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The size of breeding territory in an urban population of the Blackbird (*Turdus merula*) in Szczecin (NW Poland)

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The size and quality of breeding territory of Blackbird populations were studied in 1997–2000 in two parks of Szczecin (NW Poland). The Blackbird density as well as timing of territory occupation influenced the territory size. A significant reduction in territory size with increasing park and plot breeding birds density was recorded; moreover the territories acquired early in the season were larger than those took later on. The breeding success was found to depend mainly on female age and shrub coverage of the territory. Older females showed higher breeding success than younger ones; the success being lower in the preferred (pre-empted) territories with denser shrub coverage. The most likely explanation for distribution patterns observed in the Blackbird territories involves elements of both the ideal free and ideal despotic distributions.

1. Introduction

Reproductive success of most birds depends on their breeding at a suitable site. In a situation of heavy competition, it is important to own a territory. Our understanding of territorial behaviour of birds is incomplete, although the problem has been studied by numerous workers, e.g. Davies (1978), Stamps (1994), Tobias (1997), Goss-Custard and Sutherland (1997). However, the Blackbird (*Turdus merula)* belongs to those bird species whose territorial behaviour seems to be rather well known. The size and quality of territories occupied by urban populations of the species were studied by, i.e., Steinbacher (1953), Jackson (1954), Lind (1955), and Snow (1956). All those studies were conducted in Western Europe, where numerous ecological variables, e.g. density and the migratory status of a population, differ from those observed in Central Europe.

Originally, the Blackbird was a forest species. In the mid-1850s, it invaded cities of Western Europe. Its urban populations continue to expand northwest. However, some cities in northern Poland and Russia have yet to be colonized permanently (Mulsow & Tomiałojć 1997).

Fretwell and Lukas (1970) developed two models to explain density and distribution of individuals along gradients of habitat quality. The ideal-free distribution model proposes that the quality of most preferred habitats declines as population density increases. Thus the less preferred habitats become equally attractive as the breeding season continues, and individual fitness will be identical in preferred and less preferred habitats. Thus, the size and quality of breeding territory of both the young and old males should decrease as the breeding season progresses. The ideal-despotic model proposes that there are differences in the resource holding potential of individuals, and subordinates are forced into less suitable habitats by territorial behaviour.

Thus individual fitness is predicted to be higher in the preferred habitat than in a habitat of lower suitability. These basic models have subsequently been modified to incorporate phenotypic differences among individuals, and ideal free distributions may even occur when individuals are of unequal competitive ability (Sutherland & Parker 1985).

The aim of this study was to compare the size and quality of breeding territories of individual Blackbirds differing in their morphological characteristics, age, residency, and overwintering mode, and to identify key factors determining the size and quality of breeding territories.

2. Materials and methods

2.1. Study area

The observations were carried out in two city parks of Szczecin (420,000 inhabitants; NW Poland): Zeromski Park (Park Z, 21.9 ha) was studied in 1997–2000, while observations in Kownas Park (Park K, 16 ha) were conducted in 1998–2000. Park Z is located in the city centre (1.5 km from the nearest periphery, and 0.5 km from a forested island on the River Odra), is subjected to constant human penetration, and is surrounded by blocks of flats and streets. The canopy consists of 100- to 200-year-old, mostly deciduous trees and is dominated by oak (*Quercus sp.*), linden (*Tilia* sp.), beech (*Fagus silvatica*), and horse chestnut (*Aesculus* sp.). The understorey is very poor; the shrubberies, occupying 7% of the park's area, consist mainly of yew (*Taxus baccata*) and deciduous shrubs: spirea (*Spirea* sp.), common snowberry (*Symphoricarpos albus*), and common barberry (*Berberis vulgaris*). Because the number of breeding pairs in the study area changed during a breeding season (with a peak in May), the maximum densities had to be estimated for each year (there were 1.0, 1.2, 1.4, and 2.1 pairs/ha in 1997, 1998, 1999, and 2000, respectively). The predators occurring in the park include house marten *(Martes foina),* domestic cat, dog, Hooded Crow *(Corvus corone),* Magpie *(Pica pica),* Jay *(Garrulus glandarius),* Jackdaw *(Corvus monedula),* Kestrel *(Falco tinnunculus),* and Sparrowhawk *(Accipiter nisus).*

Park K is a part of a large green area with detached houses and gardens and merges smoothly with suburban woodlands. The intensity of pedestrian traffic is much lower than in Park Z. The canopy is formed primarily by beech (*Fagus silvatica*), European ash (*Fraxinus excelsior*), oak (*Quercus sp.*), maple (*Acer* sp.), and small-leaved linden (*Tilia cordata*). Common yew (*Taxus baccata)* and conifers, mainly common larch (*Larix decidua*), Weymouth pine (*Pinus strobus*), Norway spruce (*Picea abies*), contribute about 40% to the total tree stand. The understorey is very poor, the shrubberies occupying 9% of the park's area and consisting almost exclusively of yew. The maximum densities of Blackbirds recorded in the park in 1998, 1999, and 2000 were 1.2, 1.1, and 1.3 pairs/ha, respectively. The predators identified in the park included house marten, cat, dog, squirrel *(Sciurus vulgaris),* Magpie, Hooded Crow, Jay, Jackdaw, Tawny owl *(Strix aluco),* Kestrel, and Sparrowhawk.

The Blackbird population studied in this work is partly resident. Most of its members leave their territories once breeding is over (July, August) to reappear, in most cases, at some time between October and December; some of the birds return at the onset of the subsequent breeding season.

2.2. Data collection and processing

Observations in Park Z involved a total of 134 pairs: 22, 26, 37, and 49 pairs were observed in 1997, 1998, 1999, and 2000, respectively. In Park K, a total of 74 pairs were observed: 22, 23, and 29 pairs were under observation in 1998, 1999, and 2000, respectively. However, statistical treatment was applied to the territories of new pairs only. Territories occupied by divorced or widowed males were excluded from the analysis whenever the male stayed in the same territory. To identify the birds, most of them (about 80% of the population) were banded with colour rings.

To study how local density affects breeding territory size of the Blackbird, both parks were divided into 100 x 100 m squares and the Blackbird density was determined in each square in each year of the study. A breeding territory of a pair was assumed to belong to a square if at least 75% of the pair's territory fell within it; should 25–75% of a pair's territory be found within the square limits, the square was allocated 0.5 pair. If a given square contained less than 25% of a pair's territory, it was assumed that the pair in question did not affect the plot density, i.e. the density in the square. Whenever a territory covered parts of two squares, it was ascribed to that square which supported its larger part. If the between-square boundary divided a territory into two equal parts, the nest location decided whether the territory should be allocated to one or to the other square.

Similarly to the study of Creighton (2000), the size of a breeding territory was determined after observing each pair's movements (from 3 to 8–20 minute focal watches) and many of their territorial disputes with neighbours. Observations were carried out mainly during the time a female was building the nest prior to her first breeding attempt in the park. Because foraging is not restricted to the breeding territory (Hatchwell *et al.* 1996a, Wysocki, pers. obs.), observations on foraging birds were not used when determining territory sizes. The extent of coverage by deciduous and coniferous shrubs (measured to the nearest 1 m^2), size of canopy (tree-top density estimated in June to the nearest 10%) and understorey (estimated in the same time to the nearest 10%) were determined in each territory. Because of its very poor development in both parks, the understorey was excluded from the analysis.

The timing of territory occupation was determined from observations made at 3- to 5-day intervals during winter (i.e., until the end of February) and at 1- to 2-day intervals later on (March–July). Statistical treatment was based on pentades (five-day long intervals, for example, pentade 1 proceeded from 1 to 5 January, pentade 2 from 6 to 10 January, etc.).

The date of clutch initiation was determined from nest checks. As the majority of nests were placed 7 m above the ground, it was not possible to record the timing of laying the first egg; it was therefore assumed that the female began incubation after the third egg had been laid (day +2 of the breeding cycle). The beginning of the breeding season in both parks was determined based on the date the first egg in one of the parks was found. Statistical treatment was based on pentades (pentade 1 started at the very beginning of the breeding season).

Tarsus lengths were measured with callipers to the nearest 0.05 mm. The birds' age was determined from contrast in wing plumage (Svensson 1992).

Because the return rates were 76 and 60% for males in Park Z and Park K, respectively (Wysocki unpubl.), it was possible to compare the size of breeding territory of the same male during successive years.

2.3. Statistical treatment

The General Linear Model (GLM) was used to identify the most important factors affecting territory size and breeding success in the two parks combined. In the first model, breeding territory size was the dependent variable and fixed factors included the explanatory variables (year, park and plot density, time of territory acquisition, male age, male tarsus length; as the two parks differed in many respects, the analysis included also an individual park – K or Z – as an independent variable). In the second model, breeding success was the dependent variable and fixed factors included the explanatory variables (park, female age, territory size, territory occupation time, deciduous and coniferous shrub coverage, canopy, the number of deciduous and coniferous trees). Having found out that the parks differed in the factors decisive for breeding success, the GLM analysis was carried out for each park separately.

The relative size of each territory (S_r) was expressed as percentage of the mean territory size in the given year (S_m):

$$S_r = S/S_m \times 100$$

Significance of differences in the size of territory held by an individual in different years of its life was determined with the Wilcoxon test. ANOVA

Table 1. Mean territory size (m^2) of blackbirds in successive years of study.

	Park Z	Park K	F	P
1997	4789 ± 3834 n = 22			
1998	3398 ± 2976 n = 21	3517 ± 1585 n = 21	0.03	0.87
1999	3575 ± 2885 n = 31	3934 ± 1349 n = 17	0.11	0.74
2000	2168 ± 1138 n = 41	3404 ± 2081 n = 25	6.06	0.02

Table 2. Dependency of mean territory size of blackbirds in both parks on analysed factors (GLM analysis).

Factor	F	df	P
Free factor	91.16	1	<0.01
Park	1.43	1	0.23
T. merula density in the park	5.37	1	0.02
T. merula density in the plot	3.05	3	0.03
Occupation time	4.55	2	0.01
Male age	1.26	1	0.26
Male tarsus length	2.55	2	0.08

was used to analyse differences between territories in the extent of shrub coverage, while the Mann-Whitney U test was applied to analyse the timing of territory acquisition. Multiple regression was used to analyse the impact of territory size on the number of trees and bushed areas. Compliance to the normal distribution was tested with the Chi-square test.

3. Results

3.1. Territory size

The mean territory size in park Z varied from 4789 m^2 in 1997 to 2299 in 2000; in park K, the changes were smaller; 3306 m^2 in 2000 and 3815 in 1999. The differences between parks were significant in 2000 only (Table 1). According to GLM-analysis territory size was depending on park density, plot density, and occupation time of birds (Table 2); because there were no differences between the parks, we analysed combined data. A significant reduction in territory size with increasing park density was recorded. The mean territory size ranged from 3715 m^2 under density 1.0–1.5 pair/ha to 2299 m^2 under density 2.0–2.5 (Table 3). The same effect was observed in the case of plot density. The mean territory size varied from 4610 m^2 under density 0.5–1.0 pair/ha to 2053 m^2 under density 3.5–5.0 pair/ha (Table 3).

The territories acquired early in the season

Table 3. Dependency of mean territory size of breeding territory (m^2) on breeding density and time of territory aquisition.

Park density (pair/ha)			
1.0–1.5	2.0–2.5		
3715 ± 2621	2299 ± 1168		
n = 139	n = 35		
F = 9.70,P = 0.002			
Plot density (pair/ha)			
0.5–1.0	1.5–2.0	2.5–3.0	3.5–5.0
4073 ± 2501	3447 ± 2321	2920 ± 1786	2053 ± 1122
n = 47	n = 67	n = 30	n = 30
F = 8.01, P < 0.001			
Time of territory aquisition (pentades)			
1–10	11–20	after 20	
4073 ± 2501	3656 ± 2838	2509 ± 1345	
n = 46	n = 77	n = 51	
F = 5.75, P < 0.001			

Table 4. Shrub coverage (m^2), canopy development (%) and number of trees in territories acquired at different dates (C = coniferous, D = deciduous).

Pentade	1–10	11–20	after 20
Park Z n	32	57	21
Shrubs			
C	177 ± 289	79 ± 152	46 ± 131
D	244 ± 368	158 ± 224	38 ± 95
F = 3.99, P = 0.021			
Trees			
C	2.2 ± 3.4	1.3 ± 2.9	0.6 ± 1.1
F = 2.20, P = 0.12			
D	36.5 ± 22.6	30.1 ± 20.1	18.8 ± 12.0
F = 5.17, P = 0.007			
Canopy	56 ± 15	61 ± 17	65 ± 14
F = 2.08, P = 0.13			
Park K n	14	20	30
Shrubs			
C	521 ± 380	438 ± 415	91 ± 221
F = 11.07, P < 0.001			
Trees			
C	10.4 ± 7.1	9.4 ± 7.2	6.8 ± 7.0
F = 1.53, P = 0.23			
D	24.0 ± 10.4	21.5 ± 10.4	17.4 ± 10.0
F = 2.28, P = 0.11			
Canopy	59 ± 9	63 ± 14	72 ± 12
F = 7.33, P < 0.001			

were larger than those occupied later on. The mean territory size varied from 4073 m^2 in the case of territories acquired during pentades 1 to 10, to 2509 m^2 if the territories were acquired after pentade 20 (Table 3). A high coefficient of correlation between males and females was found in the time of taking the territory ($r = 0.67$, $P < 0.001$, $n = 174$).

Young males occupied their territories 20 days later, on average, than old males did (pentades 18 and 14, respectively), the difference in timing being significant (Mann-Whitney U test, $Z = 3.49$, $P = 0.0005$, $n_1 = 63$, $n_2 = 101$). The same is true for young males observed from one year of its life to the next (pentades 18 and 9 respectively), Wilcoxon test: $T = 2.5$; $Z = 2.7$; $n = 12$, $P = 0.007$).

The territories of young males were smaller than those of old males, but the difference was significant for those territories only that had been acquired early in the season (Pentades 1–20: young males 3029 ± 2057 m^2, $n = 36$, old males 4123 ± 2824 m^2, $n = 82$, $F_{1,116} = 4.37$, $P = 0.039$; pentade after 20: young males 2355 ± 1136 m^2, $n = 27$, old males 2814 ± 1606 m^2, $n = 19$, $F_{1,44} = 1.29$, $P = 0.26$). Also, significant differences were found between relative territory size held by a young bird in the first year of its life and that held in the following year (on average, males in their second year of life held 63% of a given year's mean territory size; one year later the territory size increased to 92%, Wilcoxon test: $T = 4.0$; $Z = 2.75$, $n = 12$, $P = 0.006$).

There were no differences in timing of occupation based on males' tarsus lengths.

3.2. Migration

Because park K is a part of a large green area with detached houses and gardens, wintering mode of blackbirds was stated for park Z only. In the population under study, males wintering in the study area acquired their territories earlier (pentade 10) than males not sighted between 1 December and 1 March (pentade 20), (Mann-Whitney U test; $Z = 3.19$, $n_1 = 8$, $n_2 = 52$, $P = 0.0014$).

Table 5. Dependency of deciduous and coniferous shrub coverage and number of trees on the size of the territory.

Park K	R^2	df	F	P
Coniferous shrub coverage	0.001	62	0.62	0.433
Number of coniferous trees.	0.11	62	7.70	0.007
Number of deciduous trees	0.42	62	45.81	<0.001
Park Z				
Coniferous shrub coverage	0.003	108	18.65	<0.001
Deciduous shrub coverage	0.15	108	0.32	0.573
Number of coniferous trees	0.001	108	0.77	0.782
Number of deciduous trees	0.38	108	67.08	<0.001

Table 6. Dependency of breeding success (number of nestlings) of blackbirds in park Z and K on analysed factors (GLM analysis).

Factor	F	df	P
Pooled data			
Free factor	11.43	1	0.001
Park	6.82	1	0.01
Female age	3.48	1	0.06
Territory size	0.20	2	0.82
Deciduous shrub coverage (DSC)	0.58	2	0.56
Coniferous shrub coverage CSC)	4.10	2	0.02
DSC + CSC	4.87	2	0.009
Canopy	2.04	2	0.13
Coniferous trees	0.21	2	0.81
Deciduous trees	1.96	2	0.14
Occupation time	1.09	2	0.34
Park Z			
Free factor	12.31	1	0.001
Female age	0.73	1	0.40
Territory size	0.58	2	0.56
Deciduous shrub coverage (DSC)	0.65	2	0.52
Coniferous shrub coverage (CSC)	3.43	2	0.04
DSC + CSC	5.69	2	0.005
Canopy	2.24	2	0.11
Coniferous trees	0.81	2	0.37
Deciduous trees	2.13	2	0.13
Occupation time	2.44	2	0.09
Park K			
Free factor	2.58	1	0.12
Female age	5.38	1	0.026
Territory size	0.75	2	0.48
Coniferous shrub coverage CSC)	0.01	2	0.94
Canopy	0.31	2	0.73
Coniferous trees	0.88	2	0.42
Deciduous trees	0.29	2	0.75
Occupation time	0.33	2	0.72

3.3. Vegetation

Shrub coverage, canopy development, and number of trees differed between territories acquired at different dates (Table 4). Those territories occupied earliest supported the most extensive shrubberies and the highest number of trees, the least extensive shrub cover and the smallest number of trees being found in territories acquired late. The opposite tendency was found in canopy development (territories acquired at the latest had the richest canopies, Table 4). In Park K, due to the very low amount of deciduous shrubs it supported, the analysis was performed for the conifers only. Territory size was highly affected by the number of deciduous trees in Park Z and by the number of deciduous and coniferous trees in Park K (Table 5). No differences between age classes in territory characteristics were found.

3.4. Breeding success

As the two parks differed greatly in the breeding success of the Blackbirds they supported, analysis of factors decisive for breeding success was carried out for each park separately (Table 6). Of the parameters that could have potentially affected the number of fledglings raised by a pair in Park K, female age was the only significant parameter. In Park Z, the significant parameters included the coniferous shrub density as well as the coniferous and deciduous shrub density combined; in addition, territory occupation time bordered on significance (Table 6).

Comparison of breeding success of young and old females showed young females in Park K to perform worse than old females, in terms of both the number of fledglings raised throughout the breeding season and in a clutch (no. of fledglings throughout breeding season: young females: 0.0 ± 0.0; n = 15; old females: 0.6 ± 1.0, n = 37, $F_{1,50}$ = 5.40, P = 0.024; fledglings/clutch: young females:

Table 7. Dependency of the breeding success on the shrub coverage.

Shrub coverage (m²)	0	1–200	201–1770
Fledglings:			
Park K			
Coniferous	1.0 ± 1.3	0.4 ± 1.1	0.2 ± 0.6
n	12	27	25
F = 3.66, P = 0.032			
Park Z			
Coniferous	2.5 ± 2.7	2.2 ± 2.8	1.7 ± 2.2
n	55	32	23
F = 0.72, P = 0.49			
All shrubs	2.5 ± 2.8	2.0 ± 2.4	2.3 ± 2.8
n	25	45	40
F = 0.25, P = 0.078			
Fledglings/brood:			
Park K			
Coniferous	0.3 ± 0.4	0.2 ± 0.5	0.1 ± 0.2
n	12	27	25
F = 1.89, P= 0.16			
Park Z			
Coniferous	1.0 ± 1.0	0.9 ± 1.3	0.7 ± 1.0
n	55	32	23
F = 0.57, P = 0.56			
All shrubs	1.1 ± 1.1	0.7 ± 0.8	0.9 ± 1.3
n	25	45	40
F = 1.15, P = 0.32			

0.0 ± 0.0, n = 15, old females: 0.2 ± 0.5, n = 37, $F_{1,52}$ = 4.23, P = 0.045).

No statistically significant difference in breeding success between young and old females was found in Park Z (no. of fledglings throughout breeding season: young females: 1.8 ± 2.1; n = 18, old females: 2.4 ± 2.7, n = 70, $F_{1,84}$ = 0.41, P = 0.52; fledglings/clutch: young females: 0.8 ± 1.0, n = 18, old females: 0.9 ± 1.1, n = 70, $F_{1,84}$ = 0.001, P = 0.98).

The highest breeding success in both parks was found in the territories devoid of shrubs (Table 7). The preference for nesting location changed during the breeding season: the nest-height increased (Park Z: 6.2 ± 4.8 m in breeding season pentade 1–6; 9.2 ± 5.8 m in pentade 7–12, 11.0 ± 6.4 m past pentade 12; $F_{2,334}$ = 21.0, P < 0.001; Park K: 5.0 ± 4.7 m, 9.3 ± 5.8 m, and 10.8 ± 5.2 m, respectively, $F_{2,197}$ = 21.2, P < 0.001); the preferred plant changed as well (at the beginning, females more often built their nests in coniferous trees and bushes, while later in the season they preferred deciduous trees; Table 8).

Although the nests placed in coniferous shrubs were more difficult to find, their success rate in the first month of the breeding season (pentades 1–6) in Park Z was lower than the overall mean rate for the same period (14% breeding success in coniferous shrubs vs. 25% in the remaining of the location, χ^2 = 3.36; P = 0.067). In Park K, the success rate was almost identical in both locations (8 vs 9%, χ^2 = 0.00; P = 0.97).

The parks differed in the timing of territory occupation. In Park Z, males acquired their territories in pentade 14.4, while in Park K in pentade 17.9 ($F_{1,184}$ = 8.45, P = 0.004). In Park Z, the territories acquired early in the season (pentades 1–10 and 11–20) produced more nestlings than those occupied later on (pentades past 20); 2.1 ± 3.0, 2.7 ± 2.6, and 1.1 ± 1.4 respectively, $F_{2,107}$ = 3.05, P = 0.051, but the number of nestlings per breeding attempt was similar (period I – 0.7 ± 1.1, II – 1.0 ± 1.1, III – 0.8 ± 1.1, $F_{2,107}$ = 0.60, P = 0.55).

Males wintering in the study area produced the same number of nestlings than males not sighted between 1 December and 1 March, (2.6 ± 2.8 and 2.9 ± 3.7 respectively, Mann-Whitney U test; Z = –0.13, P = 0.89, n_1 = 8, n_2 = 52).

In Park K, there were no differences in nestling production between territories acquired at different times (pentade 1–10: 0.4 ± 0.7, pentade 11–20: 0.3 ± 0.9 and past pentade 20: 0.5 ± 1.0, $F_{2,61}$ = 0.21, P = 0.81) or the number of nestlings per breeding attempt (pentade 1–10: 0.1 ± 0.2, pentade 11–20: 0.1 ± 0.3 and past pentade 20: 0.2 ± 0.5, $F_{2,61}$ = 0.56, P = 0.57).

Table 8. Nest number in different locations during the breeding season.

	Pentade		χ^2	P
	1–6	after 6		
Park K				
Dec. shrubs	1	2	0.03	0.85
Con. shrubs	38	4	60.66	<0.001
Dec. Trees	22	96	61.86	<0.001
Con. trees	16	11	3.15	0.076
Park Z				
Dec. Shrubs	6	15	0.08	0.36
Con. shrubs	36	5	49.31	<0.001
Dec. trees	73	189	45.86	<0.001
Con. trees	16	6	12.14	<0.001

4. Discussion

The territory sizes found in this work were comparable to those reported from other European urban populations of the species. Snow (1956) found European Blackbirds in Oxford to hold territories of a size ranging from 1600 to 2400 m², but Creighton (2001), who studied the same site, reported males holding territories ranging in size from 1530 to 5440 m². In Denmark, Lind (1955) estimated an average urban territory size at 1200 m², while Ludvig *et al.* (1994) and Jackson (1954) reported 1800 and 2000–7000 m², respectively.

As opposed to the findings of Steinbacher (1953) and Stephan (1985), density dependence was not the only explanation of the territory size in this study. The second important factor was the time of territory acquisition.

Territories occupied at different dates differed in size: those acquired late (past pentade 20) were much smaller than those occupied earlier. By defending a large territory, a bird normally has a better access to a suitable nesting site. As shown by Hoelzel (1989) for the Robin *Erithacus rube-*

cula, the size and quality of a territory may be decisive for attracting a female; Blackbird females are rarely attracted to a very small territory held by a young male (Snow 1958, Wysocki unpubl. data). Later, when all the new territories were being acquired by already paired birds, they never had to serve a function of attracting a female. Behavioural observations showed that, occasionally, after clutch loss, a female changed territory (sometimes this was accompanied by a change of the partner) by moving to a different part of a park. When this occurred, the new territory usually was very small (the smallest one had a diameter less than 30 m). Nevertheless, these small territories were seldom given up, although the neighbours were occasionally observed to strongly resist intrusion. The hypothesis that a large breeding territory increases a male European Blackbird's chances of attracting a female is supported also by the fact that there were no size differences between the territories held past pentade 20 by old and young males. Another reason why late-established territories were very small could involve a stronger resistance on the part of the territory-holders on whose territories the new territory impinges. Most of those new territories adjoined territories in which incubation or nestling-feeding was in progress. The weaker defence of a territory by its owners when the female is infertile (Birkhead & Mřller 1992, Wysocki per.obs.) may have made such late territory establishment possible. A possibility that a female selects a territory bordering the one belonging to feeding birds to increase her own breeding success (within-season conspecific attraction) cannot be ruled out either.

The relative size of a territory held by a male aged 3 years was statistically significantly larger than that held by the same male a year earlier. Similar age-dependent changes in territory size were observed in, e.g., the dunnock (*Prunella modularis*) (Davies 1992). However, these differences probably result from the fact that old birds acquire their territories earlier. Similar results were recorded by Schwabl (1983), who observed that those males that did not migrate for winter occupied territories at an earlier date and, therefore, could select optimal sites. Since Schwabl *et al.* (1980) found no differences in testosterone level between young and old blackbird males and in a wide range of avian species, this hormone plays a key role in regulating territorial aggression (see reviews by Wingfield *et al.* 1990), most probably then, the differences in the territory size stem from the fact that older males are more experienced and/or are better physically fit (Desrochers 1992, Cresswell 1998). In addition, one cannot rule out the possibility that territory size in some cases is decided upon by an individual bird size; as young Blackbirds are smaller than old (Glutz von Blotzheim *et al.* 1982, Wysocki 2002), their territories could be smaller too.

The Park Z males which were holding the same territory from one breeding season to the next were in most cases found to be able to maintain the territory in its original size and shape. Most probably, the high cost the European Blackbird incurs when occupying a new territory (Snow 1958, Wysocki pers.obs.) results in a close coupling between residency on the one hand and dominance and territory size on the other (Tobias 1997).

Numerous workers (Havlin 1963, Karlson & Källander 1977, Hatchwell *et al.* 1996a) have demonstrated that areas harbouring abundant shrub-type vegetation support high densities of the European blackbird. Also, studies focusing on blackbird nest sites indicate preferences for low shrubs (Dyrcz 1963). Karlsson and Källander (1977) found the availability of shrubs to an urban population of the European Blackbird in Sweden to be the most important determinant of territory quality, more important even than the availability of food. This has been corroborated by Landman (1991), who studied a rural population, and by Mulsow (1980), who studied an urban population. Hatchwell *et al.* (1996a) have stated that the nest exposure was the only characteristic to differ significantly between successful and unsuccessful nests: successful nests were less exposed than failed nests. After the breeding season, the evergreens provide protection during winter and are used as roosting sites (Erz 1965, Dierschke 1973).

In the present study, all the measured variables that might affect territory quality (shrub coverage, development of canopy, presence of nest-sheltering tree species), showed statistically significant differences between territories (there are no data on pedestrians, winter feeding and nest predators). Those territories acquired earliest in the season supported the most extensive shrubberies, those occupied last having much fewer shrubs. However, the coniferous shrubs served as major nest sites only during the first month of the breeding season; later on few nests were found in conifers. Most probably, the nest-hiding potential is not the only factor responsible for the European Blackbird's preference for areas with extensive shrubberies. This is indicated by the statistically significant relationship between the timing of territory occupation and the amount of deciduous shrubs in Park Z, the deciduous shrubs seldom being used for nesting either in the first month of the breeding season or later. It is certain that the lower amount of shrubs in territories acquired at a later date did not result from a reduction in the mean territory size (Table 8), but was a product of a preference change occurring during the breeding season.

Most probably, the cause of higher losses incurred by those nests hidden in conifers is their selective penetration by corvids, predominantly by the Magpie (Wysocki pers.obs.). Thus the experience accumulated by the birds is likely to have led them to avoid an ecological trap presented by an area supporting an abundant shrubbery, but offering few other, safer, breeding sites.

Tree canopies that are better developed provide a better shelter to nests built in them. As the mean height of a nest location increased during the breeding season, this is probably the reason why territories with better developed tree canopies are preferred in the later part of the breeding season. Reduction in the number of trees in the territories acquired later in time resulted from a reduction in the territory size as the breeding season proceeded (Table 8).

Thus it seems that parameters of individual territories cannot be considered out of the context of bird preferences in different parts of the breeding season. The evidence presented above demonstrates that, for the populations under study, the major function of shrubberies seems to provide safe foraging areas at the onset of the breeding season. This conclusion is corroborated by behavioural observations. In winter and at the beginning of the breeding season, the Blackbird forages most frequently in the litter underneath shrubs. The latter provide protection from Sparrowhawks, which frequently hunt in winter in both parks. Later on, as the shrubs develop leaves, the foraging Blackbirds move away from them. The shrubs may become important again should chicks leave the nest. However, since feeding parents are usually tolerated in an alien territory, it is possible for the young to move to sheltered sites in neighbouring territories, if their native ones lack shrubs (Wysocki, pers.obs.).

The most likely explanation for distribution patterns observed in Blackbird territories involves elements of both the ideal-free and ideal-despotic distribution models (Fretwell & Lucas 1970). In the study area, no differences in size territory were found between young and old males or in breeding success between territories acquired earlier and later, which is in agreement with ideal-free distribution hypothesis' prediction. Also, consistently with that hypothesis' prediction, the territory size decreased as the breeding season proceeded. Although, in Park Z, more fledglings were raised from territories acquired earlier, compared to those occupied later on (which would be suggestive of the ideal-despotic distribution model), the absence of differences in the number of fledglings per clutch demonstrates that the causes of differences should be sought in the number of clutches (the number of clutches is usually higher in territories acquired earlier) rather than in the territory quality, which is in conformity with predictions of the ideal-free distribution model. However, some of the results seem to conform to predictions of the ideal-despotic distribution hypothesis. Those predictions are supported by, firstly, difference between the parks in the timing of territory occupation. In Park Z, the territories are acquired more than 2 weeks earlier than in Park K, which, considering the mean number of fledglings raised in each park, lends support to the ideal-despotic distribution hypothesis. Secondly, territories of young males are acquired much later, which may result from worse condition of the subordinate birds; in addition, Park Z always harbours a floating population of (mostly) young males, which seems to be consistent with the ideal despotic distribution hypothesis (Edwards 1977). Moreover, the lack of differences in the number of fledglings/clutch raised between territories acquired early and late does not necessarily result from the lack of differences in territory quality, but may also be a result of the urban Blackbird population's inadequate adaptation to the growing predator pressure, the predators – until recently – avoiding centres of large cities (Marchant *et al.* 1990, Wysocki 2001).

The results point to diversity in Blackbird distribution modes in urban environment: explanation provided by the ideal despotic distribution is more appropriate in the case of Park Z (high density and breeding success), while the ideal free distribution is better suited to Park K (low density and breeding success). The same conclusions were reached by Hatchwell *et al.* (1996b) for the Blackbird and Huhta *et al.* (1998) for the Pied Flycatcher. Hatchwell *et al.* (1996b) studied woodland, farmland, and the woodland-farmland boundary. They found that Blackbirds appeared to be distributed in an ideal free manner between farmland and woodland, but there was considerable variation in habitat quality and Blackbird population parameters within woodland, suggesting an ideal despotic distribution. Huhta *et al.* (1998) stated that the distribution of Pied Flycatcher across forest stands of different sizes followed the ideal-free distribution model, whereas at the microhabitat level, age-related unequal distribution of males followed the ideal-despotic model.

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Mustarastaan esiintyminen ja pesimäreviirin koko kaupunkiympäristössä

Artikkelin kirjoittaja tutki mustarastaan pesimäreviirin kokoa ja laatua kahdessa puolalaisessa Szczecin kaupungin puistossa vuosina 1997–2000. Toisessa puistossa (koko 21,9 hehtaaria) pesi vuosittain 21–41 mustarastasparia ja toisessa puistossa (koko 16,0 hehtaaria) vastaavasti 17–25 paria. Mustarastasreviirien koko vaihteli tutkimuspuistoissa 2 299–4 789 m^2:n välillä. Reviirikoko havaittiin samansuuruiseksi kuin muissakin Euroopan kaupungeissa.

Sekä mustarastastiheys että saapumisaika reviirille vaikuttivat mustarastaan reviirikokoon. Mustarastaan reviirikoko pieneni mustarastastiheyden kasvaessa. Kun mustarastaita oli paljon (2,0–2,5 paria hehtaarilla), reviirikoko oli keskimäärin 2 299 m^2. Kun mustarastaita oli tutkimusalueella vähän (1,0–1,5 paria hehtaarilla), reviirikoko oli keskimäärin 3 715 m^2. Aikaisemmin vallattujen reviirien koko oli suurempi (4 073 m^2) kuin myöhemmin keväällä vallattujen reviirien koko (2 509 m^2). Nuoret mustarastaskoiraat saapuivat reviireilleen noin 20 päivää myöhemmin kuin vanhat mustarastaskoiraat. Nuorten mustarastaskoiraiden reviirikoko oli pienempi kuin vanhojen mustarastaskoiraiden. Pensaskerroksen peittävyys ja puuston määrä oli suurempi aikaisemmin vallatuilla reviireillä kuin myöhemmin vallatuilla reviireillä.

Lajin pesimämenestykseen vaikuttivat lähinnä naaran ikä ja reviirillä olevien pensaiden peittävyys. Vanhojen naaraiden pesimämenestys oli parempi kuin nuorten naaraiden. Pensaspeittävyys näytti vaikuttavan negatiivisesti mustarastaan pesimämenestykseen. Mustarastasreviirien jakaantumisessa ympäristöön oli piirteitä sekä ”Ideal free”- että ”Ideal despotic”-malleista. Mustarastaat valtasivat reviirin sellaisilta paikoilta, joissa niiden saama hyöty oli kulloinkin suurin mahdollinen.

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