Structure of the breeding bird assemblage of a primaeval beech-fir forest in the Šrámková National Nature Reserve, the Malá Fatra Mts

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Korňan, M. Structure of the breeding bird assemblage of a primaeval beech-fir forest in the Šrámková National Nature Reserve, the Malá Fatra Mts. Biologia, Bratislava, **59:** 219—231, 2004; ISSN 0006-3088.

The structure of a breeding bird assemblage of a primeval beech-fir forest in the Malá Fatra Mts, the Western Carpathians was studied in the period 1997–2001. A 27.5 ha (500 × 550 m) forest interior study plot was established for bird censusing. Population abundances were estimated by means of an improved version of the mapping method from April to mid-July. Altogether, 57 bird species (52 breeders) were recorded within the reserve during the 5-year period. Of these, 48 species bred in the study plot reaching a mean density of 58.17 ± 3.60 pairs/10 ha (CV = 6.18%). The year assemblage densities varied between 52.15–61.20 BP/10 ha. The Shannon diversity index (H') varied between 4.10–4.36 bites. The evenness index (J') reached values between 0.78–0.82. The year rarefaction estimates [$E\,(S_{100\,\mathrm{pairs}})$] were 22.77–25.16 species. The year rarefaction estimates on area [$E\,(S_{10\,\mathrm{ha}})$] varied between 19.46–21.30 species. Bird species diversity was comparable to other mixed primeval stands in the Western Carpathians e.g. Dobroč and Badín reserves. In total, seven species were characterized as dominant ($\geq$ 5%): *Fringilla coelebs*, *Erithacus rubecula*, *Sylvia atricapilla*, *Parus ater*, *Phylloscopus collybita*, *Regulus regulus*, and *Prunella modularis.* The species structure and relative abundance of the bird assemblage showed high temporal stability. Major differences were found in assemblage composition in comparison to the past survey in the reserve. A serious need for reevaluation and new rigorously designed quantitative inventory surveys of the Slovak reserve network is stressed.

Key words: bird community, primeval beech-fir forest, mapping method, population density, rarefaction, the Šrámková National Nature Reserve, Slovakia.

Introduction

Natural old growth forests represent the unique remains of original ecosystems and usually function as core areas in most ecological networks. They are identified as areas of high nature conservation value from the landscape ecology aspect. In Slovakia most primeval forests create a backbone of the existing nature reserve system and in the near future will be transformed into special areas of conservation (SAC) or special protection areas (SPA) meeting the criteria of NATURA

2000. Therefore, it is crucial to describe and analyze structure of these ecosystems for the management of other man made forest ecosystems and nature conservation aims.

Due to these reasons, the original fragments of close to primeval or natural forest were the subject of long term studies in the Western Carpathians for a long time. The first monitoring plots were set up by Prof. Dr. A. ZLATNÍK in the E Carpathians in the period 1935–1938 (VOLOŠČUK, 1998). Later, surveys of original representative forest ecosystems were conducted in order to establish a network of nature reserves (ZLATNÍK, 1959) that later become part of the ecological network system e.g. territorial systems of ecological stability, ECONET, etc. The nature reserves of the Malá Fatra National Park were also the subject of basic inventory surveys for nature conservation and also complex quantitative ecological studies (e.g. JANÍK & ŠTOLLMANN, 1981; KORŇAN, 1998a). During the 1990's rigorous quantitative inventory surveys were carried out in selected forest reserves in the national park to detect changes in ecosystem structure and evaluate the quality of previous studies and develop methodology for quantitative inventory surveys.

The Šrámková National Nature Reserve is considered to be the most valuable reserve in the national park from a forestry perspective. The reserve represents a W Carpathian beech-fir forest close to the primeval stage. In 1996, the reserve was selected as a model ecosystem to study complex ecological questions related to the organization and functioning of bird assemblages e.g. guild structure, resource partitioning, interspecific competition, ecomorphological patterns, habitat selection and population dynamics of birds under near primeval conditions. The results will also be utilized for nature conservation purposes to improve forest management practices.

The Šrámková Reserve has already been the subject of a cluster of ornithological and ecological studies (e.g. JANÍK, 1988; KORŇAN, 1998b, 2000, 2001, 2002; KORŇAN & ADAMÍK, 1999, in press; ADAMÍK et al., 2003). Most of the cited studies dealt with guild structure and resource partitioning except the older faunistic paper of JANÍK (1988) with simple quantitative analyses. This is the first paper based on the unpublished bird inventory surveys (KORŇAN, 2001, 2002) dealing with the analyses of bird community structure. The primary objectives of the present paper are as follows: (i) to analyze the quantitative structure of breeding bird assemblage censused by the mapping method over the five year period; (ii) to analyze population density, dominance, species diversity, and relationship between a number of species against the total number of breeding pairs (rarefaction curves) of the breeding bird assemblage; (iii) to add new data and contribute to the current knowledge of the breeding bird assemblage structure of mixed close to primeval forests in the W Carpathians; (iv) to review and evaluate previous bird inventory surveys in the reserve.

Study area

The study was conducted in the Šrámková National Nature Reserve, the Malá Fatra Mts (49°11′22″ N, 19°06′49″ E). The Malá Fatra Mts lie in NW Slovakia. The core zone of the reserve is spread over 243.65 ha. The investigation was carried out in a 27.5 ha (500 × 550 m) forest interior study plot representing the climax stage of a W Carpathian beech-fir forest growing on hillside granite waste. The forest has all the characteristic features of primeval stands, however, some plants species e.g. silver fir are negatively affected by air pollutants. The study plot is situated at the elevation of 825–1123 m a.s.l. (measured by the Magellan GPS ProMARK X). The reserve belongs to a cold mountain climatic zone with the mean July air temperatures 10–12 °C. Total mean annual precipitation varies between 900–1200 mm (VOLOŠČUK, 1986). The slope inclination is 20–60°.

The forest is uneven aged with considerable vertical and horizontal heterogeneity. All developmental stages of a primeval beech-fir forest occur in the study plot. The age of trees is approximately 200–250 years. Spatial structure of the developmental stages fits the Watt's 'gap phase' model, which explains the mechanisms behind the regeneration of climax forests. The original plant species composition has been preserved. The fitness of the silver fir population is significantly decreased by the emission of air pollutants. The study site is dominated by beech *Fagus sylvatica* L. (44.8%), silver fir *Abies alba* Mill. (20.2%), Norway spruce *Picea abies* (L.) Karst. (4.8%), sycamore *Acer pseudoplatanus* L. (4.3%), wych elm *Ulmus glabra* Huds. em. Moos (2.9%), and rowan *Sorbus aucuparia* L. emend. Hedl. (2.4%) with a mixture of other tree species such as, silver birch *Betula pendula* Roth, European larch *Larix decidua* Mill., Norway maple *Acer platanoides* L., and small-leaved lime *Tilia cordata* Miller. Standing dead trees reach dominance of 14.7%. The dominant tree species have strong regeneration. The canopy height is up to 45 m. The scrub layer mainly consists of hazel *Corylus avellana* L., red-berried elder *Sambucus racemosa* L., currant *Ribes* spp., and samplings of the dominant tree species. The herb layer is mainly composed of schott male ferns *Dryopteris filix-mas* (L.) Schott, lady-ferns *Athyrium filix-femina* (L.) Roth, forbs berries *Rubus* spp., Indian balsams *Impatiens glandulifera* Royle, rag worths *Senecio nemorensis* L., wood-sorrels *Oxalis acetosella* L., sweet woodruffs *Galium odoratum* (L.) Scop., coral-worts *Dentaria bulbi-*

fera L., perrenial honesties *Lunaria rediviva* L., purple colt's feet*Homogyne alpina* Cass., wood-rushes *Luzula nemorosa* (Poll.) E. Mey., small-reeds *Calamagrostis arundinacea* (L.) Roth., and small scrubs bilberries *Vaccinium myrtillus* L. A detailed description of the tree layer is given by KORŇAN (2000, 2002).

The selected study plot represents mainly the group of forest types *Fageto-Abietum* and *Fageto-Aceretum* sensu Zlatník forest phytosociological approach (VOLOŠČUK, 1986) that corresponds to the *Luzulo-Fagion* alliance, association *Abieti-Fageta* following the Braun-Blanquet classification system.

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 color plastic tape marking on tree trunks was established in the 27.5 ha rectangular study plot. Breeding bird censuses were carried out in the years 1997–2001 from April to mid-July. In total, 10–11 valid census visits per breeding season were performed in the time period beginning 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 two out of the total number of visits. At the beginning of April one night visit focused on owl registrations was carried out. The study design controlled the effects of weather and season on density estimates.

Each visit involved walking and mapping 100 m alternate grid lines beginning at one plot edge and ending on the opposite. The starting point and direction of observer movement were regularly changed so that census timing during the season was similar between different parts of the plot. The species name abbreviation system and mapping symbol system for bird activity followed KROPIL (1992). While censusing, all acoustic and visual observations, nests found or other important data relating to bird occurrence and dispersal patterns were recorded onto the visit maps at 1 : 1667 scale. Special attention was paid during census visits to contemporary contacts of territorial singing males so that the neighboring territories could be correctly distinguished. Some bird species e.g. *Turdus philomelos*, *Muscicapa striata*, *Certhia familiaris*, *Columba* ssp., *Pyrrhula pyrhulla*, and *Coccothraustes coccothraustes* caused considerable problems during the census and interpretational procedure. Censusing and the identification of territories on the species maps was based on the recommendations of NILSSON (1977), SVENSSON (1978, 1980), TOMIAŁOJĆ (1980, 1994), TOMIAŁOJĆ & LONTKOWSKI (1989), MOROZOV (1994), and KORŇAN (1996). In order to correctly identify the proportions of edge territories in the study plots, bird observations were recorded 100 m beyond the plot edge lines. Overlap of edge territories inside the study plot was estimated at 1/4 (25%), 1/3 (33%) or 1/2 (50%); however, only species with abundance equal to or higher then 0.5 pair per study plot were included in the total count of breeding pairs (territories). Further details regarding the mapping procedure and the principles of species map analyses are given in KORŇAN (1996).

Observations of individual species from visit maps were transferred to species maps beginning with the first species record in the plot. The criteria for territory interpretation were principally based on the IBCC (1969) recommendations. However, in the case of secretive species or species with poorly evolved territorial behaviour (discussed 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). Especially useful information on dispersal patterns of these species in the plot were gained during independent plot visits when foraging bird observations were recorded that were part of another study (KORŇAN, 1998b; ADAMÍK et al., 2003). In the case of species with abundance less than 0.5 pairs per plot, only breeding presence "+" denoting the stationary occurrence of a part of bird territory within the boundaries of the plot was recorded. This symbol was primarily used for species with territory sizes much larger than the study plot size such as some woodpeckers, owls, birds of prey, and corvids (TOMIAŁOJĆ, 1980; KORŇAN, 1996).

Statistical analyses

Bird community structure was analyzed on population abundance, density, species diversity, evenness, and species – area 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. It is the standard deviation divided by the mean ($CV = SD/\bar{x} \times 100$). Species with abundance lower that 0.5 pairs per study plot had a 0 value for the calculations of variation measures.

Species diversity and evenness were measured by three common formulae – Shannon diversity index (H') as an information theory measure, Simpson index (D) as a measure of concentration, and the Brillouin index (HB) (MAGURRAN, 1991). In addition, 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 ("+") in the computation of species diversity and evenness, constant numbers of densities (see Tab. 1 for the constant values) were added to these species. Similarity in structure of assemblages was measured by the qualitative Sörensen index and quantitative Czekanowski-Sörensen index (MAGURRAN, 1991). Species diversity indices and evenness were calculated using the PC statistical package NuCoSa 1.0 (TÓTHMÉRÉSZ, 1993). Variability measures, assemblage similarity indices, rarefaction values and curves were determined using MS Excel.

Only the mathematical formulae for the calculation of general evenness and rarefaction are presented further:

Evenness (equitability):

$$E = \frac{DIV}{DIV_{max}}$$

where: DIV – species diversity measured according to Shannon, Simpson, or Brillouin formulas, DIV_{max} – maximal theoretical value of these indices.

Rarefaction (James & Rathbun, 1981):

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

where: $E(Sn)$ is an expected number of species in a random sample of n individuals drawn without replacement from N individuals, 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

In total, 57 bird species were recorded within the Šrámková National Nature Reserve during the period 1997–2001 (Tabs 1, 3). The mean number of species occurring in the study site was 47.60. The maximum number, 50 species, was found in 1998, while the minimum number, 45 species, was found in 2000. Altogether, 52 breeding species were detected during the studied period in the reserve. The mean number of breeding species in the reserve was 42. The highest number, 45 species, was detected in 1998, whereas the lowest number, 40 species, was detected in 2000. 57 recorded species belonged to 9 orders according to the morphological systematics as follows: Falconiformes – 4 species (7.02%), Galliformes – 2 species (3.51%), Charadriiformes – 1 species (1.75%), Columbiformes – 2 species (3.51%), Cuculiformes – 1 species (1.75%), Strigiformes – 2 species (3.51%), Apodiformes – 1 species (1.75%), Piciformes – 5 species (8.77%), and Passeriformes – 39 species (68.42%).

In the 27.5 ha study, there were a total of 48 breeding species. The mean number of species was 38.80. The maximum number, 42 species, of breeders was found in 1999, while the minimum number, 37 species, were detected in 1997 and 2000 (Tabs 1, 3). Thirty (62.50%) breeders were present in every year. Other 6 species (in total, 36 species: 75.00%) bred in at least three years during the five-year period. *Carduelis spinus* was detected during the breeding season, usually from the end of May, however breeding was assumed only in 1999 when a stationary singing male was recorded several times in one location. However, the possibility of breeding cannot be excluded in other years. Also, recording inconspicuous *Nucifraga caryocatactes* caused serious problems due to poorly evolved territorial behavior.

The similarity of species structure between individual years was compared by the qualitative Sörensen index and quantitative Czekanowski–Sörensen index. The qualitative Sörensen index reached values 0.84–0.95. The lowest species similarity was found between years 1997 and 1999, and the highest similarity level was found between years 2000 and 2001 (Tab. 2). The Czekanowki–Sörensen index reached values 0.79–0.88. The lowest value was found between 1997 and 2001, whereas the assemblages in 1999–2000 and 2000–2001 reached the highest levels of similarity (Tab. 2). Similarity measurements indicated very low between year variability of the assemblage from qualitative and quantitative species structure. Thus, the studied community seems to be very stable regarding species structure.

Density and dominance

The mean total density was 58.17 BP/10 ha. Standard deviation (3.60) and coefficient of variation (6.18%) values were relatively small indicating very low between year variability in total density of the assemblage. The assemblage reached the highest total density, 61.20 BP/10 ha, in the year 2000, the lowest total density, 52.15 BP/10 ha, was detected in 1997 (Tab. 1).

Dominant species ($\geq$ 5%) contributed between 51.33–63.46% to the total assemblage dominance. On average, these seven species contributed 59.44% to total dominance using pooled data. All of these species reached a higher population density than 2.5 BP/10 ha. The highest values of density and dominance were reached by *Fringilla coelebs* in every year. Its dominance slightly exceeded 20% of the total assemblage dominance during the study period. Based on the pooled data, *Erithacus rubecula*, *Parus ater*, *Sylvia atricapilla*, *Regulus regulus*, *Phylloscopus collybita*, and *Prunella modularis* were dominant species. From this group, only *Erithacus rubecula* was dominant every year. The remaining species were not dominant in at least one year. In 1997, *Ficedula albicollis* was also a dominant species. This is generally an effect of population dynamics

Table 1. Year and mean abundance, density, and dominance of the breeding bird assemblage of a primaeval beech-fir forest in the Šrámková National Nature Reserve.

Species	Abundance					Density (pairs/10 ha)						Dominance (%)						SD	CV
	1997	1998	1999	2000	2001	1997	1998	1999	2000	2001	$\bar{x}$	1997	1998	1999	2000	2001	$\bar{x}$		(%)
Fringilla coelebs L., 1758	25.7	25.6	34.3	35.7	34.5	9.35	9.31	12.47	12.98	12.55	11.33	17.92	15.79	21.50	21.21	20.72	19.48	1.84	16.23
Erithacus rubecula (L., 1758)	10.7	14.5	15.6	16.2	11.2	3.89	5.27	5.67	5.89	4.07	4.96	7.46	8.95	9.78	9.63	6.73	8.53	0.92	18.59
Sylvia atricapilla (L., 1758)	8.7	7.6	12.4	15.9	14.0	3.16	2.76	4.51	5.78	5.09	4.26	6.07	4.69	7.77	9.45	8.41	7.33	1.28	29.93
Parus ater L., 1758	13.5	15.3	7.0	8.8	10.0	4.91	5.56	2.55	3.20	3.64	3.97	9.41	9.44	4.39	5.23	6.01	6.83	1.24	31.24
Phylloscopus collybita (Vieillost, 1817)	7.1	9.8	10.3	11.5	10.6	2.58	3.56	3.75	4.18	3.85	3.59	4.95	6.05	6.46	6.83	6.37	6.16	0.60	16.86
Regulus regulus (L., 1758)	8.0	11.1	9.3	9.7	9.3	2.91	4.04	3.38	3.53	3.38	3.45	5.58	6.85	5.83	5.76	5.59	5.93	0.40	11.71
Prunella modularis (L., 1758)	6.7	8.8	7.5	9.0	9.5	2.44	3.20	2.73	3.27	3.45	3.02	4.67	5.43	4.70	5.35	5.71	5.19	0.42	13.97
Ficedula albicollis (Temminck, 1815)	7.5	6.9	5.3	6.3	6.0	2.73	2.51	1.93	2.29	2.18	2.33	5.23	4.26	3.32	3.74	3.60	4.00	0.31	13.17
Certhia familiaris L., 1758	6.4	4.9	5.7	7.8	7.0	2.33	1.78	2.07	2.84	2.55	2.31	4.46	3.02	3.57	4.63	4.20	3.98	0.41	17.67
Columba palumbus L., 1758	6.9	7.0	7.3	6.5	2.0	2.51	2.55	2.65	2.36	0.73	2.16	4.81	4.32	4.58	3.86	1.20	3.71	0.81	37.39
Columba oenas L., 1758	5.3	3.0	3.5	5.0	11.0	1.93	1.09	1.27	1.82	4.00	2.02	3.70	1.85	2.19	2.97	6.61	3.48	1.16	57.42
Troglodytes troglodytes (L., 1758)	4.5	5.9	5.0	6.0	6.4	1.64	2.15	1.82	2.18	2.33	2.02	3.14	3.64	3.13	3.57	3.84	3.48	0.28	14.08
Turdus merula L., 1758	4.5	4.5	3.5	3.6	6.2	1.64	1.64	1.27	1.31	2.25	1.62	3.14	2.78	2.19	2.14	3.72	2.79	0.39	24.28
Turdus philomelos Brehm, 1831	1.8	5.5	3.2	4.8	4.7	0.65	2.00	1.16	1.75	1.71	1.45	1.26	3.39	2.01	2.85	2.82	2.50	0.54	37.21
Phylloscopus sibilatrix (Bechstein, 1793)	4.7	4.0	4.3	1.0	4.5	1.71	1.45	1.56	0.36	1.64	1.35	3.28	2.47	2.70	0.59	2.70	2.31	0.56	41.39
Sitta europaea L., 1758	1.8	4.0	2.8	4.0	5.6	0.65	1.45	1.02	1.45	2.04	1.32	1.26	2.47	1.75	2.38	3.36	2.28	0.52	39.32
Pyrrhula pyrrhula (L., 1758)	3.3	4.5	2.0	1.0	1.0	1.20	1.64	0.73	0.36	0.36	0.86	2.30	2.78	1.25	0.59	0.60	1.48	0.55	64.58
Muscicapa striata (Pallas, 1764)	3.0	3.0	3.8	o+	0.5	1.09	1.09	1.38	{0.1}	0.18	0.75	2.09	1.85	2.38	0.00	0.30	1.29	0.62	82.21
Ficedula parva (Bechstein, 1794)	3.5	1.0	1.5	2.5	1.5	1.27	0.36	0.55	0.91	0.55	0.73	2.44	0.62	0.94	1.49	0.90	1.25	0.36	50.00
Coccothraustes coccothraustes (L., 1758)	2.0	1.0	3.0	2.0	0.5	0.73	0.36	1.09	0.73	0.18	0.62	1.39	0.62	1.88	1.19	0.30	1.06	0.35	57.33
Turdus viscivorus L., 1758	1.8	2.0	1.0	2.0	1.0	0.65	0.73	0.36	0.73	0.36	0.57	1.26	1.23	0.63	1.19	0.60	0.98	0.19	33.19
Turdus torquatus L., 1758	+	2.4	1.5	1.0	1.3	{0.1}	0.87	0.55	0.36	0.47	0.45	0.00	1.48	0.94	0.59	0.78	0.78	0.32	69.98
Phylloscopus trochilus (L., 1758)	+	1.8	2.2	0.5	1.3	{0.1}	0.65	0.80	0.18	0.47	0.42	0.00	1.11	1.38	0.30	0.78	0.73	0.33	78.21
Parus palustris L., 1758	1.0	1.0	1.0	1.5	1.3	0.36	0.36	0.36	0.55	0.47	0.42	0.70	0.62	0.63	0.89	0.78	0.73	0.08	19.85
Dendrocopos leucotos (Bechstein, 1803)	1.0	0.5	0.8	1.5	0.8	0.36	0.18	0.29	0.55	0.29	0.33	0.70	0.31	0.50	0.89	0.48	0.58	0.13	40.23
Motacilla cinerea Tunstall, 1771	1.0	1.0	1.0	1.0	0.5	0.36	0.36	0.36	0.36	0.18	0.33	0.70	0.62	0.63	0.59	0.30	0.56	0.08	24.85
Regulus ignicapillus (Temminck, 1820)	—	1.0	1.5	1.0	1.0	0.00	0.36	0.55	0.36	0.36	0.33	0.00	0.62	0.94	0.59	0.60	0.56	0.20	60.86
Picoides tridactylus (L., 1758)	0.5	2.0	+	1.0	1.0	0.18	0.73	{0.1}	0.36	0.36	0.33	0.35	1.23	0.00	0.59	0.60	0.56	0.27	82.40
Scolopax rusticola L., 1758	1.0	1.0	p	p	p	0.36	0.36	0.00	0.00	0.00	0.15	0.70	0.62	0.00	0.00	0.00	0.25	0.20	136.93
Loxia curvirostra L., 1758	—	p	1.0	p	1.0	0.00	0.00	0.36	0.00	0.36	0.15	0.00	0.00	0.63	0.00	0.60	0.25	0.20	136.93
Aegithalos caudatus (L., 1758)	0.5	—	†0.25	+	0.8	0.18	0.00	0.09	{0.1}	0.29	0.11	0.35	0.00	0.16	0.00	0.48	0.19	0.12	110.81
Bonasa bonasia (L., 1758)	—	1.0	+	+	0.5	0.00	0.36	{0.1}	{0.1}	0.18	0.11	0.00	0.62	0.00	0.00	0.30	0.19	0.16	149.07
Parus major L., 1758	—	—	0.5	1.0	—	0.00	0.00	0.18	0.36	0.00	0.11	0.00	0.00	0.31	0.59	0.00	0.19	0.16	149.07
Dendrocopos major (L., 1758)	1.0	+	—	—	o+	0.36	{0.1}	0.00	0.00	{0.05}	0.07	0.70	0.00	0.00	0.00	0.00	0.13	0.16	223.61

Table 1. (continued)

Species	Abundance					Density (pairs/10 ha)						Dominance (%)						SD	CV
	1997	1998	1999	2000	2001	1997	1998	1999	2000	2001	$\bar{x}$	1997	1998	1999	2000	2001	$\bar{x}$		(%)
Anthus trivialis (L., 1758)	—	+	0.5	0.5	+	0.00	{0.1}	0.18	0.18	{0.1}	0.07	0.00	0.00	0.31	0.30	0.00	0.13	0.10	136.93
Cuculus canorus L., 1758	+	+	0.5	+	+	{0.1}	{0.1}	0.18	{0.1}	{0.1}	0.04	0.00	0.00	0.31	0.00	0.00	0.06	0.08	223.61
Parus caeruleus L., 1758	—	0.5	—	—	o+	0.00	0.18	0.00	0.00	{0.05}	0.04	0.00	0.31	0.00	0.00	0.00	0.06	0.08	223.61
Carduelis spinus (L., 1758)	p	p	0.5	p	p	0.00	0.00	0.18	0.00	0.00	0.04	0.00	0.00	0.31	0.00	0.00	0.06	0.08	223.61
Accipiter gentilis (L., 1758)	+	+	+	+	+	{0.004}	{0.004}	{0.004}	{0.004}	{0.004}	—	—	—	—	—	—	—	—	—
Dryocopus martius (L., 1758)	+	+	+	+	+	{0.1}	{0.1}	{0.1}	{0.1}	{0.1}	—	—	—	—	—	—	—	—	—
Garrulus glandarius (L., 1758)	+	+	+	+	+	{0.1}	{0.1}	{0.1}	{0.1}	{0.1}	—	—	—	—	—	—	—	—	—
Aquila chrysaëtos (L., 1758)	p	+	+	+	+	0.00	{0.001}	{0.001}	{0.001}	{0.001}	—	—	—	—	—	—	—	—	—
Cinclus cinclus (L., 1758)	+	+	p	+	+	{0.1}	{0.1}	0.00	{0.1}	{0.1}	—	—	—	—	—	—	—	—	—
Glaucidium passerinum (L., 1758)	+	p	+	o+	—	{0.05}	0.00	{0.05}	{0.05}	0.00	—	—	—	—	—	—	—	—	—
Buteo buteo (L., 1758)	+	—	—	—	p	{0.004}	0.00	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Pernis apivorus (L., 1758)	—	—	+	—	—	0.00	0.00	{0.004}	0.00	0.00	—	—	—	—	—	—	—	—	—
Strix aluco L., 1758	—	o+	+	o+	—	0.00	{0.01}	{0.01}	{0.01}	0.00	—	—	—	—	—	—	—	—	—
Nucifraga caryocatactes (L., 1758)	o+	o+	o+	—	+	{0.1}	{0.1}	{0.1}	0.00	{0.1}	—	—	—	—	—	—	—	—	—
Corvus corone cornix L., 1758	o+	o+	—	—	—	{0.05}	{0.05}	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Parus cristatus L., 1758	—	o+	—	—	—	0.00	{0.05}	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Picus canus Gmelin, 1788	o+	o+	—	—	p	{0.1}	{0.1}	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Pheonicurus pheonicurus (L., 1758)	o+	o+	—	—	—	{0.1}	{0.1}	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Delichon urbica (L., 1758)	p	p	p	p	p	0.00	0.00	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Tetrao urogallus L., 1758	p	p	p	p	p	0.00	0.00	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Corvus corax L., 1758	p	—	—	—	p	0.00	0.00	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Parus montanus Baldenstein, 1827	p	—	—	—	—	0.00	0.00	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Apus apus (L., 1758)	—	—	p	—	—	0.00	0.00	0.00	0.00	0.00	—	—	—	—	—	—	—	—	—
Total	143.4	162.1	159.55	168.3	166.5	52.15	58.95	58.02	61.20	60.55	58.17	100.00	100.00	100.00	100.00	100.00	100.00	3.60	6.18

Key: SD – standard deviation, CV – coefficient of variation. Mark plus sing ("+") indicates breeding abundance less the 0.5 territory (pair) per study plot; mark "o+" indicates breeding presence in the reserve, but the species was not detected as breeder in the study plot; mark "p" is used for species detected in the study plot as none breeders or rare visitors; mark "—" indicates absence. In the density columns, density estimates for "+" and "o+" species are given by qualified guess based on observations in the reserve and the national park. The density estimates in parenthesis {} were only roughly estimated for calculation of diversity indices and rarefaction of the assemblage. †Polygamous pair, three adult birds.

– fluctuations and population declines in individual populations.

In total, nine species were subdominant (2% ≤ 5% <) and represented 28.52% of the total assemblage using the pooled data. Their mean population density was higher than 1.5 BP/ 10 ha and less than 2.5 BP/ 10 ha. Recendent species (1% ≤ 2% <) constituted 5.08% of the assemblage. In total, four species represented this group. Population density usually varied between 0.60–1.50 BP/10 ha. The highest number of species, 28, was found for the group of subrecedents (< 1%), yet represented only 6.97% of the total dominance. All species reached mean population densities lower than 0.60 BP/10 ha. Another four species, *Picus canus*, *Parus cristatus*, *Pheonicurus pheonicurus*, and *Corvus corone cornix*, that would belong to this group bred outside the study plot. The highest level of between year variation in species breeding presence in the study plot occurred in this group. Ten species bred only in three or fewer years in the study plot during the time period (Tab. 1).

Diversity and evenness

Standard diversity indices such as Shannon, Simpson, and Brillouin were applied to estimate species diversity and evenness. These indices were selected for comparative purposes with previous studies where they have been widely used in community ecology studies for many decades. However, several authors (e.g. HURLBERT, 1971; JAMES & RATHBUN, 1981) concluded that most of these commonly used measures of biological diversity, including information theory based indices, are in many situations inappropriately used as indicators of biological diversity. Moreover, their application involves a significant loss of information because indices confound several community parameters e.g. number of species, their relative abundance, and area sampled into one non-metric number. In summary, differences attributable to the accumulation of species with increasing area are ignored, and many combination of species richness and relative abundance can produce the same value of the index (JAMES & RATHBUN, 1981). One of the

Table 2. Between year comparison of the bird assemblage similarity in species structure by qualitative Sörensen index and density structure by Czekanowski-Sörensen indicex. Only breeding species recorded in the study plot were included to the analyses.

Similarity indices Sörensen	Czekanowski-Sörensen 1997	1998	1999	2000	2001
1997	—	0.86	0.82	0.80	0.79
1998	0.89	—	0.84	0.82	0.81
1999	0.84	0.86	—	0.88	0.86
2000	0.86	0.92	0.91	—	0.88
2001	0.87	0.92	0.93	0.95	—

Table 3. Estimates of bird species diversity and evenness of the beech-fir primeval forest in the Šrámková National Nature Reserve by standard indices and rarefaction. Only breeding species recorded in the study plot were included to diversity calculations.

	1997	1998	1999	2000	2001	Mean	SD	CV
Diversity measures								
Total number of species	47	50	48	45	48	47.60	1.93	4.06
Total number of breeders	41	45	43	40	41	42.00	2.13	5.07
Number of breeders in plot	37	39	42	37	39	38.80	2.18	5.62
Shannon (H')	4.27	4.36	4.25	4.10	4.15	4.23	0.11	2.58
Brillouin (HB)	3.85	3.95	3.83	3.73	3.78	3.83	0.09	2.30
Simpson (D)	0.93	0.93	0.92	0.91	0.92	0.92	0.01	0.97
Rarefaction E ($S_{50\,\mathrm{pairs}}$)	19.39	20.00	19.48	18.08	18.27	19.04	0.88	4.63
Rarefaction E ($S_{100\,\mathrm{pairs}}$)	24.02	25.16	24.93	22.77	22.90	23.96	1.18	4.93
Rarefaction E ($S_{5\,\mathrm{ha}}$)	14.44	15.63	15.03	14.47	14.71	14.86	0.52	3.53
Rarefaction E ($S_{10\,\mathrm{ha}}$)	19.67	21.30	20.70	19.46	19.62	20.15	0.86	4.27
Evenness measures								
Evenness Shannon (J')	0.82	0.82	0.78	0.79	0.79	0.80	0.02	2.49
Evenness Brillouin (E_{HB})	0.83	0.83	0.79	0.80	0.80	0.81	0.02	2.46
Evenness Simpson (E_D)	0.95	0.88	0.94	0.94	0.94	0.93	0.03	3.24

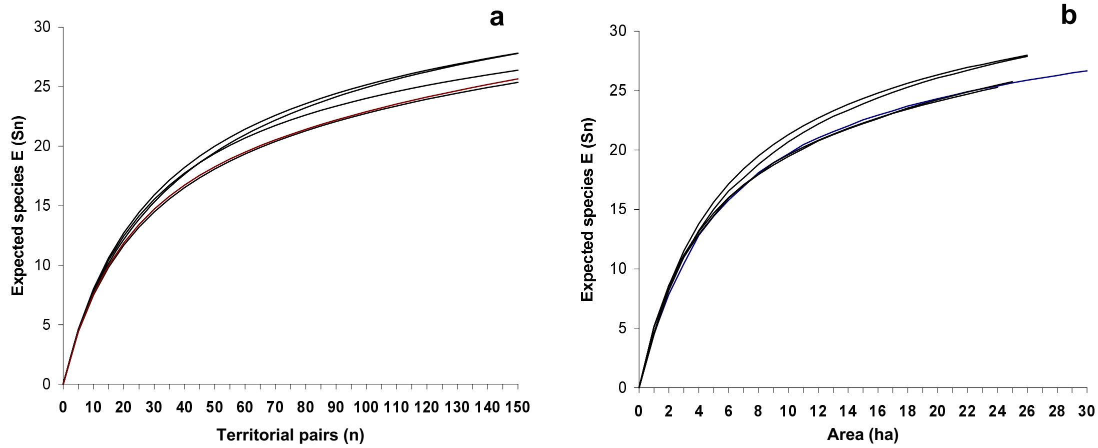

Fig. 1. Rarefaction curves for five year samples of the 27.5 ha beech-fir interior plot in the Šrámková National Nature Reserve predict the rate of species accumulation with increasing number of territorial pairs (graph a) and area (graph b). The calculations are based on the year abundance data.

alternatives to overcome this problem is the application of rarefaction (Hurlbert, 1971; Heck et al., 1975). In this study, rarefaction was applied in order to compare between seasonal species richness by standardizing samples to an equal number of individuals and equal-sized plots (Tab. 3). The relationship between expected number of species and increasing number of pairs and area was analyzed (Figs 1a, b). Evenness was expressed by a graph of species densities in a decreasing way (Fig. 2).

Values of all diversity indices were very stable (Tab. 3). Standard deviation values were close to zero. The Shannon diversity index reached a mean value 4.23. The Shannon index values varied between 4.10–4.36 bites. No significant differences were found between year comparisons. The mean value of the Brillouin diversity index was 3.83. The values varied between 3.73–3.95. This index had a similar trend as the Shannon index (Tab. 3). The values of Simpson diversity index were the most regular, mean 0.92, variation 0.91–0.93. Evenness indices were also very stable. The mean values were as follows: Shannon – 0.80, Simpson – 0.93, Brillouin – 0.81. Evenness values based on the Shannon and Brillouin diversity indices had similar trends. There were only very slight differences between years in Simpson evenness numbers. The high temporal stability in the values of diversity measures indicates a high stability of species structure of the ecosystem as well as the relative abundance of species. Similar values were estimated in other structurally similar W Carpathian close to primeval mixed forests (see Discussion).

Rarefaction species-individual and species-area curves are shown in the Figs 1a, b. The mean expected number of species per 50 pairs was 19.04 ± 0.88 species (Tab. 3). On a random sample of 100 pairs, it was 23.96 ± 1.18 species. Rarefaction $E(S_{100\,\mathrm{pairs}})$ values varied between 22.77–25.16. Values had different trends for each standardized number of pairs. The mean number of expected species on the standardized area of 5 ha was 14.86 ± 0.52 species, on an area of 10 ha, it was 20.15 ± 0.86 species. The number of expected species on the area of 5 ha varied between 14.44–15.63 species, the variation on the area of 10 ha was 19.46–21.30 species. The highest species diversity estimated by all diversity measures was found in 1998, the lowest diversity was detected in the year 2000 also by all diversity measures except the rarefaction on a standardized area of 5 ha. All evenness measures detected the highest values in 1997, whereas the lowest values were in 1999 except the Simpson evenness.

Discussion

Assemblage structure and diversity

The first quantitative studies of forest bird assemblages in Slovakia were published in the first half of 1950's. The main impetus to quantitative community ecology came from the work of the Slovak ecologist F. J. Turček and his colleagues. Turček (1952) developed his own time-quadrat method to study bird assemblage in natural groups of forest types *Fagetum typicum* and *Piceetum typicum* (GFT sensu Zlatník, 1959) in the Poľana Mts.

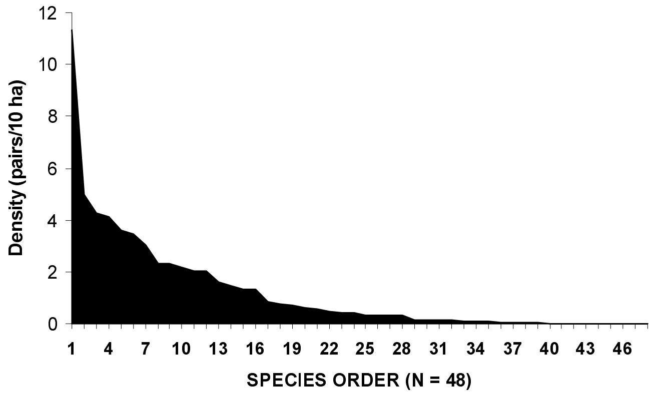

Fig. 2. Community curve of the breeding bird assemblage of the primeval beech-fir forest in the Šrámková National Nature Reserve. Pooled data from the period 1997–2001 were used. Species are ranked in descending order.

The author analyzed the density, biomass, foraging groups (guilds), and distribution of species in vertical strata in the forest. The study had a very progressive design and was ahead of its time in many aspects. The author, more than 14 years before the official principles of the concept of ecological guilds (ROOT, 1967) were formulated, had thought about functional groups of species with similar foraging requirements, feeding habits and behavior, and preferred stratum of food consumption. To date, most studies have dealt with various analyses of broadleaf forest assemblages. Relatively few studies have been focused on analyses of bird assemblages of mixed forests. Most studies are still not comparable with the present study due to differences in survey methodology, habitat classification, and study objectives. FERIANCOVÁ-MASÁROVÁ (1968, 1971, 1978) described the qualitative structure of bird assemblages of all main habitats on a regional scale in Liptov. The author also studied assemblages of mixed forest; however, due to differences in the habitat classification scheme it is not possible to compare the results because mixed forests were grouped with coniferous forests into one habitat category. FERIANCOVÁ-MASÁROVÁ et al. (1987) analyzed bird assemblages of the GFT *Fageto-quercetum* with a mixture of spruce and fir in the Sitno National Nature Reserve, the Štiavnické vrchy Protected Landscape Area. Unfortunately, only combined results for all habitat types in the reserve were presented. Consequently, it is not possible to extract data for individual habitats and compare them with the present study. TOPERCER (1989) studied the quantitative structure of breeding bird assemblages of four habitats in the Skalná alpa National Nature Reserve, the Veľká Fatra Mts, using a belt transect method. He found a total of 14 species in the total breeding bird density of 62.86 ex./10 ha (31.43 BP/10 ha) in a 200–240 year old mixed forest (GFT *Abieti-fageta superiora*). Species structure as well as population densities of individual species seem to be underestimated for all species except the chiffchaff *Phylloscopus collybita*. This species is conspicuous, sings throughout the day, and can be easily mapped with high accuracy (TIAINEN & BASTIAN, 1983). Underestimation may have been primarily caused by only two visits to the study site in one year and the differences in census methodology. The author combined three census techniques for estimating population densities (mapping method, point count, and belt transect).

Breeding bird assemblages in the Šrámková National Nature Reserve were studied using a transect method by JANÍK (1988) between 1982-84. The author studied bird assemblages in three habitat types: beech-fir and beech-sycamore forests, and meadow gaps. In the beech-fir stand, the author found a total of 34 species at the density of 489 ex./100 ha (24.45 BP/10 ha). The beech-sycamore stand had only 26 species at the total density of 520 ex./100 ha (26.00 BP/10 ha). The data appears to significantly underestimate species richness, and also the mean assemblage as well as individual population densities. The mean assemblage densities are approximately half of the values presented in this paper. In addition, common breeders such as the collared flycatcher *Ficedula albicollis*, mistle thrush *Turdus viscivorus*, firecrest *Regulus ingicapileus*, grey wagtail *Motacilla cinerea*, dipper *Cinclus cinclus*, were not detected in any habitat or were considered "rare breeders" e.g. the stock dove *Columba oenas*. In contrast, others species, for instance the fieldfare *Turdus pilaris* and whitethroat *Sylvia communis* were recorded as common breeders in forest stands. The garden warbler *Sylvia borin* was concluded to be a rare breeder in forest habitats. The most surprising "discovery" is the assessment of *Prunella collaris* as a rare breeder in the meadow gaps. These conclusions, the results, and methodological design of the study are misleading, and the interpretation of species occurrence patterns is questionable. The errors may have been caused by a low number of visits to the study site or more probably poor skills in identification of birds (e.g. *T. pilaris* versus *T. viscivorus*). The occurrence of the grey wagtail *Motacilla cinerea* and dipper *Cinclus cinclus* in the Šrámková forest was ecologically dependent on a stream habitat. Streams did not run through the plots analyzed below, thus the occurrence of these two species will not be discussed in further comparisons.

SANIGA (1994, 1995) studied breeding bird assemblages of vegetation belts in the Malá Fatra and Veľká Fatra Mts in 1989–1991 by a strip transect method. Saniga conducted censuses in transects with a total length of 3,300 m in the fir-beech belt located in two reserves. The total length of transects used for description of the spruce-beech-fir vegetation tier was 10,400 m located in six reserves. He found a total of 57 breeding species at the mean density of 75.7 BP/10 ha in fir-beech and 59 species at the mean density of 60.2 BP/10 ha in spruce-beech-fir vegetation tiers. The mean total assemblage density of spruce-beech-fir tier was not significantly different to the Šrámková forest. The Shannon diversity index was 4.46 for the fir-beech tier and 4.33 for the spruce-beech-fir tier. Surprisingly, population densities and dominance of the most abundant species are very similar to the results from the Šrámková forest, even though the study was carried out by the relative quantitative method. The occurrence of the garden warbler *Sylvia borin* and lesser whitethroat *Sylvia curruca* in the fir-beech belt, and the bramling *Fringilla montifringilla* in the spruce-beech-fir belt deviates from results in other old growth forest stands of this type in Slovakia (KROPIL, 1996a, b). Both silviid warblers were found by GŁOWACIŃSKI & PROFUS (1992) in an old-growth beech-fir stand in the Tatry Mts in Poland. Slightly higher species richness and diversity is probably due to the very large sample sizes.

Due to a high variation in population estimates produced by different quantitative methods, only mapping method studies are taken into consideration for further comparisons. Mixed primeval forests were studied on the Slovak side of the W Carpathians by KROPIL (1993, 1996a, b). KROPIL described the structure of breeding bird assemblages in the Dobroč and Badín primeval forest National Nature Reserves over a three-year period. In total, 44 species were found in a 24 ha plot in the Dobroč forest, and 42 species in a 16 ha plot in the Badín forest. The mean number of species per year in the Dobroč forest was 36, with a range 35–37. In Badín forest the mean number of species was 36, with a range 34–38. There were no significant differences in diversity estimated by the Shannon formula between year comparison of these two stands (KORŇAN, 2001). However, all Badín samples had significantly higher diversity in comparison to the Šrámková samples. The total mean density of the assemblage in the Dobroč stand (62.6 BP/10 ha) was not different from the Šrámková forest or the spruce-beech-fir tier described by Saniga (see above). The Badín stand had higher total assemblage densities – 71.0 BP/10 ha. The species structure of the Dobroč reserve was very similar to the Šrámková reserve. Eliminating raptors and large corvids, trace species with less than 0.5 territory per study plot, the only difference was in regular breeding of the willow tit *Parus montanus* and crested tit *Parus cristatus* that could be related to the presence of conifers. The crested tit *Parus cristatus* bred in Šrámková forest only in 1998 on the border of the reserve with a spruce plantation. This difference can be a result of the higher relative proportion of coniferous trees in the Dobroč forest (KROPIL, 1996a) in comparison to Šrámková forest (KORŇAN, 2000), 53% to 25%. The willow warbler *Phylloscopus trochilus*, long-tailed tit *Aegithalos caudatus*, and tree pipit *Anthus trivialis* were absent, but were regular nesters in the Šrámková forest. The occurrence of the latter two species was a result of large gaps created by a tornado in the early spring of 1998. As the result of increased heterogeneity of the forest interior, the tree pipit *A. trivialis* began breeding regularly and the willow warbler *Ph. trochilus* have increased population densities since 1998. Both species positioned their territories in the gaps or on their edges. Density and dominance values of most species were similar in both forests. The highest difference in population densities was found for the collared flycatcher *Ficedula albicollis.* Its population density (0.2 versus 2.33 BP/10 ha) in Šrámková was approximately 11 times higher than in the Dobroč forest. In contrast, the population density of this species was almost twice the size in the Badín forest compared to the Šrámková Reserve. The blackcap *Sylvia atricapilla* and chiffchaff *Phylloscopus collybita* also had higher densities in the Šrámková plot. Species structure of the Badín forest bird assemblage was even more similar. The lesser spotted woodpecker

Dendrocopus minor and willow tit *P. montanus* were absent in the Šrámková forest, but the willow warbler *Ph. trochilus*, ring ouzel *Turdus torquatus*, and firecrest *Regulus ignicapillus* were absent in the Badín forest, and the goldcrest *R. regulus* reached only very low population densities. Badín forest is typical for high breeding densities of the stock dove *Columba oenas*. It had almost three times higher population densities in comparison to the Šrámková or Dobroč forest. These differences can also be attributed to a lower proportion of coniferous trees, approximately 18%, and a lower altitude (720–760 m) of the study site in comparison to the Šrámková or Dobroč forests (720–1000 m). In addition, further variation in species structure and population densities can be attributed to different vertical and horizontal heterogeneity of the studied areas (Adamík et al., 2003). The Šramková Reserve represents an ecosystem in a mosaic state of several developmental stages, from the stage of early growing to the late developmental stages that create a very wide resource space supporting a wide range of species from floristic specialists to generalists as well as structural specialist to generalists. Presumably, the specific quantitative structure of floristic parameters in combination with structural parameters reflected in each developmental stage creating a complex mosaic spatial structure on a local scale effects the final structure of the community composition.

Pavelka & Pavelka (1990) studied three primeval beech-fir stands (Razula, Salajka, and Kutavý), the Moravskoslezské Beskydy Mts, for a period 6–7 years. The size of the study plots varied from 14.9–23.2 ha. The total number of species was 29–33, and was generally lower in comparison to the Slovak plots. Species structure was most similar to the Šrámková forest, only four breeders, the willow tit *Parus montanus*, swift *Apus apus*, pied flycatcher *Ficedula hypoleuca*, and starling *Sturnus vulgaris* did not occur in the Šrámková forest. The redstart *Phoenicurus phoenicurus* was a subrecendent species in two plots. Mean density from the three plots varied between 45.5–51.6 BP/10 ha, however, between year variation was stronger 41–61 BP/10 ha.

Głowaciński & Profus (1992) studied 100–200 year old beech-fir forest in the Strazyska Valley, the Polish Tatry National Park, during 1981–1982. They found a total of 38 species in a 10 ha study plot with the overall assemblage density of 68.2 BP/10 ha. Number of species varied between 29–35. Species composition was the most distinctive in comparison to the three Slovak plots, but the population densities of most of the species were similar apart from the robin *E. rubecula* and wood warbler *Ph. sibilatrix* having higher numbers and blackcap *S. atricapilla* lower number. The garden warbler *Sylvia borin*, lesser whitethroat *S. curruca*, greenfinch *Carduelis chloris*, pied flycatcher *Ficedula hypoleuca*, and fieldfare *Turdus pilaris* were listed, but some typical species such as the woodpigeon *Columba palumbus*, white-backed woodpecker *Dendrocopus leucotos*, collared flycatcher *Ficedula albicollis* and marsh tit *Parus palustis* found in this type of habitat in Slovakia were not recorded. The occurrence of silviid warblers and green finch could have been an effect of the forest edge, a fragmented forest patch, also causing increased species diversity in a relatively small plot.

Schaffner (1990) found only 28 species in a 70 ha plot located in *Abieti-Fagetum* natural forest reserve, the Swiss Jura Mts, during a one year study. The total mean breeding assemblage density was slightly higher in comparison to the Šrámková and Dobroč Reserves.

Storch & Kotecký (1999) meta-analysed 133 breeding bird assemblages of all habitat types (woods, clearings, steppe, open mosaic, reed, and urban habitats) from published quantitative data in the Czech Republic. They applied canonical correspondence analysis to study the effects of habitat, census techniques, and area on the general patterns of bird assemblages. Assemblage structure was measured in terms of species richness, index of dominance, and evenness. In summary, lower species richness was detected for mixed forests ($n = 14$, 25.57 ± 5.12) in comparison to deciduous forests ($n = 35$, 26.60 ± 9.10), but was higher in comparison to coniferous forests ($n = 16$, 19.31 ± 14.58). A similar pattern has been found in North American studies (James & Rathbun, 1981; James & Wamer, 1982). This pattern is, however, questionable because primary data were not rarefactioned, so the strong effects of plot size on species richness could have major effects on the final patterns and conclusions (see Results: Diversity and evenness). In contrast, Kropil (1993) detected the highest species richness in mixed primeval forests in comparison to deciduous or coniferous primeval stands. Korňan (1996) analyzed his own and Kropil's data by rarefaction and did not find a clear pattern of species richness between mixed and deciduous forests.

Acknowledgements

I wish many thanks to the Administration of the Malá Fatra National Park and the State Nature Conservancy of the Slovak Republlic for supporting this research. I also would like to express my big, "Thank you!" to I. Krno for leading my doctoral project, patience, consultations, support, and all the help. I also gratefully acknowledge the valuable field help under extreme conditions of the national park rangers, namely M. Fillo, M. Majda, Š. Bobocký, and volunteers J. Sečník, M. Bušovský, A. Bartakovics, and T. Derka for their strenuous work and understanding during study spot marking and vegetation measurements.

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Received January 15, 2003
Accepted April 10, 2003