from which the species contributing most to the spe-

cies turnover originate (cf. Table 4). Because the habitat fragments of the studied area were not homogeneous, such as for woods, but much more diversified (of an ecotone character), the results combined the level of the turnover rate with the edge effect. Worthy of notice is that habitat composition might also affect the results if there were any differences in their proportions between fragments size classes. This effect was only included indirectly (variable HABITATS) because I did not studied what area of each fragment was covered by habitat types I had distinguished.

The lower importance of individual variables such as the area size or isolation from other similar habitats means probably that in a mosaic landscape the variables defining area parameters and habitat patterns are interlinked. Bird species occurring in forest margins, besides moving between fragments, could also move into direct vicinity of man (gardens, hedges and green areas). As the built-up areas were not taken into consideration as fragments, it is difficult to asses the impact of such a phenomenon on the results obtained for extinction and colonisation rates. Nevertheless, the presence of such strongly transformed habitats in a diverse landscape should not be overlooked. It is almost certain that the proportion of such areas will increase and will be, together with other variables, more and more significant in metapopulation processes. Therefore, future studies should examine the effect of farmsteads and built-up areas as well as other elements of landscape structure on changes in bird fauna with greater care.

Species–area relationships

Do individual species show a relationship between turnover rate and sample area? If there is no such relationship for the whole bird assemblage (Table 5) one should try to understand why some species show high turnover rates in small habitat patches while others do so in large ones and what the differences should be associated with. Only two species, Pheasant and Mallard, are among those with the highest species turnover rates on both the smallest (< 1 ha) and the largest (> 26 ha) study fragments. Their occurrence, however, does not depend on area. As far as Mallard is concerned, specific size-independent water habitat features are the main factors responsible for presence of the species while occurrence of Pheasant depends on the artificial supply of the population. Another interesting point is whether the changes in species composition are random or are there some consistent patterns explaining them? Having certain species contributing to turnover more than others may not be due to the fact that they are more "variable" species. The way in which turnover rate was calculated can cause that for a given species its relative value changes over fragments of different size if the species showed some kind of incidence function.

It can be predicted that in large-area samples the percentage of species of forest interior will increase. This supposition is supported by both the absence of such species as Wood Warbler, Lesser Spotted Woodpecker *Dendrocopos minor* or Chiffchaff *Phylloscopus collybita* in small fragments and the high turnover of these species in the largest fragments. The results obtained for the smallest fragments are much more difficult to explain. One should bear in mind that individual fragments are occupied by species populations which are parts of a metapopulation. Metapopulation dynamics are a complex result of subpopulation dynamics and interchange of individuals between habitat patches occupied by subpopulations (Hanski 1994). Consequently, the existence of the species in the smallest fragments, which is the result of local extinction or recolonisation, may be related first of all to habitat quality. Taking into consideration poor habitat isolation and high permeability of isolating habitats (edge effect), habitat quality may be decisive in forming dynamics of subpopulation of a particular species. Therefore, the list of species with the highest turnover rate in the smallest patches as well as the percentage of other species in the largest areas depends mostly on the habitat type in which the research is carried out. Moreover, impact of the surrounding landscape may be more significant for temporal dynamics of animal communities than the processes in the fragment itself (Wiens et al. 1985, Hobbs 1993, Jokimäki et al. 2000). It concerns mainly birds which are the most mobile terrestrial animals and may use the matrix in different ways (Saunders et al. 1991, Balent & Courtiade 1992, Bentley & Catterall 1997).

Effects of fragmentation

The absence of species in small fragments can be attributed to reduced habitat heterogeneity because many bird species require more than one habitat types (Rolstad 1991). However, the results show also that fragments may differ in the probability of being occupied as a result of various spatial characteristics: size, habitat quality, distance to other patches and resistance of the landscape matrix.

As the remnants of natural habitats in altered surroundings in terrestrial conditions may not be treated as islands, it is worth considering what factors determine the differences. Nowadays it is recognized that what happens within the fragments often results from the phenomena of a wider, landscape-related context. The effects of edges on bird populations and assemblages are usually important, but not always the same. In highly fragmented landscapes in geographical latitudes such as Central Europe many bird species show major movements of an unknown nature, from year to year (Jokimäki et al. 2000, Doherty & Grubb 2002). There are some studies of species dispersion, but they usually refer to forest species (e.g. Matthysen et al. 1995), whereas there is a lack of studies concerning species movements in more heterogeneous habitats in agricultural landscapes. Thus it is difficult to discern the changes in species composition caused by dispersion of individuals because of alterations in habitat structure and configuration from casual changes (stochasticity). For this reason, the relationships found are related to resident and migrant species together, although the set of variables of substantial importance in explaining the variability in groups of different migratory status can be different (Tworek 2003).

Although nowadays a lots of ecosystems are intensely fragmented most researches of changes in species composition comes from short-term studies. My study is an example of longer ones, in which the metapopulation dynamics is followed in a great number of fragments to assess extinction/colonisation and turnover rates, and to relate these parameters with habitats and landscape characteristics. The results support the argument that the effects of fragmentation are influenced by the landscape context (Brotons et al. 2003). They also suggest that species responses may vary in landscapes with different matrix qualities. Important insights on the mechanisms how species respond to a landscape structure could be brought by researches focused on the role of species flexibility in resource use and their exploratory behavior. An attempt to know the genetic adaptation of species to fragmentation from the functional effect of environmental plasticity of a species may be a challenging task in future researches on habitat fragmentation.

ACKNOWLEDGEMENTS

I thank Zbigniew Głowaciński, Jan Pinowski, and Jacek Wasilewski for valuable comments on earlier drafts of this manuscript. Through their remarks, two anonymous reviewers also considerably improved the quality of the manuscript. The help of Henryk Sułek was appreciated during bird censuses and Róża Kaźmierczakowa during vegetation descriptions. In 1996–1998 this study was supported by the Polish State Commitee for Scientific Research (grant No. 6P04G00910).

REFERENCES

Baguette M., Deceuninck B., Muller Y. 1994. Effect of spruce afforestation on bird community dynamics in a native broad-leaved forest area. Acta Oecol. 15: 275–288.

Balent G., Courtiade B. 1992. Modelling bird communities and landscape patterns relationships in a rural area of South-Western France. Landscape Ecol. 6: 195–211.

Bentley J. M., Catterall C. P. 1997. The use of bushland, corridors and linear remnants by birds in southeastern Queensland, Australia. Conserv. Biol. 11: 1173–1189.

Bibby C. J., Burgess N. D., Hill D. A. 1992. Bird census techniques. Academic Press, London.

Brotons L., Mönkkönen M., Martin J. L. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. Am. Nat. 162: 343–357.

Cieślak M. 1994. The vulnerability of breeding birds to forest fragmentation. Acta Ornithol. 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.

Doherty P. F., Grubb T. C. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83: 844–857.

Gilpin M., Hanski I. 1991. Metapopulation dynamics. Academic Press, London.

Głowaciński Z. 1981. Stability in bird communities during the secondary succession of a forest ecosystem. Ekol. pol. 29: 73–95.

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.

Hanski I. 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63: 151–162.

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., Huhta E., Mönkkönen 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.

MacArthur R. H., Wilson E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton.

Mason C. F. 2001. Woodland area, species turnover and the conservation of bird assemblages in lowland England. Biodiv. Conserv. 10: 495–510.
Matthysen E., Adriaensen F., Dhondt A.A. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented landscape. Oikos 72: 375–381.
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.
Petersen B. S. 1998. The distribution of Danish farmland birds in relation to habitat characteristics. Ornis Fennica 75: 105–118.
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.
Saunders D. A., Hobbs R. J., Margules C. R. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5: 18–29.
StatSoft Inc. 1997. Statistica for Window. Tulsa OK. Polish Edition by StatSoft Polska Sp. z o.o. Kraków, Poland.
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.
Tworek S. 2003. Local extinction, colonisation and turnover rates of breeding birds in fragmented landscapes: differences between migratory guilds. Ornis Fennica 80: 49–62.
Wiens J. A., Crawford C. S., Gosz J. R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45: 421–427.
Wilcove D. S., McLellan C. H., Dobson A. P. 1986. Habitat fragmentation in the temperate zone. In: Soulé M. E. (ed.). Conservation Biology. The science of scarcity and diversity. Sinauer Associates, Massachusetts, USA, pp. 237–256.

STRESZCZENIE

[Czynniki wpływające na czasową dynamikę ptasich zgrupowań w krajobrazie mozaikowym]

Badania prowadzone były w latach 1995–1999 w południowej Polsce, w krajobrazie rolniczym (Tab. 1). Na obszarze badań wyznaczono powierzchnie badawcze stanowiące pozostałości naturalnych/półnaturalnych siedlisk (fragmenty). Podzielono je na 5 klas wielkości, ze względu na powierzchnię, która wahała się od 0.2 do 40.0 ha (Tab. 2). Poszczególne fragmenty opisano przy pomocy 17 zmiennych charakteryzujących ich strukturę, usytuowanie w krajobrazie i cechy otoczenia (Tab. 3). Przy pomocy metody kartograficznej wykonywano liczenia ptaków w każdym z fragmentów. Na tej podstawie określano liczbę par lęgowych (N), liczbę gatunków (S) oraz tempo ekstynkcji (E), kolonizacji (C) i wymiany gatunkowej (TR). Tempo wymiany gatunkowej obliczono wg formuły: $TR = (E + C)/(S1 + S2) \times 100\%$, gdzie E oznacza liczbę gatunków, które zniknęły z powierzchni (ekstynkcja), a C — liczbę gatunków, które pojawiły się na powierzchni (kolonizacja), między dwoma kolejnymi sezonami lęgowymi, a S1, S2 to liczby wszystkich gatunków lęgowych we fragmencie w tych samych sezonach lęgowych. Nie wykryto istotnej zależności między liczbą ekstynkcji i kolonizacji a wielkością fragmentów (Fig. 1). Tempo ekstynkcji nie różniło się istotnie od tempa kolonizacji w żadnej klasie wielkości badanych fragmentów (Fig. 2). Fragmenty różniły się natomiast zarówno pod względem składu gatunków ptaków, które miały największy udział w wymianie gatunkowej, jak i pod względem procentowego udziału poszczególnych gatunków w całkowitym tempie wymiany (Tab. 4). Do gatunków mających największy udział w całkowitym tempie wymiany należały: gąsiorek *Lanius collurio*, bażant *Phasianus colchicus*, krzyżówka *Anas platyrhynchos*, potrzos *Emberiza schoeniclus*, grzywacz *Columba palumbus* i cierniówka *Sylvia communis* (Fig. 3). Największy udział w wyjaśnieniu zmienności w tempie ekstynkcji, kolonizacji i wymiany gatunkowej miała zmienna określająca liczbę siedlisk (HABITATS). Żadna ze zmiennych nie znalazła się natomiast wśród mających istotne znaczenie we wszystkich trzech modelach regresji (Tab. 5). Mniejsze znaczenie pojedynczych cech, takich jak wielkość fragmentów czy stopień izolacji od innych, podobnych siedlisk, wskazuje że w zróżnicowanym siedliskowo krajobrazie zmienne określające parametry badanych fragmentów i strukturę siedlisk są ze sobą wzajemnie sprzężone. W dużych fragmentach wzrasta udział gatunków leśnych, które nie występują w niewielkich fragmentach. Z kolei brak pewnych gatunków w niewielkich fragmentach może wynikać z mniejszego zróżnicowania siedliskowego. Istnienie gatunku w najmniejszych fragmentach można zatem wiązać przede wszystkim z jakością siedlisk, która — przy słabej izolacji w warunkach rolniczego krajobrazu i w konsekwencji dużej „przenikalności" środowisk izolujących — może mieć decydujące znaczenie w kształtowaniu dynamiki liczebności subpopulacji gatunków występujących w takich środowiskach. Wpływy otaczającego krajobrazu mogą mieć nawet większe znaczenie dla dynamiki zgrupowań ptaków niż procesy mające miejsce w obrębie fragmentów. Dotyczy to zwłaszcza ptaków, które jako zwierzęta najbardziej mobilne wykorzystują otoczenie na wiele sposobów.