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Structure of the breeding bird assemblage of a primeval alder swamp in the Šúr National Nature Reserve

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Abstract: The structure of a breeding bird assemblage of a primeval alder swamp in the Šúr National Nature Reserve (the Danube Basin) was studied in the period 1992–1995. A 16 ha forest interior study plot was established for bird censusing. Population abundances were estimated by a combined version of the mapping method from the end of March to the beginning of July. Altogether, 42 breeders were recorded and the mean total density of species total across years was 125.15 ± 12.73 pairs/10 ha (CV = 10.17%). Two species were eudominant ($\geq 10\%$): Sturnus vulgaris and Anas platyrhynchos, and six species were dominant ($5\% \leq 10\% <$): Ficedula albicollis, Fringilla coelebs, Phylloscopus collybita, Parus major, Sylvia atricapilla, Erithacus rubecula. The Shannon diversity index (H') varied between 3.98-4.10 bites. The evenness index (J') reached values between 0.79-0.81. Expected species diversity in a random sample of 100 pairs calculated by rarefaction [$E(S_{100 \text{ pairs}})$] was 21.35 ± 0.92 species derived as a mean value from the years 1992-1995. The mean rarefaction estimate on the area [$E(S_{10 \text{ ha}})$] was 22.75 ± 1.58 species. Bird species richness and diversity were significantly higher in the study plot in comparison to the mean value of European wet alder forests. These results are comparable with the values of structural assemblage parameters of the primeval stands dominated by alder within the Białowieża National Park, Poland.

Key words: bird community; primeval alder swamp; mapping method; population density; rarefaction; Slovakia

Introduction

Primeval stands and their avian assemblages have specific features that make them easily distinguishable from man made secondary habitats and their assemblages. One of the main characteristics is the combination of high species richness with low densities of individual species (Tomiałojc & Wesołowski 2004). This feature of pristine forest is a general rule regardless to some extent of climatic zone. Some of these structural features are as follows: impressive height of trees, multistorey profile of stands, diverse tree community, large amount of dead timber, uprooted trees, dead standing stems, stumps and old fallen logs. Such complex structural feature forms a unique system of ecological niches that can support high species diversity.

The Šúr National Nature Reserve (681.4 ha) forms the largest patch of primeval alder swamp (334.7 ha), association *Carici elongatae-Alnetum*, in the Slovak Republic that is one of the best preserved in Central Europe. The reserve has been object to a number of zoological and ecological studies due to close distance from the Biological Station of the Comenius University, Bratislava. Currently, it is one of the best-studied reserves in the country.

The first bird faunistic studies in Svätojurský Šúr were carried out during the period 1929–1942 (Turček

1941; Ferianc 1943). Ferianc (1943) synthesised and summarised the faunistic data from the historical bird occurrence records, dermatological collections and his own observations carried out in 1941–1942. The study did not analyse species structure of individual habitats. It rather gives a general list of species occurring in this site with some notes on distribution, abundance and character of occurrence. Kupcová (1972, 1980) studied bird assemblages of majority of characteristic habitats of the reserve in the years 1969–1971. The study was focused on basic quantitative description of habitat assemblages and their seasonal dynamics counted by a belt transect method. Kupcová (1972, 1980) studied only the forest edge avifauna of the alder swamp.

In previous studies, due to lack of data on precise description of the bird assemblage by a standard census technique, an interior and an edge forest study plot of identical size were established in order to gain a complex picture on the structure of the alder forest bird assemblages. The study was supposed to detect the level of degradation of pristine ecosystem indicated in the structure of bird assemblage. Due to one-year census in 1995 (Korňan 1996), the data from the forest edge plot have not been analysed in the present study. The primary objectives of this paper are as follows:

(1) to analyse quantitative structure of the forest interior bird assemblage from the aspects of species

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richness, abundance, population densities, dominance, diversity and evenness;

- (2) to analyse guild structure by a priori approach following Wiens (1989) concept;
- (3) to compare the alder swamp assemblage with similar ecosystems on the European scale.

Study area

The Šúr National Nature Reserve is located in the Danube basin near the south-eastern part of the Malé Karpaty Mts approximately 12 km north-east from the city of Bratislava in the territory of the town of Svätý Jur and the village of Chorvátsky Grob (districts of Senec and Pezinok). The reserve is surrounded by the Moravod water channel in North-West and South and by the Čierna voda stream in the East. This wetland ecosystem started to evolve approximately 10,000 years ago in the early Holocene. Svätojurský Šúr evolved in a terrain depression created by tectonic activities. These processes created a shallow lake filled out by the Carpathian streams. The streams slowly deposited gravel, sand and mud followed by the plant successional series into the current stage. The reserve was part of a wetland belt spreading along foothills of the Malé Karpaty Mts from the present city of Bratislava to the towns of Modra and Bernolákovo. The area of the reserve spreads over 681.39 ha, out of which the area of the buffer zone is 307.29 ha (State list of the State Nature Conservation of the Slovak Republic 2007). The reserve lies at the altitude 128-132 m a.s.l. (Kupcová 1972). The area of Svätojurský Šúr belongs to the warmest parts of the former Czechoslovakia with the mean annual temperature 9.6 °C (Janota 1967). The mean annual rainfall is 657 mm.

Originally, six Carpathian streams used to run into the swamp, yet three of them regularly dried out from July until September (Podhradský 1961). Presently, the Fofovský Stream is the only water source flooding the area, however, it also dries out in the mentioned period (Kupcová 1972). In the past, the water regime of the reserve was disturbed by drainage and ameliorations that negatively affected dynamics of the swamp ecosystem. The first channel through the Šúr wetland was excavated in 1896 what significantly lowered the surface water level. Another channel transferring the natural waterways of the Carpathian streams deluging the ecosystem was dug out in the period 1941–1943. The wetland almost completely dried out and was hit by several fires. A nature reserve was established in 1952 that partly saved the rare ecosystems. Later, it has become the Ramsar and IBA site of the international importance (Hora & Kaňuch 1992).

In the best preserved site, the ecosystem of the alder swamp interior was selected as a study plot. The whole forest covers 334.7 ha. The forest is uneven-aged, 40–120 years old. The oldest part in the core zone has a character of a primeval stand and was approximately 107 years old in 1995 (Korpel 1989). A 16 ha study plot (400×400 m) was placed into this part. The plot was located approximately 250–300 m from the forest edge. The area is regularly flooded from the end of March or the beginning of April until the end of June or mid July. The maximum water level up to 80 cm was recorded in 1992, in the following years it reached only 50 cm.

Tree canopy is strongly dominated by Alnus glutinosa (423.78 ex./ha, 90.20%), with biggest trees reaching the height of 31 m and width of 72 cm. Salix cinerea (42.19

ex./ha, 8.98%) and *Ulmus laevis* (3.84 ex./ha, 0.82%) grow at much lower densities. Quercus robur (4 ex./16 ha) and Padus racemosa (2 ex./16 ha) very rarely occur, too. Abundance of these two species was exactly measured during nest searching in the whole plot. Standing dead trees (42.19 ex./ha) created gaps in the tree canopy. Bush coverage is very low, somewhere totally absent, except about a 100 m wide belt in the north-western part of the study plot edge where dense bush layer of Salix cinerea grew. Frangulla alnus and young saplings of Ulmus laevis occur infrequently in the bush layer. Admixture of Rosa spp., Padus racemosa and young samplings of Alnus glutinosa grew at very low densities. Herb layer primarily consisted of Carex riparia, Urtica dioica, Convolvulus arvensis, Galium spp. and Polygonum spp. Less common were Carex elongata, Carex paniculata, Iris pseudacorus, Lycopus europaeus, Dryopteris filis mas, etc. The alder swamp belongs into the Alnion qlutinosae alliance, association Carici elongatae-Alnetum medioeuropeum following the Braun-Blanquet classification system (Michalko et al. 1986).

Quantitative description of vegetation structure and floristics of the 16 ha study plot was conducted by the $11.3~\mathrm{m}$ (0.04 ha) circular plot method originally proposed for studies on bird-habitat relationships (Noon 1981; Korňan 1996). Totally, 13 circular plots randomly spaced were used for a detailed description of the plot. The measurements were taken in September 1995. The mean height of the bush layer was 1.90 m. The density of shrubs was 836.50 ex./ha. The mean height of herb layer was 1.04 m. The estimated mean closest distance between two trees was 5.40 m, while between two bushes it was 8.01 m. The horizontal foliage coverages in the 10 height classes were as follows: 98.5% (0-0.3 m), 97.7% (0.3-1 m), 57.7% (1-2 m), 17.3% (2-3 m), 25.0% (3-5 m), 29.6% (5-7 m), 39.2% (7-10 m),57.3% (10–15 m), 58.5% (15–20 m), 56.9% (> 20 m). Wood biomass in the oldest part ($\geq 80 \text{ years}$) was 580-790 m³ ha⁻¹, the mean annual volume biomass production in the stands dominated by mature seed trees reached 16 m³ ha⁻¹ (Korpel 1989).

Material and methods

Bird censusing

Population densities were estimated by the combined version of the mapping method (Tomiałojć 1980; Korňan 1996). In order to construct an effective orientation system within the study plot, a 50×50 m grid system based on a colour plastic tape marking on tree trunks was established in the 16 ha (400×400 m) squared study plot. Breeding bird censuses were carried out in the years 1992–1993 and 1995 from the end of March to early July. Totally, 11–14 valid visits per breeding season were performed, starting at 04:30 and ending usually by 9:00 CET (sometimes by 10:00 CET) for morning visits, from 16:00 to 19:30 CET for evening visits, and from 19:00 to 22:00 CET for night visits. The proportion of evening visits was always three out of the total number of visits. At the beginning of April, one night visit focused on owl registrations was carried out.

Some bird species, e.g., Columba spp., Streptopelia turtur, Turdus philomelos, Muscicapa striata, Certhia familiaris, Carduelis carduelis, Chloris chloris and Coccothraustes coccothraustes caused considerable problems during census and interpretational procedure. Censusing and the identification of territories on the species maps

Table 1. Structure of tree vegetation of the primeval alder swamp in the Šúr National Nature Reserve sampled by the 11.3 m diameter circular plot method. Totally, 13 randomly spaced circular plots were used for the characteristics.

Species	Abundance (n)	Density (ex./ha)	Dominance (%)	Mean height (m)	Mean trunk width (cm)
Alnus glutinosa	221	423.78	90.20	18.31	33.98
Salix cinerea	22	42.19	8.98	3.92	4.64
Ulmus laevis	2	3.84	0.82	8.90	17.25
Quercus robur*	4	0.25		_	_
Padus racemosa*	2	0.13		_	_
Live trees totally	245	469.80	-	16.94	31.21
Standing dead trees	22	42.19	=	6.23	30.14

Explanations: * – Densities of these species were too low to be covered and sampled by the circular plots. Abundance and density of the species were estimated from their occurrence in the whole 16 ha plot. The data were gathered when the whole plot was checked for the mallard and starling nests.

was based on recommendations of Nilsson (1977), Svensson (1978, 1980), Tomiałojć (1980, 1994), Tomiałojć & Lontkowski (1989), Morozov (1994), and Korňan (1996). Abundance of semi-colonial and non-territorial species such as Anas platyrhynchos and Sturnus vulgaris was estimated by direct nest counts during the bird censuses and extra visits. Nest trees were marked by a white chalk to avoid double nest counts. Usually, the nest searches were carried out independently of census visits and separately for A. platyrhynchos (the first half of April) and $S.\ vulgaris$ (second half of May). Nest losses were not included into the abundance estimates of S. vulgaris. In order to correctly identify the proportions of edge territories in the study plot, bird registrations were recorded to 100 m distance beyond the plot edge lines. Overlap of edge territories to the study plot was estimated on 1/4, 1/3, 1/2, however, only species with abundance even or higher than 0.5 pair per study plot were included in the total count of breeding pairs (territories). Any further details regarding the mapping procedure and the principles of species map analyses are given in Korňan's (1996) thesis.

Registrations from visit maps were transferred onto species maps using number order beginning from the first species record in the plot. The criteria for territory interpretation were principally based on the IBCC recommendations (IBCC 1969). The minimum number of registration required before a cluster of registrations was accepted as a territory was four registrations per 12-14 valid visits and three registrations per 8-11 valid visits. However, in the case of some secretive species or species with not well-evolved territorial behaviour (mentioned above), species-specific minimum number of registrations (acceptance level of territory), and other criteria required to accept a cluster of registrations as a territory may have been modified (Svensson 1978). Useful information on distributional patterns of these species in the plot was gained during independent plot visits, especially during the nest counts. In case of species with abundance less than 0.5 pair per plot, only breeding presence "+" denoting the stationary occurrence of a part of bird territory within the boundaries of the plot was stated. This symbol was primarily used for the species with territory sizes much larger than the study plot, such as some woodpeckers, owls, birds of prey, and corvids (Tomiałojć 1980; Korňan 1996). Species breeding in the forest interior (150 m behind the forest edge) that were not detected in the study plot were marked by "o+", indicating breeding in the forest interior but outside the study plot.

Guild and migratory habit classifications

Foraging guild categorisation and species classification into individual categories was based on the studies by Korňan (1996) and Korňan & Adamík (2007). In addition, real field

observations of foraging birds and nest site records from swamp were used for more precise allocation. Species were classified into the guild categories by means of a priori approach (Wiens 1989; Korňan 2005), mainly based on previous studies. Foraging guild classification was primarily based on the results of a posteriori statistical guild classification (Korňan & Adamík 2007) and was combined with the original a priori classification (Korňan 1996).

All species detected in the study plot in the period 1992–1995 were partitioned into 10 foraging guild categories (Appendix). The category "outside forest foragers" combines several foraging guilds together such as raptors, granivores, water foragers, etc.; therefore it can be understood as an "artificial" category, not a guild from functional aspect in the trophic chains. If a species belonged into several guild categories, it was characterised by a proportional, respectively, percentage membership in a guild category. Proportions in guild categories were subjectively estimated (Appendix). The guild densities were calculated from the population densities in Table 2, based on guild membership information in the Appendix.

Nesting quilds

B – bush nesters, nests located in shrub vegetation up to 2 m in height;

C – canopy nesters, open nests built in the canopy of trees above 2 m from ground;

G – ground nesters, open or domed nests located on the ground or built in grass, herb or forb vegetation;

H – hole nesters, nests built in tree cavities or semicavities regardless of height.

Foraging guilds

AF – arboreal flycatchers, insectivorous passerines feeding on flying or staying insects by hawking or sallying primarily in the canopy layer;

 ${\rm AQ}$ – water foragers, species foraging in the surface water in the forest;

BG – bark gleaners, insectivorous passerines foraging primary from tree bark by gleaning;

FG – foliage gleaners, mainly insectivorous passerines foraging mainly from leaves, twigs, and branches by gleaning and hovering;

VE – vegetarians (granivores), species consuming plants or their parts independently of foraging height and type of nutrition;

HF – herb layer foragers, mainly insectivorous passerines feeding in grass, herb and forb vegetation layer by gleaning and hovering;

Table 2. Year and mean abundance, density and dominance of the breeding bird assemblage of the primeval alder swamp in the Šúr National Nature Reserve.

a		Abundance		Density (pairs/10 ha)			Dominance (%)			(ID	CV			
Sp	ecies	1992	1993	1995	1992	1993	1995	\bar{x}	1992	1993	1995	\bar{x}	SD	(%)
	Sturnus vulgaris L., 1758	39.0	33.0	36.0	24.38	20.63	22.50	22.50	18.14	18.64	17.25	18.01	1.88	8.33
	Anas platyrhynchos L., 1758	33.0	23.0	20.0	20.63	14.38	12.50	15.83	15.35	12.99	9.58	12.64	4.25	26.87
3.	Ficedula albicollis (Temminck, 1815)	18.0	15.0	17.7	11.25	9.38	11.06	10.56	8.37	8.47	8.48	8.44	1.03	9.78
	Fringilla coelebs L., 1758	16.2	14.8	19.5	10.13	9.25	12.19	10.52	7.53	8.36	9.34	8.41	1.51	14.34
	Phylloscopus collybita (Vieillot, 1817)	14.4	12.0	23.0	9.00	7.50	14.38	10.29	6.70	6.78	11.02	8.17	3.61	35.12
	Parus major L., 1758	10.1	14.2	11.2	6.31	8.88	7.00	7.40	4.70	8.02	5.37	6.03	1.33	17.93
	Sylvia atricapilla (L., 1758)	11.5	10.3	13.0	7.19	6.44	8.13	7.25	5.35	5.82	6.23	5.80	0.85	11.66
	Erithacus rubecula (L., 1758)	10.7	10.8	9.4	6.69	6.75	5.88	6.44	4.98	6.10	4.50	5.19	0.49	7.58
	Parus caeruleus L., 1758	7.3	7.2	7.6	4.56	4.50	4.75	4.60	3.40	4.07	3.64	3.70	0.13	2.83
	Certhia familiaris L., 1758	7.7	6.5	5.2	4.81	4.06	3.25	4.04	3.58	3.67	2.49	3.25	0.78	19.34
	Columba oenas L., 1758	3.7	3.0	5.0	2.31	1.88	3.13	2.44	1.72	1.69	2.40	1.94	0.63	26.02
	Sitta europaea L., 1758	4.3	4.0	3.4	2.69	2.50	2.13	2.44	2.00	2.26	1.63	1.96	0.29	11.75
	Muscicapa striata (Pallas, 1764)	4.7	3.2	3.3	2.94	2.00	2.06	2.33	2.19	1.81	1.58	1.86	0.52	22.46
	Troglodytes troglodytes (L., 1758)	4.5	2.7	3.6	2.81	1.69	2.25	2.25	2.09	1.53	1.72	1.78	0.56	25.00
	Prunella modularis (L., 1758)	2.8	3.0	4.4	1.75	1.88	2.75	2.13	1.30	1.69	2.11	1.70	0.54	
	Oriolus oriolus (L., 1758)	3.0	2.0	3.0	1.88	1.25	1.88	1.67	1.40	1.13	1.44	1.32	0.36	21.65
	Anthus trivialis (L., 1758)	5.0	+	2.5	3.13	$\{0.2\}$	1.56	1.56	2.33	0.00	1.20	1.17		100.00
	Coccothraustes coccothraustes (L., 1758)	2.5	3.0	1.5	1.56	1.88	0.94	1.46	1.16	1.69	0.72	1.19		32.73
	Passer montanus (L., 1758)	-	_	7.0	0.00	0.00	4.38	1.46	0.00	0.00	3.35	1.12		173.21
	Dendrocopos major (L., 1758)	2.0	2.2	2.4	1.25	1.38	1.50	1.38	0.93	1.24	1.15	1.11	0.13	9.09
	Turdus merula L., 1758	2.5	1.8	1.5	1.56	1.13	0.94	1.21	1.16	1.02	0.72	0.97	0.32	26.54
	Columba palumbus L., 1758	2.8	1.0	0.5	1.75	0.63	0.31	0.90	1.30	0.56	0.24	0.70	0.76	84.40
	Dendrocopos minor (L., 1758)	1.5	+	2.0	0.94	$\{0.2\}$	1.25	0.73	0.70	0.00	0.96	0.55	0.65	89.21
	Turdus philomelos Brehm, 1831	1.5	1.0	1.0	0.94	0.63	0.63	0.73	0.70	0.56	0.48	0.58	0.18	24.74
	Certhia brachydactyla Brehm, 1820	1.5	1.0	1.0	0.94	0.63	0.63	0.73	0.70	0.56	0.48	0.58	0.18	24.74
	Parus palustris L., 1758	1.0	1.3	0+	0.63	0.81	$\{0.2\}$	0.48	0.47	0.73	0.00	0.40	0.43	88.79
	Garrulus glandarius (L., 1758)	1.0	1.0	0+	0.63	0.63	$\{0.2\}$	0.42	0.47	0.56	0.00	0.34		86.60
	Dryocopus martius (L., 1758)	1.2	+	+	0.75	$\{0.2\}$	$\{0.2\}$	0.25	0.56	0.00	0.00	0.19		173.21
	Hippolais icterina (Vieillot, 1817)	_	_	1.0	0.00	0.00	0.63	0.21	0.00	0.00	0.48	0.16		173.21
	Carduelis chloris (L., 1758)	p	+	1.0	0.00	$\{0.2\}$	0.63	0.21	0.00	0.00	0.48	0.16		173.21
	Carduelis carduelis (L., 1758)	p	p	1.0	0.00	0.00	0.63	0.21	0.00	0.00	0.48	0.16		173.21
	Serinus serinus (L., 1766)	p	P	1.0	0.00	0.00	0.63	0.21	0.00	0.00	0.48	0.16		173.21
	Cuculus canorus L., 1758	0.8	$^{\mathrm{o}+}$	0+	0.50	$\{0.2\}$	$\{0.2\}$	0.17	0.37	0.00	0.00	0.12		173.21
	Streptopelia turtur (L., 1758)	0.8	p	$^{\mathrm{o}+}$	0.50	0.00	$\{0.2\}$	0.17	0.37	0.00	0.00	0.12	0.29	173.21
	Buteo buteo (L., 1758)	*+	+	+	$\{0.1\}$	$\{0.1\}$	$\{0.1\}$	0.00	_	_	_	_	_	_
	Strix aluco L., 1758	+	+	+	$\{0.1\}$	$\{0.1\}$	$\{0.1\}$	0.00	_	_	_	_	_	_
	Corvus corone cornix L., 1758	+	+	0+	$\{0.1\}$	$\{0.1\}$	$\{0.1\}$	0.00	_	_	_	_	_	_
	Accipiter gentilis (L., 1758) Falco cherruq Grey, 1834	o+ -	o+ *+	+		$\{0.03\}$		0.00	_	_	_	_	_	_
		_		_	0.00	$\{0.03\}$		0.00	_	_	_	_	_	_
	Locustella fluviatilis (Wolf, 1810)	_	+	*+	0.00	$\{0.2\}$	0.00	0.00	_	_	_	_	_	_
	Ciconia nigra (L., 1758)	_	_		0.00	0.00	$\{0.03\}$	0.00	_	_	_	_	_	_
	Corvus corax L., 1758	_	_	+	0.00 0.00	0.00	$\{0.03\}$	0.00	_	_	_	_	_	_
	Accipiter nisus L., 1758 Phylloscopus sibilatrix (Bechstein, 1793)	-	-	o+	0.00	0.00 0.00	$\{0.03\}$	0.00 0.00	_	_	_	_	_	_
	Fulica atra L., 1758	-	p	p	0.00	0.00	0.00	0.00	_	_	_	_	_	_
	Jynx torquilla L., 1758	p	- D	_	0.00	0.00	0.00	0.00	_	_	_	_	_	_
	Dendrocopos medius (L., 1758)	_	p	_	0.00	0.00	0.00	0.00	_	_	_	_		_
	Dendrocopos leucotos (Bechstein, 1803)	_	p p	_	0.00	0.00	0.00	0.00	_	_	_	_	_	_
	Sylvia communis Latham, 1787	_	p	_	0.00	0.00	0.00	0.00	_	_	_	_	_	_
	Phylloscopus trochilus (L., 1758)	_	p	_	0.00	0.00	0.00	0.00	_	_	_	_	_	_
50.	1 regree of the trocine (D., 1100)		р		0.00	0.00	0.00	0.00						

Explanations: SD – standard deviation of density; CV – coefficient of variation of density. Mark plus sign ("+") indicates breeding abundance less than a 0.5 territory (pair) per study plot; mark "o+" indicates breeding presence in the reserve, but the species was not detected as a breeder in the study plot; mark "p" is used for species detected in the study plot as non-breeders or rare visitors; mark "-" indicate absence; * – nest in the study plot. In the density columns, density estimates for "+" and "o+" species are given by qualified guess based on observation in the reserve. Only "o+" species breeding in the forest interior, approximately 150 m from the forest edge, were included to the species list in the Table. Densities of "o+" species breeding and occurring only in the edge of the reserve (0–150 m forest belt from the edge toward interior) were not estimated. The density estimates in parenthesis {} were only roughly estimated for calculation of diversity indices and rarefaction of the assemblage.

LF – litter foragers, invertebratophagous passerines feeding on and within the litter layer by gleaning or specific strategy called leaf-lifting;

 ${\rm O}$ – outside forest foragers, described above;

TP – trunk probers, insectivorous species foraging in the trees trunk xylem or bark by pecking, probing or drilling; R – raptorial guild (vertebratophags), birds of prey and owls feeding primary on vertebrates.

Migratory habits

R – residents, sedentary species staying all year round in the nesting site, local movements not exceeding 200 km;

M – short-distance migrants, species wintering in the Mediterranean region;

T – tropical migrants, species wintering in tropical Africa south of the Sahara Desert.

$Statistical\ analyses$

Bird assemblage structure was studied from the aspects of population abundance, density, species diversity, evenness and species richness – sample size relationship (rarefaction). Standard deviation (SD) and coefficient of variation (CV) were applied to estimate variation between years. Standard deviation was applied to measure the variability between years. The use of n-1 in the denominator was applied instead of n. Coefficient of variation was applied to measure the relative dispersion in the sample. Species with abundance lower that 0.5 pair per study plot had a 0 value for the calculations of variation measures.

Species diversity and evenness were measured by three common formulas - Shannon diversity index as an information theory measure, Simpson index as measure of concentration, and Brillouin index (Magurran 1991). In addition, the rarefaction as an alternative to traditional diversity indices was also applied (Hurlbert 1971; Heck et al. 1975). To include species with very low population densities ("+") for computations of species diversity and evenness, constant numbers of densities (see Table 2 for the constant values) were added to these species. A separate rarefaction curve was calculated for each year. Similarity in structure of assemblages was measured by qualitative Sörensen index and quantitative Czekanowski-Sörensen index (Magurran 1991). Species diversity indices and evenness were calculated in the PC statistical package NUCOSA 1.05 (Tóthmérész 1993). Variability measures, assemblage similarity indices, rarefaction values and curves were calculated in MS Excel.

Only the mathematical formulas for computation of rarefaction and evenness are presented further: *Evenness (equitability):*

$$E = \frac{\text{DIV}}{\text{DIV}_{\text{MAX}}},$$

where DIV – species diversity measured according to Shannon, Simpson, or Brillouin formulas; DIV $_{\rm MAX}$ – maximal theoretical value of these indices.

Rarefaction:

$$E(S_n) = \sum_{i=1}^{S} \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right],$$

where $E(S_n)$ is an expected number of species in a random sample of n individuals drawn without replacement from N individuals that is sum of all individuals of all species in a assemblage, S is the total number of species found in the study plot in a year, N_i is the number of individuals in species i.

Results

Species structure

Totally, 50 species including transmigrants and vagrants were detected in this ecosystem in the period 1992–1995, out of which 43 species were breeders (Tables 2, 3). The mean yearly species richness in the forest interior was 36.33 breeders in the study period. 42 breeders were recorded in the study plot; the mean species richness in the plot was 33.33 species. The highest number, 35 species, was found in 1995, whereas the lowest species richness, 32 species, was detected in 1992. Twenty-six species were constantly recorded in the study plot in each year of the study period, while 16 species occurred only in some of the years. In fact, five of them bred in the plot in two years and 11 species nested only in one year of the three-year study period. From the faunistic aspect, breeding of Falco cherrug and Ciconia nigra are important national records. Both species had nests in the study plot. Phylloscopus sibilatrix and less common Ph. trochilus can be considered as transmigrants due to high abundance in the end of April and the first half of May, and later absence. Most of the nonbreeding species are vagrants from the forest edge, ponds, surrounding agricultural habitats and forests in the Malé Karpaty Mts.

The similarity of assemblage structure between years was compared by the qualitative Sörensen index and quantitative Czekanowski-Sörensen index. The qualitative Sörensen index reached values of 0.81–0.92. The highest similarity (0.92) was found between years 1992 and 1993. Qualitative comparisons of the years 1992–1995 showed the lowest value 0.81. A little higher similarity (0.82) was detected between years 1993-1995. The Czekanowski-Sörensen index reached values of 0.85–0.88. The highest similarity value 0.88 was detected between 1992 and 1993. The computation of similarity of quantitative assemblage structure between years 1992–1995 and 1993–1995 resulted in the same similarity value 0.85 for both year pairs. Coefficients of assemblage stability in the three-year study period showed relatively stable structure from both qualitative and quantitative aspects.

Density and dominance

The total mean breeding bird assemblage density of the interior alder swamp was 125.15 pairs/10 ha (further p/10 ha) in the three-year period (1992–1995). The highest total assemblage density, 134.38 p/10 ha, was found in 1992, and the lowest value, 110.63 p/10 ha, in 1993. The quantitative species structure of the breeding bird assemblage is given in Table 2, community curve of the breeding bird assemblage is presented in Fig. 2.

Eudominant species ($\geq 10\%$) contributed by 30.65% to the total assemblage abundance based on mean values. The yearly variation was 28.27–33.49%. Only two species, *Sturnus vulgaris* and *Anas platyrhynchos*, belonged into this dominance class when considering the mean dominance values. *Anas platyrhynchos* did not belong into this dominance class in 1995 when it

Table 3. Estimates of bird species diversity and evenness of the primeval alder swamp in the Šúr National Nature Reserve by standard indices and rarefaction. Only species breeding within the 16 ha study plot were taken into the calculations (including species marked as "+"). Shannon index is calculated in bites.

Diversity measures	1992	1993	1995	Mean	SD	CV
Total number of species	38	44	42	41.33	3.06	7.39
Total number of breeders	33	35	41	36.33	4.16	11.46
Number of breeders in plot	32	33	35	33.33	1.53	4.58
Shannon (H')	4.07	3.98	4.10	4.05	0.06	1.54
Brillouin (HB)	2.52	2.45	2.54	2.50	0.05	1.89
Simpson (D)	0.91	0.91	0.92	0.91	0.01	0.63
Rarefaction $E(S_{50pairs})$	17.32	16.22	17.16	16.90	0.59	3.51
Rarefaction $E(S_{100pairs})$	22.03	20.30	21.74	21.35	0.92	4.33
Rarefaction $E(S_{5ha})$	19.35	16.89	18.92	18.39	1.31	7.13
Rarefaction $E(S_{10ha})$	23.88	20.95	23.41	22.75	1.58	6.92
Evenness measures						
Evenness Shannon (J')	0.81	0.79	0.80	0.80	0.01	1.25
Evenness Brillouin (E_{HB})	0.82	0.80	0.81	0.81	0.01	1.23
Evenness Simpson (E_D)	0.94	0.94	0.95	0.94	0.01	0.61

reached a dominance value of 9.58% only. Sturnus vulgaris reached the highest mean density and dominance in the assemblage, contributing by 18.01% to the total with low between-year variation (CV = 8.33%). The mean density of this species was 22.50 p/10 ha and varied between 20.63–24.38 p/10 ha. Anas platyrhynchos contributed to the total abundance by 12.64% and reached the mean density 15.83 p/10 ha with very high variation 12.50–20.63 p/10 ha (CV = 26.87%). In 1995, Phylloscopus collybita was among eudominant species with the dominance value 11.02%, but this happened only in one year, probably in the fluctuation time.

Dominant species ($5\% \le 10\% <$) contributed by 42.04\% to the total assemblage abundance, with a vearly variation between 27.95–43.56%. Totally, six species (Ficedula albicollis, Fringilla coelebs, Phylloscopus collybita, Parus major, Sylvia atricapilla, Erithacus rubecula) can be characterised as dominants based on mean values. In the period studied, E. rubecula and P. major did not belong to dominants every year. In comparison to other species, F. albicollis had the highest mean density (10.56 p/10 ha) and dominance (8.44%), with low between-year variation (CV = 9.78%). The mean density of F. coelebs was 10.52 p/10 ha (9.25-12.19 p/10 ha; CV = 14.34%),contributing by 8.41% to the assemblage. Phylloscopus collybita reached a mean density of 10.29 p/10 ha (8.17%) with very high variability (7.50-14.38 p/10 ha;CV = 35.12%). Parus major had a mean density of 7.40 p/10 ha (6.03%), with a variability between 6.31– 8.88 p/10 ha (CV = 17.93%). Sylvia atricapilla had a mean density of 7.25 p/10 ha and contributed by 5.80% to the assemblage with the density variation 6.44-8.13 p/10 ha (CV = 11.66%). Erithacus rubecula formed 6.44 p/10 ha (5.19%) of the total assemblage density and had relatively low between-year variation (5.88-6.75 p/10 ha; CV = 7.58%).

Subdominant species ($2\% \le 5\%$ <) represented 6.95% of the total assemblage abundance with the annual variation between 10.00–25.26%. Based on mean dominance values, only two species (*Parus caeruleus*,

Certhia familiaris) belonged to subdominants. These two species belonged into this group constantly every year, while the other nine species only in one or two years in the three-year study period. Certhia familiaris and Columba oenas reached relatively high mean density (4.04 and 2.44 p/10 ha) and dominance (3.25% and 1.94%) compared to the other types of lowland forests (Bureš & Maton 1984–1985; Chytil 1984, 1990; Pavelka 1988; Bohuš 1993, 2000; Korňan 1996). This could be caused by proximity of the site to the Malé Karpaty Mts where these species are common, and by the high occurrence of cavities.

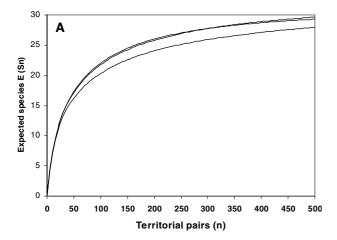
Recedent species ($1\% \le 2\% <$) contributed by 15.15% (range 8.05–11.81%) to the total assemblage abundance. In total, ten species belonged into this group. Columba oenas, Sitta europaea, Muscicapa striata, Troglodytes troglodytes, Prunella modularis and Oriolus oriolus had higher densities and more stable annual variability in comparison to the others (CV = 11.75-26.02%).

Subrecedent species (< 1%) contributed by 5.20% (range 2.99–5.51%) to the total assemblage abundance. Fourteen species belonged among subrecents, yet only five species Turdus merula, Columba palumbus, Dendrocopos minor, Turdus philomelos and Certhia brachydactyla were constantly present in all years in the study period.

Species diversity and evenness

Mean and yearly values of species diversity indices, evenness and rarefaction are shown in Table 3. Based on all diversity measures it is possible to conclude that the values of bird diversity had similar trend. Simpson diversity index showed slightly lower ability to distinguish annual variability reflected in similar index values among years in comparison to the other diversity measures (Table 3).

Shannon species diversity index values did not show statistically significant differences when tested by t-student test for pair-wise comparisons. The index reached the highest value 4.10 bites in 1995, whereas



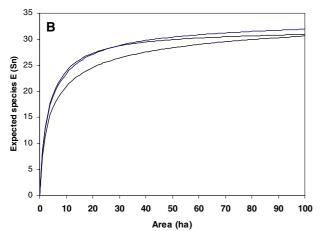


Fig. 1. Rarefaction curves for three year samples 1992, 1993, and 1995 of the 16 ha interior alder swamp census plot in the Šúr National Nature Reserve. Figures shows the relationship between expected species richness E (Sn) estimated by rarefaction and increasing samples of territorial pairs (A) and area (B). The calculations are based on year density data including species with very low population densities ("+"). For these species, density estimates given in parenthesis in Table 2 were used for calculations

the lowest value was 3.98 bites in 1993. Brillouin and Simpson indices detected similar diversity pattern, yet the Simpson index had the same value 0.91 in both years (1992–1993) that indicated its lower sensitivity.

Evenness index values did not have identical trends, either. The Shannon and Brillouin indices reached the highest values 0.81 and 0.82 in 1992. The Shannon evenness index had the lowest value 0.79 in 1993 as well as the Brillouin evenness index 0.80. In contrast, the Simpson evenness index reached the highest value 0.95 in 1995 and identical values 0.94 in 1992–1993.

Rarefaction was selected as a less biased method of diversity measurements in comparison to the common diversity indices. The expected species richness $E(S_n)$ was calculated in the relationship with the increasing sample of territorial pairs and area (Figs 1A, B). Expected species richness on all standardised sample sizes of territorial pairs and areas were the highest in 1992 that did not correspond to diversity estimates gained

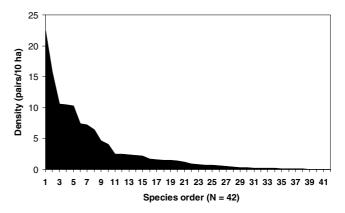


Fig. 2. Community curve of the breeding bird assemblage of the alder swamp in the Šúr National Nature Reserve. Pooled data from the period 1992–1995 were used. Only species breeding in the 16 ha study plot are ordered. Species are ranked in descending order.

Table 4. Guild and migratory habit structure of the bird assemblage within the primeval alder swamp in the Šúr National Nature Reserve in the period 1992–1995. Mean density and dominance values for the period were calculated for each category. All breeders including the "o+" category were used for the calculations.

	Number of species	Density	Dominance
Foraging guilds			
1. Foliage gleaners	15	46.36	36.71
2. Outside forest foragers	16	29.02	22.97
3. Arboreal flycatchers	3	19.34	15.31
4. Water foragers	2	7.92	6.27
5. Bark gleaners	3	7.21	5.71
6. Litter foragers	5	6.05	4.79
7. Herb layer foragers	2	4.41	3.49
8. Vegetarians	7	3.11	2.46
9. Trunk probers	5	2.56	2.02
10. Raptors	4	0.33	0.26
Nesting guilds			
1. Hole nesters	18	61.72	48.98
2. Ground nesters	9	35.39	28.09
3. Canopy nesters	17	16.31	12.94
4. Shrub nesters	8	12.59	9.99
Migratory guilds			
1. Short-distance migrants	19	68.58	54.30
2. Tropical migrants	15	29.42	23.29
3. Residents	25	28.31	22.41

by the indices (Table 3). The expected species diversity in random sample of 50 and 100 pairs was 17.32 and 22.03 species. The estimate on the area of 5 ha and 10 ha was 19.35 and 23.88 species. All rarefaction calculations detected the lowest values in 1993 that correspond to the diversity estimated by the Shannon and Brillouin indices. The rarefaction estimate on random samples of 50 and 100 pairs was 16.22 and 20.30 species, respectively in 1993. The estimates on the area of 5 ha and 10 ha were 16.89 and 20.95 species, respectively (Table 3).

Guild structure and migratory habits Foraging guilds

Totally, 10 categories of foraging guilds were classified

by a priori approach based primarily on literature information and foraging observations during bird censusing (Table 4). Guild membership of bird species is given in the Appendix. One guild category, outside forest foragers, can be understood as artificial combining all species primarily feeding outside the forest swamp regardless their real guild memberships. This category, consisting mainly of waterfowl, raptors and corvids, had the second highest dominance value 22.97% and density 29.02 p/10 ha. In total, 16 species belonged at least partly into this guild. The high proportion of outside forest foragers may reflect that alder swamp is an island surrounded by agricultural land and other types of cultural landscape habitats, which attracts many species for foraging.

Foliage gleaners represented the most dominant guild consisting of 15 species with the mean combined density 46.36 p/10 ha, contributing by 36.71% to the assemblage (Table 4). Arboreal flycatchers reached the third highest guild density (19.34 p/10 ha), constituting 15.31% of the assemblage. The guild was composed of only three species. The mean density and dominance of the other guilds were significantly lower. The mean dominance value of these categories did not exceed 7%. Water foragers consisting of only two species constituted 6.27% of the assemblage with the mean density 7.92 p/10 ha. The guild density is approximately by 50% lower compared to the breeding densities due to the outside forest foraging. Species ecologically dependent on trunk, constituting only up to 8% of the assemblage, were divided into two guilds: bark gleaners were represented by two species of treecreepers and Sitta europaea and bark probers by five species of woodpeckers. The density of the bark gleaners (7.21 p/10 ha; 5.71%) was almost three times higher than the density of the trunk probers (2.56 p/10 ha; 2.02%). Lower vegetation strata foragers were split into two guilds herb layer foragers and litter foragers. The herb layer foragers, comprising two species, had very low density (4.41 p/10 ha; 3.49%) that indicated underdeveloped understorey vegetation and very low density of shrubs. The litter foragers comprising five species reached very low density (6.05 p/10 ha; 4.79%) that was probably caused by a limited coverage of litter microhabitat due to presence of surface water along alder trees. Vegetarians were the second species richest guild. Seven species at least partly belonged to vegetarians. However, their relative contribution 3.11% (2.46 p/10 ha) was one of the smallest. Raptorial guild represented by four species contributed on average only by 0.26% (0.33 p/10 ha) to the total density. Very low between-year fluctuations were found in the guilds of the arboreal flycatchers and raptors, the other guilds showed visible between-year changes in density and dominance values.

Nesting guilds

Hole nesters were the most species rich and dominant guild (Table 4). Totally, 18 hole nesters represented this guild, out of this number three species did not breed in the plot. This guild represented approximately half

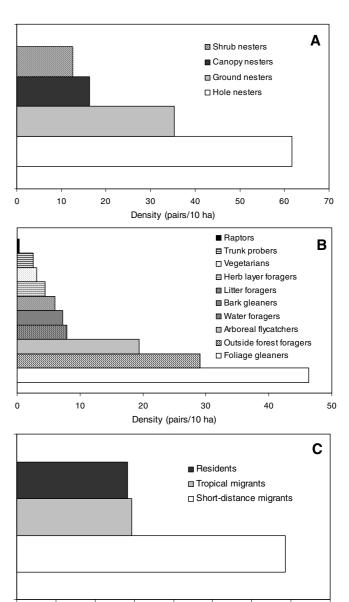


Fig. 3. Mean densities of nesting (A) and foraging (B) guilds of the breeding bird assemblage of the alder swamp in the study period 1992–1995 within the Šúr National Nature Reserve. Mean densities of bird migratory habits are indicated in diagram C. Only breeding species detected in the 16 ha study plot were included in the analysis.

40

Density (pairs/10 ha)

50

(48.98%) of the assemblage density (61.72 p/10 ha). Members of this guild were not only typical cavity nesters, but also semi-cavity breeders such as Musci-capa striata and treecreepers. The highest density of hole nesters reflects the tree structure of the stand with many old decaying trees full of natural cavities. Natural number of cavities on some trees was so high that there were several breeding pairs of $Sturnus\ vulgaris$ on a single tree. Ground nesters having the second highest mean density 35.39 p/10 ha reached a dominance of 28.09%. The guild consisted of nine species, only six of them were breeders. This finding is a little bit surprising due to the presence of surface water during most of the

breeding season. Many of these species bred on exceeding island-like land along air roots of alder trees that topped the flooded ground. Canopy nesters contributed by 12.94% (16.31 p/10 ha) to the assemblage. The guild had 17 species and all were nesters. This low number was caused by the fact that the majority of passerine canopy insectivores nested in cavities. Another factor explaining this low number may be the fairy transparent and uniform structure of alder canopies. Shrub nesters constituted 9.99% (12.59 p/10 ha) of the assemblage due to very low density of suitable shrubs in the larger part of the plot. Eight species can be at least partly characterised as bush nesters. Two of them were not nesters. Only an approximately 100 m belt in the NW part of the plot was densely covered by willow (Salix cinerea) shrubs to support higher densities of understorey bush breeders. Very low between-year variability of densities indicated temporally stable nesting guild structure.

Migratory habits

Density of short distance migrants (68.58 p/10 ha) was the highest out of the migratory groups, contributing by more than half (54.30%) to the assemblage. Totally, 19 species belonged to short distance migrants. Tropical migrants, totally 15 species, had the second highest mean dominance 23.29% (29.42 p/10 ha) that indicated very warm climate of the site. However, they were overdominated in 1993 by residents. Twenty-five species belonged to residents. Although, residents were the most species rich, their mean dominance value 22.41% (28.31 p/10 ha) was the lowest. Only very low between year density fluctuations were detected that reflects a very stable structure of the migratory habit groups of the bird assambalge.

Discussion

Past studies in the alder forest

The primeval swamp of the Jurský Šúr National Nature Reserve belongs to the most threatened wetland habitats in Europe due to habitat destruction primarily by drainage and amelioration. Before the drainage plant constructed in the 1940s and the 1950s, the water level in spring was higher by 0.4–0.5 m on average, even several meters in local terrain depressions (Ferianc 1943). That time some parts of the reserve were accessible only by boat.

The first studies dealing with bird fauna of the reserve were completed in the 1940s (Turček 1941; Ferianc 1943). Ferianc (1943) summarised previous faunistic records, faunistic papers and own observations. He listed 112 bird species including transmigrants and vagrants. Forty-one species could be characterised as forest habitat breeders, including the edge zone. Several "potential" alder forest breeders (Phylloscopus sibilatrix, Phoenicurus phoenicurus, Falco tinnunculus, Milvus migrans, Lanius collurio, Acrocephalus palustris and Carduelis spinus) can be indirectly inferred from the Ferianc (1943) species list, however, they were not

proved to be nesters in this study. Past breeding records were mostly described without any site or habitat specificity; therefore it is difficult to estimate species habitat relationships in that period. Some of these species currently breed in other habitats of the reserve. In addition, Ferianc critically evaluated occurrence records of other authors. Five species, Falco subbuteo, Actitis hypoleucos, Acrocephalus melanopogon, A. paludicola, and Locustella fluviatilis, were recorded by Jirsík, Petényi, and Turček (Ferianc 1943). Presently, of them only L. fluviatilis is a regular breeder in the alder swamp and surrounding habitats. Extremely important was a breeding record of Carduelis spinus on an alder tree in 1895 (Nagy & Warga in Ferianc 1943).

The first complex study on the structure of bird assemblages and their seasonal dynamics in the most typical habitats in the reserve was conducted in 1969–1971 by Kupcová (1972, 1980). The quantitative structure of bird assemblages of alder swamp edge was studied by a belt transect method during three consecutive breeding seasons. The author detected only 38 breeding species in the forest ecotone, which is significantly less in comparison to 50 species detected in the forest edge in 1995 (Korňan 1996). The total breeding bird density was 187.5 p/10 ha, which is 12.2% less in comparison to the estimate of total breeding bird density 213.69 p/10 ha in 1995. Because this article is focused on the interior assemblage, the results of these two studies will not be further compared.

$European\ scale\ comparison$

Oelke (1987) summarised the results of quantitative studies of bird assemblages of wet alder Alnion glutinosae stands in Europe. Totally, data sets of 29 assemblages studied mainly in Western Europe and published in the period 1930-1984 were used for the synthesis (Table 5). The size of study plots varied between 0.36– 80 ha what might have drastic effects on data comparability since the results were not standardised by rarefaction techniques. In addition, the author synthesised bird count results conducted by different census methods that could seriously violate data comparability assumptions due to differences in applicability and accuracy of bird count methods. The mean total bird assemblage density for the pooled data set of 29 bird counts was 88.2 p/10 ha (range 14-279 p/10 ha). Compared to these values, the Jurský Šúr assemblage reached much higher values than the mean, it was 125.15 p/10 ha in the swamp interior and 213.69 p/10 ha in the swamp edge. The species richness in the pooled data set also showed much lower mean value, 26 species (range 4-47), in comparison to the Jurský Šúr assemblage in which 32–35 breeders were recorded in individual years in the swamp interior and 50 breeders in one year in the swamp edge. Moreover, dramatic differences can be seen in the assemblage structures when comparing densities of the first 15 species ordered by dominance values (Table 5). Following the results of the synthetic study, *Phyl*loscopus trochilus, Turdus merula, Sylvia borin, Turdus philomelos, Sylvia communis, Anthus trivialis and

Table 5. Comparison of diversity, evenness, and the mean species densities and their standard deviations between bird assemblages of *Alnion glutinosae* stands in Europe (Oelke 1987) and the forest interior of this habitat in the Šúr National Nature Reserve. Oelke (1987) summarized data of 29 censuses of wet alder stands in the period 1930–1984. For comparative purposes the Shannon diversity index and evenness based on natural logarithms was applied because it was used in Oelke's study.

Assemblage parameters	Oelke's summarized data	Šúr NNR	
Mean species richness	26	33.33	
Minimum richness/plot in the sample	3	32	
Maximum richness/plot in the sample	47	35	
Mean species diversity	2.65 ± 0.50	2.81 ± 0.04	
Total species number in all plot/s	103	42	
Minimum diversity/plot in the sample	1.04	2.76	
Maximum diversity/plot in the sample	3.24	2.84	
Mean evenness	0.87 ± 0.07	0.80 ± 0.01	
Mean total assemblage density (pooled data)	88.2 p/10 ha	125.15 p/10 ha	
Minimum total assemblage density	14 p/ 10 ha	110.63 p/ 10 ha	
Maximum total assemblage density	$279~\mathrm{p}/~10~\mathrm{ha}$	$134.38 \text{ p}/\ 10 \text{ ha}$	
Dominant species	Density (p/ 10 ha)	Density (p/ 10 ha)	
Phylloscopus trochilus	9.0 ± 8.4	=	
Fringilla coelebs	8.2 ± 7.5	10.52 ± 1.51	
Sturnus vulgaris	6.2 ± 9.5	22.50 ± 1.88	
Turdus merula	5.8 ± 6.6	1.21 ± 0.32	
Sylvia borin	4.8 ± 4.7	_	
Phylloscopus collybita	4.6 ± 3.8	10.29 ± 3.61	
Troglodytes troglodytes	4.4 ± 3.2	2.25 ± 0.56	
Erithacus rubecula	4.2 ± 2.5	6.44 ± 0.49	
Parus major	4.2 ± 2.7	7.40 ± 1.33	
Sylvia atricapilla	4.2 ± 3.5	7.25 ± 0.85	
Turdus philomelos	2.8 ± 2.0	0.73 ± 0.18	
Sylvia communis	2.6 ± 1.5	_	
Anthus trivialis	2.2 ± 1.6	1.56 ± 1.56	
Parus caeruleus	2.1 ± 1.3	4.60 ± 0.13	
Farus caerateus	2.1 ± 1.0	4.00 ± 0.15	

Hippolais icterina were among the 15 most common species, yet three of them, P. trochilus, S. borin and S. communis, were not recorded in the Jurský Šúr assemblage and the rest of them had lower population densities in the assemblage. In contrast, Anas platyrhynchos, Ficedula albicollis, Certhia familiaris, Columba oenas, Sitta europaea, Muscicapa striata and Prunella modularis, were not listed in Oelke's work. Anas platyrhynchos and F. albicollis belonged to dominant species in the interior and edge assemblages, while M. striata was among dominants in the edge assemblage. In conclusion, it is very difficult to explain these major differences in the assemblage structure due to lack of information on habitat structure, floristics, landscape composition, presence of water, etc. in Oelke's paper.

Morozov (1992) studied breeding bird assemblage of a 20–50 year mesophylic grey alder forest with luxuriant herb layer in the Valdai Uplands (subboreal zone of north-west Russia). In total, 28 species were detected by the combined version of the mapping method in a 18.4 ha census plot in the four year study period (1986–1989). Yearly variability of richness was 21–23 species. The total mean breeding bird density was 102.65 p/10 ha that is comparable to the mean assemblage density in an ash-alder riverine forest (Circaeo-Alnetum) in the Białowieża National Park, also representing a subboreal type characterized by admixture of spruces (Tomiałojć & Wesołowski 1996). The as-

semblage was dominated by Fringilla coelebs, Sylvia atricapilla, Ficedula hypoleuca, Turdus pilaris, Sylvia borin, Phylloscopus trochilus and Turdus iliacus. There are many species not occurring in the Central European alder habitats that are typical of northern wetland forests, while F. hypoleuca is functionally fully equivalent to F. albicollis. Nevertheless, the species richness is significantly lower in the Valdai Uplands grey alder stand, which is caused partly by the young successional stage and geographic location affecting local food abundance, availability, and niche organisation in the ecosystem.

Primeval alder stands in the Białowieża forest Tomiałojć et al. (1984) established monitoring plots in two types of primeval forests, alder swamp Carici elongatae-Alnetum (25 ha) in 1976 and ash-alder riverine forest Circaeo-Alnetum (25 and 33 ha) in 1975 within the Białowieża National Park, Poland. The 25 ha Carici elongatae-Alnetum plot and the 33 ha Circaeo-Alnetum plot have been censused by mapping method until now. The second, 25 ha Circaeo-Alnetum, plot was censused only in 1975–1979. The total breeding bird density in the swamp Carici elongatae-Alnetum was estimated on 78.0 p/10 ha in 1990–1994 (Tomiałojć & Wesołowski 1996) and 87.8 p/10 ha in 1995–1999 (Wesołowski et al. 2002). The 33 ha plot of the association Circaeo-Alnetum reached a mean of 105.1 p/10

ha in 1990–1994 and 112.8 p/10 ha in 1995–1999 (Wesołowski et al. 2002). The total mean breeding assemblage density in the second plot of this association censused only in the period 1975–1979 was 75.8 p/10 ha (Tomiałojć et al. 1984). From the long-term monitoring data, it is possible to conclude that the total mean breeding assemblage densities increased in the second half of the 1990's. Numerical increases in these stands increased simultaneously in all plots and could not be attributed to changes in local environmental factors such as food resources, weather condition or habitat structure (Wesołowski et al. 2002). The authors suggest that environmental factors acting on a larger geographic scale, outside the study area, could have been involved in development of these patterns.

In order to compare species richness and total density estimates of the analysed census plots with the Jurský Šúr data, the combined data sets from the period 1992–1993 and 1995 from the two published data sources were used for this purpose (Tomiałojć & Wesołowski 1996; Wesołowski et al. 2002). The total mean breeding density of the alder swamp Carici elongatae-Alnetum (25 ha) in the 3-year period was $82.00 \pm 8.32~\mathrm{p}/10~\mathrm{ha}$ (CV = 10.15%) with the minimum extreme value 76.80 p/10 in 1993 and the maximum extreme value 91.60 p/10 in 1995. The mean species richness of the assemblage in the 3-year period was 35.33 \pm 1.15 species per year (CV = 3.27%). In total, 41 breeding species were recorded in the plot. The minimum richness was 34 species in 1992, yet the maximum richness was 36 species detected in 1993 and 1995. The total mean breeding density of the ash-alder riverine forest Circaeo-Alnetum (33 ha) in the 3-year period was $107.98 \pm 9.84 \text{ p/}10 \text{ ha (CV} = 9.12\%)$. The minimum extreme density was 98.64 p/10 ha in 1992, whereas the maximum extreme value was 118.26 p/10 ha in 1995.Totally, 55 breeders were detected within the study plot in the 3-year sample size. The mean species richness of the assemblage was 47.00 ± 2.00 species per year (CV = 4.26%). The minimum richness was 45 species detected in 1993, while the maximum richness was 49 species recorded in 1995. The extremely high species richness and occurrence of a high number of silviid warblers, finches and other edge species in the study plot is caused by forest edge having over 1000 m (Tomiałojć et al. 1984). The second ash-alder forest Circaeo-Alnetum (25 ha) censused only in the five-year period (1975– 1979) reached the mean breeding assemblage density $75.80 \pm 7.24 \text{ p/}10 \text{ ha}$ (CV = 9.56%). The mean species richness in this study plot was 37.00 ± 1.73 species with the minimum extreme value 34 species in 1978 and maximum extreme value 38 species in 1979. Totally, 48 nesters were recorded in the five-year period in the study plot. The species diversity and population densities of this assemblage were also affected by approximately 350 m forest edge creating boundary with non-forest habitats. Species richness of the three compared study plots is similar to the values found in the primeval alder swamp in the Jurský Šúr, whereas the Polish habitats reached visibly lower total breeding bird

densities. The higher total species richness is primarily caused by plot size effects and larger spatial extent of the Białowieża Forest compared to the island type of alder habitat in the Šúr NNR. When comparing the species richness and total breeding bird density of the forest edge habitat in Jurský Šúr and the values of 33 ha ash-alder "peninsula" plot, the edge of the Jurský Šúr swamp reached comparable species richness 50 breeding species per year, yet much higher total breeding bird assemblage density of 213.69 p/10 ha. This could have been caused partly by the 16 ha census plot 150×1065 m in the shape of letter "L", while the Polish plot has irregular rectangular shape and was not designed to census primarily forest edge assemblage (Korňan 1996). This is the principal problem of the comparison. Consequently, it is difficult to conclude if the edge assemblage of the Jurský Šúr can reach higher species richness due to limited one-year period of censusing, plot size and shape. Definitely, it belongs to the most species diversified and dense bird assemblages of alder stands on the European scale when compared with the report of Oelke (1987).

To compare diversity of the Białowieża alder forests directly with the Šúr alder forest, a rarefaction from Polish primary data from the period 1992–1993 and 1995 was calculated on a standardized sample of 100 pairs and area of 10 ha. Both Białowieża forests reached higher species diversity. Mean rarefaction value of the alder swamp $Carici\ elongatae\text{-}Alnetum\ calculated}$ as expected number of species in the random samples of 100 pairs from 1992–1993 and 1995 was 24.35 \pm 0.17 species. In the same period, the mean value in the Šúr swamp was 21.35 \pm 0.92 species.

Guild and migratory habit structure of the avian assemblage was compared with these features of the Białowieża assemblages. The assemblages were divided into guilds by means of a priori approach (Tomiałojć et al. 1984). Their classification system is not based on real foraging observations and consequent statistical analyses of such data with the result of a posteriori analysis. Foraging guild classification of the Šúr assemblage is also a priori, but is based on a posteriori guild model of primeval beech-fir forest (Korňan & Adamík 2007). The comparison is, therefore, only partly compatible, especially in the cases of nesting guilds and migratory habits. To prepare compatible comparison, several guild categories from the Šúr alder forest guild model have to be joined into one guild category equivalent to the Białowieża Forest guild model or opposite. The bark gleaners and the trunk probers of the Šúr forest were combined to create a category equivalent to bark insectivores. The litter foragers and herb layer foragers of the Šúr forest were joined to establish a category equivalent to ground insectivores. The foliage gleaners and the arboreal flycatchers were transformed into the category of the crown insectivores. The other guild categories were comparable without transformations. The years 1990–1994 from the Białowieża monitoring period 1975-present were selected for comparison with the Šúr guild data (Tomiałojć & Wesołowski 1996). Table 8 of

the paper was also recalculated to get dominance values of the guilds for the comparisons. The estimated density of raptors (predators) was 0.5 p/10 ha in the Circaeo-Alnetum assemblage. A little lower value (0.3 p/10 ha) was found in the Carici elongatae-Alnetum assemblage. The raptor density was comparable in the Šúr forest (only 0.33 p/10 ha). Density of vegetarians (8.5 p/10 ha) was the highest in Circaeo-Alnetum assemblage. The density of vegetarians in the Carici elongatae-Alnetum assemblage was 6.9 p/10 ha, while in the similar habitat type in the Šúr forest the density was only 3.11 p/10 ha. The density of the ground insectivores was the highest in Circaeo-Alnetum assemblage (30.7 p/10 ha), followed by the Carici elongatae-Alnetum assemblage (24.8 p/10 ha). The lowest value was in the Šúr assemblage (10.46 p/10 ha). This could have been caused by regular spring floods that disable food searching in the lower vegetation strata. The density of the bark insectivores was similar in both Białowieża plots, 8.1 and 7.4 p/10 ha, respectively. A little higher value was estimated in the Šúr forest (9.77 p/10 ha). Yet, the dominance of bark insectivores was a little higher in both Białowieża habitats (8.44% and 9.55%) than in the Šúr alder swamp (7.74%). The Carici elongatae-Alnetum assemblage of the Šúr forest showed the highest density of the crown insectivores (65.70 p/10 ha). The density of the crown insectivores in the Circaeo-Alnetum assemblage was 48.2 p/10 ha, whereas in the Carici elongatae-Alnetum assemblage it was only 38.1 p/10 ha. This could presumably have been caused by lower leaf density and more open canopy of the Białowieża alder stands containing many gaps after tree falls. The higher total density of the breeding bird assemblage in the Šúr alder swamp was another factor shading this pattern. When comparing the dominance of crown insectivores among the three plots, the values were almost the same (50.21% and 49.16% versus 52.24%).

Comparison of nesting guilds was easier. Only transformation of the shrub and the ground nesters from the Šúr guild model into one category of the ground nesters of the Białowieża guild classification system was needed for comparison. The density of ground nesters (47.98 p/10 ha) was the highest in the Šúr assemblage. This was partly caused by the high population densities of Anas platyrhynchos that was attracted for breeding by water floods of the forest. The Circaeo-Alnetum assemblage had a value of 26.8 p/10 ha. The lowest value (21.2 p/10 ha) was in the Carici elongatae-Alnetum assemblage. The canopy nesters were equivalent to the crown nesters. The crown nesters reached the highest density (41.2 p/10 ha) in the Circaeo-Alnetum assemblage. The density of crown nesters in the Carici elongatae-Alnetum assemblage in the Białowieża Forest was lower (30.7 p/10 ha). The lowest number (16.31 p/10 ha) was found in the Šúr forest assemblage. In contrast, the hole nesters had the highest density (61.72 p/10 ha) in the Šúr assemblage. Presumably, the very high density of Sturnus vulgaris affected this pattern. The Circaeo-Alnetum assemblage

followed by the density $35.7~\rm p/10$ ha. The lowest density $(25.7~\rm p/10~\rm ha)$ was found in the Carici elongatae-Alnetum of the Białowieża Forest. The differences in densities of the nesting guilds between the two Polish plots were strongly affected by the higher total density of the Circaeo-Alnetum assemblage. When comparing dominance values, the numbers were almost the same. Consequently, the plots are structurally very little different.

For comparison of migratory habits, it was necessary to combine two categories of the Białowieża classification, the residents in the region and the true forest residents, into one category of residents of the classification model of the Súr alder assemblage. The densities of all migratory habit categories were higher in the Šúr assemblage; the density of tropical migrants in the Šúr alder forest was 29.42 p/10 ha. The Circaeo-Alnetum assemblage had a lower value (21.9 p/10 ha). The lowest density (15.0 p/10 ha) was found in the Carici elongatae-Alnetum of the Białowieża Forest. The shortdistance migrants reached a density of 68.58 p/10 ha in the Šúr assemblage, whereas in the Circaeo-Alnetum assemblage their density was 57.7 p/10 ha and in the Carici elongatae-Alnetum 42.5 p/10 ha. Smaller differences were in densities of residents between the Carici elongatae-Alnetum of the Šúr Reserve (28.31 p/10 ha) and the Circaeo-Alnetum assemblage of the Białowieża Forest (24.4 p/10 ha). Again, the lowest number of residents was found in the Carici elongatae-Alnetum assemblage of the Białowieża Forest (20.5 p/10 ha). The overall lower numbers of migratory groups could have been partly caused by the lower values of total breeding bird densities in the Polish plots. This hypothesis is supported by the dominance values of migratory groups that were almost the same between the three compared plots. We can conclude that the three plots are not different from the aspect of bird migratory habits.

All Białowieża stands used in the comparisons were dominated by $Fringilla\ coelebs$ that was the only species reaching regularly densities exceeding 20 p/10 ha. It was the only eudominant species similar in its dominance position to $Sturnus\ vulgaris$ in the Šúr swamp. $Erithacus\ rubecula$ belonged to dominant species in all alder stands, with population densities above 5 p/10 ha. The second position in the Šúr plot was occupied by $Anas\ platyrhynchos$, whose population densities were probably dependent on the level of surface water in the plot.

Eight species exceeded the dominance threshold of 5% in the Šúr NNR, whereas five species were in this dominance class in the three Białowieża plots based on pooled data from 1992–1995. The Carici elongatae-Alnetum swamp plot was dominated by Fringilla coelebs, Erithacus rubecula, Ficedula albicollis, Phylloscopus collybita, and Turdus philomelos. Equivalent habitat in the Šúr NNR was predominantly occupied by Sturnus vulgaris, Anas platyrhynchos, Ficedula albicollis, Fringilla coelebs, Phylloscopus collybita, Parus major, Sylvia atricapilla, and Erithacus rubecula. All Białowieża dominant species were found in this class in

the Šúr swamp, except T. philomelos. In the edge riverine swamp Circaeo-Alnetum plot, five dominant species (F. coelebs, S. vulgaris, E. rubecula, F. albicollis, T. philomelos) were detected, while F. coelebs, E. rubecula, Phylloscopus sibilatrix and Troglodytes troglodytes belonged into this class in the interior plot of this habitat censused in 1975–1979. The remaining species breed in much lower numbers. Densities of approximately 60\% nesters in the swamps did not exceed 3 p/10 ha. The Polish alder dominated swamps had an admixture of native Picea abies trees that significantly influenced species structure of the stands. Coniferous specialists such as Regulus regulus, R. ignicapillus, Parus ater, P. cristatus, P. montanus, Picoides tridactylus, Pyrrhula pyrrhula, Nucifraga caryocatactes and Glaucidium passerinum were recorded as breeders in the period 1975–2004, some in fairly high numbers. Based on these comparisons, it can be concluded that alder swamps are extremely diverse ecosystems with only very broad species composition and population density patterns depending on local environmental conditions, forest structure and geographical location.

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Appendix. A priori classification of species into guild and migratory habit types detected in the interior primeval alder swamp in the $\check{\text{S}}$ úr National Nature Reserve in the period 1992–1995.

a :		Guild types	Migratory habits		
Species	nesting	foraging	Migratory habits		
Accipiter gentilis	C	R	R		
Accipiter nisus	$^{\mathrm{C}}$	R	M		
Anas platyrhynchos	G	O–AQ	M		
Anthus trivialis	\mathbf{G}	$_{ m LF}$	T		
Buteo buteo	$^{\mathrm{C}}$	O	R-M		
Carduelis carduelis	$^{\mathrm{C}}$	O–VE	M-R		
Carduelis chloris	B-C	O–VE	R(0.7), M(0.3)		
Certhia brachydactyla	H	$_{ m BG}$	R		
Certhia familiaris	Н	BG	R		
Ciconia nigra	C	O–R	T		
Coccothraustes coccothraustes	$^{ m C}$	VE (0.6), FG (0.4)	M(0.7), R(0.3)		
Columba oenas	Н	O-VE	M		
Columba palumbus	C	O-VE	M		
Corvus corax	Č	0	R		
Corvus corone cornix	$\ddot{ ext{C}}$	O (0.9), R (0.1)	R		
Cuculus canorus	_	FG	T		
Dendrocopos leucotos	Н	TP	R		
Dendrocopos major	H	TP	R		
Dendrocopos medius	H	TP	R		
Dendrocopos minor	H	TP	R		
Dryocopus martius	H	TP	R		
Erithacus rubecula	G	AF	M (0.8), R (0.2)		
Falco cherrug	$\tilde{ ext{C}}$	O (0.8), R (0.2)	M		
Ficedula albicollis	H	AF	T		
Fringilla coelebs	C	FG	M		
Fulica atra	Ğ	O–AQ	M (0.9), R (0.1)		
Garrulus glandarius	Č	R (0.4), LF (0.4), VE (0.2)	R		
Hippolais icterina	Č	FG	T		
Jynx torquilla	H	LF	$\stackrel{\mathtt{l}}{\mathrm{T}}$		
Locustella fluviatilis	G	LF–HF	$\stackrel{\mathtt{l}}{\mathrm{T}}$		
Muscicapa striata	H	AF	$\stackrel{\mathtt{l}}{\mathrm{T}}$		
Oriolus oriolus	C	FG	$\overset{\mathtt{l}}{\mathrm{T}}$		
Parus caeruleus	H	FG	R		
Parus major	H	FG	R		
Parus palustris	H	FG	R R		
Passer montanus	H	O–FG	R R		
Phylloscopus collybita	G	FG	$_{ m M-T}^{ m R}$		
Phylloscopus sibilatrix	G	FG	T		
Phylloscopus trochilus	B–G	FG	$\overset{\mathtt{l}}{\mathrm{T}}$		
Prunella modularis	В	HF	M		
Serinus serinus	C	O–VE	M		
Sitta europaea	Н	BG	R		
	C	O–VE	т Т		
Streptopelia turtur	Н	O (0.2), R (0.8)	R		
Strix aluco Sturnus vulgaris	Н	O (0.8), LF (0.1), FG (0.1)			
· ·	В		$egin{array}{c} \mathbf{M} \\ \mathbf{T} \end{array}$		
Sylvia atricapilla	В	${ m FG}$ ${ m FG}$	T		
Sylvia communis Troglodytes troglodytes	G–B	HF	M–R		
Trogioaytes trogioaytes Turdus merula	G-в В	LF			
	В	$_{ m LF}$	$_{ m M-R}$		
Turdus philomelos	D	ГГ	1V1		

Guild and migratory habit categories: nesting guilds: B – bush nesters, C – canopy nesters, G – ground nesters, H – hole nesters; foraging guilds: AF – arboreal flycatchers, AQ – water foragers, BG – bark gleaners, FG – foliage gleaners, VE – vegetarians (granivores), HF – herb layer foragers, LF – litter foragers, O – outside forest foragers, C – trunk probers, C – raptorial guild (vertebratophags); migratory habits: C – residents, C – short-distance migrants, C – tropical migrants.