DENSITY-DEPENDENT HABITAT SELECTION IN NIGHTINGALE (*Luscinia megarhynchos* C. L. B r e h m) IN SELECTED WINDBREAKS OF SW SLOVAKIA

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Abstract

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The study is based on the theory that birds at low population density occupy the most suitable habitat, whereas with increasing the density, a part of the population occupies marginal habitats at a greater range. The population density of the nightingale (*Luscinia megarhynchos*) was monitored by means of the territory mapping method in windbreaks of SW Slovakia during six breeding seasons. The population of nightingale reached its maximum in 2000 (45 breeding pairs, 3.55 BP/ha) and the minimum in 1997 (31 breeding pairs, 2.44 BP/ha). Comparing the vegetation structure of nightingale territories occupied in both years (1997 and 2000) and territories occupied just in the year at the highest population density (2000), the two types of habitat selected by nightingale were distinguished by means of discriminant analysis. The habitat selected in both years was characterized by lower herb cover values, higher tree diversity values and smaller shrubs. At the high population density, a part of the population selected also the habitat with higher herb cover values, lower tree diversity values and taller shrubs. Considering the spatial structure of a windbreak network, the windbreak intersections and dead-ends were preferred by nightingale, whereas the straight windbreak sections were selected only at the high population density. To support the definition of optimal and suboptimal habitat for nightingale in windbreaks of SW Slovakia, reproductive conditions of population should be acknowledged. To determine the general habitat selection, the year-to-year fluctuations in population density should be considered, hence the short-term ecological studies give just weak implications.

Key words: habitat preference, discriminant function analysis, *Luscinia megarhynchos*, ecology

Introduction

The nightingale *Luscinia megarhynchos*, C. L. B r e h m is widespread in central, southern and western Europe. In Slovakia, it breeds in southern regions of the country in lowlands, basins and hills up to 800 m a. s. l. (Mošanský, Danko, 2002). The breeding biotopes are in riparian forest stands, broadleaved forest ecotones, groups or belts of bushes situated in open land, windbreaks, field woodlots, non-managed gardens, cemeteries and parks in suburban areas (Hudec et al., 1983; Mošanský, Danko, 2002). The species selects similar biotopes throughout its whole distribution area (Glutz von Blotzheim, Bauer, 1988; Tomiałojć, Stawarczyk, 2003).

Windbreak strips are typical features of agricultural landscapes in Slovakia, as well as in C and W Europe. In windbreaks of Podunajská nížina lowland (SW Slovakia) the nightingale species is the one of the dominant species (Krištín, 1987; Némethová et al., 1998) breeding in well-developed and dense windbreaks (Némethová, Tirinda, 2005). Similarly, nightingale species dominate in communities of Východoslovenská nížina lowland windbreaks (SE Slovakia; Mošanský, 1996), in windbreaks of S Moravia (Balát, 1986), as well as in windbreaks of Hungary (Legány, 1991).

Habitat selection is a process dependent on the population density, since birds at low density select the most suitable habitat, whereas with increasing density, the suboptimal habitat is also occupied (Fretwell, Lucas, 1970). The habitat and territory selection in nightingale was found to be density-dependent in a riparian forest of NE Austria (Grüll, 1981). The density-dependent use of habitat has been demonstrated also in bird species breeding in agricultural landscape, e.g. in Britain (Chamberlain, Fuller, 1999; Hinsley et al., 1996; Benson, Williamson, 1972) and in Austria (Straka, 1995).

The changes in population density lead into two possible situations: (1) the individuals occupy greater territories at low population density, whereas at high population density the individuals build smaller territories as a result of intra-population competition. It could be assumed that there is a greater diversity of microhabitats in greater territories, and thus the smaller territories are suboptimal; (2) the dimensions of territories do not change with increasing/decreasing the population density. Individuals at low population density select only the best habitats, whereas at high population density a part of the population occupies marginal habitats. Moreover, the territories occupied at the lowest population density are chosen also at the highest population density.

In this paper, we focused on the habitat selection in the nightingale *Luscinia megarhynchos* considering the population density of the species. The aims of the present study were: (i) to record the changes in population density of nightingale breeding in windbreaks of SW Slovakia during the period 1996–2002, (ii) to examine the differences between the area of territory at low and at high population density, (iii) to analyse the habitat selection at low and high population density.

Material and methods

Study area

The research was conducted in a network of 12 windbreaks situated in the agricultural landscape near the city of Šamorín, SW Slovakia. The network consists of windbreaks established in the 1950s to alleviate wind erosion and drought, and to improve the water balance of the area. The dominant tree species in the locality are

Acer campestre, A. negundo, A. pseudoplatanus, Fraxinus excelsior, Ulmus carpinifolia, Tilia cordata, Populus x euroamericana, Robinia pseudoacacia, Gleditsia triacanthos, Quercus robur, Prunus avium. The shrub layer is composed of young individuals of *Ulmus carpinifolia, Acer negundo,* and such shrub species as *Sambucus nigra, Rosa canina, Rubus caesius, Crataegus oxyacantha, Ligustrum vulgare, Evonymus europaea, Clematis vitalba, Cornus sanguinea, Pyrus communis, Syringa vulgaris*. The nearest forest is in contact with the studied network, but considering the short-distance effect of forests, only one of the 12 corridors could be affected by the forest.

The average width of windbreaks is 18.4 m (min. 10.7 m, max. 25.0 m), the total length of the studied windbreaks is 7.02 km and their total area is 12.68 ha.

Bird censuses

The field observations were carried out during the breeding seasons 1996–2002 (except of the year 1998). The distribution of breeding territories of nightingale was estimated by means of the combine version of the mapping method (Tomiałojć, 1980). The locality was mapped 8–11 times per a breeding season. The position of singing males in the field was unambiguosly registered onto species map. The registrations from one season were transferred onto one map per windbreak, and territories were identified according to the recommendations of Tomiałojć (1980). The length of the territory was measured from the map, the width of the territory was determined as the width of the windbreak. In the case, a path went within the windbreak and the singing male was registered just on one side of the path, the width of the territory was measured from the path to the end-side of the windbreak. The area of the territory was the length multiplied by the width.

Habitat sampling

Habitat surveys were carried out in the late summer after the bird censuses were completed. The vegetation was measured at 20 m long windbreak sections situated in nightingale territories. The composition and structure of vegetation was characterized as suggested by James, Shugart (1970) and Janda, Řepa (1986) considering the linear form of windbreaks. The number of characterized territories (samples) was 54.

The vegetation characteristics included: number of trunks of trees (per 100 m^2), mean trunk diameter at a breast height (cm), basal area (cm^2/100 m^2), mean height of small shrubs (cm; only shrubs smaller than 1 m were regarded), mean height of trees (m), mean distance between tree trunks (m), mean distance between shrubs (m), proportion of fallen foliage in the ground cover (%), vegetation volume (%) in different layers (0–0.3 m, 0.3–1 m, 1–3 m, 3–7 m, 7–9 m, above 9 m), total herb cover (%), total shrub cover (%), total tree cover (%), number of tree genera.

Each of the 20 m long sample was characterized also by its width (m) and distance from the nearest dead-end or intersection of windbreaks (m).

Data analysis

To compare the area of nightingale territories in breeding seasons with the highest and the lowest population density the t-test was used. Before performing the test, the area was log transformed to ensure the normal distribution.

The t-test was used also to find out the differences in the values of vegetation characteristics measured in the two sample (territory) groups: 1) 24 territories occupied just in the breeding season of the highest population density 2) 30 territories occupied in the breeding season of the lowest population density and simultaneously in the season of the highest population density. Because the test assumes the normal distribution, test for normality was performed to each of the variable. The habitat variables that did not fit the normal distribution were log transformed (length, area) or arcsine transformed (proportional variables).

The habitat selection in nightingale in windbreaks was evaluated by means of the discriminant analysis (DFA) using the STATISTICA software (StatSoft, Inc., 1994). In course of the analysis the forward stepwise method was used to select the minimal set of variables significantly separating the two sample (territory) groups. The territories were characterized by 18 vegetation parameters as well as by the distance from the nearest windbreaks end or intersection and the sample width (Table 1). It is assumed that the data entering the discriminant analysis

T a b l e 1. Averages (x) and standard deviations (s.d.) of variables in two groups of territories and results of the t-test (d.f. – degree of freedom, P – significant value). Group 1: territories occupied by nightingale just in the breeding season 2000 (the highest population density); Group 2: territories occupied by nightingale in the breeding season 1997 (the lowest population density) and simultaneously in 2000.
Variables listed were used in the discriminant function analysis (DFA).
[a]habitat variables that did not fit the normal distribution were log-transformed (variables coded log) or arcsine transformed (variables coded arcsine) before the DFA and t-test were carried out.

Variable	Transformation[a]	Group 1 (N = 24)		Group 2 (N = 30)		t-value	d.f.	P
		x	s. d.	x	s.d.			
Number of trunks of trees (per 100 m^2)	-	36.54	11.48	42.77	16.24	-1.586	52	0.119
Trunk diameter at breast height (cm)	-	14.99	4.04	15.64	5.64	-0.472	52	0.639
Basal area (cm^2/100 m^2)	log	9567.69	3835.79	13515.84	6675.17	-2.114	52	**0.039**
Shrub height (cm)	-	61.25	10.02	53.91	9.55	2.747	52	**0.008**
Tree height (m)	-	12.15	2.50	12.57	2.65	-0.595	52	0.555
Tree-tree distance (m)	-	2.72	1.03	2.81	1.03	-0.338	52	0.736
Shrub-shrub distance (m)	-	1.97	1.13	1.97	0.75	0.003	52	0.998
Proportion of fallen foliage in ground cover (%)	arcsine	29.06	23.69	36.08	19.72	-1.298	52	0.200
Vegetation volume in the layer of 0–0.3 m (%)	arcsine	75.98	17.20	69.45	16.41	1.703	52	0.095
Vegetation volume in the layer of 0.3–1 m (%)	arcsine	59.87	11.85	57.34	11.30	0.751	52	0.456
Vegetation volume in the layer of 1–3 m (%)	arcsine	67.49	14.09	65.57	14.26	0.503	52	0.617
Vegetation volume in the layer of 3–7 m (%)	arcsine	82.23	12.44	84.66	12.15	-0.831	52	0.410
Vegetation volume in the layer of 7–9 m (%)	arcsine	60.55	20.91	66.00	24.45	-0.779	52	0.440
Vegetation volume in the layer above 9 m (%)	arcsine	41.39	22.85	49.90	26.50	-1.130	52	0.264
Total herb cover (%)	-	45.94	24.19	25.45	13.93	3.905	52	**< 0.001**
Total shrub cover (%)	-	43.00	27.87	49.12	18.16	-0.972	52	0.335
Total tree cover (%)	-	111.58	32.71	113.55	27.11	-0.242	52	0.810
Number of tree genera	-	4.58	1.72	5.03	1.90	-0.901	52	0.372
Distance from the nearest windbreak end or intersection (m)	log	206.46	164.13	100.30	114.78	3.198	52	**0.002**
Sample width (m)	-	17.96	4.27	20.14	5.74	-1.547	52	0.128

T a b l e 2. The number of breeding pairs and density of the nightingale (*Luscinia megarhynchos*) in windbreaks of SW Slovakia.

Breeding season	1996	1997	1999	2000	2001	2002
Number of breeding pairs	38	31	36	45	39	32
Density (BP/ha)	3.00	2.44	2.84	3.55	3.08	2.52

represent a sample from a multivariate normal distribution (Legendre, Legendre, 1983), and this is why the transformed variables were used in the analysis.

Results

Population density and area of nightingale territories

The population density of the nightingale (*Luscinia megarhynchos*) in selected windbreaks of SW Slovakia varied between 31 breeding pairs in 1997 and 45 breeding pairs in 2000 (Table 2). Nightingale established greater territories in 1997 (mean area 994.8 m^2) than in 2000 (mean area 800.4 m^2), but the difference was not significant ($t = -0.227$, d.f. = 74; $P = 0.821$). However, some of the territories in the year of high population density were placed in windbreak sections, which were not chosen in the year of low population density. This phenomenon was evident already during the field work.

Habitat selection in nightingale at low and high population density

Using the forward stepwise DFA, four variables which significantly discriminate two sets of territories were selected: 24 territories occupied only in 2000 and 30 territories occupied in 1997 as well as in 2000. The four variables mentioned above were: total herb cover, distance from the nearest windbreak end or intersection, shrub height and number of tree genera as seen from the standardized discriminant function coefficients and the correlations between the discriminating variables and the discrimination function (Table 3).

T a b l e 3. The results of the discriminant analysis: standardized discriminant function coefficients and pooled-within-groups correlations between discriminating variables and discriminant function.

	Standardized discriminant function coefficients	Correlations variable – DFA axis
Total herb cover	-0.697	-0.637
Distance from the nearest windbreak end or intersection	-0.562	-0.522
Shrub height	-0.447	-0.448
Number of tree genera	0.422	0.147

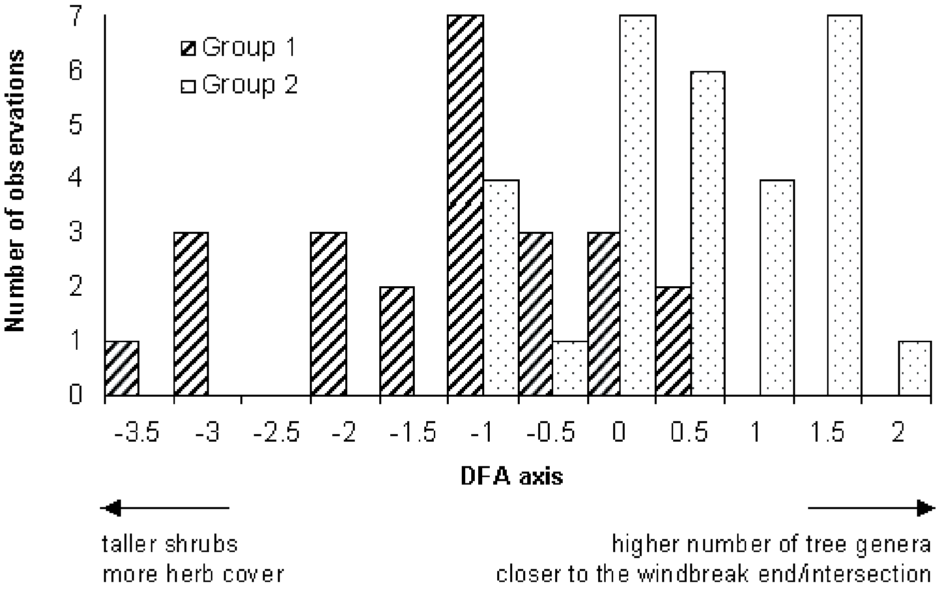

Fig. 1. Distribution of Nightingale territories according to the discriminant function. Territories separated in Group 1 and Group 2 as in the Table 1.

The efficiency of the discriminant function analysis was high, as it is indicated in the posterior probability test (44 of 54 territories – 81.48% were correctly classified). The distribution of the territories on the DFA axis shows only a small overlap between the two territory groups (Fig. 1).

The habitat selected by nightingale in 1997 and simultaneously in 2000 was characterized by a higher number of tree genera (x_2 = 5.0) and smaller shrubs (x_2 = 53.9 cm). The undergrowth was formed with lesser herbs (herb cover 25.5%; Table 1). In the year 2000 of the high density, a part of the population selected also the habitat with lower tree diversity values (x_1 = 4.6), higher herb cover values (x_1 = 45.9%) and taller shrubs (x_1 = 61.3 cm; Table 1). Considering the spatial structure of a windbreak network, windbreak intersections and dead-ends were preferred by nightingale, as seen from the value of a distance from the nearest windbreak end or intersection in Group 2 (x_2 = 100.3 m; Table 1). On the other hand, the straight windbreak sections were selected only at the high population density (x_1 = 206.5 m; Table 1). Three of the four selected variables showed significant differences between the two sets of territories: total herb cover, distance from the nearest windbreak end or intersection, shrub height (Table 1). Moreover, a significant difference was found in the variable basal area (Table 1), which was not selected by means of the forward stepwise DFA. Regarding this vegetation variable, nightingale species prefer more trees (larger basal area of trees) in their territories, whereas territories characterized by a smaller basal area are occupied only at their high population density.

Discussion

The population density of the nightingale (*Luscinia megarhynchos*) in selected windbreaks of SW Slovakia varied between 2.44 and 3.55 BP/ha. In windbreaks of Východoslovenská nížina lowland (SE Slovakia), the breeding density of nightingale reached 2.0 BP/ha (Mošanský 1996). A comparison with other studies dealing with breeding birds in windbreaks of Slovakia is not possible, because other techniques than a territory mapping method were used to estimate the population densities of birds. The published data on territory area of nightingale breeding in windbreaks are known neither from Slovakia, nor from other countries.

In the present study the difference between the area of territory in the year of low population density and in the year of high population density was not significant. The position and dimensions of nightingale territories were found to be dependent on the population density in the willow and poplar mead in NE Austria (Grüll, 1981). As the population density increased, at first the territories became smaller which was caused by separating of occupied territories. Subsequently suboptimal habitats were also occupied. However, the optimal preferred territories were selected each year (Grüll, 1981).

A relationship between the territory area and population density was registered in some bird species occurring in forest fragment and linear stream vegetation of eastern Bohemia (Storch, 1998). Similar conclusion was confirmed for the whitethroat *Sylvia communis* in hedgerows of English farmland, where it had unusual large territories in the year of low population density (Benson, Williamson, 1972). The territories were actually more than twice larger than in the year of high population density (Benson, Williamson, 1972).

The results of the present study emphasize that nightingale species in the year of the highest population density select a habitat which was not used in the year of the lowest population density. At first, nightingale in studied windbreaks occupy a habitat with higher tree diversity, smaller shrubs, lesser herbs in the undergrowth and situated closer to the windbreak intersection or a dead-end. At the high population density a part of the population occupies windbreak sections with lower tree diversity, taller shrubs and more herbs in undergrowth, which are situated closer to the central part of windbreaks.

Similar study was conducted in the agricultural landscape of Austria, where the red-backed shrike *Lanius collurio* increased its population density (Straka, 1995). In the year of the lowest population density the red-backed shrike selected only habitats with a high shrub density. On the other hand, in the year of the highest population density the species occupied also habitat with scarce shrubs. Moreover, the territories occupied at the lowest population density were chosen also at the highest population density (Straka, 1995). The similar situation holds true for the wren *Troglodytes troglodytes* in the agricultural landscape of Great Britain. The species at low population density selected only forest fragments, whereas at high population density the species occupied also hedgerows (Benson, Williamson, 1972).

It could be assumed, that the habitat selected by nightingale only in 2000 (territory group 1) represents the suboptimal habitat, whereas the habitat selected in 1997 and simultaneously in 2000 (territory group 2) is the optimal one for nightingale. To support the assumption, reproductive conditions of the population in the studied windbreaks have to be known. Two situations could be misleading: 1) very low population density, when the optimal habitat is not saturated; 2) long-term high population density, when the optimal and suboptimal habitats are occupied for more years. To determine the general habitat selection, the year-to-year fluctuations in population density should be considered, hence the short-term ecological studies give just weak implications.

According to our results we conclude, that the area of nightingale territory is not density-dependent in windbreaks of SW Slovakia. However, at high population density nightingale occupies places which it does not use at low population density.

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References

Balát, F., 1986: The avian component of a well-established windbreak in the Břeclav area. Folia Zool., *35*: 229–238.

Benson, G.B.G., Williamson, K., 1972: Breeding birds of a mixed farm in Suffolk. Bird Study, *19*: 34–50.

Chamberlain, D.E., Fuller, R J., 1999: Density-dependent habitat distribution in birds: issues of scale, habitat definition and habitat availability. J. Avian Biol., *30*: 427–436.

Fretwell, S.D., Lucas, H.L. Jr., 1970: On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor., *19*: 16–36.

Glutz von Blotzheim, U., Bauer, K.M., 1988: Handbuch der Vögel Mitteleuropas. Band 11. Passeriformes (2. Teil). AULA-Verlag, Wiesbaden, 1226 pp.

Grüll, A., 1981: Untersuchungen über das Revier der Nachtigall (*Luscinia megarhynchos*). J. Orn., *122*: 259–285.

Hinsley, S.A., Pakeman, R., Bellamy, P.E., Newton, I., 1996: Influences of habitat fragmentation on bird species distributions and regional population sizes. Proc. R. Soc. Lond. B, *263*: 307–313.

Hudec, K. (ed.), 1983: Birds – Aves, part III. Fauna of Czechoslovakia, vol. 23 and 24 (in Czech). Academia, Praha, 1236 pp.

James, F.C., Shugart, H.H., 1970: A quantitative method of habitat description. Audubon Field Notes, *24*: 727–736.

Janda, J., Řepa, P., 1986: Methods of quantitative research in ornithology (in Czech). SZN, Praha, 158 pp.

Kristín, A., 1987: Bird communities in selected windbreaks of Žitný ostrov and notes on the breeding of some bird species (in Slovak). Biológia, Bratislava, *42*: 163–173.

Legány, A., 1991: Significance of shelter-belts and rows of trees in respect of ornithology and nature conservancy (in Hungarian). Aquila, *98*: 169–179.

Legendre, L., Legendre, P., 1983: Numerical Ecology. Elsevier, Amsterdam–Oxford–New York, 420 pp.

Mošanský, L., 1996: The breeding birds of windbreaks of the East Slovakian lowland (in Slovak). Natura Carpatica, *37*: 183–190.

Mošanský, L., Danko, Š., 2002: Nightingale (*Luscinia megarhynchos*) (in Slovak)., In Danko, Š., Darolová, A., Krištín, A. (eds), Birds distribution in Slovakia, VEDA, Vydavateľstvo SAV, Bratislava, p. 463–464.

Némethová, D., Tirinda, A., Kocian, Ľ., 1998: The breeding bird community of the Žitný ostrov windbreaks (in Slovak). Tichodroma, *11*: 59–70.

Némethová, D., Tirinda, A., 2005: The influence of intersections and dead-ends of line-corridor networks on the breeding bird distribution. Folia Zool., *54*: 123–134.

StatSoft, Inc., 1994: STATISTICA for the Windows operating system. Quick reference, 149 pp.

Storch, D., 1998: Densities and territory sizes of birds in two different lowland communities in eastern Bohemia. Folia Zool., *47*: 181–188.

Straka, U., 1995: Zu Bestandsentwicklung und Habitatwahl des Neuntöters (*Lanius collurio*) in einem Ackerbaugebiet in südlichen Weinviertel (Niederösterreich) in den Jahren 1985 bis 1993. Egretta, *38*: 34–45.

Tomiałojć, L., 1980: The combined version of the mapping method., In Oelke, H. (ed.), Proc. VI. Int. Conf. Bird Census Work, Göttingen, p. 92–106.

Tomiałojć, L., Stawarczyk, T., 2003: Avifauna of Poland. Vol. II (in Polish). Wyd. Pro Natura, Wroclaw, 870 pp.

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