Ornis Fennica 81:33–39. 2004

Territory size and habitat selection in subadult and adult males of Black Redstart (*Phoenicurus ochruros*) in an urban environment

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Received 28 August 2003, accepted 14 October 2003

Territory size, distribution of territories and habitat selection were studied in Black Redstart (*Phoenicurus ochruros*) populations in three urban habitats (garden city, old and new housing estates) of Prague (Czech Republic). We tested if the territory size and quality of territories occupied by adult and subadult males differed from each other. Average territory size of the adult males was 1.21 ± 0.80(SD) ha and of the subadult males 1.08 ± 0.58(SD) ha. This difference was not statistically significant. Moreover, males of particular age-class were not spatially clustered. Microhabitat analysis shows that the habitat selection depends on the presence of buildings. Apparently buildings offer a good nesting, singing and foraging places for the Black Redstart. The territory size of Black Redstarts differed between habitats, being largest in the garden city (1.98 ± 1.06 (SD) ha), intermediate in the old housing estate (1.48 ± 0.45 (SD) ha) and smallest in the new housing estate (0.85 ± 0.33 (SD) ha). Our results indicate that in urban environment the relationships between adult and subadult territory owners differ from those referred to in mountain villages.

1. Introduction

The Black Redstart, *Phoenicurus ochruros* (S. G. Gmelin, 1774), a small European passerine exhibiting delayed plumage maturation, is a suitable model for studies of variation in territory quality and spatial relationships between the two age categories of males. Subadult males have female-like, grey-brown plumage; second-year and older males (adults) are characterized by black face, throat and breast, grey-black forehead and crown, and grey mantle-back area. The Black Redstart occupies various habitats: dry, rocky zones, mountain habitats in higher altitudes and anthropogenous environments, i. e. villages, towns and industry agglomerations (Cramp 1988, Zamora 1991). In Europe the highest densities of this species are reported from the mountain and urban habitats (Hagemeijer & Blair 1997). In mountain villages the subadult males are displaced by earlier arriving adults to suboptimal and/or peripheral village zones with few, usually also young neighbours (Landmann & Kollinsky 1995). The males compete for the territories in the centre of human settlement, and the differences between territories of subadult and adult males may ensue from sharp gradient of resources. The situation may be different in large agglomerations owing to even distribution of human settlement and less harsh environmental conditions than in mountain villages.

We studied the Black Redstart territory distribution in three representative city habitats (i. e. garden city, new and old housing estate) to test whether there is any difference in the quality of territories occupied by subadult and adult males. We used the territory size, and proportion of microhabitats in the territory as a measure of the territory quality. Following the concept of economic defendability (Krebs & Davies 1993), we assumed smaller territories to be of higher quality (Davies 1992, Searcy & Yasukawa 1995).

We compared the distances between territories of subadult and adult males within each locality to find whether there are clusters of males of the same age. Another aim of this study was to test if the presence of vertical surfaces is the major criterion of territory choice.

2. Material and methods

2.1. Study sites

The study was carried out in three types of urban habitats situated in Prague (50°06'N 14°30'E, 280–380 m a. s. l.) in 1998 and 1999 viz. garden city, old (from 60's) and new (built in last 5 years) housing estate. The garden city adjoins the old housing estate, both are situated in NW side of the town, the border was made by the highway. The new housing estate is situated on the other side (NE) of Prague agglomeration. Size of the localities was 24.9–124.9 ha; they differed mainly in a vegetation structure (Kruskal-Wallis test for high dense trees with undergrowth: $H_{2,30} = 22.7$, $P < 0.05$) and types and density of buildings (Table 1). In the garden city, there were no houses higher than 3 floors. In contrast, buildings up to 5 floors occurred in the old housing estate. In the new housing estate there were even 6 to 12 floor high buildings standing close to each other. The borders of investigated areas were changed from the first season to the second one relative to human influence on localities. The influence of the year was tested in the GLM: year, habitat type and age of male were taken as dependent variables in the model, territory size as the independent one; there were found the significant effect of the year ($F_{1,54} = 16.87$, $P < 0.05$) and between effect of habitat and year ($F_{2,54} = 4.21$, $P < 0.05$, $n = 66$; whole model $R^2 = 39.93\%$). So, the combination of the habitat and the year was given as a single variable "locality" to simplify the model. For that reason, the term "locality" means "one habitat in one season" for all the following analysis.

2.2. Bird surveys

Localities were visited during the breeding season weekly (over 10 visits per locality, i. e. 150 to 300 min of observations per bird, from 3:00 to 7:00 CET) and all the activities of birds were recorded and mapped. Birds were observed with a 8 x 50 telescope. Only the data from the first breeding were taken into account. All the locations transferred to one map for each locality enabled us to estimate territory boundaries. The territory size was assessed as the area delimited by lines drawn closely outside (5 m) of the lines connecting marginal points where the territory owner was observed (minimal convex polygon), with the exception of evidently remote observations. Colour rings for exact individual identification marked the birds settled in overlapping territories mainly. We have mapped from 8 to 19 territories per locality.

2.3. Microhabitat measurements

Microhabitats were classified into five categories on the basis of vegetation structure, ground type, and presence of buildings (Table 1). Proportions of microhabitats in territories were taken from the maps. The same procedure was done for the control plots, areas of the approximately circular shape and the same average size as territories, randomly placed (by uninitiated person) into maps of studied areas (ten plots per locality).

Table 1. Proportion (in %) of different microhabitats in studied localities (i.e. garden city, old housing estate and new housing estate), and their overall areas.

Microhabitat	Garden city		Old housing estate		New housing estate	
	1998	1999	1998	1999	1998	1999
Overall area (ha)	109.3	124.9	54.8	57.9	24.9	62.8
Built-up area	14.22	14.18	15.50	15.93	14.67	15.96
Bare grounds	26.76	25.26	33.81	33.56	28.49	24.06
Herbaceous vegetation	3.02	3.03	12.74	12.46	10.86	18.42
Low rare trees with undergrowth	34.30	31.83	12.56	13.03	44.05	40.81
High dense trees with undergrowth	23.04	24.69	25.42	25.02	1.88	0.74

2.4. Statistical testing

Mann-Whitney U-test was applied to compare the proportion of each microhabitat between territories and the control plots. To test the dependence of territory size on microhabitat composition of territory we performed multiple linear regression analysis (forward stepwise variable selection, critical value for variable removal $P = 0.05$). To measure potential habitat-dependent and/or age-dependent differences in territory size we compared the territory sizes using GLM procedure (locality and male age were taken as the independent variables, territory size as the dependent one, between effect of these variables was also computed in the model). The proportions of one chosen microhabitat (differing in territories and control plots) in territories of subadult and adult males were compared by ANCOVA when territory size variance was taken as a covariate. We used log-transformed values of territory size and areas covered by specific microhabitats in these analyses. All the analyses were computed using STATISTICA 6.0 software.

Another studied feature was the mutual position of Black Redstart territories. The distance of each territory from the nearest subadult territory and from the nearest adult territory was defined as the shortest distance between the territory borders. These distances were compared by Wilcoxon matched-pair rank test (using S-Plus 4.0 software). Year-to-year territory overlap on each locality was defined as the proportion of territories situated at the same position in both years of the study. The position of two territories was considered as the same if at least 25% of territory area occupied in the second year was placed over the first year territory area.

The significance level is $P < 0.05$ for territory sizes, and distances between neighbouring territories. To keep the overall error of the five tests set below 5% we used Bonferroni correction (Sokal & Rohlf 1995) in the analyses of microhabitat composition of territories and randomly generated areas; in these analyses the significance level is $P < 0.01$.

3. Results

The parameters of 37 territories occupied by adult males and 29 occupied by the subadults were recorded. Average territory size was 1.15 ± 0.51(SD) ha; range 1.08–4.05 ha. Territory sizes of subadult (1.08 ± 0.58(SD) ha) and adult males (1.21 ± 0.80(SD) ha) did not differ (GLM: $F_{1,54} = 1.62$, ns, n = 66, Table 2). The locality had considerable effect on territory size (GLM: $F_{5,54} = 6.20$, $P < 0.001$, whole model $R^2 = 39.93\%$, n = 66, Table 2). The interaction between variables had no considerable effect on the model. Garden city in 1998 differed from all other localities except from the old housing estate; the largest territories were found there, the breeding density was 0.09 pairs/ha only (Table 2). In contrast, the smallest territories

Table 2. Adult and subadult males' average territory sizes (± SD), and breeding densities (pairs/ha) found in three urban habitats of Prague.

	Garden city		Old housing estate		New housing estate	
	1998	1999	1998	1999	1998	1999
Adult males	2.46 (± 1.38)	0.95 (± 0.64)	1.65 (± 0.42)	0.72 (± 0.26)	0.96 (± 0.23)	0.98 (± 0.50)
Subadult males	1.66 (± 0.76)	0.73 (± 0.36)	1.21 (± 0.42)	1.14 (± 0.74)	0.85 (± 0.28)	0.75 (± 0.08)
Breeding density	0.09	0.15	0.18	0.13	0.40	0.14

were found in the garden city in the season 1999. However, the breeding density in the garden city was 0.15 pairs/ha in this season (Table 2).

In 1999 the territories there were concentrated to the same regions as in the previous season (68.4% of territories were placed over the territories from the last season). The same situation was found in the old housing estate, where 62.5% of the territories overlapped between the years. In the new housing estate, only 22.2% of them were situated likewise. No cases of presence of the same ringed male (about 20% of males) in his last year territory were recorded in any of the localities. Presumably, there is a possibility that some of the non-marked adult males occupied the same territory during both years.

Comparison of the microhabitat proportions between the territories and control plots shows significant difference for built-up areas only (Mann-Whitney U-test: $Z = 2.44$, $P < 0.05$, $n = 132$). The higher proportion of buildings was found in territories (Fig. 1). Regression analysis shows a significant negative dependence of the territory size on the proportion of the territory area covered by buildings ($r = -0.37$, $F_{1,64} = 9.88$, $P < 0.05$, $R^2 = 13.37\%$). In smaller territories the proportion of build-up area was higher. The distribution of territories in ordination space based on the proportion of microhabitats was not affected by the owner's age (Fig. 2). The territories occupied by adult and subadult males did not differ in the representation of built-up areas (ANCOVA: $F_{1,62} = 0.38$, ns, $n = 66$).

The breeding sites were occupied randomly relative to owner's and neighbour's age (Wilcoxon rank test: $Z = 0.10$, ns, $n = 61$), there were no significant differences in distances between adult and subadult nearest neighbour relative to owner's age. Thus, the birds did not form any clusters composed exclusively by the same age category.

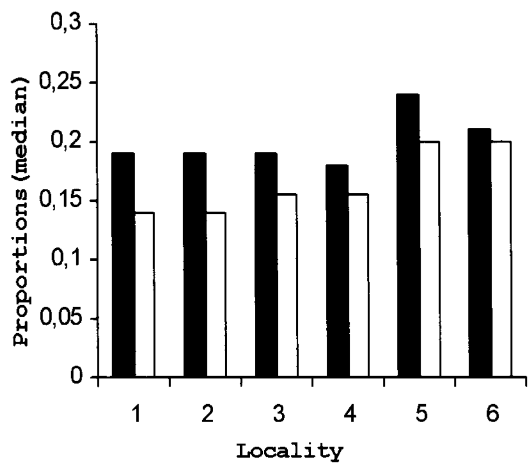

Fig. 1. Median values of proportions of built-up area in occupied territories (black columns) and control plots (white columns). Localities: (1) garden city in 1999; (2) garden city in 1998; (3) old housing estate in 1999; (4) old housing estate in 1998; (5) new housing estate in 1999; (6) new housing estate in 1998.

4. Discussion

4.1. Territory quality

Previous studies suggest overall structural diversity (Andersson 1995, Landmann & Kollinsky 1995) and particularly structural diversity of buildings (Weggler 2001) to be a criterion of habi-

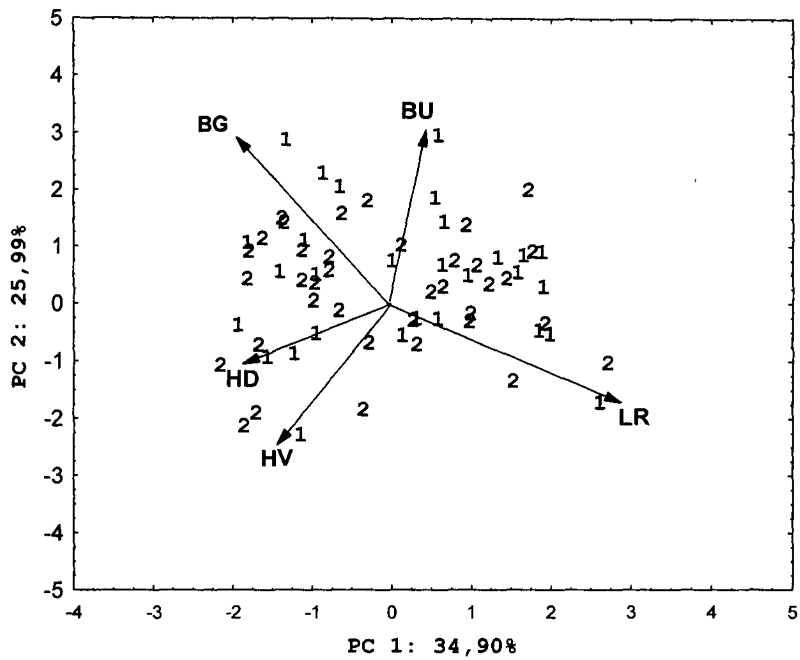

Fig. 2. Distribution of the territories occupied by subadult (1) and adult (2) males in the ordination space determined by the first two principal components based on the proportion of different microhabitats in the territories. BU = built-up area; BG = bare grounds; SG = surfaced grounds without vegetation; HV = herbaceous vegetation; LR = low (less than 2 m) rare trees with undergrowth; HD = high and dense trees (over 2 m) with dense undergrowth.

tat selection of Black Redstart. Our analysis of microhabitat composition of Black Redstart territories suggested presence of vertical surfaces as a possible criterion of habitat selection. The vertical walls seem to be the only common feature of different habitats inhabited by Black Redstarts (rocky, bleak land, and modern cities or industrial agglomerations; Cramp 1988). The walls in human settlements, and the rocks in montane areas represent the potential nest sites (Weggler 2001) and the food source (the insects resting frequently on the surfaces exposed to sun, or hilltoping around their tops) for the Black Redstart. The top position of the singing male should be important for the control of all the territory area and the possible intruders. The visibility and audibility of the male sitting on the top position is much better for the other individuals. So, the presence of suitable vertical surfaces should determine the size of the area occupied by male. Contrastingly, in some other urban breeders the negative relationships between bird abundance and built structure proportion were found (Jokimäki 1999).

The proportion of built-up area differs significantly between the real territories and control plots (Fig. 1). In the garden city, the larger territories were situated in the areas of villas surrounded by large gardens, while numerous but smaller territories were found in areas where family houses stand close to each other, i.e. forming long rows. The houses in the new housing estate are very similar and spaced in regular distances, what may explain the absence of preferences for particular regions. Accordingly to this observation, the regression analysis shows the significant dependence of the territory size on the proportion of the area covered by buildings in the territory. The larger territories included the higher proportion of non-preferred microhabitats (i. e. those, which proportion in territories was not significantly higher than in control plots). The territories in new housing estate were the smallest during both seasons. Larger territory area may be needed mainly in the garden city for the acquisition of a sufficient number of walls in the situation, when the buildings are far from each other in the areas covered by large gardens. However, the cause of such a pattern would arise from the food competition in garden-covered areas (Solonen 2001). The concentration of the other breeding bird species is higher than in more urbanized areas of garden city. These are less attractive for most species. If the food and nest sites availability are equal, as the urbanization increases, the density of breeding pairs increases (Kosiński

2001). Such a bird-human relationship (safe zones hypothesis) may explain the observed distribution and density pattern of Black Redstart's territories as well.

4.2. Territory size

The territory size of Black Redstart varies according to different habitats occupied by the species in Europe. We have found a wide variation in territory size (range 0.22–4.05 ha) in the urban habitats we studied. The Black Redstarts inhabiting montane areas occupy fairly smaller territories of the average size 0.28 ha for subadult and 0.57 ha for adult males (Landmann & Kollinsky 1995). The density of breeding pairs and the number of singing males per kilometer of transect in Alpine valleys suggest the smaller territory size as well: 4.5–9 pairs per 10 ha, 4.3–6.9 males per 1 km of transect respectively (Landmann 1987, Kollinsky & Landmann 1996). The territory size varies between 0.35–7.4 ha (Nesenhöner 1956, Menzel 1983, Cramp 1988) in urban landscape. These examples illustrate the plasticity of the territory size, demonstrated by the comparison between different habitat types, and seen within one habitat type as well.

4.3. Comparison of subadult and adult males

Territory parameters showed no differences between the territories occupied by the two age categories of males, contrary to findings of Weggler (2001) in mountain villages, where young males occupied territories less structurally diversified than adults. Breeding sites in our localities were occupied randomly relative to the owner's and the neighbour's age, and the birds did not form clusters of the same age category. Subadults were not displaced to peripheral areas. The density of breeding territories varied from 0.09 to 0.4 pairs per 1 ha in our localities. These values are low in comparison with Black Redstart population in mountain villages. The territories of subadults are situated rather marginally and solitarily in the mountain village zones. Such a pattern, when subadults are separated from the adult males in suboptimal habitats, should facilitate avoidance of competition of the young males with the adult, more experienced ones (Procter-Gray & Holmes 1981). The distance of subadult's territory from the adult's one is expected to be larger in situations of high competition than in the environment with evenly distributed resources and lesser competition in which the territories are randomly distributed (as in urban habitats studied, where the birds choose from a sufficient amount of preferred habitats).

Acknowledgements. We thank P. Štys, T. Grim and D. Frynta for critical reading of the first draft of the manuscript, and T. Janikova for improving the English. We also thank R. Bowman, I. Krams and T. Solonen and some anonymous referees for valuable comments on the manuscript. We are very grateful to J. Jokimäki for his constructive suggestions and provisioning some useful literary resources. This research was supported by FRVŠ grants No. 1689/1999 and 1770/2001, Charles University (GA UK) grant No. 93/1998, and institutional grant provided by Czech Ministry of education, Youth and Sports No. J13-98113100004.

Aikuisten ja esiaikuisten mustaleppälintukoiraiden reviirikoosta ja elinympäristönvalinnasta kaupunkiympäristössä

Artikkelin kirjoittajat tutkivat eri-ikäisten mustaleppälintukoiraiden reviirikokoa, reviirien sijoittumista ja elinympäristönvalintaa Prahassa vuosina 1998–1999. Tutkimusalueet sijaitsivat puistomaisessa kaupunginosassa, vanhalla asuntoalueella (ikä noin 60 vuotta) sekä uudella asuntoalueella (ikä noin 5 vuotta). Puistomaisessa kaupunginosassa ei ollut yli 3-kerroksisia kerrostaloja, vanhalla asutusalueella oli 5-kerroksisia taloja ja uuden asutusalueen talot olivat lähellä tosiaan sijaitsevia, 6–12 kerroksisia rakennuksia. Mustaleppälintu on sopiva mallilaji eri-ikäisten koiraiden elinympäristönvalinnan tutkimiseen, koska eri-ikäisten koiraiden höyhenpuvut ovat selvästi erilaisia.

Kirjoittajat olettivat, että pienemmät reviirit olivat laadukkaampia kuin suuret reviirit. Vanhojen koiraiden keskimääräinen reviirikoko (1,21 ha, n = 37) ei eronnut esiaikuisten koiraiden reviirikoosta (1,08 ha, n = 29). Mikrohabitaattitason analyysi osoitti, että rakennusten esiintyminen vaikutti mustaleppälinnun habitaatinvalintaan.

Pienikokoisilla reviireillä rakennetun alan osuus oli suurempi kuin suuremmilla reviireillä. Ilmeisesti rakennukset ovat hyviä pesimä-, laulu- ja ruokailupaikkoja mustaleppälinnuille. Lajin reviirikoossa esiintyi vaihtelua habitaattien välillä. Reviirin keskikoko oli suurin puistomaisessa kaupunginosassa (1,98 ha) ja pienin uudella asuntoalueella (0,85 ha). Vanhalla asuntoalueella reviirin keskikoko oli 1,48 ha.

Toisin kuin vuoristokylissä on havaittu aikaisemmin, eri-ikäisten mustaleppälintukoiraiden reviirit eivät laadultaan eronneet kaupunkialueella toisistaan. Mustaleppälintujen reviirit eivät olleet kaupungissa myöskään ryhmittyneet ikäluokittain. Oletettavasti nämä erot johtuvat siitä, että resurssit ovat jakautuneet kaupunkialueella tasaisemmin ja kilpailu reviireistä on kaupungissa vähäisempää kuin vuoristokylissä.

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