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STRUCTURE AND VERTICAL DISTRIBUTION OF THE BREEDING BIRD COMMUNITIES IN THE POLISH TATRA NATIONAL PARK

STRUKTURA I WYSOKOŚCIOWE ROZMIESZCZENIE LĘGOWYCH ZESPOŁÓW PTAKÓW W POLSKIM TATRZAŃSKIM PARKU NARODOWYM

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Abstract: The basic structural features of the breeding bird communities with regard to the biotope zonation of the Polish Tatra Mountains were defined in the breeding seasons 1981 and 1982. In the studied gradient series from the beech-fir forests of the lower montane zone up to the highest peaks such values as the number of species (S), density (N) and species diversity (H') are clearly functions of altitude. The decrease in the number and density of the bird communities (S and N) along the gradient from the lowest to the highest altitudes is visibly of hiperbolic type. The bird species diversity (H') and biomass (B) pass through two phases: their values decrease sharply in the forest and dwarf pine zones, and then stabilize on a similar low level. In the mountain forest dominate the ubiquist species: *Fringilla coelebs* and *Erithacus rubecula* (N over 15 per cent). The thick dwarf pine bushes are dominated by *Prunella modularis* (over 30 per cent), the alpine meadows with clumps of dwarf pine bushes - by *Anthus spinoletta* (over 50 per cent), the alpine zone - by *Prunella collaris*. On the sample plots a total of 55 bird species were identified; in the whole Polish Tatra National Park (ca. 212 km^2) there were an estimated 44000-67000 pairs, out of which about 90% of the pairs or breeding territories were found in the forests (ca. 150 km^2).

Key words: bird communities, biomass, breeding season, density, high mountains, species diversity, vertical distribution, Tatra National Park, Poland.

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Treść: W sezonach lęgowych 1981 i 1982 określono podstawowe cechy strukturalne lęgowych zespołów ptaków na tle zonacji siedliskowej Tatr Polskich. W badanej serii gradientowej od dolnoreglowych lasów bukowo-jodłowych po najwyższe szczyty wartość takich wskaźników, jak liczba gatunków (S), zagęszczenie (N) i różnorodność gatunkowa (H') jest wyraźnie funkcją wysokości terenu nad poziom morza. Spadek wielkości zespołów (S i N) w gradiencie od najniższych do najwyższych położeń przebiega wyraźnie hiperbolicznie. Różnorodność gatunkowa i biomasa ptaków (B) kształtują się w dwóch fazach: ich wartość spada ostro w stadiach lasu i kosówki, po czym stabilizuje się na zbliżonym niskim poziomie. W reglach zdecydowanie dominują gatunki ubikwistyczne: *Fringilla coelebs* i *Erithacus rubecula* (N powyżej 15%). W zwartej kosówce dominuje *Prunella modularis* (powyżej 30%), w strefie hal z kępami kosówki - *Anthus spinoletta* (powyżej 50%). Strefę alpejską najsilniej wydziela *Prunella collaris*. Na powierzchniach próbnych wykazano w sumie 55 gatunków ptaków, których liczebność dla całego polskiego Tatrzańskiego Parku Narodowego (ok. 212 km^2) oszacowano na 44000-67000 par, z czego na lasy (ok. 150 km^2) przypada około 90% par lub rewirów lęgowych.

I. INTRODUCTION

The knowledge of the Polish Tatra birds is based mainly on the observations of Wodzicki (1851), Schauer (1862), Karliński (1882) and Kocyan (1884, also museum collections), as well as on more recent studies of Domaniewski (e.g. 1927) and Ferens (1954a, 1962). This basic bibliography is supplemented with smaller contributions from such authors as Sokołowski (1953),

Ferens (1954b), Marchlewski (1959), Wasilewski (1969), Głowaciński , Jakubiec, Profus (1983), Cichocki (1986), as well as with the data included in monographs and books (e.g. Sokołowski 1958, Ferens 1962, Tomiałojć 1990). The avifauna of the Slovak Tatra is also quite well known, and the works of such authors as Balat, Havlin, Hudec (1955), Ferianc, Feriancova (1956), Klima (1959), Pikula (1962) and Mošansky (1974) contain not only detailed faunal descriptions but also ecological estimations based partly on quantitative field methods. The works provide analyses of bird communities in a wide variety of biotopes of the Slovak, i.e. southern Tatra (e.g. Mošansky 1974) and of species distribution in the seasonal aspect (e.g. Klima 1959).

However, there are no detailed descriptions of the breeding bird communities based on absolute number estimations, that would allow a more precise analysis of the structure and functional features of the Tatra ornithocenoses. Such estimations are expected to be a reliable starting point for future studies of the role of birds in the Tatra biocenoses as well as for keeping a record of changes in the native bird communities and populations.

This paper aims to (1) present a detailed description of the structure of the breeding bird communities with regard to the biotope zonation of the Polish Tatra, (2) show altitudinal changes in these communities, (3) make a closer presentation of the place of the northern Tatra in the avifauna of the Carpathians and compared with other mountain regions.

II. DESCRIPTION OF THE STUDIED AREA

The Tatra are the highest massif in the Carpathians (Gerlach 2663 m above sea level). This area however, is not very large (750 km^2) - about 70 times smaller than the Alps (Atlas Tatrzańskiego Parku Narodowego 1985). Only one fifth of the Tatra (ca. 150 km) is in Poland, while the remaining part with the highest peaks lies within the borders of Czecho-Slovakia. The highest peak in the Polish Tatra is Rysy (2499 m a.s.l.). The geomorphology and relief of the Tatra today are the product of intensive local Pleistocene glaciations. As for their geological structure and relief, the Tatra are subdivided into three distinct units: (1) granite Eastern, i.e. High Tatra, (2) a little lower Western Tatra built mainly of sedimentary rocks (limestone, dolomite), and (3) limestone Bielskie Tatra lying on the Slovak side. Within the Polish Tatra some scientists distinguish also (4) the Subalpine or Zakopane Tatra with less high-mountain relief than the former three units (Klimaszewski 1988).

The Tatra climate exhibits high-mountain features typical of the moderate climate at the borderline of oceanic and continental climatic zones. What is of particular significance to living organisms, are high annual and daily temperature amplitudes as well as quite heavy precipitation in the summer period (the monthly average about 250 mm). The average annual temperatures in 1951-1960 ranged from 4.9°C in Zakopane (844 m above sea level), 2.5°C near Lake Morskie Oko (1400 m), 1.2°C in Dolina Pięciu Stawów Polskich (the Valley of Five Polish Ponds) (1668 m), -0.8°C at Kasprowy Wierch (1891 m), down to -3.8°C at Łomnica (2635 m). The annual amplitude however, drops together with the altitude; for example, in the years 1951-1960 menioned above, it ranged from 19.6°C in Zakopane to 13.3°C at Łomnica. The annual temperature amplitudes in the Tatra valleys are higher (e.g. extreme ranges for Zakopane are 66, with a maximum of 32°C and minimum of -34°C), compared with the peaks (e.g. at Łomnica 48°C, with a maximum of 18°C and minimum of -30°C). In the alpine zone of the Polish Tatra the summer season practically disappears (maximum temperature in the day is < 0°C), while the winter lasts from about 117 days in Zakopane up to 200 days at Kasprowy Wierch. The average annual precipitation increases from the lower regions (1096 mm in Zakopane in 1951-1960) up to the peaks (1825 mm at Kasprowy Wierch). The period of continuous lingering of the snow cover lasts from 86 days in Zakopane to 207 days at Kasprowy Wierch.

A typical feature of the Tatra climate are strong and frequent winds on the peaks (the so-called "halny" wind) and winds falling down one side of the mountain while masses of air accumulate on the other side of the range. The altitudinal layout of the thermal and precipitation zones in the Tatra is modified by a sharp differentiation of the local climates (Orlicz 1962).

The Tatra nature and relief are greatly diversified on a relatively small area. Moreover, the environmental factors emerging from the vertical formation,

varied types of bedrock, different slope expositions, as well as wind, avalanches and human activity - all these determinants exert a powerful influence on these high mountains. The studies were carried out in the Polish Tatra National Park (orig. TPN). The study areas (of 10 up to 65 ha) where censuses were taken in 1981 and 1982, were located in the altitudinal gradient illustrating a full range of the zonal biotopes of the northern slopes of the Tatra. The studies focused on the granite High Tatra, i.e. on the region of Morskie Oko and Dolina Pięciu Stawów Polskich, where seven study areas were located. Only one study area was placed in the limestone Zakopane Tatra (Fig. 1). The map of forest and brushwood communities of the Tatra National Park made by Myczkowski et al. (1974) was used to locate the study areas. They included the lower montane zone (beech-fir forest - I), upper montane zone (thick spruce forest - II), subalpine zone (dwarf pine bushes - III -IV), alpine zone (alpine meadows with rockslides - V-VI), subnival zone (bare rocks and rockslides - VII-VIII). The foothill zone does not reach the northern foot of the Tatra. In the past the Zakopane valley was covered with mixed forests including *Abies alba, Picea excelsa* and *Fagus sylvatica.* Centuries ago these forests were cut down by the pioneer settlers and are now replaced by houses and cultivated fields (Fabijanowski 1962, Zarzycki, Zwolińska 1984).

I - beech-fir forest in Dolina Strążyska (the Strążyska Valley). A sample plot of 10 ha was located in 100-200-year old Carpathian beechwood *Fagetum carpaticum tatricum* on a limestone bedrock (according to Myczkowski, Lesiński 1974 - the *Luzulo-Fagetum* associations), to the left of Strążyski Potok, on the slopes of Samkowa Czuba, at an altitude of 960-1100 m. Apart from the dominating beeches *Fagus sylvatica* and firs *Abies alba*, there are occasional spruces *Picea excelsa* and sycamores *Acer pseudoplatanus* (Fabijanowski 1962, Myczkowski, Lesiński 1974). This fragment of a mixed forest in the lower montane zone, which is well-preserved and mostly of the climax type, has a relatively balanced spatial structure. It is only in some places on the lower steep slopes that the forest floor and undergrowth are sparser. A detailed floristic and phytosociological description of the upper layers of this beechwood was provided by Myczkowski and Lesiński (1974), and of the region of Sarnia Skała near the sample plot, east of Potok Strążyski by Horvat et al. (1980) and Piękoś (1968). The censuses of birds were taken on the folowing days: 8, 19, 29 May, 9, 28 June, 11 July 1981 and 11, 12, 18, 22 May, 9, 16 June, 2 July 1982.

II - natural thick spruce forest by Rybi Potok (the Rybi Stream). A sample plot of 13.5 ha was located at an altitude of 1300-1400 m in the climax thick spruce forest *Piceetum tatricum* on a granite bedrock (Myczkowski, Lesiński 1974), at the height of Włosienica, close to the upper forest border at the foot of Żabi Mt. Occasional *Pinus cembra* occur in the thick spruce forest of *Picea excelsa.* Abundant moss and occasional *Dryopteris austriaca* appear on the forest floor which is sparse and covered with blocks of rock, while stones and trees are overgrown with lichen.

The bird censuses were taken on the following days: 9, 20, 30 May, 11, 27 June, 13 July 1981 and 19, 25, 28 May, 8, 17 June, 4 July 1982.

III - heterogenous dwarf pine bushes in the region of Morskie Oko. A sample plot of 30 ha was located at an altitude of 1400-1580 m, immediately above the upper forest border, on the slopes of the Miedziane-Opalone mountain ridge. The plot covered thick and luxuriant dwarf pine *Pinus mughus* included in the sub-group *Mughetum carpaticum silicicolum* (Myczkowski et al. 1974), with some *Sorbus aucuparia* var. *glabrata* (15-20 per cent of the plot), *Betula carpatica* (about 15 per cent), and *Salix silesiaca* et *S. caprea* (about 5 per cent). The lower dwarf pine zone is characterized by spruce-stone pine biogroups (10-30 per cent of the plot) which are remnants of a relic *Cembro-Piceetum* forest. Montane herb communities appear occasionally in the dwarf pine bushes.

The sample plot is crossed by tourist trails: a section of the blue one: the road by Rybi Potok - Opalone, and the yellow one traversing Morskie Oko. On these trails the censuses were taken on the following days: 10, 26-27 June, 11-12 July 1981 and 12, 27 May, 8, 16-19 June, 6 July 1982.

IV - upper homogenous dwarf pine community. A sample plot (a total of 36 ha in 1981 and 40 ha in 1982) was located in three groups of dwarf pine forest *Mughetum carpaticum silicicolum* (Myczkowski, Lesiński 1974), at an altitude of 1550-1720 m, along the blue trail at Opalone, Świstówka Roztocka, and in Dolina Pięciu Stawów Polskich at Wyżna Kopa, as well as along the yellow

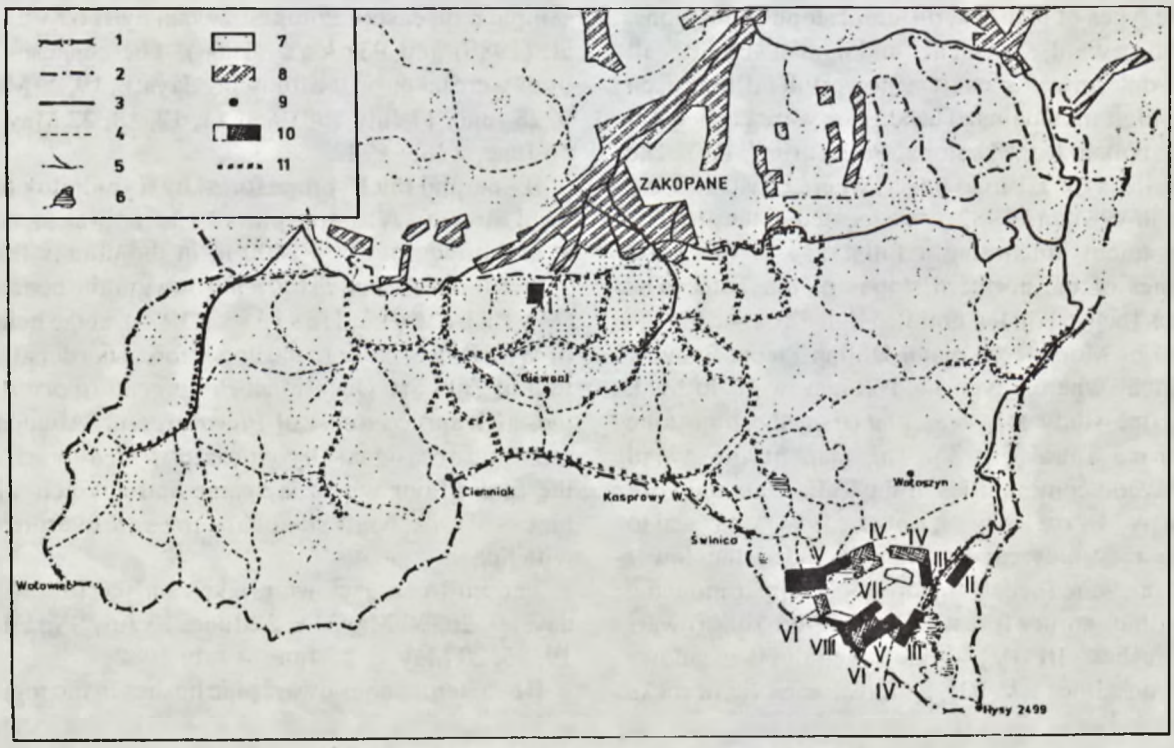

Fig.1. Schematic map of the Tatra National Park with the sample plots I-VIII. Numbers: 1 - state border, 2 - border of the National Park, 3 - roads, 4 - tourist trails, 5 - streams, 6 - lakes, 7 - forests, 8 - built-up areas, 9 - selected mountain peaks, 10 - sample plots I-VIII (explanations in the text - p.67-69), 11 - regions of supplementary censuses

Ryc.1. Schematyczna mapa Tatrzańskiego Parku Narodowego z zarysem powierzchni badawczych I-VIII. Oznaczenia: 1 - granica państwa, 2 - granica Parku Narodowego, 3 - drogi, 4 - szlaki turystyczne, 5 - potoki, 6 - jeziora, 7 - lasy, 8 - tereny zabudowane, 9 - niektóre szczyty górskie, 10 - powierzchnie próbne I-VIII (objaśnienia w tekście - str.67-69), 11 - trasy liczeń uzupełniających

trail at the foot of Mnich. The plot comprised homogenous strongly trailing dwarf pines, which - going upwards - become less luxuriant and change into alpine meadows and rubble. Clumps of herb communities appear among the dwarf pines. It is only occasionally that stunted forms of *Sorbus aucuparia* and *Salix silesiaca* are found in this zone.

The censuses of birds were taken at the same time as on plot III.

V - alpine meadows with occasional clumps of dwarf pine bushes. Sample plots (a total of 65 and 60 ha) were located on alpine meadows at an altitude of 1600-1800 m on Hala za Mnichem, and in Dolina Pięciu Stawów Polskich. The plots comprised natural alpine meadows dominated by high mountain turf of the *Trifido-Distichetum* association. A considerable part of the sample plots (15-25 per cent) was covered with granite alpine rubble overgrown with the *Oxyrio-Saxifragetum carpaticae* association (P a w ł o w s k a 1962). Patches of dwarf pine occupy about 10 per cent of the plot.

The bird censuses were taken at the same time as on sample plot III.

VI - upper alpine meadows and scree. A sample plot of 35 ha was located at an altitude of 1720-2000 m in the upper part of Hala za Mnichem and at Szpiglasowa Perć. The area is dominated by alpine rubble and cones of rockslides. In the lower parts of the studied area there are herb plant associations *Oxyrio-Saxifragetum* and *Luzuletum spadiceae*, which are typical of the alpine zone (P a w ł o w s k a 1962). There are small clumps of dwarf pine which disappears on the higher alpine rubble.

The bird censuses were taken mainly along the yellow tourist trail on the following days: 26-27 June, 11-12 July 1981 and 27 May, 8, 16, 19 June 1982.

VII - crags and rockslides in the subnival zone. An approximate sample plot of 45 ha was composed of two sections (20+25 ha) located among the rocks at an altitude of 1900-2120 m, in the region of Przełęcz Szpiglasowa (2114 m) and also in a cirque at

Świstówka Roztoczańska and Opalony Wierch (2124 m). The sparse vegetation in this zone is represented by few flower plants, high mountain turf and lichen communities. Only occasionally can small dwarf pines be found. In small cirques and recesses exposed to the north, patches of snow and ice linger for most of the breeding season.

The bird censuses were taken at the same time as on sample plot VI.

VIII - top steep ridges of rock in the region of Szpiglasowy Wierch (2171 m) and Miedziany (2233 m). The observations were made along the arete and a sample plot was not fixed because the area did not favour counting. The data were recorded on the basis of some censuses taken on the days mentioned for sample plot VI. Information referring to *Tichodroma muraria* was provided by other, incidental observers, i.e. alpinists who know this bird.

The studies did not include the azonal biotopes formed in the stream valleys and anthropogenic biotopes such as once grazed meadows within the Tatra forests.

III. METHODS

The bird number estimations were made by the mapping method (E n e m a r 1959, and others), with the modifications increasing its efficiency suggested by T o m i a ł o j ć (1980). The field conditions, time-and technique limits made it impossible to locate and efficiently view the sample plots of similar sizes and of a comparable area/circumference ratio (the edge effect problem). It was assumed (cf. K e n d e i g h 1974, C o u s i n s 1977 and others) that the sample area in a biotope that is complex and rich in birds should not be smaller than 10 ha (Carpathian beechwood) and in semi-open and open biotopes with a lower bird density - 20 ha (upper alpine meadows changing into rocks). In some cases the location of larger plots was further complicated by a mosaic character of the biotopes. It was also assumed that the sample plots which were forcibly elongated (e.g. in the lower dwarf pine thicket), could not be narrower than 100 m. In the biotopes that were difficult to view, especially in the dwarf pine thicket and on steep rocks, tourist trails were used in the observations.

The observations were made at different times of the day when the weather was good and the birds active. The observations in the rain, thick fog, and strong wind were of complementary significance. Two observers worked simultaneously and a double census was treated as one counting. In the breeding season the censuses were taken 5-7 times in the forest biotopes and at least 3 times in clear, top biotopes. The beginning and end of the breeding season in the Tatra are contingent on the altitude (cf., e.g. the thermal seasons of the year according to O r l i c z 1962). Going upwards, the season is two times shorter in the region of Dolina Pięciu Stawów Polskich, compared with the vicinity of Zakopane. Therefore the bird censuses at higher altitudes were taken 1-2 weeks later than in the forests of the lower montane zone.

When summing up the censuses, single occurrences of birds were excluded. The exception were the unrepeated occurrences of specimens or pairs which revealed signs of nesting (collecting the nest material, food and defending the territory) or whose behaviour led to finding the nest. The birds which were found in a given biotope only in tiny numbers ($N < 0.1p/10$ ha) and which probably nested close to the sample plot, were included in the breeding community as complementary ones and marked with "+". Incidental species in a given biotope were marked in the same way (e.g. *Motacilla cinerea* in the forest community). An arbitrary number 2 was attributed to those species (the lowest integer whose logarithm is > 0) for the species diversity estimations according to S h a n n o n ' s formula H' taken from information theory. When the biomass was estimated, the arbitrary values of 0.1p/10 ha were attributed to them. These calcuations refer to such regions as the extremely sparse bird communities on the top rocks.

In order to make a rough estimate of the number of birds in the whole Polish Tatra National Park, irregular censuses were taken and treated as supplementary to the mapping method (MM). These countings were carried out on belts whose width depended on the clearness of the biotope (see p. 85).

The species diversity H' was calculated according to the formula:

$$H' = -\sum_{i=1}^{s} p_i \log p_i,$$

where S - species number in the community, p - fraction of the specimens of the i-th species (e.g. L l o y d, Z a r, K a r r 1968, P i e l o u 1975).

The evenness or equitability was calculated by means of the J' formula:

$$J' = H'/H'_{max},$$

where $H'_{max} = \log S$, while H' and S are as above (e.g. Tramer 1969).

The formulae H' and J' were also used for the biomass of the described communities by replacing the number of specimens in p with a fraction of the total biomass for the i-th species (cf. Głowaciński, Weiner 1977, 1980, Głowaciński 1981).

To calculate the hypothetical bird species richness of a given biotope with any number of specimens in a sample, the rarefaction index $E(S_n)$, widely used in American works, was applied:

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

where S - number of species in the community, N - number of breeding pairs (or specimens) in the whole community, N - number of breeding pairs (specimens) of the i-th species, n - any number of birds in the sample, but smaller than N. (Peet 1974, Raup, Stanley 1984; see also James, Wamer 1982, and Jermaczek 1990).

The rarefaction index allows the determination of the theoretical expected number of species on the basis of the size and number structure of the samples taken at random from different plots.

The similarity estimation of bird communities was made on the basis of Renkonen's formula (1938) Re:

$$Re = \sum_{i=1}^{s} w_i,$$

where w_i - the common percentage of the i-th species domination in the comparable communities.

IV. ZONAL DIFFERENTIATION OF THE BIRD COMMUNITIES

The bird communities described in the altitudinal gradient of the Tatra (Tables I-VII) reveal a spectral zonal differentiation typical of high mountains. It is seen mainly in the size of the communities measured by the species number and composition.

1. Species richness and density

In the eight studied biotopes of the Tatra a total of 55 nesting bird species were identified (Tables I-VII). Although the results of the censuses do not include all the bird species occurring in the Polish Tatra, they certainly cover the basic composition of the avifauna of this mountain region.

As expected, the biggest bird community was found in the beechwood of the lower montane zone (community I, Table I). In the seasons 1981 and 1982, 38 breeding species were found there (i.e. almost 70 per cent of the species in the studied gradient series); their total density was about 66 and 70 pairs in 10 ha. The species which dominate this community are: *Fringilla coelebs* ($\bar{x}$ = 22 per cent of the specimen number), *Erithacus rubecula* (16 per cent), *Phylloscopus sibilatrix* (12.5 per cent) and *Parus ater* (7.5 per cent). It can be safely assumed that these are the species that dominate the Carpathian beechwood in the whole Carpathians (cf. Bocheński 1960, 1970, Kozłowski 1974, Głowaciński 1990), as well as the beechwood of the lower montane zone of the Karkonosze mountains (Dyrcz 1973) and even most of the old deciduous forests in the lowlands. 10 species occurred in tiny number on this area (N = 0.1 p/10 ha - marked with "+"). One of these species, *Motacilla cinerea* is a bird closely connected with mountain streams and lakes. Thus in the mainland biotopes of the Tatra this species should be treated as incidental.

In the spruce forest of the Tatra upper montane zone the bird species number is lower by about 1/3 (25 species) than in the beechwood. The density is half as high (about 36 p/10 ha) compared with the previous community (Table II). The dominance of the two ubiquitous species - *Fringilla coelebs* and *Erithacus rubecula* (30 per cent each) is even greater in the upper montane forest than in the beechwood. The subsequent species prefer coniferous forests: *Regulus regulus, Parus ater, Prunella modularis, Turdus torquatus* and *Parus cristatus*. In the transitional zone between the upper montane forest and

TABLE I

Species composition and density of breeding birds in the Tatra beechwood of the lower montane zone (habitat and bird community I)

Skład gatunkowy i zagęszczenie ptaków gnieżdżących się w tatrzańskiej buczynie(siedlisko i zespół ptaków I)

Species / Gatunek	Number of pairs per 10 ha / liczba par na 10 ha		
	1981	1982	$\bar{x}$
Fringilla coelebs	12.5	17.5	15.0
Erithacus rubecula	10.5	11.0	10.8
Phylloscopus sibilatrix	10.0	7.0	8.5
Parus ater	5.5	4.7	5.1
Phylloscopus collybita	3.5	3.5	3.5
Phylloscopus trochilus	1.5	4.7	3.1
Pyrrhula pyrrhula	2.5	3.0	2.8
Turdus philomelos	2.0	1.7	1.9
Turdus merula	2.5	1.0	1.8
Parus montanus	2.0	1.5	1.8
Sylvia atricapilla	1.3	2.0	1.7
Parus major	1.2	2.0	1.6
Turdus viscivorus	1.0	1.5	1.3
Ficedula parva	1.0	1.0	1.0
Prunella modularis	0.5	1.5	1.0
Sitta europaea	1.0	1.0	1.0
Strix aluco	1.0	1.0	1.0
Muscicapa striata	1.0	0.6	0.8
Dryocopus martius	0.3	1.0	0.7
Anthus trivialis	1.0	-	0.5
Certhia familiaris	1.0	-	0.5
Coccothraustes coccothraustes	1.0	-	0.5
Regulus regulus	1.0	-	0.5
Aegithalos caudatus	+	1.0	0.5
Turdus pilaris	+	1.0	0.5
Garrulus glandarius	0.5	-	0.3
Carduelis spinus	0.2	0.2	0.2
Tetrastes bonasia	0.3	-	0.2
Dendrocopos major	+	0.1	0.1
Cuculus canorus	+	+	+
Troglodytes troglodytes	+	+	+
Carduelis chloris	+	-	+
Ficedula hypoleuca	+	-	+
Loxia curvirostra	-	+	+
Sylvia borin	-	+	+
Sylvia curruca	-	+	+
Turdus torquatus	+	-	+
Motacilla cinerea (stream / potok)	+	-	-
Total/Razem	65.8	69.0	68.2

the belt of dwarf pine the bird community numbers 17 species of the density of about 17 pairs in 10 ha (Table III). This heterogenous biotope is the borderline of vertical ranges of 11-12 forest species. At the same time the alpine zone species occur there: *Anthus spinoletta* and *Phoenicurus ochruros*, the latter coming from this type of biotope and now also common in open and anthoropogenic lowland biotopes. The species decisively dominating this climatic and vegetation zone and most typical there (38.5 per cent of the specimens) is *Prunella modularis*. This species also dominates the higher zone of the homogenous dwarf pine (46.6 per cent). Together with *Anthus spinoletta* (38.1 per cent), it constitutes as much as 5/6 of the specimen number in the community which is composed of 10 bird species. (Table IV). In both seasons the tundra form of *Luscinia s. svecica* as well as boreal-alpine *Acanthis flammea* represented in the Tatra by the form *Acanthis flammea cabaret* (cf. Hanzak 1953) were found in this biotope. Still in this mountain zone *Turdus torquatus* was regularly noted in the breeding seasons; this species nests in the dwarf pine community. This zone is occasionally penetrated by *Acan-*

TABLE II

Species composition and density of breeding birds in the Tatra spruce forest of the upper montane zone (II)
Skład gatunkowy i zagęszczenie ptaków gnieżdżących się w tatrzańskim górnoreglowym borze świerkowym (II)

Species / Gatunek	Number of pairs/Liczba par				
	1981		1982		$\bar{x}$
	13.5 ha	10 ha	13.5 ha	10 ha	10 ha
Fringilla coelebs	12.5	9.3	17.4	12.9	11.1
Erithacus rubecula	16.5	12.2	13.2	9.8	11.0
Regulus regulus	4.7	3.5	4.0	3.0	3.3
Parus ater	4.0	3.0	4.4	3.3	3.2
Prunella modularis	1.2	0.9	4.2	3.1	2.0
Turdus torquatus	2.0	1.5	2.0	1.5	1.5
Parus cristatus	2.0	1.5	1.5	1.1	1.3
Nucifraga caryocatactes	0.5	0.4	0.5	0.4	0.4
Turdus viscivorus	0.7	0.5	0.2	0.2	0.4
Pyrrhula pyrrhula	1.0	0.7	+	+	0.4
Carduelis spinus	1.0	0.7	-	-	0.4
Turdus merula	1.0	0.7	-	-	0.4
Troglodytes troglodytes	0.3	0.2	0.2	0.2	0.2
Garrulus glandarius	0.5	0.4	+	+	0.2
Certhia familiaris	0.5	0.4	-	-	0.2
Turdus philomelos	+	+	0.3	0.2	0.1
Motacilla cinerea (stream/potok)	+	+	0.1	0.1	0.1
Phylloscopus collybita	-	-	0.2	0.2	0.1
Anthus trivialis	+	+	+	+	+
Tetrao urogallus	+	+	-	(+)	+
Loxia curvirostra	-	(+)	-	-	+
Parus montanus	-	-	+	+	+
Phoenicurus phoenicurus	-	-	+	+	+
Regulus ignicapillus	-	-	+	+	+
Picoides tridactylus	-	(+)	-	(+)	(+)
Total/Razem	48.4	35.9	48.2	36.0	36.3

TABLE III

Species composition and density of breeding birds in the Tatra heterogenous dwarf pine in the subalpine zone (III)

Skład gatunkowy i zagęszczenie ptaków gnieżdżących się w heterogenicznej kosówce tatrzańskiej w strefie subalpejskiej (III)

Species / Gatunek	Number of pairs/Liczba par				
	1981		1982		$\bar{x}$
	30 ha	10 ha	30 ha	10 ha	10 ha
Prunella modularis	19.0	6.3	21.0	7.0	6.7
Phylloscopus collybita	7.0	2.3	8.5	2.8	2.6
Fringilla coelebs	4.0	1.3	6.0	2.0	1.7
Phylloscopus trochilus	3.0	1.0	7.0	2.3	1.7
Erithacus rubecula	4.0	1.3	5.0	1.7	1.5
Sylvia atricapilla	3.5	1.2	3.0	1.0	1.1
Parus ater	2.0	0.7	1.5	0.5	0.6
Phoenicurus ochruros	-	-	1.5	0.5	0.3
Anthus spinoletta	3.0	1.0	0.5	0.2	0.2
Anthus trivialis	-	-	1.0	0.3	0.2
Motacilla cinerea (stream/potok)	1.0	0.3	-	-	0.2
Pyrrhula pyrrhula	1.0	0.3	-	-	0.2
Regulus regulus	1.0	0.3	-	-	0.2
Sylvia curruca	-	-	0.5	0.2	0.1
Turdus torquatus	-	-	0.5	0.2	0.1
Loxia curvirostra	-	-	+	+	+
Nucifraga caryocatactes	+	+	-	-	+
Total/Razem	48.5	16.0	56.0	18.7	17.4

TABLE IV

Species composition and density of breeding birds in the higher Tatra homogenous dwarf pine in the subalpine zone (IV)

Skład gatunkowy i zagęszczenie ptaków gnieżdżących się w wyżej położonej homogenicznej kosówce tatrzańskiej w strefie subalpejskiej (IV)

Species / Gatunek	Number of pairs/Liczba par				
	1981		1982		$\bar{x}$
	36 ha	10 ha	36 ha	10 ha	10 ha
Prunella modularis	15.0	4.2	27.2	6.8	5.5
Anthus spinoletta	17.0	4.7	17.4	4.4	4.6
Luscinia s. svecica	1.0	0.3	5.0	1.3	0.8
Acanthis flammea	1.0	0.3	1.6	0.4	0.4
Phoenicurus ochruros	1.2	0.3	1.0	0.3	0.3
Sylvia atricapilla	1.0	0.3	-	-	0.2
Motacilla cinerea (stream/potok)	+	+	0.8	0.2	0.1
Motacilla alba	-	-	0.4	0.1	0.1
Acanthis cannabina	+	+	+	+	+
Turdus torquatus	+	+	+	+	+
Total/Razem	36.2	10.1	53.4	13.5	12.0

TABLE V

Species composition and density of breeding birds in the alpine meadows with occasional clumps of dwarf pine in the alpine zone (V)

Skład gatunkowy i zagęszczenie ptaków gnieżdżących się w obrębie łąk wysokogórskich z kępami kosówki w strefie alpejskiej (V)

Species / Gatunek	Number of pairs/Liczba par				
	1981		1982		$\bar{x}$
	60 ha	10 ha	60 ha	10 ha	10 ha
Anthus spinoletta	30.5	4.7	24.5	4.1	4.4
Prunella modularis	11.5	1.8	14.2	2.4	2.1
Phoenicurus ochruros	2.5	0.4	3.0	0.5	0.4
Motacilla cinerea (stream / potok)	1.5	0.2	0.7	0.1	0.2
Luscinia s. svecica	-	-	1.7	0.3	0.1
Acanthis flammea	+	+	0.5	0.1	0.1
Acanthis cannabina	+	+	+	+	+
Oenanthe oenanthe	-	-	+	+	+
Prunella collaris	-	-	+	+	+
Total/Razem	46.0	7.1	44.6	7.5	7.3

this cannabina, which comes from the lowland and foothill open biotopes. The repeated occurrences of this species in the summer season are indicative of high prkbability babilityof its nesting here. The bird community identified in the alpine meadows with clumps of dwarf pine is very similar and not much sparser. In two seasons 9 breeding and possibly breeding bird species whose total density was slightly higher than 7 pairs in 10 ha (Table V) were identified. It is a biotope of narrow spectral ranges of *Luscinia s. svecica* and *Acanthis flammea*. A strictly alpine faunal element *Prunella collaris* as well as *Oenanthe oenanthe* which is widely spread in the Holarctic zone occur here for the first time. *Acanthis cannabina* is still noted here (category of occurrence "+"). As for the number, the dominating species here are the same ones as in the previous zone, but in a reversed sequence; the population of *Anthus spinoletta* prevails (ca. 60 per cent of the specimens), while *Prunella collaris* is less numerous.

In the higher parts of the alpine zone there were recorded only 7 species whose total density was about 7 pairs per 10 ha (Table VI). In this zone *Anthus spinoletta* still prevails (50% of the specimens) and the share of *Prunella collaris* increases as that of a congeneric species - *Prunella modularis* decreases. As in the previous bird community *Oenanthe oenanthe* also occurs rather infrequently. The source regions of streams in this mountain zone are rarely reached by *Motacilla cinerea* (category "+").

More or less the same number of bird species lives in the upper regions of the alpine rubbles and rocky walls as in the previous biotope, but the species density is lower, i.e. 3.7 pairs per 10 ha for the two studied seasons (Table VII). This zone is characterized by *Prunella collaris* (almost 50 per cent of specimens), *Anthus spinoletta* and species of a wider habitat tolerance, such as *Phoenicurus ochruros* and *Oenanthe oenanthe*. Very rarely does *Tichodroma muraria* occur within the sample area; this species is typical of some rocky mountains of southern Eurasia (L ö h r l 1976). In the seasons 1981-1982 the sample plot was within the breeding territory of some species of a wide ecological and geographical range, such as for example *Falco peregrinus* which is now very rare in central Europe.

It was noted that in the top regions of the rock ridges only 3-4 bird species of a tiny number (cat. "+") had their breeding territories. It was assumed that this extremely scarce bird community reaches a density of 0.1 pair in 10 ha.

This zone is inhabited by *Tichodroma muraria* which was noted in the studied aea in the 70-80ties by alpinists such as M. B a ł a, M. D ą s a l, J. J a s i ń s k i and W. W i s z (J. B a r y ł a - personal

TABLE VI

Species composition and density of breeding birds in the higher regions of alpine meadows with rockslides in the alpine zone (VI)

Skład gatunkowy i zagęszczenie ptaków lęgowych wyższych partii łąk alpejskich z osuwiskami skalnymi w strefie alpejskiej (VI)

Species / Gatunek	Number of pairs/Liczba par				
	1981		1982		$\bar{x}$
	35 ha	10 ha	35 ha	10 ha	10 ha
Anthus spinoletta	14.0	4.0	11.5	3.3	3.6
Phoenicurus ochruros	4.0	1.2	5.0	1.4	1.3
Prunella collaris	5.0	1.4	2.0	0.6	1.0
Prunella modularis	1.0	0.3	4.5	1.3	0.8
Motacilla cinerea (stream / potok)	+	+	-	-	+
Falco tinnunculus	-	-	+	+	+
Oenanthe oenanthe	-	-	+	+	+
Total/Razem	24.0	6.9	23.0	6.6	6.7

TABLE VII

Species composition and density of breeding birds in the almost bare rocks and alpine rubble in the subnival zone (VII)

Skład gatunkowy i zagęszczenie ptaków lęgowych odsłoniętych skał i rumoszu skalnego w strefie subniwalnej (VII)

Species / Gatunek	Number of pairs/Liczba par				
	1981		1982		$\bar{x}$
	20 ha	10 ha	25 ha	10 ha	10 ha
Prunella collaris	3.0	1.5	5.5	2.2	1.8
Anthus spinoletta	1.0	0.5	4.0	1.6	1.0
Phoenicurus ochruros	+?	+?	3.0	1.2	0.6
Oenanthe oenanthe	-	-	1.0	0.4	0.2
Falco peregrinus	0.2	0.1	-	-	0.1
Corvus corax	+	+	-	-	+
Falco tinnunculus	-	-	+	+	+
Tichodroma muraria	-	(+)	-	(+)	(+)
Total/Razem	4.2	2.1	13.5	5.2	3.7

comm.). Every year the top rocks are within the reach of breeding sites of *Corvus corax, Falco peregrinus* and *F. tinnunculus*, which were noted alternately in both seasons, probably nest irregularly here.

Generally, as for the bird species number, the lowermost biotopes which are ornithologically the richest (S = 35 and 29) (ca. 1000 m above sea level) in the studied profile of the Tatra differ from the highest and most meagre (S = 3-4) ones by about one order of magnitude. In other words, the diversity of a bird community decreases by about 3 species together with the increase of altitude by about 100 m. However, this change is not of proportional but hyperbolic type rather (Fig. 2). The bird specimen number is a similar decreasing function of altitude, but the difference in the specimen number between the extreme communities (N from ca. 70 p/10 ha to 0.1 p/10 ha) is much bigger than the difference in the number of species, and goes up to two orders of magnitude (Table VIII, Fig. 2). The sizes of bird communities so changing in the studied gradient series from the beechwood of the lower montane zone up to the rock grounds of the subnival zone reflect the simpler and simpler biotope structure (mainly vegetation) and the increasing pressure of the physical factors on the bird populations.

The expected number of bird species in the particular biotopes of the Tatra National Park was

determined by means of the calculus of probability and rarefaction formula $E(S_n)$ (Fig. 3). According to these estimations, the highest theoretical species accumulation is noted in the beech forest in the lower regions of the mountains, which is confirmed by empirical data. The simulated biotope capacity of the alpine and subnival zones is low and follows a shifting pattern. What is interesting is the theoretical accumulation rate of bird species in those biotopes where the numbers of species were initially similar. For example, the accumulation of a bigger bird species number is more probable in the spruce forest of the upper montane zone than in the heterogenous dwarf pine. Lesser divergences are noted in this respect in higher and therefore more meagre biotopes.

A comparison of the species number (S) and the average density (N) of birds in the particular communities (Table VIII, Fig. 4) points to a strong correlation of these characteristics ($r = 0.96$). The specimen (pair) number per the statistical bird species drops from the lower montane zone up to the subnival biotopes. In the top communities only one specimen (community VII) or even a fraction of a specimen (VIII) represents a species, whereas in the richest beechwood community this ratio is 1 : 3.6. In other words, the more meagre and ecologically restrictive biotopes limit the specimen and species number of the bird communities to a various degree (cf. C o d y 1980). The restrictions on the population sizes are more severe.

2. Species diversity and evenness

The species diversity of the Tatra bird communities, understood in the sense of the H' index (e.g. L l o y d, Z a r, K a r r 1968), follows a slightly different pattern as compared with the species number and density. If this index is to be estimated on the basis of the specimen number (H'_n) or the biomass of adults (H'_b), it turns out that in both cases the diversity drops from the beechwood (I) up to the

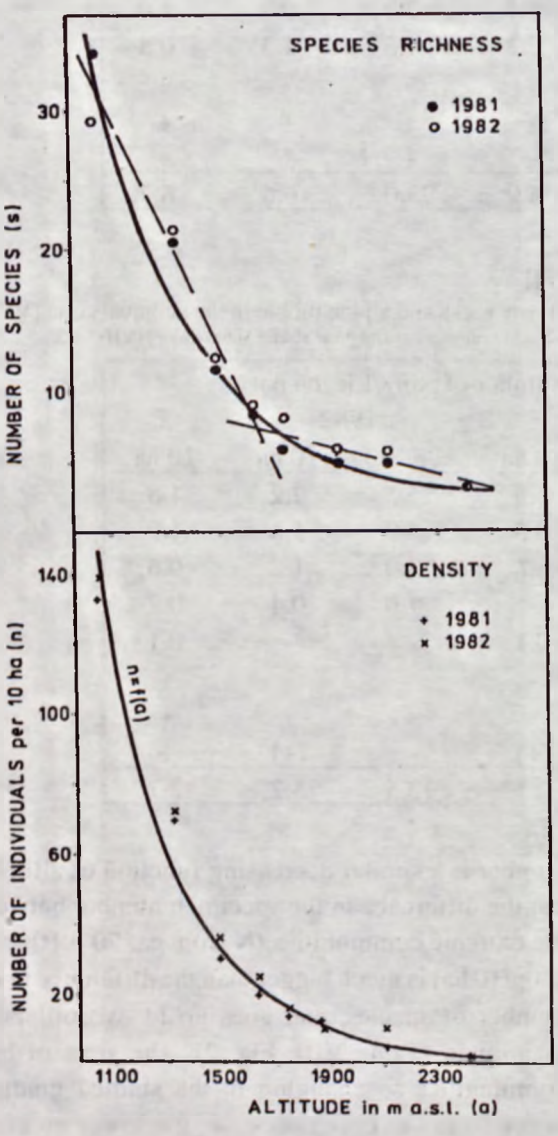

Fig.2. Curves of the decrease in bird species richness (S) and density (N) from beechwoods up to rocky peaks of the Polish Tatra

Ryc.2. Krzywe obrazujące spadek bogactwa gatunkowego (S) i zagęszczenia (N) ptaków od lasów bukowych po skaliste szczyty Tatr Polskich

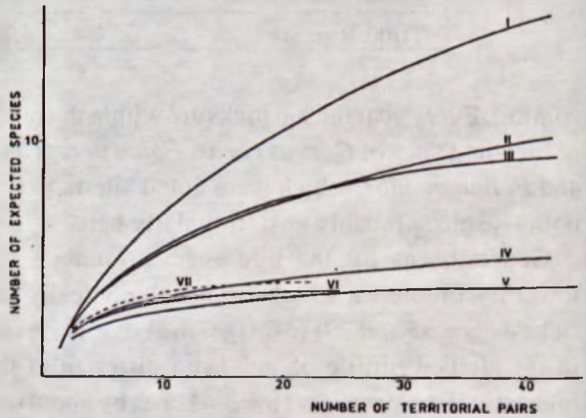

Fig.3. Rarefaction curves of the theoretical accumulation of bird species in the studied Tatra biotopes (I-VII)

Ryc.3. Krzywe rarefakcji obrazujące teoretyczną akumulację gatunków ptaków w badanych siedliskach tatrzańskich (I-VII)

TABLE VIII

Species number (S), density (N), species diversity (H') and equitability (J') of the bird communities in the studied Tatra biotopes I-VIII in 1981 (a) and 1982 (b). N - number of breeding pairs in 10 ha, H'_n and H'_b - species diversity described on the basis of the number of specimens or pairs (n) and the biomass (b), J'_n and J'_b - equitability for n and b

Liczba gatunków (S), zagęszczenie (N), różnorodność gatunkowa (H') i struktura dominacji gatunkowej (J') w zespołach ptaków badanych siedlisk tatrzańskich I-VIII w latach 1981 (a) i 1982 (b). N - liczba par na 10 ha, H'_n i H'_b- różnorodność gatunkowa opisana na podstawie liczby osobników (n) i biomasy (b), J'_n i J'_b - wskaźniki udziału gatunków w zespołach dla wartości n i b

		Biotopes Siedliska	S		N		H'_b		H'_n		J'_n		J'_b	
			a	b	a	b	a	b	a	b	a	b	a	b
I	<	Beechwood Buczyna	35	29	65.8	68.8	4.0	3.8	4.0	3.8	0.8	0.8	0.8	0.8
II	<	Spruce forest Świerczyna	21	22	35.9	36.0	3.0	2.8	3.3	3.0	0.7	0.6	0.7	0.7
III	><	Dwarf pine	12	13	16.0	18.7	2.9	2.8	2.8	2.9	0.8	0.8	0.8	0.8
IV	><	Kosodrzewina	9	9	10.1	13.5	1.9	1.9	2.0	2.0	0.6	0.6	0.6	0.6
V	><	Alpine meadows	6	9	7.1	7.5	1.6	1.9	1.4	1.9	0.6	0.6	0.5	0.6
VI	><	Hale	5	6	6.9	6.6	1.6	2.0	1.6	2.2	0.7	0.8	0.7	0.9
VII	><	Bare rocks	5	5	2.1	5.2	1.6	1.9	1.5	1.9	0.7	0.8	0.7	0.8
VIII	><	Szczytowe skały	3	3	0.2	0.2	1.5	1.5	0.9	0.5	0.9	0.9	0.6	0.3

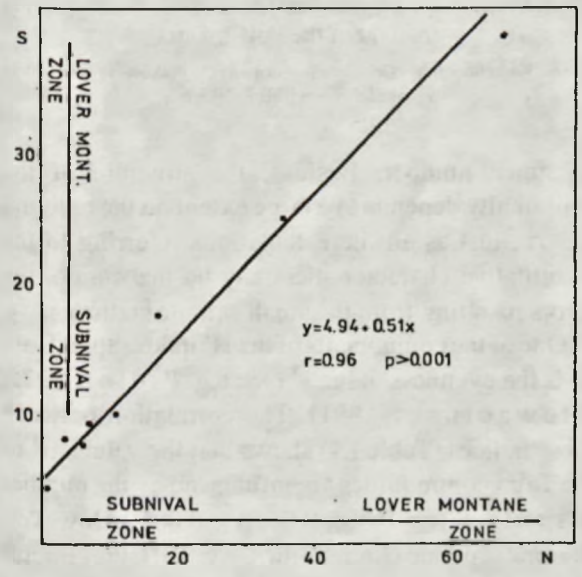

Fig.4. Correlation between the numbers of species (S) and specimens (N) in the zonal bird communities of the Tatra National Park. N is the average number of pairs in 10 ha for the breeding seasons 1981 and 1982

Ryc.4. Zależność między liczbą gatunków (S) a liczebnością osobników (N) w zonalnych zespołach ptaków Tatrzańskiego Parku Narodowego. Wartość N stanowi średnią liczbę par na 10 ha dla sezonów lęgowych 1981 i 1982

homogenous dwarf pine community (IV or V), and then remains more or less stable (Table VIII, Fig. 5). The expected decrease in the species diversity from the richest communities to the sparsest ones at the upper forest border is not always monotonic. It is most evident in the case of the H'_n value which, especially in the season 1982, soars for the heterogenous dwarf pine community (III), compared with the neighbouring communities (II and IV). Therefore, by applying the species diversity formula, it was possible to prove the ecotonal character of the zone at the borderline between th upper montane forests and the subalpine dwarf pine. However, the values of H'_n indicate that this ecotone is only weakly distinguished in the avifauna structure. Other indices, such as S, N and B (Figs. 2 and 6) do not suggest that it is an ecotone at all. It seems that groups of trees and single trees in the dwarf pine community favour a gentle transition from the avifauna of mountain forests to that of the shrubs and meadows of the alpine zone. The curves of the species diversity H'_n and H'_b however, inflect sharply in the dwarf pine zone (habitats IV or V) and then remain on a quite uniform level of 1-2 bits (Fig. 5). As for the species diversity, two basic bird formations appear: the forest formation together with the transitional zone

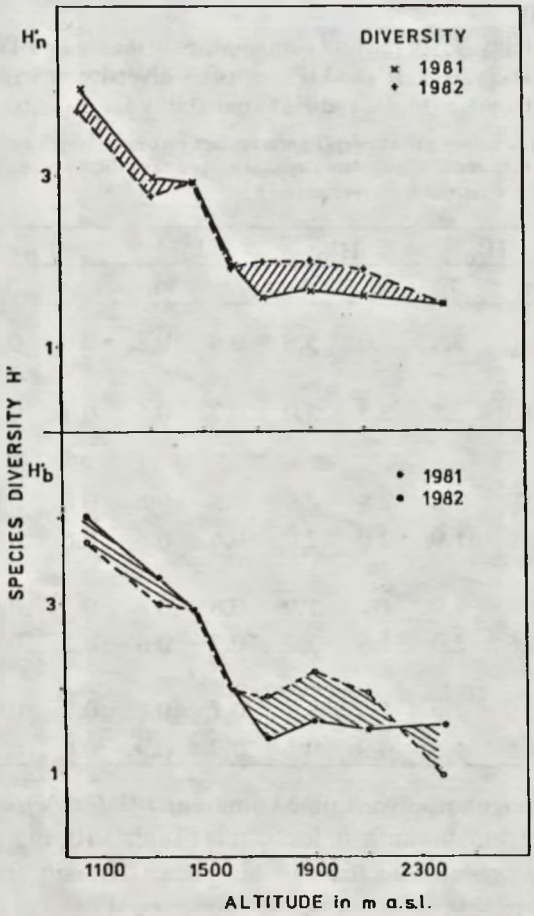

Fig.5. Species diversity (H') of bird communities in the biotope differentiation of the Polish Tatra, calculated with regard to number of specimens (H'_n) and biomass (H'_b)

Ryc. 5. Różnorodność gatunkowa (H') zespołów ptaków na tle zróżnicowania siedliskowego Tatr Polskich obliczona w odniesieniu do liczby osobników (H'_n) i biomasy (H'_b)

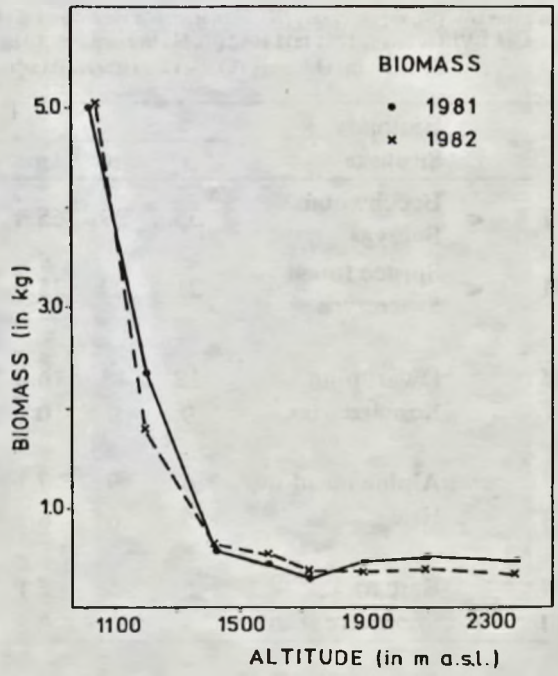

Fig.6. Biomass (in kg per 10 ha) of adults in the altitudinal gradient of the Polish Tatra

Ryc.6. Kształtowanie się biomasy dorosłych ptaków w gradiencie wysokościowym Tatr Polskich

to the dwarf pine bushes (I-III) and more meagre, i.e. the alpine one (IV-VII).

What is characteristic are the similar indices of bird species diversity in the communities of hetero- and homogenous dwarf pine community (III and IV) in the two studied seasons (Fig. 5). Although they are not sufficient to determine the stability of the bird communities, they suggest that the avifauna in these zones is more stable than in other biotopes. Also the community of the arbitrary subalpine region (VIII) reveals the same species diversity (H'_n) in both years of study, but at the same time it shows a clear seasonal changes in the diversity calculated on the basis of the bird biomass H'_b. This result is obvious, as the diversity of the extremely sparce community is far greater with respect to the biomass than to the specimen number. Besides, the structure of the community depends to a large extent on the external factors, just as all the calculations referring to the quantitative characteristics may be inaccurate, the errors resulting from the small sample statistics.

One of the components of the H' index (apart from S) is the evenness value J' (see e.g. P i e l o u 1975, G ł o w a c i ń s k i 1981). The correlation between these indices (Table IX) shows that the values H' of the Tatra communities are influenced by the number of species S ($r = 0.88 - 0.96$, $p < 0.001$). However, in some separate communities, e.g. VIII, the structure of the species dominance J' markedly influenced a higher or lower H' (see J'_n and H'_n, J'_b and H'_b - - Table VIII). It was not proved that the structure of species dominance J' was dependent exclusively on the sizes of the described bird communities. However, there is a close similarity between the species diversities calculated for both variants H'_n and H'_b ($r = 0.93$ and 0.98, with $p < 0.001$).

TABLE IX

Correlation matrix of the structural indices of the Tatra bird communities. S - number of species, H' - species diversity, J' - equitability (= evenness). The last two indices have been calculated with regard to the number of specimens (n) and biomass (b). The coefficients of correlation (r) and probability (p) have been presented separately for both study years in a double row

Macierz korelacji wskaźników strukturalnych tatrzańskich zepołów ptaków. S - liczba gatunków, H' - różnorodność gatunkowa, J' - struktura dominacji gatunkowej. Dwa ostatnie wskaźniki obliczono w odniesieniu do liczby osobników (n) i biomasy (b). Współczynniki korelacji (r) i wartości prawdopodobieństwa (p) podano osobno dla obu lat badań w podwójnym szeregu

	H'_n	S	J'_n	H'_b	J'_b	
H'_n	1.00	0.96^{*}	0.28^{***}	0.98^{*}	0.72^{**}	1981
	1.00	0.95^{*}	-0.01^{***}	0.93^{*}	0.51^{***}	1982
S	-	1.00	0.18^{***}	0.95^{*}	0.59^{**}	1981
	-	1.00	-0.23^{***}	0.88^{*}	0.34^{***}	1982
J'_n	-	-	1.00	0.12^{***}	0.47^{***}	1981
	-	-	1.00	-0.24^{***}	-0.04^{***}	1982
H'_b	-	-	-	1.00	0.71^{**}	1981
	-	-	-	1.00	0.72^{**}	1982
J'_b	-	-	-	-	1.00	1981
	-	-	-	-	1.00	1982

* $p < 0.001$ ** $p < 0.05$ *** $p > 0.01$

3. Biomass of adults

The total biomass of birds (excluding the young) in the described series of communities is from 5.10 kg in 10 ha (beechwood - I) to 0.27 kg in 10 ha (alpine meadows - V) on average for both seasons. The biomass of birds in the Tatra beechwood and in the spruce wood of the upper montane zone is 16 to 7 times bigger than in the subalpine and alpine biotopes (Table X) respectively. The biomass of all the bird communities formed above the upper forest border remains on a quite uniform low level from 251 up to 650 ($\bar{x}$ = 266-609 g/10 ha; Table XI, Fig. 5).

In the beechwood of the lower montane zone the biomass of birds was dominated by the pair *Strix aluco* ($\bar{x}$ = 1300 g/10 ha) and the subsequent one was *Fringilla coelebs* ($\bar{x}$ = 690 g/10 ha). In the spruce forest the dominating species were - *Fringilla coelebs* ($\bar{x}$ = 511 g/10 ha) and *Erithacus rubecula* ($\bar{x}$ = 396 g/10 ha). In the zones from the dwarf pine bushes up to the alpine meadows (III-VI), the most numerous species constituted the biggest part of the biomass; these species were: *Prunella modularis* ($\bar{x}$ = 255 g/10 ha, i.e. 40 per cent - zone III; $\bar{x}$ = 210 g/10 ha, i.e. 47 per cent - IV), *Anthus spinoletta* (x = 150 g/10 ha, i.e. 56 per cent - V; $\bar{x}$ = 122 g/10 ha, i.e. 38 per cent - VI). In the top regions of the Tatra, the size of the biomass of the sparse avifauna is markedly influenced by bigger birds (e.g. *Corvus corax*, and *Falco* spp.), than the ones which occur in lower and more densely populated biotopes.

4. Indicator and characteristic species

Looking at the spectral ranges of the particular bird species (Table XI) it is not possible to distinguish strictly indicator species (i.e. the ones which show a strong habitat preference) for each of the described biotopes. The zones of bird occurrence are here usually broader than it would follow from the distribution of the sample plots. Besides, many bird species are multizonal or even azonal (e.g. *Phoenicurus ochruros, Acanthis cannabina, Phylloscopus trochilus, Sylvia atricapilla*), which is related more to the structure of the biotope rather than to the mountain zonation.

In mountain forests it is possible to identify only the characteristic species, i.e. preferring the given biotopes (highest density). The present data confirm the facts known to field ornithologists that in the Carpathian beechwood these are mainly *Ficedula parva, Phylloscopus sibilatrix* and *Tetrastes bonasia*. The bird characteristic of the spruce wood are *Regulus ignicapillus, Picoides tridactylus* and *Nuci-*

TABLE X

Biomass (grams per 10 ha) of adult birds in the studied Tatra biotopes
Biomasa (gramy na 10 ha) ptaków dorosłych w badanych siedliskach tatrzańskich

		Kind of biotope / Rodzaj siedliska		1981	1982	$\bar{x}$
I		Beechwood Buczyna		5012	5097	5055
II		Spruce forest Świerczyna		2374	1780	2077
III	>	Dwarf pine Kosówka	heterogenous heterogeniczna	569	650	610
IV			homogenous homogeniczna	389	512	450
V	>	Alpine meadows Łąki wysokogórskie	with dwarf pine z kępami kosówki	256	276	266
VI			without dwarf pine bez kęp kosówki	332	300	316
VII	>	Bare rocks Otwarte skały, turnie		531	322	426
VIII				393	251	322

fraga caryocatactes. Such species as *Pyrrhula pyrrhula, Regulus regulus, Loxia curvirostra* and *Turdus torquatus* are present in both forest types, up to the highest tree biogroups.

In the highest dwarf pine area (communities IV-V) the most indicative species is the boreal-alpine *Acanthis flammea* and to some extent also *Luscinia s. svecica*; the occurrence of the latter one is limited to the upper dwarf pine close to the lakes in Dolina Pięciu Stawów Polskich and in Hala Gąsienicowa (supplementary data from June 1983). It is not absolutely certain whether the latter species nests regularly in the Tatra. In the dwarf pine and on the alpine meadows (communities III-VII), i.e. in the whole subalpine and alpine zones of the Tatra, *Anthus spinoletta* and to some extent also *Phoenicurus ochruros* (alpine subpopulation) can be regarded as indicator species. In the zones of open alpine meadows and alpine rubble the indicator species are *Prunella collaris* and infrequently *Oenanthe oenanthe*. The steep top rocks are characterized by *Tichodroma muraria*, although this zone is most strongly dominated by some bigger birds not limited in their occurrence to this high mountain biotope (*Falco tinnunculus, Falco peregrinus, Corvus corax* and others).

Two species of broadest spectra of occurrence are *Prunella modularis*, reaching from the lowest regions up to the highest clumps of the dwarf pine (biotopes I-VI) and *Motacilla cinerea* connected with watersides, whose occurrence does not correspond to the altitudinal zonation and which reaches the regions of stream sources (also I-VI).

TABLE XI

Range spectra of the breeding bird species in the altitudinal zonation of the Polish (northern) Tatra biotopes. I - beechwood, II - spruce foret, III - dwarf pine with spruce and stone pine groups, IV - homogenous dwarf pine, V - alpine meadows with dwarf pine, VI - alpine meadows and rocky deris, VII - alpine meadows and rocks, VIII - bare rocks

Spektra zasięgowe lęgowych gatunków ptaków na tle wysokościowej zonacji siedliskowej Tatr Polskich (północnych). I - buczyna dolnoreglowa, II - świerczyna górnoreglowa, III - kosówka z biogrupami świerka i limby, IV - kosówka homogenna, V - łąki alpejskie (hale) z kosówką, VI - łąki alpejskie i osuwiska skalne, VII - łąki alpejskie i skały, VIII - otwarte skały (turnie)

Zonal habitats / Siedliska zonalne Species / Gatunki	I	II	III	IV	V	VI	VII	VIII
	Altitude in m a. s. l./Wysokość w m n. p. m.							
	960--1100	1300--1400	1400--1580	1500--1720	1600--1800	1700--2000	1900--2100	above 2100m
Carduelis chloris	***							
Ficedula hypoleuca	***							
Sylvia borin	***							
Aegithalos caudatus	-----							
Coccothraustes coccothraustes	-----							
Dendrocopos major	-----							
Dryocopus martius	-----							
Muscicapa striata	-----							
Tetrastes bonasia	-----							
Turdus pilaris	-----							
Ficedula parva	-----							
Parus major	-----							
Sitta europaea	-----							
Strix aluco	-----							
Phylloscopus sibilatrix	===							
Parus montanus	-----	***						
Turdus philomelos	-----	-----						
Turdus merula	-----	-----						
Turdus viscivorus	-----	-----						
Carduelis spinus	-----	-----						
Certhia familiaris	-----	-----						
Garrulus glandarius	-----	-----						
Troglodytes troglodytes	***	-----						
Pyrrhula pyrrhula	-----	-----	-----					
Phylloscopus trochilus	-----		-----					
Sylvia curruca	***		-----					
Sylvia atricapilla	-----		-----	-----				
Phylloscopus collybita	-----	-----	-----					
Fringilla coelebs	===	===	-----					
Erithacus rubecula	===	===	-----					
Parus ater	===	-----	-----					
Regulus regulus	-----	-----	-----					
Anthus trivialis	-----	***	-----					
Loxia curvirostra	***	***	***					
Turdus torquatus	***	-----	-----	***				
Motacilla cinerea	***	-----	-----	-----	-----	***		
Prunella modularis	-----	-----	===	===	-----	-----		
Phoenicurus phoenicurus		***						
Picoides tridactylus		***						
Regulus ignicapillus		***						
Tetrao urogallus		***						
Parus cristatus		-----						
Nucifraga caryocatactes		-----	***					
Anthus spinoletta			-----	-----	-----	-----	-----	
Phoenicurus ochruros			-----	-----	-----	-----	-----	
Motacilla alba				-----				
Luscinia s. svecica				-----	-----			
Acanthis flammea				-----	-----			
Acanthis cannabina				***	***			
Oenanthe oenanthe					***	-----	-----	
Prunella collaris					***	-----	-----	
Falco tinnunculus						***	***	***
Falco peregrinus							***	***
Corvus corax							***	***
Tichodroma muraria							***	***

--- less than 1 pair / mniej niż 1 para, ----- 1 ≥ 5 pairs / 1 ≥ 5 par, === 5 ≥ 10 pairs / 5 ≥ 10 par, === 10 ≥ 15 pairs per 10 ha/10 ≥ 15 par na 10 ha,
*** rare nesting species signed with + in Tables I-VII / rzadkie gatunki oznaczone znakiem + w tabelach I-VII

5. Vertical distribution of some pairs of the congeneric bird species

Among the Tatra birds it is possible to distinguish several pairs of congeneric species whose vertical ranges and habitat selectivities are separate or partly overlapping. The most characteristic and superseding species which are taxonomically close in this mountain region are *Anthus trivialis* and *A. spinoletta* as well as *Prunella modularis* and *P. collaris*.

A comparison of the results obtained by the census method on the eight zonal plots (Fig. 7) provides a quite clear although certainly a little simplified picture of the vertical distribution of the birds with regard to the degree of the habitat preferences of the particular species.

Anthus trivialis is a species typical of thin forests and of forest ecotones. In the Polish Tatra it reaches the upper forest border and heterogenous dwarf pine (up to 1550 m above sea level), where its density is higher than in the beechwood. *Anthus spinoletta* occurs in the heterogenous dwarf pine community; it reaches its optimum of occurrence (the highest N) in the upper regions and in the places where the dwarf pine penetrates the region of the alpine meadows (1400-1800m above sea level). The limit of the vertical range of this species i the Polish High Tatra is in the rocky bare ridges in the subnival zone, i.e. it reaches a little higher than 2100 m above sea level. The zone where the two *Anthus* species overlap is the upper forest border and dwarf pine thicket with tree biogroups. According to Klima (1959), the separate-occurrence zones of these species on the southern slopes of the High Tatra is almost the same as on the Polish northern slopes, the only difference being that the optimum of the occurrence of *Anthus trivialis* was at the upper forest border composed partly of *Larix decidua* which was not found on the northern slopes.

The *Anthus* species nest on the ground in the grass and undergrowth; *Anthus trivialis* practically does not go beyond the trees, whereas *A. spinoletta* sticks to shrubs, even if they are very thin.

The vertical range of *Prunella modularis* stretches continuously from the lowermost regions up to the alpine meadows with clumps of dwarf pine at an altitude of about 2000 m (Fig.7). This species reaches its highest density (6.3-7 p/10 ha) in the lower dwarf pine community (zone III). An outline of the range of *Prunella modularis* for the Slovak Tatra was presented by Klima (1959). The replacement congeneric species of *Prunella collaris* was found already in the upper dwarf pine community passing into the alpine meadows, at an altitude of about 1650 m and it reached the rocky peaks (up to 2100 m above sea level).

This species reaches its optimum of occurrence in the zone of open alpine meadows, at an altitude of 2000 m. The region where the vertical ranges of both representatives of the genus *Prunella* in the Polish Tatra overlap is at an altitude of 1600-2000 m. In the Slovak Tatra it is almost the same but slightly lower, at an altitude of 1500-1970 m (Klima 1959). It should be noted that the area of occurrence of *P. collaris* in the Slovak Tatra is much broader (by almost 600 m) and is 1500-2600 m, with the hypsometric optimum at 1800-2300 m (Mošansky 1974). Higher ranges of some species on the southern side of the Slovak Tatra are noted for a number of other species (e.g. *Anthus trivialis* - up to 1700 m, *Acanthis flammea* - 2000 m), although it is not a rule. This is due mainly to the fact that the Slovak Tatra are higher than Polish and the southern exposition of the slopes dominating there moves the bioclimatic zones upwards (there is no beechwood zone), compared with the respective zones on the northern slopes of the Polish Tatra. The differences in ranges in the comparable works follow partly from the fact that different census methods were applied. The mapping method used in this study on some fixed sample plots gives the most accurate number estimations of the breeding avifauna, whereas the method of censuses on continuous transects applied by Balat et al. (1955) and Klima (1959) provides a relative but clearer diagram of these ranges in the hypsometric profile of the mountains.

The problem of zonal separation of other congeneric species, such as *Phoenicurus phoenicurus* and *Ph. ochruros*, *Acanthis cannabina* and *A. flammea* or *Parus major* and *P. cristatus* (see Table XI) requires special and more accurate field studies.

6. The faunal and geographical status of the identified species

The bird communities described here are dominated by common species of central European lowlands and highlands. Most of these species belong to the forest fauna and the limit of their hypsometric range is at the upper forest border or in

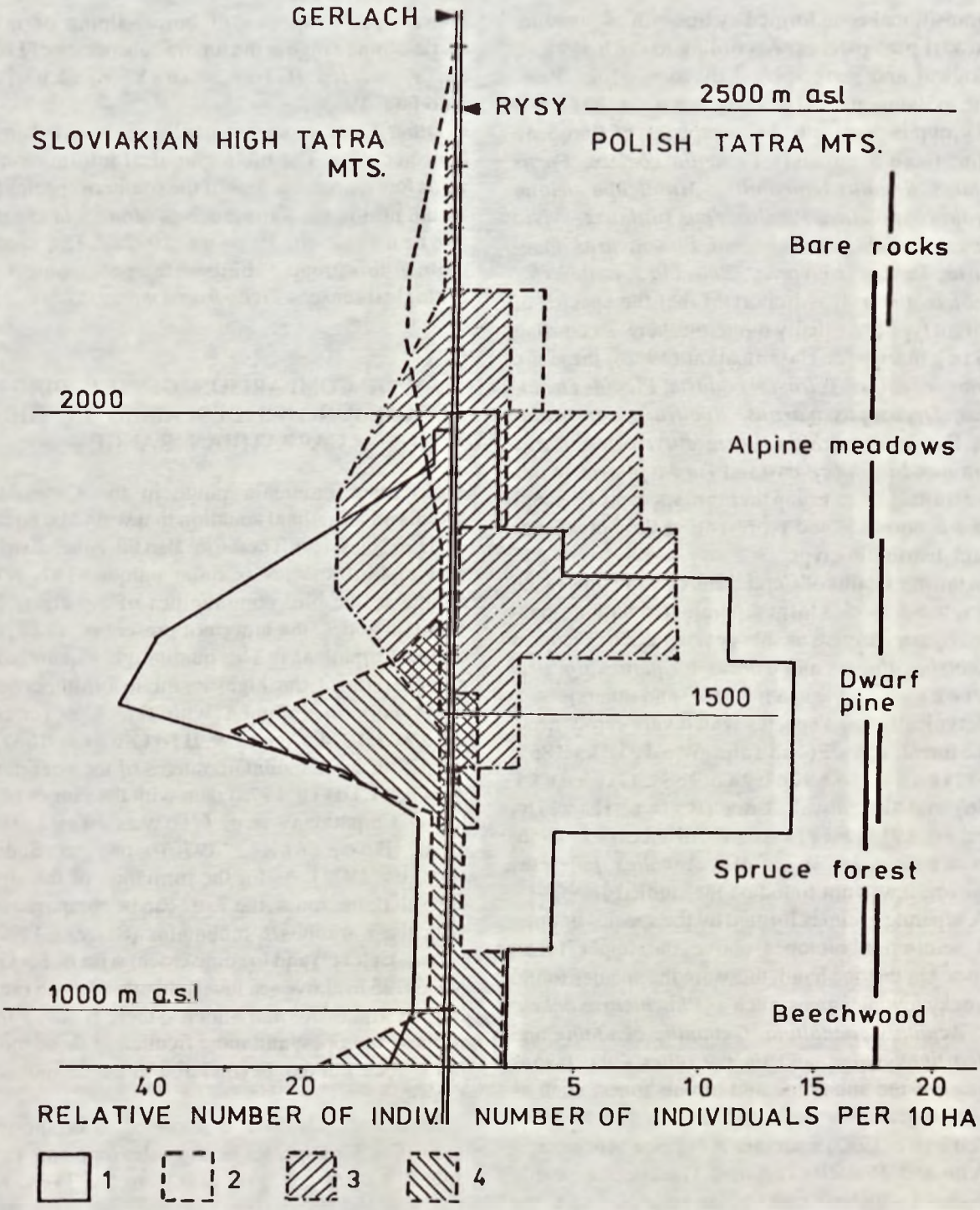

Fig.7. Distribution of two congeneric species typical of the Tatra avifauna: *Anthus trivialis/Anthus spinoletta* and *Prunella modularis/Prunella collaris*. Data for the Slovak Tatra according to K l i m a (1959); the compared results were obtained by different methods and presented in the diagram in a different way. 1 - vertical range of *Prunella modularis*, 2 - *P. collaris*, 3 - *Anthus spinoletta*, 4 - *A. trivialis*

Ryc.7. Rozmieszczenie dwóch charakterystycznych dla awifauny Tatr par gatunków kongenerycznych: *Anthus trivialis/Anthus spinoletta* i *Prunella modularis/Prunella collaris*. Dane dla Tatr Słowackich podano według K l i m y (1959); porównywane wyniki uzyskano różnymi metodami i wykazano je na wykresie w nieco odmienny sposób. 1 - zasięg pionowy *Prunella modularis*, 2 - *P. collaris*, 3 - *Anthus spinoletta*, 4 - *A. trivialis*

the transitional zone formed by tree groups invading the dwarf pine patches. According to the historical, ecological and geographical division of the Palearctic avifauna made by Stegmann (1938), this bird group is dominated by the species of European origin; these are mainly *Fringilla coelebs, Parus cristatus, Regulus ignicapillus, Muscicapa striata, Ficedula hypoleuca, Phylloscopus sibilatrix, Sylvia atricapilla, Erithacus rubecula, Phoenicurus phoenicurus, Turdus viscivorus, T. merula T. philomelos* and *Strix aluco*. It is important that the species of Siberian type are equally numerous here. According to Stegmann's classification (1938), these are *Tetrao urogallus, Tetrastes bonasia, Picoides tridactylus, Dryocopus martius, Nucifraga caryocatactes, Pyrrhula pyrrhula, Loxia curvirostra, Parus montanus, Ficedula parva* and *Turdus pilaris*. In this Siberian-taiga bird group there are species of discontinuos occurrence and representing the boreal-mountain distribution type.

In the mountains of Central Europe and thus in the Tatra, these species form separate populations classified by taxonomists as subspecies, such as *Picoides tridactylus alpinus* and *Turdus torquatus alpestris* (Ferens 1962, Ferianc 1979 and others).

A typically taiga species which very rarely nests in the forests of the Polish Tatra (Wodzicki 1851, Karliński 1882, Kocyan 1884, Cichocki 1986) and the Slovak Tatra (Balat, Havlin, Hudec 1955, Ferianc, Feriancova 1956, Mošansky 1974) is also *Aegolius funereus*; however, it was not found on the studied areas.

A separate group is formed by the species of open and semi-open biotopes above the upper forest border. On the one hand, these are the species found on rocky lowland areas, such as *Phoenicurus ochruros, Acanthis cannabina, Oenanthe oenanthe* and *Falco tinnunculus*, and on the other - the taxons typical of the subalpine and alpine zones, such as *Acanthis flammea cabaret* (see Hanzak 1953, Jakubiec 1992) *Luscinia s. svecica, Anthus spinoletta* and *Prunella collaris*. The species strictly connected with bare rocks of the subalpine up to the subnival zones is the paleomontane *Tichodroma muraria*. It occurs also in low rocky mountains (e.g. the Pieniny) and therefore it cannot be considered as typical of high mountains. In the Tatra the only typically alpine species is *Prunella collaris*. A boreal-alpine species is *Acanthis flammea*, which is included by Stegmann (1938) in the Siberian fauna type. A species of boreal-alpine or rather arctic-alpine range is the tundra subspecies of *Luscinia s. svecica* (Głowaciński, Jakubiec, Profus 1983).

Other fauna types are hardly represented in the collected data. The bibliographical information reveals few representatives of the southern species that would nest in the Tatra, such as *Monticola saxatilis* (Ferens 1954b, Profus 1992a). The species close to this group of birds in the geographical and ecological sense is *Tichodroma muraria*.

V. A COMPARISON OF THE BIRD COMMUNITIES DESCRIBED IN THE CARPATHIAN RANGE

No other mountain range in the Carpathians reveals an altitudinal zonation that would be equally clear and classical. Therefore also the zonal distribution of bird species is quite unique. This refers mainly to the bird communities of the alpine and subnival zones, the latter not present in other parts of the Carpathians. The qualitative - quantitative composition of the high-mountain ornithocenoses have more in common with the Alps (cf. e.g. Bezzel 1974, Glutz v. Blotzheim 1987) or even with some mountain ranges of the continental Asia (cf. Złotin 1975) than with the ranges of the lower Carpathians (e.g. Głowaciński 1969, 1990, Bocheński 1970) or the Sudetes (Dyrcz 1973). As for the formation of the alpine and subalpine zones, the Tatra can be compared only with the Karkonosze mountains (Śnieżka 1602 m above sea level) and to some extent with Babia Góra Mt. (1725 m above sea level). In other Polish ranges of the Carpathians and Sudetes, there is only a trace of these biotopes, and most frequently these mountains does not go beyond the zone of mountain forests.

If *Anthus spinoletta* is assumed to be the most indicative bird species of the subalpine and alpine zones, it turns out that apart from the Tatra, Karkonosze and Babia Góra (where both these zones are fully formed), this indicator was also noted in some relatively low mountain massifs deprived of the typically alpine or even subalpine zones.

In Poland these mountains include the Bieszczady (Tarnica 1346 m, marginal subalpine zone with *Alnus viridis*, and open Eastern Carpathian meadows, so called "poloninas"), the Gorce (Turbacz

1310 m, only open top glades), Pilsko Mt. (1557 m, marginal zones of dwarf pine and subalpine meadows), Śnieżnik Kłodzki Mt. (1427 m, only subalpine meadows and top peat bogs), the Izerskie Mountains (Wysoka Kopa 1127 m, marginal zones of dwarf pine and subalpine meadows).

The alpine character of the avifauna is strenghtened by the occurrence of such species as *Prunella collaris* (apart from the Tatra also in the Karkonosze, at Babia Góra, single pairs in the Bieszczady and at Śnieżnik), *Acanthis flammea* and *Luscinia s. svecica* (apart from the Tatra also in the Karkonosze and *Acanthis flammea* also in the Śnieżnik massif; e.g. Tomiałojć 1972, Dyrcz 1973, Głowaciński, Jakubiec, Profus 1983, Cichocki 1986). In Poland, the main refuge of all these species is in the Tatra. Although the basic composition of the alpine and subalpine ornithocenoses repeats to a various degree in these mountains, the qualitative-quantitative relations between the bird communities above the upper forest border in the Tatra differ considerably from those in the lower mountain massifs mentioned above (cf. Głowaciński 1969, Bocheński 1970, Dyrcz 1973). Since these communities in various mountain ranges are not equally well-known, it is impossible now to make more accurate comparisons.

The breeding avifauna of the Tatra subalpine forests and the avifauna of forests of other Carpathian regions have quite a lot in common (Bocheński 1960, 1970, Kozłowski 1974, Głowaciński 1990, Cichoń, Zając 1991).

Comparing the structures of the bird communities of these biotopes (Table XII), we can conclude that the level of similarity Re of the forest aggregations of birds of the Polish Carpathians and Tatra is usually higher than 50 per cent.

The similarity levels of the communities of beechwood and lower montane mixed forests dominated by spruces and firs as well as lower and higher montane spruce forests are higher and amount to Re = 57.0-67.1 and 65.5-72.2, respectively. Thus the mixed forests of the lower montane zone are the region of a gentle transition from the avifauna of the beechwood to that of the spruce wood of the upper montane zone. The similaripy ylevel between the avifaunas of the natural spruce forest of the upper montane zone in the Polish Tatra and the Turbacz natural reserve in the Gorce is high and amounts to 72.2 per cent. As for their structure, the breeding communities of the Tatra forests belong to practically the same formations of subalpine birds as the ones which are typical of the whole Polish Carpathians and probably other central European mountains. A comparison with the materials of Dyrcz (1973) and Z. Jakubiec (unpubl.) shows that these high levels of similarity can also refer to the avifaunas of the forests of the Karkonosze National Park and of the massif of Śnieżnik.

However, a comparison of the structures of bird communities of the Carpathian and Karkonosze beechwood of the lower montane zone with the old lower-lying beechwoods (e.g. on the Sudety foothill - about 300 m above sea level; Jakubiec 1972) points to significant differences between the avifaunas of these zones. The differences lie mainly in the size of the described communities (in the sense of S and N), as well as in a considerable number of typically lowland elements in the foothill forest (e.g. *Parus caeruleus, Dendrocopos medius*) and elements that are synanthropic to some extent (e.g. *Sturnus vulgaris, Passer montanus, Corvus monedula*), which are not present in typically mountain forests.

VI. NUMBER ESTIMATION OF BIRDS IN THE POLISH TATRA NATIONAL PARK

Using the sample estimations of the number of birds in the particular biotopes, it is possible to make a rough estimate of the number of these birds on a larger-aea scale. Such attempts were made especially in West European countries (e.g. Dybbro 1976, Bezzel, Lechner 1978, Rheinwald 1982, Verbreitungsatlas der Brutvögel 1980). The most accurate estimations were performed in the region of Lake Constance (Bodensee 1670 km^2) and Kanton Zürich (1729 km^2) with the application of special methods (Schuster et al. 1983, Weggler 1991).

The number estimation of the whole breeding avifauna in the Tatra National Park was based on the data from the particular sample plots for the MM (I-VIII, see p. 69),and also on supplementary transect censuses in a fifty-meter belt in the forests and a hundred-meter belt in the biotopes which were easier to study. The results were extrapolated on the whole area of the biotopes occupied by individual species. In the case of the species for which the methods and times of censuses were not good enough (e.g. *Loxia*

TABLE XII

Comparison of the qualitative-quantitative composition of the bird communities in the subalpine forests of the Polish Carpathians and Tatra on the basis of Renkonen's formula (Re). Symbols: BE - beechwood, MC - mixed and pure coniferous forest, MS - mixed coniferous forest with domination of spruce, SW - spruce wood in the upper montane zone; Ta- Tatra Mts, Bi - Bieszczady Mts., (Cichoń, Zając 1991, data from 1987), Tu - Turbacz nature reserve in Gorce Mts (Kozłowski 1974), Ka - Kamienica watershed in Gorce Mts (Głowaciński 1990). Similarity classes for Re = 55-65, 66-75 and over 75 have been distinguished

Porównanie składu gatunkowo-ilościowego zespołów ptaków lasów reglowych polskich Karpat i Tatr w oparciu o formułę Renkonena (Re). Oznaczenia: BE - buczyna, MC - dolnoreglowy bór jednolity świerkowy i mieszany, MS - bór mieszany z dominacją świerka, SW - górnoreglowa świerczyna; Ta - Tatry, Bi - Bieszczady (Cichoń, Zając 1991 z 1987), Tu - rezerwat Turbacz w Gorcach (Kozłowski 1974), Ka - zlewnia Kamienicy w Gorcach (Głowaciński 1990). Wyróżniono klasy podobieństwa dla Re = 55-65, 66-75 i powyżej 75

BE-Ta	BE-Bi	BE-Tu	BE-Ka	MC-Ka	MS-Ka	SW-Tu	SW-Ta	
-	57.8	61.5	67.1	64.5	64.0	56.2	53.5	BE-Ta
	-	59.4	59.9	62.5	57.8	56.2	50.0	BE-Bi
		-	57.0	61.3	58.0	65.0	57.3	Be-Tu
			-	73.0	80.4	51.2	49.9	BE-Ka
				-	83.9	68.6	65.5	MC-Ka
					-	59.2	59.0	MS-Ka
						-	72.2	SW-Tu
							-	SW-Ta

curvirostra, Corvus corax, Nucifraga caryocatactes), the estimations were made on the basis of all the field observations and frequency of occurrences.

From 10 May to 10 June 1982: 1- Dolina Białego - Upłaz Kalacki, 2 - Dolina Potoku Strążyskiego - Przełęcz na Grzybowcu, 3 - along Małołącki Potok from its sources to Gronik, 4 - the tourist trail Morskie Oko - a cirque at Świstówka, 5 - the trail Morskie Oko - Włosienica, 6 - the road along Potok Kościeliski, 7 - Dolina Strażyska - Sarnia Skała - Dolina Białego, 8 - the vicinity of Morskie Oko, Dolina pod Mnichem, 9 - the road Kiry - Hala Ornak.

In June 1983: 1 - Kuźnice - the Murowaniec hostel - Stawy Gąsienicowe, 2 - Kasprowy Wierch - Staw Kurkowski, 3 - Kuźnice - Kalatówki, 4 - Hala Kalatówki, Kondratowa, Kopieniec Wielki, Jaworzyna and Rusinowa, 5 - the Czerwone Wierchy range, 6 - Kobylarz - Hala Miętusia - Dolina Małej Łąki, 7 - Dolina Chochołowska, 8 - Dolina Olczyska, 9 - Jaszczurówka - Stawy Toporowe.

In June 1986 a census was taken along the trail Hala Miętusia - Wantule.

The number of bird species identified in the Tatra National Park was estimated at about 44000-67000 territories (Table XIII). In the years 1981-1983 about 55 000 breeding pairs lived in the TNP, whereof about 50 000 bird pairs were found in the mountain forests. The two most numerous species, i.e. *Fringilla coelebs* and *Erithacus rubecula* constitute as much as 30-35 per cent of the avifauna of the Polish Tatra National Park.

Special direct number estimations of *Cinclus cinclus* and *Motacilla cinerea* were made in the Polish Tatra by W. Cichocki and P. Mielczarek (in print). In the years 1985-1989 in the streams of the TNP these researchers identified 45, 35, 48, 38 and 55 breeding pairs and territories of *Cinclus cinclus*, respectively. A low number of territories of this sedentary species in the seasons 1986 and 1988 should be associated with severe winters preceding the breeding seasons; particularly severe was the winter of 1987/88. The highest number of territories in the season of 1989 on the other hand, may be related to a very mild winter of 1988/89.

In the same years the number of *Motacilla cinerea* was estimated to be 74, 66, 102, 72 and 133 breeding pairs and territories, respectively. The connection between the weather conditions in the Tatra with the number of this migratory species as well as the reasons for considerable number differences are hard to explain.

About 500 territorial pairs and birds which do not form monogamic territorial pairs (e.g. *Cuculus ca-*

TABLE XIII

Number of estimation of the territories or breeding pairs occupied by the most numerous and medium number bird species of the Polish Tatra National Park. The basic data are for the years 1981-1982 and the supplementary ones for 1981-1986.

Szacunkowa liczba rewirów zajętych przez najliczniejsze i średnio liczne gatunki ptaków polskiego Tatrzańskiego Parku Narodowego. Główne dane pochodzą z lat 1981-1982, uzupełniające - z lat 1981-1986.

	Species Gatunek	Number of breeding pairs and territories Liczba rewirów i par lęgowych
(1)	*Fringilla coelebs*	11000 - 16000
	Erithacus rubecula	11000 - 15000
	Parus ater	3500 - 5000
	Regulus regulus	3500 - 4500
	Prunella modularis	2000 - 4000
	Anthus spinoletta	2000 - 2500
	Parus cristatus	1000 - 2000
	Turdus torquatus	1000 - 2000
	Sylvia atricapilla	1000 - 2000
	Anthus trivialis	1000 - 2000
	Phylloscopus trochilus	1000 - 1500
	Pyrrhula pyrrhula	1000 - 1500
	Phylloscopus collybita	500 - 1000
	Certhia familiaris	400 - 800
	Carduelis spinus	400 - 800
	Turdus melura	300 - 600
	Turdus philomelos	300 - 600
	Turdus viscivorus	300 - 600
	Phylloscopus sibilatrix	300 - 500
	Regulus ignicapillus	250 - 500
	Garrulus glandarius	250 - 500
	Troglodytes troglodytes	200 - 400
	Loxia curvirostra	200 - 400
	Prunella collaris	150 - 300
	Turdus pilaris	150 - 300
	Apus apus	100 - 200
	Parus major	100 - 200
	Tetrastes bonasia	70 - 200
	*Motacilla cinerea**	66 - 133
	Sylvia curruca	50 - 100
	Phoenicurus phoenicurus	50 - 100
	Saxicola rubetra	50 - 100
	Aegithalos caudatus	50 - 100
	Sitta europaea	50 - 100
	Parus montanus	50 - 100
	*Nucifraga caryocatactes***	30 - 100
(37)	*Cinclus cinclus**	35 - 55
(38-55)	Other species/Inne gatunki	300 - 620
	Total/Razem	~ 44000 - 67000

* After Cichocki and Mielczarek (in print)
Według Cichockiego i Mielczarka (w druku)

** Nesting in Eastern (High) Tatras only (Ferens, Wasilewski 1985)
Gnieździ się tylko w Tatrach Wysokich (Ferens, Wasilewski 1985)

norus) are found among rarer species such as *Muscicapa striata, Oenanthe oenanthe* (30-60 territories), *Coccothraustes coccothraustes* (25-50), *Corvus corax* (15-30), *Falco tinnunculus, Strix aluco, Dryocopus martius, Dendrocopos major, Ficedula parva* (10-20) and *Cuculus canorus* (30-60 males).

The rarest and most interesting species have been discussed in the following chapter.

VII. OCCURRENCE OF SOME RARE AND THREATENED SPECIES - REMARKS ON BIRD PROTECTION IN THE TATRA NATIONAL PARK

The Tatra are one of Europe's most important refuges of high-mountain and boral-alpine species. A number of distinct animal forms and plant communities originated here (Tatrzański Park Narodowy 1955, 1962, Fudakowski 1965 and others). This biological aspect was the main reason for establishing the Tatra National Park.

Also in the bird communities described here (Tables I-VII, XI), there are a number of species that are rare and limited in their occurrence to very specific biotopes (*Tichodroma muraria, Prunella collaris, Luscinia s. svecica, Picoides tridactylus* and others), or previously widely spread but today present only locally and threatened with extinction (*Tetrao urogallus, Falco peregrinus*).

In the case of the Tatra, the main question is: how big are the populations of such typically alpine and subalpine species as *Prunella collaris* or *Anthus spinoletta*? Table XIII provides a simplified answer to this question. The extrapolation of the data obtained on the sample areas shows that the population of *Prunella collaris* in the Polish Tatra National Park numbers approximately 150-300 (the former being more probable) territories (breeding pairs), which means that this is by far the richest habitat of this species in Poland. In the Karkonosze that are most similar (in our geographical region) to the Tatra, the number of breeding pairs of this species on the Polish side does not probably exceed 10 (Dyrcz 1973). In other Polish mountain ranges the number of this species is from a few (the Bieszczady, Śnieżnik Mt.; e.g. Głowaciński 1969, Tomiałojć 1990) up to a dozen or so pairs (Babia Góra Mt.; Bocheński 1970). The population of *Anthus spinoletta* is much larger and in the Polish Tatra it numbers 2000-2500 breeding pairs. This species, compared with the former one, occupies broader zonal ranges, and together with *Prunella modularis* they dominate above the upper forest border. Thus the Tatra population of *Anthus spinoletta* is capable of rapid regeneration after heavy losses caused by external factors. For instance, on 17 June 1982 in the middle of the breeding season a several-hour snowfall observed in Dolina Pięciu Stawów Polskich brought about the covering of almost all nests of *Anthus spinoletta* and destruction of some hatches, mainly the ones in the *pullus* stage, i.e. from the phenological optimum. The survivors were chiefly the earlier hatches with fully-fledged youngs and the later ones - in the egg stage. Thus in the season 1982 the population of *Anthus spinoletta* was exposed to the disruptive selection, which however does not seem to be a regular phenomenon here.

In the upper regions of the dwarf pine zone a small breeding population of *Acanthis flammea* lives. Its number in the Polish Tatra, estimated on the basis of the extrapolation of the data for the sample plots, is 20-40 breeding territories. The former data (Wodzicki 1851, Karliński 1882) and the contemporary ones (e.g. Kania, Wasilewski 1969, Feriance 1979, Winiecki 1979 and Cichocki 1986) show that this species has nested in the Tatra for a long time, maintaining the continuity of occurrence. Direct proofs are also provided by the present studies, in the course of which birds defending their territories and bringing food were observed. Moreover, in the middle of June 1982 Z. Jakubicc found a nest with eggs.

In the same biotope but more limited to the region of alpine post-glacial lakes, a small population of the tundra form of *Luscinia s. svecica* has originated (Głowaciński, Jakubicc, Profus 1983). This apparently recent (1980-81?) population concentrates in Dolina Pięciu Stawów Polskich (ca. 10 breeding territories in 1982). Additional studies carried out in the Polish Tatra resulted in finding only one singing male in the dwarf pine thicket near Długi Staw above Hala Gąsienicowa. So far, there has been no information about nesting of this species in other parts of the Tatra. Some observations in the Karkonosze (Dyrcz 1973) suggest that this form of *Luscinia s. svecica* may also nest in the Sudetes.

In the case of the above bird species no signs of threat from the local anthropogenic factors have

been noted. Changes in the populations of these species are more likely to come about under the impact of natural physical and biological factors. The protection of their refuges in the Polish Tatra in the form of a national park is sufficient at present and seems so in the long run, too.

This cannot be said about an extremely sparse population of *Tichodroma muraria*. In the Polish Tatra the number of the breeding pairs does not exceed 10 (see Głowaciński 1992) and 20 pairs in the Slovak Tatra (cf., e.g. Ferianc 1979). Besides, this species is strongly ecologically specialized (biotope, food) and therefore more threatened than *Luscinia s. svecica*, the latter being equally numerous in the Tatra and revealing signs of expansion in the geographical scale. The biggest number of *Tichodroma muraria* was observed on Raptawickie Turnie and Kominiarski Wierch (Cichocki 1986, also after J. Baryła - personal comm.). Since little is known about the situation of this species in the Tatra, one practical conclusion seems to be justified: accurate records of the breeding sites of this bird species should be kept and the species protected from human penetration. It is possible that the Tatra population of *Tichodroma muraria* is limited by some ecological birds of prey, e.g. *Corvidae*. In such a case active protection should be considered.

A representative of the Polish avifauna, extremely small in number, which nests in the Tatra, is also *Falco peregrinus* (Tomiałojć 1990). This species found in 1981 in the region of the top sample plots (Mnich, Wrota Chałubińskiego, Szpiglasowa Przełęcz), revealed signs of nesting (frequent patrolling of the same territory, loud call of one bird at the end of the possible laying - 12 July 1981). It is also highly probable that the observed birds formed the pair described by Cichocki (1986). Also *Aquila chrysaetos* was identified in the Polish Tatra. When controlling the sample plots in the seasons 1981 and 1982, the authors of the present paper noted single, typically variegated birds of this species, which were circulating in the region of Wołoszyn, Granaty, Świstówka Roztocka. Those could have been the birds which were nesting in the Western Tatra (Cichocki 1986) or coming from the Slovak Tatra (Ferianc 1977), and whose breeding territory overlaps with the Polish High Tatra (cf. Ferens, Wasilewski 1985). Many facts indicate that not more than one pair of each of the species, i.e. *Falco peregrinus* and *Aquila chrysaetos* nests in the Polish Tatra National Park.

In the forests and lower rocks of the Tatra National Park nest 6-7 pairs of *Bubo bubo* (Ferens, Wasilewski 1985, Profus 1992b). Little is known about the size of the Tatra population of gallinaceous birds, especially *Tetrao urogallus* and *Lyrurus tetrix*. According to Podobiński (e.g. 1960, 1979) and reports of the workers of the Tatra National Park, approximately 50-100 specimens of *Tetrao urogallus* and 30-40 specimens of *Lyrurus tetrix* occur in the Polish Tatra, and current lek arenas of both these species are found. Since it is a national park, these birds are not hunted for in the Tatra, and it is probably thanks to this form of protection that their populations have been more or less stable for years.

The Tatra are an important place of occurrence of the very rare *Picoides tridactylus*. Its number in the Polish Tatra is estimated at 20-50 breeding pairs. This estimation is partly confirmed by the observation of Wasilewski (1969). In the summer 1968 this author identified a total of 31 feeding specimens of *Picoides tridactylus* in fresh windfalls at different places in the Tatra forests. As these observations were rather random, the real size of the Tatra population of this species must have been much bigger.

The significance of the Tatra as a refuge for rare and singular species is much greater than selectively described here. Many bird species come to breed here only occasionally (e.g. *Monticola saxatilis* - Ferens 1954b), and the possible occurrence of some other species is not certain (e.g. *Charadrius morinellus* - an adult with two fledglings was seen on 13 July 1988, on the slopes of Małołączniak Mt - 1900 m a.s.l.; Czerwiński 1992) or even controversial (e.g. *Gyps fulvus* - Wodzicki 1851, cf. Tomiałojć 1990). The Tatra National Park protects the unique alpine biotopes which can also be inhabited by the bird species which come here incidentally from other geographical zones (e.g. *Apus melba* - Mošansky 1974, Cichocki 1984). Besides, there are some species (e.g. *Strix uralensis, Dendrocopos leucotos, Phylloscopus bonelli*), which are expected to occur in the forests of the northern Tatra, but whose presence there has not yet been proved.

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STRESZCZENIE

Badania ornitologiczne w Tatrach mają ponad stuletnią historię, lecz znajomość fauny ptaków tych gór z ekologicznego punktu widzenia ogranicza się właściwie do kilku prac wykonanych po słowackiej stronie Tatr. Prezentowane tu badania ten wycinek wiedzy o ptakach tatrzańskich w znacznym stopniu wzbogacają, a w szczególności wnoszą nowe dane do awifauny Tatrzańskiego Parku Narodowego.

Celem tej pracy było: (1) opisanie struktury lęgowych zespołów ptaków wykształconych w typowych biotopach Tatr Polskich, (2) określenie strefowego zróżnicowania tych zespołów według pięter roślinno-klimatycznych oraz (3) porównanie ich z awifauną odpowiednich siedlisk niektórych innych rejonów górskich.

Badania terenowe przeprowadzono w sezonach lęgowych 1981 i 1982 na ośmiu powierzchniach próbnych (od 10 do 65 ha), rozmieszczonych we wszystkich głównych siedliskach tatrzańskich, poczynając od buczyny reglowej (od ok. 960 m n.p.m.), a kończąc na piętrze turniowym (do ok. 2230 m n.p.m.). Badania te skoncentrowano w Tatrach Wysokich - w rejonie Morskiego Oka i Doliny Pięciu Stawów Polskich, a tylko jedną powierzchnię (dolnoreglową) zlokalizowano w obrębie Tatr Zakopiańskich (ryc. 1). Ten ekologiczny opis ptaków

odnosi się tym samym prawie do pełnego przekroju przez siedliska zonalne północnych stoków Tatr, poza którymi znalazły się jednak naturalne laski limbowe oraz sztuczne lub półnaturalne świerczyny w obrębie dawnych dolnoreglowych lasów bukowo-jodłowych.

Terenowe oceny liczebności ptaków prowadzono metodą kartowania, z zastosowaniem modyfikacji zwiększających jej efektywność. Dla szacunkowej oceny liczby ptaków całego polskiego Tatrzańskiego Parku Narodowego - w uzupełnieniu metody kartograficznej - prowadzono nieregularne sondażowe liczenia na pasach o szerokości zależnej od przejrzystości siedliska. Oceniono wartości tak podstawowych charakterystyk jak liczba gatunków (S), zagęszczenie (N), różnorodność gatunkowa (H') i stan biomasy (B) poszczególnych zespołów ptaków. Odwołując się do rachunku prawdopodobieństwa i wskaźnika rarefakcji $E(S_n)$ obliczono ponadto oczekiwaną liczbę gatunków w zepołach w oparciu o próbkowe dane liczebne z różnych powierzchni badawczych. Różnorodność gatunkową obliczano za pomocą wskaźnika Shannona H', którego formuła wywodzi się z teorii informacji.

W ośmiu zbadanych siedliskach (I-VIII, por. tabela XI) Tatrzańskiego Parku Narodowego stwierdzono łącznie 55 gniazdowych gatunków ptaków, które stanowią podstawowy zestaw ornitofauny lęgowej obszaru tatrzańskiego.

Zgodnie z oczekiwaniami największy zespół (najwyższe S i N) ptaków wykazano dla starej buczyny w Dolinie Strążyskiej pod Samkową Czubą (tabela I). Zdecydowanymi dominantami liczebnymi w tym zespole są zięba *Fringilla coelebs* (22% osobników), rudzik *Erithacus rubecula* (16%), świstunka *Phylloscopus sibilatrix* (12,5%) i sosnówka *Parus ater* (7,5%), czyli gatunki należące do grupy dominantów buczyn reglowych w całym łuku Karpat, a nawet większości starodrzewi liściastych na nizinach. W naturalnym tatrzańskim borze świerkowym u podnóży Żabiego przeważają liczebnie dwa ubikwistyczne gatunki - *Fringilla coelebs i Erithacus rubecula* (po 30%). Następne w kolejności są już jednak gatunki preferujące lasy szpilkowe, do których należą: mysikrólik *Regulus regulus*, sosnówka *Parus ater*, płochacz pokrzywnica *Prunella modularis*, drozd obrożny *Turdus torquatus* i sikora czubatka *Parus cristatus* (tabela II).

W strefie przejściowej między borem górnoreglowym a pasem zarośli kosówki kończy swoje pionowe zasięgi 11-12 gatunków leśnych. Zarazem pojawiają się tu gatunki strefy alpejskiej: siwerniak *Anthus spinoletta* i - rozpowszechniony też w otwartych antropogenicznych siedliskach nizinnych - kopciuszek *Phoenicurus ochruros*. Zdecydowanym dominantem (38,5% osobników) i najbardziej charakterystycznym gatunkiem jest tutaj *Prunella modularis* (tabela III). Gatunek ten panuje liczebnie również wyżej w strefie kosówki homogenicznej (46,6%), gdzie silnie wzrasta udział *Anthus spinoletta* (38,1%). Oba te gatunki stanowią tu aż około 5/6 liczby osobników w zespole (tabela IV). W tym siedlisku w Dolinie Pięciu Stawów Polskich odnotowano tundrową formę podróżniczka *Luscinia s. svecica*, a na szerszym obszarze Tatr również borealno-alpejską czeczotkę *Acanthis flammea*. Bardzo podobny i niewiele uboższy jest zespół ptaków zasiedlających strefę łąk wysokogórskich (hal) z kępami kosówki (tabela V). Jest to siedlisko leżące jeszcze w wąskich spektrach zasięgowych *Luscinia s. svecica* i *Acanthis flammea cabaret*. Pojawia się tu po raz pierwszy ściśle wysokogórski element fauny - płochacz halny *Prunella collaris* i szeroko rozpowszechniona w holarktyce białorzytka *Oenanthe oenanthe*. W strefie tej zdecydowanie dominuje jednak *Anthus spinoletta* (ok. 60% osobników). Wyższe partie krainy hal z rumowiskami skalnymi zasiedla 7-8 gatunków o zagęszczeniu wynoszącym zaledwie 2,1-6,9 par na 10 ha (tabela VI i VII). Strefę tę najbardziej wydzielają *Prunella collaris* (prawie 50% osobn.), *Anthus spinoletta* oraz gatunki o szerszej tolerancji siedliskowej - *Phoenicurus ochruros* i *Oenanthe oenanthe*. W szczytowych partiach grzbietów skalnych notowano rewiry jedynie 3-5 gatunków ptaków w liczebnościach zaledwie śladowych, umownie szacowanych na 0,1 pary na 10 ha; do gatunków tych należą: pomurnik *Tichodroma muraria*, kruk *Corvus corax*, sokół wędrowny *Falco peregrinus*, pustułka *Falco tinnunculus* i orzeł przedni *Aquila chrysaetos*. Pod względem liczby gatunków ptaków (S) siedliska najniżej położone (ok. 1000 m n.p.m.) są najbogatsze, a ze wzrostem nad poziom morza o każde 100 m zespół ptaków ubożeje o około 3 gatunki. Zmiana ta nie przebiega jednak proporcjonalnie, lecz hiperbolicznie (ryc. 2). Spadek liczby gatunków i zagęszczenia ptaków, idąc ku górze, zbiega się wyraźnie z coraz prostszą strukturą siedlisk i wzrostem reżimu czynników fizycznych. Oceny wychodzące z formuły rarefakcji $E(S_n)$ zbieżnie z danymi empirycznymi wskazują, że największa teoretyczna akumulacja gatunków oczekiwana jest w buczynie w dolnych partiach Tatr (ryc. 3). W przeciwieństwie do tego siedliska na bardzo niskim i zmiennym poziomie kształtuje się symulowana chłonność ornitologiczna biotopów strefy alpejskiej i subniwalnej. Silna korelacja (r=0,96) liczby gatunków i osobników (ryc. 4) w zespołach zmieniających się w porządku hipsometrycznym wskazuje na kierunkowe zmiany liczby osobników przypadających na statystyczny gatunek. O ile w zespołach szczytowych na 1 gatunek ptaka przypada zaledwie 1 osobnik lub jego ułamek to w najbogatszym zespole buczynowym proporcja ta wynosi 1:3,6. Również różnorodność gatunkowa awifauny, obliczona w odniesieniu do osobników (H'_n) i biomasy (H'_b), jest wyraźnie funkcją wyniosłości terenu nad poziom morza. Różnorodność ta spada ostro w stadiach lasu i kosówki, po czym wyrównuje się bądź wykazuje pewne oscylowanie (ryc. 5). Łączna biomasa

ptaków dorosłych w opisanej serii zespołów (tabela X) wynosi dla obu sezonów od 5,1 kg. (buczyna) do 0,3 kg na 10 ha (hale z kępami kosówki). Biomasa ptaków buczyny tatrzańskiej i górnoreglowych świerczyn jest odpowiednio większa aż o około 16 i 7 razy niż w siedliskach subalpejskich (kosówka) i alpejskich. Stan biomasy zespołów ptaków wykształconych ponad górną granicą lasu jest dość wyrównany na stosunkowo niskim poziomie od 251 do 650 g na 10 ha (ryc. 6).

Porównania zespołów ptaków odpowiednich siedlisk Tatr, Beskidów i niektórych innych gór wskazują (tabela XII), że lęgowa awifauna lasów tatrzańskich należy w gruncie rzeczy do tych samych formacji reglowych ptaków jakie cechują całe Karpaty Północne, a nawet i Sudety. Stopień podobieństwa zespołów ptaków borów górnoreglowych (Re zwykle ponad 70%) jest jednakże wyższy niż lasów dolnoreglowych (70% > Re > 55%). Stopień rozwoju awifauny wysokogórskiej w Tatrach jest nieporównywalnie większy niż w innych środkowoeuropejskich górach ze strefą alpejską, co podkreśla silny przyrodniczy indywidualizm Tatr.

Pewne różnice zachodzą między ornitofauną południowych i północnych stoków Tatr. Wskazują na to m.in. porównania pionowych zasięgów niektórych gatunków kongenerycznych i charakterystycznych dla tych gór (ryc. 7). Różnice te polegają nie tylko na wyższych zasięgach niektórych gatunków, ale i innym usytuowaniu ich optimum występowania (maks. N), związanego z nieco odmienną strefowością siedliskową Tatr północnych i południowych.

Liczebność wykazanych w Tatrzańskim Parku Narodowym gatunków-ptaków oszacowano na 44000-67000 rewirów. W latach 1981-1983 obszar tego Parku (ok. 212 km^2) zasiedlało prawdopodobnie około 55000 par, z tego 50 000 par lub rewirów ptaków (ok. 90%) przypada na lasy reglowe. Aż 30-35% awifauny polskiego Tatrzańskiego Parku Narodowego stanowią dwa najliczniejsze gatunki: *Fringilla coelebs* i *Erithacus rubecula* (tabela XIII). Około 500 par terytorialnych i ptaków nie tworzących monogamiczne terytorialne pary (np. *Cuculus canorus*) przypada na gatunki rzadsze, wśród których znajdują się m.in. takie rzadkości, jak *Tichodroma muraria* (ok. 10 rewirów i par) *Luscinia s. svecica* (ok. 10) *Picoides tridactylus* (20-50), *Falco peregrinus*, *Aquila chrysaetos* (1-2), *Bubo bubo* (6-7), *Tetrao urogallus* (50-100 osobn.), *Lyrurus tetrix* (30-40 osobn.) czy *Acanthis flammea* (20-40 rewirów lęgowych). Specjalne kontrole stanu liczebnego pluszcza *Cinclus cinclus* i pliszki górskiej *Motacilla cinerea* przeprowadzili W. Cichocki i P. Mielczarek (w druku); w latach 1985-1989 na potokach TPN wykazali oni obecność od 35 do 55 rewirów i par lęgowych pluszcza oraz od 66 do 133 par pliszki górskiej. Najniższy stan obu gatunków odnotowano, po ostrej zimie w 1986 r., a szczyt liczebny - wykazany w sezonie 1989 - można wiązać z poprzedzającą go bardzo łagodną zimą.