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Diurnal migration of birds in the Carpathian Mountains – characteristics, barrier effect and comparison with other regions in Poland

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Abstract. Despite the development of technically advanced methods of studying bird migration, classical visual observations remain a source of valuable data allowing a broad analysis of the picture of diurnal migration at a given site. We employed visual observations to investigate the spatial and temporal pattern of diurnal migration of birds in the Polish part of the Carpathians. During autumns 2011-2013, 28 localities distributed over the area were surveyed by experienced observers, while 12 localities were researched in spring 2015. The data collected allowed the determination of passage intensity indices and the timing of migration for more than 100 species in autumn and about 70 species in spring. Mean passage intensity was more than 3 times higher in autumn than in spring, with the highest recorded in the first half of October and mid-March, respectively. Compared to autumn, the peak of diurnal migration was shifted to later hours in spring. The passage occurred primarily along the N-S axis, followed by the NE-SW axis. No consistent evidence of a barrier effect of the Carpathians – expressing as a reduction in passage intensity in intra-mountain locations or in higher elevated areas – has been detected in this study. The cluster analysis showed that the assemblage structure of migratis in the mountain regions located in the south of Poland (Carpathian Mts., Karkonosze Mts., Świętokrzyskie Mts.) were more similar to each other than to a region situated far to the north on the Baltic coast.

Key words: visible migration, migration stream, concentration of passage, migration barrier, flyway, passerines, pigeons, waterbirds, birds of prey.

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I. INTRODUCTION

Despite increasing knowledge on bird migrations in Poland, still relatively little is known about how the passage of individual species contributes to the full migration pattern. Some data on this subject can be provided by permanent trapping of migrants, usually at stopover sites, where birds congregate, feed and rest during breaks in active migration. Using this method, it is possible to characterise the migration of a wide range of passerines (DORKA 1966; DYRCZ 1981; AUGUSTYN 2008; BOBREK et al. 2016; VAVŘÍK et al. 2016) or waders (MEISSNER & REMISIEWICZ 1998; MEISSNER et al. 2006). Other effective methods include ornithological radar or other automatic recording techniques (SCHMALJOHANN et al. 2008; SCHMIDT et al. 2017). However, if we lack such data, the method that allows the most complete understanding of the migration dynamics and phenology of the entire assemblage of diurnal migrants at

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a given site, and furthermore an assessment of its species composition, is classical visual observations (Berthold 2001; Schmaljohann et al. 2008; SCHMIDT et al. 2017). This method has been successfully used in studies of diurnally migrating birds, both in Poland (ABRASZEWSKA-KOWALCZYK 1974; DYRCZ 1981; BELA et al. 2011), and other countries (DORKA 1966; ALERSTAM 1978; WILLIAMS et al. 2001; HÜPPOP et al. 2006; KORNER-NIEVERGELT et al. 2007; SACKL et al. 2014; VAVŘík et al. 2016). The resulting indices of migration intensity show a positive correlation with the results of radar surveys, despite the lower numerical values (BRUDERER et al. 2012; SCHMIDT et al. 2017). At the same time, the effectiveness of visual observations increases for species forming flocks and for lower flight heights, as radar surveys face technical difficulties in determining flock sizes and detecting birds flying lower than 50 m above the ground (SCHMALJOHANN et al. 2008; SCHMIDT et al. 2017). Since, under Central European conditions, a large part of the diurnal migration takes place at heights of up to 200 m above the ground (BRUDERER & LIECHTI 2004; HÜPPOP et al. 2006; BRUDERER et al. 2012; ASCHWANDEN et al. 2020), it seems reasonable to use a relatively simple and inexpensive visual method that additionally allows to characterise the migration of individual species. Visual observations are also widely used in bird monitoring and surveys carried out for planning and investment purposes, as national guidelines recommend the use of this method in field surveys (wind farms: CHYLARECKI et al. 2011, power lines: MANIA-KOWSKI et al. 2013). Unfortunately, most of the data obtained from such monitoring initiatives are not being published and do not add to the knowledge of bird migration (NEUBAUER & SIKORA 2015).

Most Polish migration studies focus on the Baltic coast region, where migration is concentrated (Busse 1976; Busse & HALASTRA 1981; BELA et al. 2011) due to the presence of an extensive marine area, which for most landbirds is an obstacle (barrier) to migration (BERTHOLD 2001; NEWTON 2008). Passage in the inland part of Poland is less concentrated due to the small number of large-scale topographic structures affecting migration routes (leading lines; MUELLER & BERGER 1967; ALERSTAM 1978; Åkesson 1993), which translates into dispersal of the migrating birds' flux over a large area and so-called broad front migration (BRUDERER 1996; BERTHOLD 2001). More concentrated inland passage tends to

occur along the river valleys (BINGMAN et al. 1982; BERTHOLD 2001; LUGOVOY 2005) and in mountainous regions (DORKA 1966; DYRCZ 1981; BRUDERER & JENNI 1990; KORNER-NIEVERGELT et al. 2007), as high ridge chains shape the migration routes (BRU-DERER 1996; WILLIAMS et al. 2001; BRUDERER & LIECHTI 2004; NEWTON 2008). However, data and analyses from the Carpathians are scarce in this regard.

The goal of the present study was to investigate the spatial and temporal pattern of diurnal migration of birds in the Polish part of the Carpathians, including the determination of migration dynamics and phenology, species composition and migration directions. The regional specificity of migration was assessed by comparing the results obtained in the Carpathians with available data on the characteristics of daily bird migration in other regions of Poland. An attempt was also made to verify the role of the Carpathians as a barrier against bird migration, with the expectation that migration intensity at locations at higher altitudes and further in the interior of the mountain range (and therefore more distant from its outer boundary) would be lower than at locations lower and closer to the edge of the mountain area.

II. MATERIAL AND METHODS

Study area and field methods

The study covered the north-western part of the Carpathian chain, located within Poland's borders (an area of about 19.6 thousand km²), which is comprised of three subprovinces: Outer Western Carpathians, Central Western Carpathians and Eastern Beskids (KONDRACKI 2013; Fig. 1). In this area, 28 observation posts (localities) were set up from which daily counts of migratory birds were conducted (Fig. 1, Table 1). The spatial distribution of the surveyed localities was non-random. They were placed predominantly on hilltops - forest-free mountain peaks providing good visibility and covering as much of the skyline as possible, while ensuring reasonable spatial representativeness. A single count (a few hours' observation) was carried out by one person, but usually two observers were responsible for a given locality, who performed successive counts alternately. Overflying birds were detected and identified visually and by voice, with the naked eye and with the help of binoculars/observation scopes. All birds



Fig. 1. Study area and the distribution of observation localities on the background of mesoregion boundaries (according to KONDRACKI 2013) and digital elevation model (based on SRTM; http://srtm.csi.cgiar.org/).

Table 1

Coordinates [longitude (X) and latitude (Y)] and altitude (m asl) of autumn (2011-2013) and spring (2015) observation localities. Localities where no spring observations were carried out are marked '-'. Spatial distribution of localities in the study area – see Fig. 1

Locality		Autumn			Spring	
No.	X	Y	m asl	Х	Y	m asl
1	18°44' 24" E	49°45' 13" N	455	_	_	_
2	18°46' 50" E	49°48' 14" N	351	-	-	_
3	18°53' 43" E	49°32' 57" N	619	18°53' 43" E	49°32' 57" N	619
4	18°57' 18" E	49°32' 44" N	880	-	-	_
5	19°7' 42" E	49°42' 22" N	395	-	-	_
6	19°13' 30" E	49°47' 14" N	748	19°13' 30" E	49°47' 14" N	748
7	19°14' 4" E	49°32' 36" N	1175	-	-	_
8	19°40' 52" E	49°29' 4" N	680	19°40' 37" E	49°28' 56" N	690
9	19°41' 14" E	49°41' 57" N	502	19°41' 14" E	49°41' 57" N	502
10	19°46' 54" E	49°45' 14" N	859	_	-	_
11	19°50' 41" E	49°27' 23" N	656	_	-	_
12	20°6' 21" E	49°37' 59" N	711	_	-	_
13	20°10' 52" E	49°26' 15" N	597	_	-	_
14	20°18' 50" E	49°55' 10" N	266	20°18' 50" E	49°55' 10" N	266
15	20°28' 34" E	49°24' 52" N	719	_	-	_
16	20°41' 33" E	49°25' 22" N	660	20°45' 21" E	49°23' 31" N	487
17	21°5' 6" E	49°23' 1" N	679	21°5' 16" E	49°23' 5" N	713
18	21°32' 46" E	49°39' 9" N	328		49°39' 9" N	328
19	21°33' 23" E	49°31' 20" N	385	_	-	_
20	21°40' 42" E	49°26' 1" N	480	21°41' 7" E	49°26' 0" N	450
21	21°46' 32" E	49°23' 32" N	534	_	-	_
22	22°6' 46" E	49°15' 46" N	600	22°6' 45" E	49°15' 41" N	601
23	22°12' 1" E	49°46' 2" N	373	_	-	_
24	22°33' 43" E	49°24' 25" N	552	22°35' 10" E	49°25' 12" N	554
25	22°42' 26" E	49°3' 24" N	776	-	-	_
26	22°42' 38" E	49°13' 52" N	556	_	-	_
27	22°42' 47" E	49°37' 9" N	463	22°42' 47" E	49°37' 9" N	463
28	22°50' 43" E	49°6' 17" N	703	-	_	_

detected were counted, including those not identified to a species level. Detection distance and height were limited by the observer's ability to detect passing birds and by local field conditions, which did not always allow the entire area around the locality to be covered by observation. The inability to identify the species mostly concerned small passerines and was usually due to too great a distance between the observer and the passing bird, poor visibility or audibility conditions (e.g. observation conducted against the light or during wind blow) or a short observation time, making it impossible to capture diagnostic features of the bird reliably. In autumn, the surveys were conducted in 2011-2013. Three localities (No. 16, 22 and 24) were surveyed for three seasons, one (No. 3) for two, and the others only for one season. In spring, birds were surveyed in 2015 at 12 of the 28 localities monitored in autumn (Table 1). In some cases, the location of the spring observation post was slightly shifted relative to the autumn one to obtain the most favourable possible view. Counts were carried out at regular intervals, usually once a week, only in autumn at localities 3, 11, 16, 22, 24 and 28 every 3-4 days. In autumn, observations were carried out during the periods: 1.09-16.11.2011, 14.08-18.11.2012 and 15.08-19.11.2013, while in spring 7.03-5.05.2015. At a single locality in autumn, between 11 and 49 counts were made - depending on the season and the number of years of observation - while in spring each locality was visited 9 times. Counts were conducted during the day, starting 1-2 hours after sunrise. Depending on the length of the day, they lasted 7-10 hours. A total of 488 counts (lasting 4151 hours) were carried out in all autumns and 108 counts (989 hours) in spring. As only selected bird species were recorded during autumn 2011, data from that year were used only for some analyses (see values marked* in Appendix 1). In all other cases, only the results obtained in 2012-2013 at 19 localities were used (Tables 1 & 2), where 319 field counts lasting a total of 2751 hours were carried out. Priority was given to distributing the observations evenly throughout the season, so the fieldwork was generally not dependent on weather conditions, with the exception of particularly unfavourable ones (heavy, prolonged rain or snow, high winds, all-day fog), when the count was postponed to the nearest possible date.

Data processing and analysis

Visual monitoring of bird migration, especially when passage is not highly concentrated, faces the problem of separating migrating birds from those making only local movements (MUELLER & BERGER 1967), especially as an unknown proportion of those not currently on the wing (e.g. resting, foraging) are also migrating. To avoid the use of an arbitrary classification, the seasonal dynamics of the observations and indices of passage intensity included all observed individuals. It should therefore be borne in mind that these results include a mixture of individuals in active flight, those that have stopped during migration and local birds not undertaking long-distance movements. The passage intensities of the whole assemblage at the observation localities were presented separately for spring and autumn as (i) the value for certain locality (number of individuals divided by the number of survey hours), (ii) the value for the tenday period of a month (average for all localities) and (iii) the value for the whole study area (average for all localities). The parameter used for comparisons between localities and time periods was the average number of individuals recorded during 10 standard hours of observation (individuals/10 h), hereinafter referred to as passage intensity. An analogous measure was used for particular species (Appendices 1 & 2), with passage intensity calculated as the number of individuals divided by the number of survey hours in the period between phenologically earliest and latest observation of a species. If the number of observations was less than 10 for a species, this parameter was not calculated.

Species richness

Individuals identified to the species level were used to assess species richness. However, the total number of species found in a given ten-day period appeared to be positively related to the number of hours spent surveying (PEARSON's correlation; spring: r=0.927; P=0.003; df=5; autumn: r=0.753; P=0.012; df=8). Therefore, a different measure was used in the analysis of seasonal changes in species richness – the mean number of species recorded during 1 hour of observation in a given ten-day period.

Diurnal passage dynamics

Differences in diurnal passage dynamics between spring and autumn were verified using the MANN-WHITNEY U test. This test requires independence of variables, therefore, due to the flocking of birds during migration, the diurnal passage dynamics was presented as the number of observations (obs./h) recorded per hour in consecutive hours counted from sunrise, which meets the independence condition. As surveys did not usually start at full hours relative to sunrise, each 60-minute count period was included in the hour in which it started. The sunrise time of the site located in the centre of the region was used as a reference. In order not to include resting birds, only observations for which the direction of flight was recorded were used in the analysis, so those certainly involving birds in flight.

Flight direction

Distributions of flight directions were presented for individual localities and all of them combined, separately for spring and autumn. Flight directions were analysed for species in which this parameter was determined for at least 50% of individuals in a given migration season (in spring or in autumn). Using PEARSON's correlation, the relationship between passage intensity at observation localities and their altitude and distance from the outer border of the Carpathians was examined. For the latter, the geographical distance was measured to the nearest point of the outer border of the mountain chain of the Carpathians (according to KONDRACKI 1989; light grey area on the left panel of the Fig. 1), not only the Polish part. For some analyses, the assemblage of observed species was divided into groups (Appendices 1 & 2). The division was based on the dominant groups of diurnal migrants observed in the studied region. Five species groups were distinguished: (1) passerines (Passeriformes), (2) pigeons (Columbiformes), (3) birds of prey (Accipitriformes et Falconiformes), (4) waterbirds (excluding species covered in the preceding groups) and (5) other (all remaining species).

Structure of the assemblage

The structure of the assemblage observed in the Carpathians was compared with assemblages of migrants reported in visual passage surveys conducted in other regions of Poland – on the Baltic coast (Busse 1976; Busse & HALASTRA 1981; about 500-550 km to the N and NW of the northern border of the Carpathians), in the Świętokrzyskie Mountains (NALEPA 2014; about 100 km to the N) and in the Karkonosze Mountains (DYRCZ 1981; about 250 km to the NW). Due to differences in the way

results are reported in some papers and seasons, to allow comparisons, data for some groups of species (Anser spp., Buteo spp., Circus spp., Fringilla spp., *Mergus* spp., *Larus argentatus* complex + *L. fuscus*, Loxia spp., Passer spp., Phylloscopus spp., Turdus philomelos + T. iliacus) were combined and analysed together. In the first step, the matrix of abundances of each species/group in compared regions was created. To facilitate comparisons, relative values were used, assuming the sum of abundance of all species in a given region as 100. These data were then subjected to a hierarchical clustering of migrant assemblages recorded in particular regions. To build a dendrogram, the BRAY-CURTIS distances of similarity and the group average linking method were used (MCALEECE et al. 1997; MAGURRAN 2004).

Data curation, storage, processing and visualisation was performed using MS Office Access and Excel 2010, as were basic calculations (including coefficient of variation and PEARSON's correlation). The map was prepared in ArcGIS 10.2.2, while the geographical distances and altitudes were measured in Google Earth Pro 7.3.6.9345. The MANN-WHIT-NEY U test was performed in R ver. 4.0.5 (R CORE TEAM 2021), while cluster analysis in BioDiveristy Pro ver. 2 (MCALEECE et al. 1997).

Abbreviations

I-XII – months; when followed by superscript indicate the ten-day period (e.g., III² – second ten-day period of March).

III. RESULTS

The material analysed included 8 657 observations of 47 098 individuals from the autumn of 2011 (when only selected bird species were counted), 34 560 observations of 253 106 individuals from the autumns of 2012-2013 and 6 984 observations of 26 604 individuals from the spring of 2015. Species identity was determined for 92.2%, 97.3% and 97.0% of the individuals recorded in these periods, respectively.

Appendices 1 and 2 show the basic characteristics of the autumn and spring records of each species. In spring, the most numerous species observed were Starling *Sturnus vulgaris*, followed by Fieldfare *Turdus pilaris*, Chaffinch *Fringilla coelebs*, Common Crane *Grus grus* and Woodpigeon *Columba palumbus* (Appendix 2). In autumn, on the other hand, Chaffinch was by far the dominant species, ahead of Woodpigeon, Rook *Corvus frugilegus*, Starling and Barn Swallow *Hirundo rustica* (Appendix 1).

Species richness

A total of 117 bird species were recorded in spring (Appendix 2). On average, 5.2 species were observed per hour (SE=0.1), with a maximum of 5.7 species in III³, although values were similar in the first five ten-day periods of spring (Fig. 2). Noticeably fewer (on average 4.5 and 4.4 species per hour) were observed at the end of survey period, in IV^3 and V^1 . In the autumn, 149 species were recorded (Appendix 1). At this time of year, an average of 6.8 species were recorded per hour (SE=0.1). The highest values (8.3-8.7 species; Fig. 2) were recorded during IX^3-X^2 , and during the rest of the season they were lower (5.2-7.2 species). The total number of species that were shared across spring and autumn was 111 (Appendices 1 & 2). Between 41 and 79 species were recorded at surveyed 12 observation localities in spring, 58.5 (SE=3.2) species on average, while between 49 and 91 species were recorded at 19 localities in autumn, with an average of 72.7 (SE=2.4) (Table 2).

Passage intensity

In spring, the passage intensity averaged 269.4 individuals/10 h (SE=35.0) at a single observation locality, while in autumn it was much higher, reaching 863.1 ind./10 h (SE=105.5). Passerines were recorded with the highest frequency in both seasons, followed by waterbirds, pigeons and birds of prey in spring, and pigeons, waterbirds and birds of prey in autumn (Table 3). The proportion of other species was marginal in both seasons.

The variation in the passage intensity between localities was moderate (Fig. 3, Table 2), with the coefficient of variation being slightly higher in autumn (CV=53.3%) than in spring (CV=45.0%). In autumn, the passage intensity was highest at the western and eastern edges of the study region. In spring, on the other hand, the highest values were recorded in the central part of the region, although the lack of data from the westernmost localities makes an unambiguous assessment difficult (Fig. 3). Nevertheless, in spring, it was found that the passage intensity at the locality increased significantly with the distance from the outer border of the Carpathian range (PEAR-SON's correlation; r=0.803; P=0.002; df=10; Fig. 4a). In autumn, the equivalent relationship was reversed, although not statistically significant (r=-0.4; P=0.09; df=17; Fig. 4b). However, after excluding the data from locality 3 (the outlier marked with an arrow in Fig. 4b), the relationship became statistically significant (r=-0.517; P=0.028; df=16). In contrast, the passage intensity at the locality was not related to the altitude in either spring (r=0.044; P=0.892; df=10) nor autumn (r=-0.18; P=0.460; df=17).

Seasonal dynamics

Relatively high passage intensity values were recorded in spring already in the first ten-day period of the counts (Fig. 2, Table 3). This parameter (measured by the number of individuals) reached its highest values during III2-IV1, with peaks for passerines recorded in III² and IV¹ and for non-passerines in III². The latter was mainly due to the increased intensity for waterbirds, as in pigeons the peak occurred in III³ and in birds of prey in III¹ (Table 3). From the 2nd ten-day period of April onwards, the total passage intensity decreased to reach a minimum at the end of the study period. In autumn, on the other hand, the passage intensity was lowest in the initial phase of the season (Fig. 2, Table 3). It increased in the following ten-day periods, reaching its highest values between the IX³ and the end of X. A peak occurred in X1-X2 and resulted from the conjunction of the maximum values of the indices for passerines and pigeons, while counts for birds of prey and waterbirds peaked later, in X2-X3 and X3-XI1 respectively (Table 3). Passerines were numerically dominant - their proportion reached 68.5% in spring (ten-day period values: 61.6-81.0%) and 85.5% in autumn (69.2-92.0%) (Fig. 2, Table 3).

Diurnal dynamics

The diurnal distribution of spring observations differed significantly from that of autumn observations (MANN-WHITNEY U test; Z=17.991; P<0.001). In autumn, most observations were recorded in the 1st, 2nd and 3rd hours after sunrise (Fig. 5) and in the following hours the intensity of observations steadily decreased. In spring, the peak was recorded later than in autumn – in the 3rd and 4th hour after sunrise, although in the first two hours the intensity of



Fig. 2. The seasonal dynamics of passage intensity (bars; No. of individuals per 10 h) and species richness (points; No. of species per 1 h), recorded in consecutive 10-day periods. The vertical dashed line indicates a break in counts between 6.V. and 13.VIII. The whiskers represent the standard error. In case of passage intensity, only the positive whiskers are shown (grey for Passeriformes, black for Non-Passeriformes).

Table 2

The number of counts and hours spent on observation, mean observation intensity, measured as the number of individuals recorded during 10 hours of observation in the studied period (7 Mar-5 May and 14 Aug-19 Nov) and the number of observed species in each of the studied autumn (2012-2013) and spring (2015) observation localities. In case of the localities studied during both autumn seasons (No. 3, 16, 22, 24), the mean seasonal number of species is shown. Localities where no spring observations were carried out are marked '–'

		Autumn				S	Spring	
Locality No.	No. of counts	No. of hours	No. of ind./10 h	Species No.	No. of counts	No. of hours	No. of ind./10 h	Species No.
1	14	120	1224.2	83	-	-	-	_
2	14	120	1655.8	88	-	-	-	-
3	28	245	2067.0	76	9	82	251.6	49
6	14	122	596.3	78	9	83	167.0	66
7	13	112	656.4	50	-	-	-	-
8	14	120	793.3	67	9	80	396.0	46
9	13	111	793.2	79	9	83	175.5	62
10	14	120	708.4	70	-	-	-	-
12	13	110	429.9	73	-	-	-	-
14	14	121	448.8	91	9	84	129.2	61
16	28	242	738.1	76.5	9	85	368.1	79
17	14	121	533.3	70	9	82	220.6	63
18	14	121	632.0	49	9	82	346.8	47
20	14	122	501.8	67	9	82	467.0	68
22	28	242	706.0	66.5	9	82	410.1	55
23	14	117	681.9	73	_	-	_	-
24	28	242	1146.1	77	9	82	175.7	65
26	14	121	505.8	78	-	-	_	-
27	14	122	1581.1	69	9	82	125.6	41

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Table 3

Observation intensity (No. of individuals per 10 h of count) in the ten-day periods of the consecutive months and the whole spring and autumn season for particular groups of migrants and all species together. The Roman numeral in the first column represents the month, while the superscript – the ten-day period. Species-to-groups assignments are given in Appendix 1 and 2

Ten-day period	Passerines	Pigeons	Waterbirds	Birds of prey	Other	Total
III ¹	166.3	6.7	35.2	29.1	1.5	238.8
III ²	284.0	17.4	124.7	27.4	1.4	454.9
III ³	252.9	40.1	88.5	20.6	0.9	403.0
IV^1	278.7	31.4	25.0	13.8	1.0	350.0
IV ²	142.1	20.0	9.4	16.4	0.8	188.7
IV ³	84.0	3.3	11.8	14.9	1.7	115.7
V^1	64.6	11.0	6.2	14.8	3.5	100.1
spring	184.4	21.0	43.7	19.0	1.4	269.4
VIII ²	157.4	46.6	7.7	18.2	3.7	233.5
VIII ³	290.2	51.4	20.9	21.8	2.6	387.0
IX1	291.2	24.3	24.6	25.8	3.2	369.1
IX ²	500.2	18.5	6.2	23.5	2.8	551.2
IX ³	1185.5	113.2	24.4	25.3	2.4	1350.7
X^1	1870.5	276.6	25.5	25.0	2.2	2199.9
X ²	1706.9	210.2	42.1	36.0	2.2	1997.4
X ³	900.4	2.2	60.8	33.2	2.3	998.8
XI ¹	610.4	4.7	59.4	15.5	2.9	692.8
XI ²	334.1	2.0	19.4	11.9	2.2	369.5
autumn	738.3	68.7	29.7	23.9	2.6	863.1



Fig. 3. The variation in the passage intensity (No. of individuals per 10 h) between observation localities (denoted by numbers) in spring (dark grey) and autumn (light grey).



Fig. 4. Relationship between the passage intensity and distance of surveyed localities from the outer boundary of the Carpathian range, for spring (a) and autumn (b) migration period.

observations was also high (Fig. 5). After the peak period, the intensity decreased steadily and only in the last, 12th hour (which, however, included only three hours of observation) a slightly higher value was recorded than in the preceding hour (Fig. 5).

Flight directions

The direction of flight was determined in spring and autumn for 64.6% and 87.5% of individuals, respectively. Spring was dominated by flights to the north (42% of individuals), followed by north-east (24%), east (12%) and north-west (8%; Fig. 6). Each of the remaining directions were chosen by 3-4% of birds. In autumn, the flight directions were almost exactly opposite to those in spring – the dominant direction was south (40% of individuals), ahead of south-west (34%), west (16%) and south-east (5%). Each of the other directions was chosen by less than 2% of birds (Fig. 6).

The distributions of flight directions at particular localities sometimes deviated significantly from the above averaged pattern and showed regional specificity (Figs 7a & 7b). In autumn, in the western part of the Carpathians, a split was apparent between localities where westerly flights predominated or had a significant share (localities 1-2, 10), and those where southerly flights dominated (localities 3, 6, 8-9; Figs 1 & 7a). In the central and eastern part



Fig. 5. The diurnal dynamics of passage in spring and autumn localities – the mean number of observations recorded during the consecutive hours after the sunrise. As surveys did not usually start at full hours relative to sunrise, each 60-minute count was included in the hour in which it started (e.g. hour 1 covers count periods starting between 0 and 59 minutes after the sunrise). No. of counts conducted in spring (top row) and autumn (bottom row) are given above the chart.



Fig. 6. Spring and autumn distributions of flight directions for all localities combined. N – No. of individuals.



Fig. 7. Autumn (a) and spring (b) distributions of flight directions for each of the individual localities (denoted by numbers) in the surveyed region.

of the study region, a south-westerly or southerly flights prevailed at most localities, while the proportion of a westerly flights was considerably smaller. In spring, much more limited material was collected, deriving from only 10 localities (Fig. 7b). It did not show as pronounced regional variation as in the autumn and, in addition, the distributions of flight directions were clearly multimodal at some localities.

Similarity of the assemblage structure from different regions

For all regions combined, i.e. Carpathians (this study), Karkonosze Mts. (Dyrcz 1981), Świętokrzyskie Mts. (NALEPA 2014) and Baltic Coast (Busse 1976; Busse & HALASTRA 1981), the quantitative similarity in the structure of migrant assemblages reached 39%, both in autumn (Fig. 8a) and spring (Fig. 8b). The cluster analysis showed that in autumn the assemblages from the Carpathians and Karkonosze Mts. shared the most similar structure (58%), while the Baltic Coast was characterised by the highest dissimilarity from all other regions (Fig. 8a). Analogous results were obtained in spring, except that the dendrogram does not include the Karkonosze Mts., for which data was not available, thus no comparisons with this mountain range could be made. So in spring, the highest similarity was found between the Carpathians and the Świętokrzyskie Mts. (49%; Fig. 8b).



Fig. 8. Dendrograms illustrating the Bray-Curtis similarities between the autumn (a) and spring (b) diurnal migrant assemblages of some regions in Poland for which comparable visual passage survey data was published (BUSSE 1976; BUSSE & HALASTRA 1981; DYRCZ 1981; NALEPA 2014).

IV. DISCUSSION

Bird migration in the Carpathian Mountains

The shape of the seasonal dynamics of passage intensity, characterised by a single peak in the middle of the season and minima at the beginning and end of the period, resembles the typical patterns reported in many studies based on systematic bird migration observations (cf. DORKA 1966; BUSSE & HALASTRA 1981; CHRISTEN 2006; KORNER-NIEVERGELT et al. 2007; AUGUSTYN 2008; BELA et al. 2011; NALEPA 2014). This indicates that the results obtained in our study predominantly address the phenomenon of bird migration in this region. This is also supported by the recorded flight directions of the observed individuals, as well as the changes in the species richness. A comparison of the intensity during peak periods

with the minimum values allows us to conclude (assuming constant levels of local bird activity during the study period) that most of the observations concerned migrants. The contribution of birds originating from local populations was undeniably evident, although not heavily influenced the results. Based on the strongly marked dynamics of autumn passage, it can be concluded that the fraction of non-migrating birds is smaller in autumn than in spring, when there was a smoother rise and fall in the passage intensity. The migration dynamics also suggests that the timing of the fieldwork ensured that the migration period in the Carpathians was covered sufficiently to characterise the passage of a large group of species. Certainly, however, the migration of some early spring or late autumn migrants also took place outside the fieldwork period. It should be emphasised that the migration picture obtained is not complete, as it only covers birds migrating during the day, while the nocturnal passage, the characterisation of which is beyond the scope of the research method used (NEW-TON 2008), involves a significant fraction of birds migrating at a given site (Hüppop et al. 2006; BRUD-ERER 2017). Moreover, at least in autumn, nocturnal migration is phenologically distinct from diurnal and mostly occurs earlier - it has been estimated that, under Central European conditions, about 80% of nocturnal migrants pass by 15 September and more than 80% of diurnal migrants after this date (DORKA 1966). The picture is further complicated by the fact that some – especially late – migrants may migrate during both day and night (DORKA 1966; NEWTON 2008; BRUDERER 2017).

The higher species richness of the assemblage observed in the Carpathians in autumn compared to spring is probably related to more intense migration at this time of year. Analogous results were obtained e.g. in the Świętokrzyskie Mts. (NALEPA 2014) and in the Swiss Highlands (CHRISTEN 2006), where the indices of species richness and migration intensity were also higher in autumn. However, this is not a constant pattern, as, for example, on the northern German coast, spring and autumn migration had similar intensities (HÜPPOP et al. 2006). In contrast to, for example, the Świętokrzyskie Mts. (NALEPA 2014), the Karkonosze Mts. (Dyrcz 1981) or the Jeseníky Mts. (VAVŘík et al. 2016), in the Carpathians there was a marked migration of waterbirds, recorded here in both seasons. This indicates that migration routes of birds associated with aquatic environments

may also lead through mountainous areas, despite general knowledge that this group avoids crossing mountain ranges during migration (BRUDERER & JENNI 1990; NEWTON 2008).

The results indicate that the passage of diurnal migrants in the Carpathians is directed, with certain directions being chosen with unequal frequency. The directions preferred during spring and autumn migration are opposite, with the same sequence of dominance in both seasons. In the study region, diurnal passage occurs primarily along the N-S axis, with slightly lower numbers along the NE-SW axis. The E-W axis is only the third most important, chosen by 2-3 times fewer birds than each of the previous axes, whereas the least intensive passage occurs along the NW-SE axis. What is remarkable is the low proportion of directions opposite to the standard direction of migration in a given season. This confirms that reverse migration, common in coastal locations and near large bodies of water (Åkesson 1999; BERTHOLD 2001; HÜPPOP et al. 2006), is less important in the mountains (cf. also Dyrcz 1981). It should be noted, however, that in the Carpathians the magnitude of this phenomenon may be underestimated, because for a certain fraction of birds (approx. 12% in autumn and 35% in spring) the direction of flight has not been determined in the field. There are no comparative data from other regions of the country, collected over wide area and for a broad set of species, which would allow to trace the main migration routes of diurnal migrants in Poland. The only available results come from the Polish Baltic coast. They indicate that in this region the dominant direction of autumn migration is shifted more to the west compared to the Carpathians; south-west and west directions prevail there, while the share of the southern direction is small (e.g.: BUSSE & HALASTRA 1981; KANIA 1981; REMISIEWICZ et al. 1997; but cf. BUSSE et al. 2001). This is strongly influenced by the W-E course of the southern Baltic coastline, along which most of the species migrating through this region proceed.

Within central Europe, the broad front bird migration occurs mainly along the NE-SW axis (BRUDERER 1982, 1996, 2017; SZÉP 1992; BERTHOLD 2001; HÜPPOP et al. 2006; RÖSSLER & SCHAUER 2014). Its deviation in the Carpathians towards the N-S axis may be due to several reasons. The first may be the specific qualitative and quantitative composition of the migrant assemblage, as the passage directions are species- and population-diversified (BAUMGART-NER & BRUDERER 1985; SZÉP 1992; HÜPPOP et al. 2006; SACKL et al. 2014). The existence of such differences is partly confirmed by comparisons of the dominance structure, showing greater similarity of the migrant assemblage in the Carpathians to other mountain ranges of southern Poland than to the Baltic coast. A second reason for differences in passage directions may be that a significant fraction of the birds observed in the Carpathians follow an eastern migratory route, leading to or through the eastern Mediterranean. This would follow the hypothesis that most birds (at least passerines) from central and eastern European populations migrate via this route in autumn (BUSSE 2001). Such an explanation cannot be rejected on the basis of the data collected in this study, but in the light of this hypothesis it is difficult to explain the low proportion of passage along the NW-SE axis in the Carpathians, which should prevail for the eastern route (BUSSE 2001). Therefore, another plausible explanation for the dominance in the Carpathians the N-S migration axis seems to be a local deviation of the standard European migration direction (NE-SW) due to the topography of the mountain chain (BAUMGARTNER & BRUDERER 1985; BRUDERER 1982, 1996). This is because using the N-S axis ensures that the Carpathians are crossed by the shortest possible route - across the chain, while following the NE-SW axis (the second most frequent option) necessitates a route that is only slightly longer, which may favour those directions among the migrants. In contrast, proceeding along the NW-SE axis would imply several hundred kilometres over areas of the eastern Carpathians, due to the southeastern course of the mountain chain across Ukraine and much of Romania. This may be one of the reasons for the low proportion of birds flying this direction at surveyed locations. To verify to what extent Carpathian topography does shape the migration direction, data from areas located in the foreland of this mountain range would be necessary. It should be emphasised that the above considerations apply to the entire set of diurnal migrants and, for individual species, the results may show more explicit directional preferences and different underlying reasons (cf. detailed papers covering migration of selected species or groups of birds in the Carpathians: Boвкек et al. 2017a; b; 2018; 2019; 2020; WILK et al. 2018).

To summarise, the most distinct features characterising diurnal bird migration in the studied part of the Carpathians include:

 a definite quantitative dominance of passerines, both in spring and autumn, and a marked migration of waterbirds;

- higher species richness of migrants in autumn than in spring;

- more than 3-times higher intensity of autumn migration compared to spring migration;

- the presence of a distinct autumn migration peak, covering the last ten-day period of September and the whole of October;

- a shift of the diurnal migration peak in spring towards later hours compared to autumn;

- the predominance of passage along the N-S and NE-SW axis, with little contribution of other directions;

- a different spatial pattern of migration intensity between central and peripheral areas depending on the season (cf. further below).

Migration in the Carpathians compared to other regions in Poland

There are few sufficiently detailed data to allow comparative analysis of the structure of diurnal migrant assemblages in Poland, and there has been no quantitative and qualitative comparisons of this structure in different regions of the country so far. The results of the present analysis show that the migrant assemblages from all concerned regions (the Carpathians, the Karkonosze Mts., the Świętokrzyskie Mts. and the Baltic coast) were comparable, resulting in quantitative similarities at the level of 39-58% in autumn and 39-49% in spring. Nevertheless, the mountain regions located in the south of the country were more similar to each other than to this situated a few hundred kilometres to the north on the Baltic coast. It is worth noting that differences between regions were also marked in respect of the dominant migrant species. In autumn, in the case of the Carpathians and the Karkonosze Mts., the most numerous migrants were species of the genus Fringilla spp., in the Świętokrzyskie Mts. it was the Fieldfare Turdus pilaris, and on the Baltic coast the Starling Sturnus vulgaris (BUSSE & HALASTRA 1981; DYRCZ 1981; NALEPA 2014). In contrast, the dominant species in spring included the Chaffinch Fringilla coelebs (the Świętokrzyskie Mts. and the

Baltic coast; BUSSE 1976; NALEPA 2014) and the Starling (the Carpathians; this study). Despite these differences, it is remarkable that within the group of the 10 most abundant taxa in each region, there were many recorded in each of the compared regions. In autumn, as many as five taxa belonged to this group: Fringilla spp., Barn Swallow Hirundo rustica, Great Tit Parus major, Siskin Spinus spinus and Woodpigeon Columba palumbus. In addition, in three of the four regions, the 10 most abundant species included Fieldfare (all mountainous regions) and Starling (cf. BUSSE & HALASTRA 1981; DYRCZ 1981; NALEPA 2014 and this study). In spring, in each of the three regions compared (no data available for the Karkonosze Mts.), the ten dominant species included Chaffinch, Starling, Skylark Alauda arvensis and Woodpigeon (cf. BUSSE 1976; NALEPA 2014 and this study). This suggests that in Poland, which has a predominantly lowland landscape without distinct geographical barriers for migration, the core of the qualitative structure of diurnal migrants is similar. On the other hand, inter-regional differences, both qualitatively and - above all - quantitatively, are visible in the comparisons made, particularly between mountainous regions and the Baltic coast. It can be assumed that these differences are all the greater the distance separating the compared regions, although the influence of other factors, such as habitat differences, cannot be excluded. To verify this claim, however, more comparative data are needed from different regions of the country, in particular from lowland areas located far from mountain ranges or the sea coast. It should also be borne in mind that the oldest of the compared datasets were gathered several decades earlier than the most recent ones, so the substantial changes in the environment and avian populations that have taken place during this period can have a major impact on migrant assemblages. Therefore, the results of the comparison should be taken with caution.

The Carpathians as a barrier for bird migration

One of the determinants of bird migration routes is the existence of ecological barriers ('barrier effect'; HENNINGSSON & ALERSTAM 2005; ASCHWANDEN et al. 2020). When reaching an area on the route where it is difficult or impossible to cross it, renew energy stores or rest, which for landbirds could be, for example, a sea area, a high mountain range, a desert or an ice field (ALERSTAM 2001; BERTHOLD 2001; HEN- NINGSSON & ALERSTAM 2005), migrants can choose one of two basic strategies: (i) continue flying over unfavourable area or (ii) modify the route and avoid (bypass) it (Alerstam 2001; Newton 2008; Brud-ERER 2017). The unwillingness to overcome 'obstacles' along the route, involving, among other things, taking additional risks, increased migration costs or the need for specific physiological and behavioural adaptations (ALERSTAM 2001; HENNINGSSON & ALER-STAM 2005), may cause migrants to locally concentrate in places where they have to 'decide' whether to attempt to cross the barrier or to bypass it. The phenomenon of concentration of migrating birds associated with an ecological barrier is particularly characteristic of seashores (ALERSTAM 1978; Åkesson 1993; BRUDERER 2017), as land birds are averse to flying over extensive water areas (NEWTON 2008). Mountainous areas can also concentrate migrants in certain places, e.g., where updrafts are created due to topography, facilitating altitude gain which is particularly important for birds crossing mountain ranges using gliding flight (BOHRER et al. 2012; BRUDERER 2017).

Mountains can also act as a barrier which disrupts migration or impedes resting for some bird species, especially those migrating at lower altitudes (BER-THOLD 2001; BRUDERER 2017). This leads to a concentration of migrants along the outer mountain ridges, in valleys and mountain passes (BRUDERER & JENNI 1990; BRUDERER 1996; WILLIAMS et al. 2001; BRUDERER & LIECHTI 2004; PEDRINI et al. 2008; FRANZOI et al. 2021). Mountains can also lead to a deviation of the local (secondary) direction of passage from the primary direction typical of a particular migratory stage, as demonstrated in the case of the Alps (BRUDERER & JENNI 1990; BRUDerer 1996; Bruderer & Liechti 2004; Rössler & SCHAUER 2014). However, strength of this influence depends on the spatial context - relation of the approaching direction of birds and the course of the mountain range (Aschwanden et al. 2020). Moreover, the influence of the mountain ranges is weather-dependent and manifests itself more strongly in unfavourable conditions, e.g., heavy cloud cover and strong headwinds (BRUDERER & JENNI 1990; BRUDERER 1996; WILLIAMS et al. 2001). The barrier effect is attributable to typical characteristics of mountain areas, such as increased altitude and varied topography (disrupting the pattern of air currents, atmospheric fronts, precipitation and limiting longdistance visibility), specificity of mountain habitats,

the severity of the local climate and instability of the weather (BRUDERER & JENNI 1990; PEDRINI et al. 2008; BRUDERER 2017). These external factors interact with species- and population-specific ones, such as geographical origin, capabilities, mode, distance, altitude or direction of flight and habitat selectivity, as well as with individual-specific factors, such as general physiological state, energy stores or experience of the individual (BRUDERER & JENNI 1990; BRUDERER 1996; BERTHOLD 2001; NEWTON 2008; PEDRINI et al. 2008).

The effect of the mountain chain barrier and its influence on bird migration was extensively studied in the Alps, amongst others by comparing species composition, migration intensity and flight behaviour (including direction) in the northern Alpine foothills and in the mountains (BRUDERER & JENNI 1990; BRUDERER 2017; ASCHWANDEN et al. 2020). In the present study, a similar method was adopted, however, due to the lack of data from the Carpathian foothills, analyses were made using data collected within the mountains, comparing migration intensity at different altitudes and at different distances from the outer border of the Carpathian range. We failed to confirm the relationship between migration intensity and the altitude of the locality. However, this may be due to the relatively low variability in the study sample – in autumn the difference in altitude between the highest and lowest locations was only 909 m, with a standard deviation of 206.4 m, and in spring even lower - 482 m and 142.6 m, respectively (Table 1). It can be assumed that with the relatively small number of locations surveyed and the low variability in altitude, the detection of a relationship was unlikely. Without the inclusion of the highest elevated areas (exceeding 2000 m asl) in the analysis, the result obtained should not be considered definitive. The relationship between migration intensity and distance from the Carpathian boundaries, on the other hand, was unclear, indicating a possible weak barrier effect occurring during autumn, and no such effect (and even a signal of inverse relationship) for spring migration.

Similarly, as it has been shown for the eastern Alps (Aschwanden et al. 2020), which are higher than the Carpathians, some results suggest an influence of the mountain chain on certain aspects of bird migration. In the Carpathians, for example, this is evidenced by the dominance of passage along the N-S axis rather than along the NE-SW axis, which is predominant in Europe (cf. discussion above). Nevertheless, this influence is not so pronounced as to become apparent on a large spatial scale, through a reduction in migration intensity in intra-mountain locations compared to those on the fringes of the chain or in higher-altitude areas compared to those lying lower. The results obtained therefore indicate that the Carpathians do not, in this respect, constitute a distinct barrier channelling a broad front bird migration in this part of Central Europe. It is worth bearing in mind, however, that the lack of data from neighbouring areas significantly limits the possibilities for comparison, including, for example, the detection of bird concentration in the northern foreland of the mountains during autumn. Thus, inference is limited to observations made within the Carpathians themselves, making it difficult to detect a barrier effect to migration for this mountain range on a wider geographical scale.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Appendix 1. Descriptive parameters of migration of particular bird species in the Carpathian Mts., recorded during field counts carried out in autumn seasons 2012–2013. Some values (marked *) refer to the wider period of 2011-2013. For each species, the number of observations (Obs.), the number of individuals (Ind.), the date of first and last observation in the season, the average number of observations (Obs./10 h) and individuals (Ind./10 h) per 10 hours of count (calculated for the period between the first and last record of certain species) are given. For the species recorded less than 10 times, some values (marked '-') were not calculated. In the last column, each species was assigned to one of the following groups of migrants: passerines (pas), pigeons (pig), birds of prey (bop), waterbirds (wat) or other (oth). Species sorted based on number of observed individuals.

No.	Species	Obs.	Ind.	Observ	vation	Obs./10 h	Ind./10 h	Group
				First	Last			
1	Fringilla coelebs L.	6657	83185	14 VIII	19 XI	24.20	302.4	pas
2	Columba palumbus L.	1054	18199	14 VIII*	11 XI*	3.17*	57.1*	pig
3	Corvus frugilegus L.	193	17602	16 VIII*	16 XI*	0.55*	46.7*	pas
4	Sturnus vulgaris L.	676	15447	15 VIII	11 XI	2.62	59.8	pas
5	Hirundo rustica L.	1710	14997	15 VIII	21 X	8.23	72.1	pas
6	Turdus pilaris L.	767	11283	18 VIII	19 XI	2.93	43.0	pas
7	Parus major L.	1004	7410	15 VIII	19 XI	3.66	27.0	pas
8	Spinus spinus (L.)	818	7405	16 VIII	19 XI	3.01	27.2	pas
9	Alauda arvensis L.	699	4447	15 VIII	16 XI	2.61	16.6	pas
10	Buteo buteo (L.)	2256	4093	14 VIII*	19 XI*	8.17*	15.6*	bop
11	Carduelis carduelis (L.)	635	3915	14 VIII	18 XI	2.31	14.3	pas
12	Anthus pratensis (L.)	1330	3658	16 VIII	16 XI	5.01	13.8	pas
13	Linaria cannabina (L.)	591	3392	15 VIII	19 XI	2.16	12.4	pas
14	<i>Coccothraustes coccothraustes</i> (L.)	436	2706	25 VIII	19 XI	1.81	11.2	pas
15	Emberiza citrinella L.	677	2674	15 VIII	18 XI	2.48	9.8	pas
16	Grus grus (L.)	90	2529	24 VIII*	11 XI*	0.54*	15.6*	wat
17	Chloris chloris (L.)	642	2512	14 VIII	18 XI	2.34	9.2	pas
18	Delichon urbicum (L.)	260	2315	15 VIII	5 X	1.64	14.6	pas
19	Periparus ater (L.)	454	2302	16 VIII	19 XI	1.67	8.5	pas
20	Corvus corax L.	785	2231	15 VIII*	19 XI*	3.29*	8.3*	pas
21	Motacilla alba L.	767	2208	14 VIII	31 X	3.34	9.6	pas
22	Anthus trivialis (L.)	1113	2110	14 VIII	21 X	5.33	10.1	pas
23	Pyrrhula pyrrhula (L.)	578	1978	16 VIII	19 XI	2.12	7.3	pas
24	Fringilla montifringilla L.	404	1910	23 IX	18 XI	2.72	12.9	pas
25	Cyanistes caeruleus (L.)	469	1824	15 VIII	18 XI	1.72	6.7	pas
26	Turdus viscivorus L.	516	1824	16 VIII	18 XI	1.90	6.7	pas
27	Loxia curvirostra L.	292	1727	16 VIII	19 XI	1.07	6.3	pas
28	Phalacrocorax carbo (L.)	108	1519	17 VIII	16 XI	0.41	5.8	wat
29	Corvus monedula L.	94	1323	16 VIII*	17 XI*	0.29*	4.0*	pas
30	Garrulus glandarius (L.)	686	1314	14 VIII*	18 XI*	2.53*	4.5*	pas
31	Corvus cornix L.	196	1185	14 VIII*	18 XI*	0.68*	3.6*	pas
32	Accipiter nisus (L.)	933	1061	14 VIII*	18 XI*	2.86*	3.2*	bop
33	Motacilla flava L.	192	783	15 VIII	6 X	1.16	4.7	pas
34	Aegithalos caudatus (L.)	81	709	16 VIII	19 XI	0.30	2.6	pas
35	Chroicocephalus ridibundus (L.)	40	674	15 VIII	18 XI	0.15	2.5	wat
36	Anas platyrhynchos L.	75	654	15 VIII	15 XI	0.29	2.5	wat
37	Passer montanus (L.)	80	633	15 VIII	17 XI	0.29	2.3	pas
38	Anser anser (L.)	21	632	22 IX*	15 XI*	0.12*	3.5*	wat
39	Ciconia ciconia (L.)	37	571	15 VIII*	2 X*	0.2*	2.7*	wat
40	Anser albifrons (Scop.)	6	506	2 X*	9 XI*	-	-	wat
41	Prunella modularis (L.)	213	470	18 VIII	4 XI	0.92	2.0	pas
42	Turdus merula L.	209	432	16 VIII	18 XI	0.77	1.6	pas

43	Falco tinnunculus L.	333	417	14 VIII*	16 XI*	1.17*	1.4*	bop
44	Nucifraga caryocatactes (L.)	278	416	14 VIII*	19 XI*	1.11*	1.5*	pas
45	Turdus philomelos C.L. Brehm	153	340	18 VIII	11 XI	0.62	1.4	pas
46	Anser fabalis s. lato (Lath.)	7	304	28 IX*	11 XI*	-	-	wat
47	Larus cachinnans Pall.	66	299	18 VIII	16 XI	0.26	1.2	wat
48	Streptopelia decaocto (Friv.)	81	289	16 VIII*	15 XI*	0.21*	0.7*	pig
49	Pica pica L.	152	285	15 VIII*	18 XI*	0.48*	0.9*	pas
50	Phoenicurus ochruros (S.G.	144	282	15 VIII	16 XI	0.54	1.1	pas
	Gmel.)		-		-			1
51	Dendrocopos major (L.)	244	263	14 VIII	19 XI	0.89	1.0	oth
52	Falco subbuteo L.	206	262	14 VIII*	12 X*	1.14*	1.4*	bop
53	Clanga pomarina (C.L. Brehm)	172	233	15 VIII*	13 X*	1.43*	1.9*	bop
54	Ardea cinerea L.	96	224	15 VIII	15 XI	0.37	0.9	wat
55	Accipiter gentilis (L.)	192	204	14 VIII*	18 XI*	0.59*	0.6*	bop
56	Columba oenas L.	64	184	18 VIII*	28 X*	0.24*	0.7*	pig
57	Circus aeruginosus (L.)	144	178	16 VIII*	3 XI*	0.67*	0.8*	bop
58	Vanellus vanellus (L.)	12	169	17 VIII	9 XI	0.05	0.7	wat
59	Phylloscopus collybita (Vieill.)	127	156	16 VIII	27 X	0.58	0.7	pas
60	Acanthis flammea (L.)	40	155	28 IX	19 XI	0.29	1.1	pas
61	Serinus serinus (L.)	66	153	14 VIII	4 XI	0.27	0.6	pas
62	Sitta europaea (L.)	122	152	16 VIII	18 XI	0.45	0.6	pas
63	Ardea alba L.	27	144	1 IX	10 XI	0.14	0.7	wat
64	Lullula arborea (L.)	51	144	18 VIII	28 X	0.24	0.7	pas
65	Poecile montanus (Conrad)	72	143	16 VIII	18 XI	0.27	0.5	pas
66	Lanius collurio L.	94	125	14 VIII	21 IX	0.79	1.0	pas
67	Pernis apivorus (L.)	94	124	14 VIII*	13 X*	0.49*	0.7*	bop
68	Dryocopus martius (L.)	120	121	14 VIII	18 XI	0.44	0.4	oth
69	Picus viridis L.	117	118	14 VIII	18 XI	0.43	0.4	oth
70	Cygnus olor (J.F. Gmel.)	42	113	18 VIII	11 XI	0.17	0.5	wat
71	Regulus regulus (L.)	55	112	19 VIII	15 XI	0.22	0.5	pas
72	Ciconia nigra (L.)	58	109	15 VIII*	4 X*	0.32*	0.6*	wat
73	Erithacus rubecula (L.)	76	104	16 VIII	18 XI	0.28	0.4	pas
74	Mergus merganser L.	13	91	25 VIII	10 XI	0.06	0.4	wat
75	Emberiza schoeniclus (L.)	58	90	17 VIII	10 XI	0.24	0.4	pas
76	Turdus iliacus L.	26	86	13 X	15 XI	0.31	1.0	pas
77	Sylvia atricapilla (L.)	53	80	14 VIII	5 X	0.33	0.5	pas
78	Circus cvaneus (L.)	74	79	24 IX*	16 XI*	0.67*	0.7*	bop
79	Troglodytes troglodytes (L.)	14	77	15 IX	4 XI	0.10	0.5	pas
80	Passer domesticus (L.)	15	74	17 VIII	15 XI	0.06	0.3	pas
81	Saxicola rubetra (L.)	39	73	16 VIII	27 IX	0.30	0.6	pas
82	Phasianus colchicus L.	55	69	16 VIII	16 XI	0.21	0.3	oth
83	Lanius excubitor L.	63	67	17 VIII	18 XI	0.24	0.3	pas
84	Lophophanes cristatus (L.)	39	67	19 VIII	16 XI	0.16	0.3	pas
85	Riparia riparia (L.)	13	60	23 VIII	15 IX	0.16	0.7	pas
86	Poecile palustris (L.)	38	59	25 VIII	19 XI	0.16	0.2	pas
87	Muscicana striata (Pall)	35	55	14 VIII	6 X	0.21	0.3	pas
88	Aquila chrysaetos (L.)	42	51	18 VIII*	18 XI*	0.17*	0.2*	hon
89	Apus apus (L.)	22	49	14 VIII	25 IX	0.17	0.4	oth
90	Motacilla cinerea Tunst	${23}$	38	16 VIII	6 X	0.14	0.2	pas
91	Picus canus LF Gmel	36	37	23 VIII	18 XI	0.14	0.2	oth
92	Gallingon gallingon (I)	3	31	1 IX	29 IX	-	-	wat
93	Falco vespertinus I	18	27	17 VIII*	4 X*	0.1*	0.1*	hon
94	Buteo lagonus (Pont.)	25	$\frac{2}{26}$	11 X*	15 XI*	0 33*	0.1	hon
95	Curruca communis Lath	17	20	15 VIII	15 IX	0.16	0.2	nas
96	Anthus cervinus (Pall)	14	16	13 IX	20 X	0.13	0.1	nas
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97	Dryobates minor (L.)	14	16	23 VIII	26 X	0.07	0.1	oth
98	Oriolus oriolus (L.)	13	16	15 VIII	5 IX	0.19	0.2	pas
99	Cuculus canorus L.	13	15	16 VIII	5 X	0.08	0.1	oth
100	Sterna hirundo L.	4	15	25 VIII	1 IX	-	-	wat
101	Dendrocopos leucotos (Bechst.)	14	14	24 VIII	16 XI	0.06	0.1	oth
102	<i>Oenanthe oenanthe</i> (L.)	11	14	23 VIII	22 IX	0.11	0.1	pas
103	Certhia familiaris L.	12	13	26 VIII	19 XI	0.05	0.1	pas
104	<i>Emberiza calandra</i> L.	3	13	21 IX	12 X	-	-	pas
105	Falco peregrinus Tunst.	12	12	14 VIII*	6 XI*	0.04*	0.0*	bop
106	Pandion haliaetus (L.)	11	12	4 IX*	21 X*	0.08*	0.1*	bop
107	Anthus spinoletta (L.)	6	11	20 X	11 XI	-	-	pas
108	Larus argentatus Pont.	1	11	11 XI	11 XI	-	-	wat
109	Phoenicurus phoenicurus (L.)	10	11	26 VIII	17 X	0.07	0.1	pas
110	Perdix perdix (L.)	1	10	17 VIII	17 VIII	-	-	oth
111	Ficedula hypoleuca (Pall.)	7	8	15 VIII	16 IX	-	-	pas
112	Saxicola rubicola (L.)	6	8	24 VIII	20 X	-	-	pas
113	Falco columbarius L.	7	7	14 IX*	16 XI*	-	-	bop
114	Larus fuscus L.		7	20 X	20 X	-	-	wat
115	Numenius arquata (L.)	2	1	24 VIII	29 IX	-	-	wat
116	Circus pygargus (L.)	6	6	I'/ VIII*	9 X*	-	-	bop
117	Phylloscopus trochilus (L.)	6	6	14 VIII	26 VIII	-	-	pas
118	Streptopelia turtur (L.)	5	6	23 VIII*	10 IX*	-	-	pıg
119	Larus canus L.	5	5	/ IX	27 X	-	-	wat
120	Plectrophenax nivalis (L.)	3	5	15 XI	1/XI	-	-	pas
121	Regulus ignicapilla (1emm.)	4	5	22 IX	20 X	-	-	pas
122	Milvus migrans (Bodd.)	4	4	18 VIII*	31 X*	-	-	bop
123	Picoides tridactylus (L.)	4	4	19 VIII	20 X	-	-	oth
124	Haliaeetus albicilla (L.)	3	3	11 X*		-	-	bop
125	Jynx torquilla L.	3	3	19 VIII	7 IX	-	-	oth
126	Curruca curruca (L.)	3	3	25 VIII	2 IX	-	-	pas
127	Curruca nisoria (Bechst.)	2	3	18 VIII	19 VIII	-	-	pas
128	Mareca strepera (L.)		2	13 X	13 X	-	-	wat
129	Bombycilla garrulus (L.)	2	2	19 X	18 XI	-	-	pas
130	Falco cherrug J.E. Gray	2	2	18 IX*	4 X*	-	-	bop
131	Linaria flavirostris (L.)		2	31 X	31 X	-	-	pas
132	Phylloscopus sibilatrix (Bechst.)		2	31 VIII	31 VIII	-	-	pas
133	<i>Remiz pendulinus</i> (L.)		2	28 IX	28 IX	-	-	pas
134	Tringa glareola L.	2	2	18 VIII 21 VIII	18 VIII 25 IV	-	-	wat
135	Tringa nebularia (Gunn.)	2	2	31 VIII 2 IV	25 IX	-	-	wat
130	Turdus torquatus L.	2	2	2 IX 1 IX	14 X	-	-	pas
13/	Asio flammeus (Pont.)		1	1 IX		-	-	oth
138	Circaetus gallicus (J.F. Gmel.)		1	4 IX*	4 IX*	-	-	bop
139	Coturnix coturnix (L.)		1	19 VIII	19 VIII	-	-	oth
140	Crex crex (L.)		1			-	-	wat
141	Dendrocoptes medius (L.)		1	14 X	14 X	-	-	oth
142	Ehren.)	1	1	25 VIII	25 VIII	-	-	oth
143	Egretta garzetta (L.)	1	1	29 IX	29 IX	-	-	wat
144	Ficedula albicollis (Temm.)	1	1	19 VIII	19 VIII	-	-	pas
145	Hydrocoloeus minutus (Pall.)	1	1	10 XI	10 XI	-	-	wat
146	Locustella fluviatilis (Wolf)	1	1	16 XI	16 XI	-	-	pas
147	Locustella naevia (Bodd.)	1	1	18 VIII	18 VIII	-	-	pas
148	Pluvialis squatarola (L.)	1	1	14 IX	14 IX	-	-	wat
149	Tringa totanus (L.)	1	1	17 VIII	17 VIII	-	-	wat

Appendix 2. Descriptive parameters of migration of particular bird species in the Carpathian Mts., recorded during field counts carried out in spring 2015. For each species, the number of observations (Obs.), the number of individuals (Ind.), the date of first and last observation in the season, the average number of observations (Obs./10 h) and individuals (Ind./10 h) per 10 hours of count (calculated for the period between the first and last record of certain species) are given. For the species recorded less than 10 times, some values (marked '-') were not calculated. In the last column, each species was assigned to one of the following groups of migrants: passerines (pas), pigeons (pig), birds of prey (bop), waterbirds (wat) or other (oth). Species sorted based on the number of observed individuals.

No.	Species	Obs.	Ind.	Obser	vation	Obs./10 h	Ind./10 h	Group
	1			First	Last			1
1	Sturnus vulgaris L.	396	4896	7 III	5 V	4.00	49.5	pas
2	Turdus pilaris L.	216	2888	7 III	3 V	2.23	29.8	pas
3	Fringilla coelebs L.	715	2824	7 III	5 V	7.23	28.6	pas
4	Grus grus (L.)	39	2416	8 III	19 IV	0.55	33.8	wat
5	Columba palumbus L.	362	1775	8 III	3 V	3.80	18.6	pig
6	Buteo buteo (L.)	796	1365	7 III	5 V	8.05	13.8	bop
7	Alauda arvensis L.	370	1253	7 III	5 V	3.74	12.7	pas
8	<i>Hirundo rustica</i> L.	246	674	30 III	5 V	4.03	11.0	pas
9	Linaria cannabina (L.)	222	535	7 III	5 V	2.24	5.4	pas
10	Motacilla alba L.	246	366	7 III	5 V	2.49	3.7	pas
11	Phalacrocorax carbo (L.)	27	362	9 III	25 IV	0.37	4.9	wat
12	Anthus pratensis (L.)	166	361	8 III	5 V	1.71	3.7	pas
13	Corvus corax L.	221	352	7 III	5 V	2.23	3.6	pas
14	Parus major L.	118	335	7 III	5 V	1.19	3.4	pas
15	Corvus frugilegus L.	21	319	8 III	3 V	0.24	3.7	pas
16	Carduelis carduelis (L.)	135	290	8 III	5 V	1.39	3.0	pas
17	Emberiza citrinella L.	183	280	7 III	5 V	1.85	2.8	pas
18	Vanellus vanellus (L.)	47	271	7 III	1 V	0.52	3.0	wat
19	Garrulus glandarius (L.)	109	265	7 III	5 V	1.10	2.7	pas
20	Columba oenas L.	89	225	7 III	3 V	0.92	2.3	pig
21	Ciconia ciconia (L.)	81	217	16 III	3 V	1.00	2.7	wat
22	Chloris chloris (L.)	113	203	7 III	3 V	1.17	2.1	pas
23	Corvus cornix L.	111	197	8 III	5 V	1.14	2.0	pas
24	Turdus viscivorus L.	122	192	7 III	5 V	1.23	1.9	pas
25	Turdus philomelos C.L. Brehm	76	165	14 III	5 V	0.85	1.8	pas
26	Larus cachinnans Pall.	61	147	9 III	5 V	0.67	1.6	wat
27	Anthus trivialis (L.)	64	134	29 III	3 V	0.98	2.1	pas
28	Accipiter nisus (L.)	131	132	8 III	5 V	1.35	1.4	bop
29	Pica pica L.	74	131	7 III	3 V	0.76	1.4	pas
30	Periparus ater (L.)	41	124	7 III	21 IV	0.55	1.7	pas
31	Anser anser (L.)	4	112	8 III	17 III	-	-	wat
32	Falco tinnunculus L.	103	109	8 III	5 V	1.06	1.1	bop
33	<i>Coccothraustes coccothraustes</i> (L.)	41	94	8 III	5 V	0.42	1.0	pas
34	Cyanistes caeruleus (L.)	49	90	7 III	5 V	0.50	0.9	pas
35	Corvus monedula L.	24	89	16 III	3 V	0.30	1.1	pas
36	Spinus spinus (L.)	20	88	8 III	3 V	0.21	0.9	pas
37	Ciconia nigra (L.)	53	80	21 III	5 V	0.68	1.0	wat
38	Delichon urbicum (L.)	25	76	13 IV	5 V	0.65	2.0	pas
39	Chroicocephalus ridibundus (L.)	10	76	14 III	21 IV	0.15	1.2	wat
40	Turdus merula L.	59	71	8 III	5 V	0.61	0.7	pas
41	Accipiter gentilis (L.)	61	66	7 III	3 V	0.63	0.7	bop
42	Clanga pomarina (C.L. Brehm)	51	62	4 IV	3 V	0.93	1.1	bop
43	Ardea cinerea L.	45	57	8 III	3 V	0.47	0.6	wat

44	Anser fabalis s lato (Lath)	2	57	8 III	4 IV	_	_	wat
45	Fringilla montifringilla L	21	54	8 III	12 IV	0.36	0.9	nas
46	Mergus merganser I	32	24 46	9 III	3 V	0.36	0.5	wat
40 17	Phoenicurus ochruros (S G	40	40	17 III	5 V	0.50	0.5	nac
т/	Gmel)	70		1 / 111	5 V	0.50	0.0	pas
18	Pyrrhula pyrrhula (I)	25	12	8 III	2 V	0.27	0.5	nac
40	Motacilla flava I	23	42	24 III	$\frac{2}{3}$ V	0.27	0.5	pas
49 50	Turdus iliacus I	11	28	24 III 21 III	17 W	0.31	0.0	pas
51	A agithalog agudatus (L.)	0	20	0 III	1/1V	0.43	1.5	pas
51	Circus geruginosus (L.)	25	27	0 III 22 III	$\frac{2}{2}$ V	- 0.51	- 0.5	pas
52 52	Circus deruginosus (L.)	22	27	23 III 19 IV	2 V 5 V	0.31	0.5	bop
55 51	Saxicola rubelra (L.)	28	27 24	10 I V 22 III	5V 5V	0.83	1.1	pas
54 55	Anga platurburgh og I	32	24	23 III 9 III		0.43	0.5	pas
55	Ands platyrnynchos L.	16	54 24	0 III 15 III		0.23	0.4	wat
50 57	Prunella modularis (L.)	10	34 22	13 III		0.18	0.4	pas
5/	Apus apus $(L.)$	9	33	24 IV		-	-	oth
58 50	Serinus serinus (L.)	26	32		3 V	0.58	0.7	pas
59	Picus viridis L.	23	25	/ 111		0.26	0.3	oth
60	Dendrocopos major (L.)	23	23	8 111	28 IV	0.27	0.3	oth
61	Passer montanus (L.)	6	21	8 111	26 IV	-	-	pas
62	Dryocopus martius (L.)	20	20	7 III	28 IV	0.23	0.2	oth
63	Poecile montanus (Conrad)	15	19	7 III	19 IV	0.21	0.3	pas
64	<i>Oenanthe oenanthe</i> (L.)	9	19	5 IV	18 IV	-	-	pas
65	Aquila chrysaetos (L.)	14	16	17 III	3 V	0.18	0.2	bop
66	Circus cyaneus (L.)	13	15	8 III	12 IV	0.22	0.3	bop
67	Lullula arborea (L.)	12	15	8 III	16 III	0.69	0.9	pas
68	Saxicola rubicola (L.)	11	15	30 III	1 V	0.21	0.3	pas
69	Regulus regulus (L.)	3	15	16 III	12 IV	-	-	pas
70	Erithacus rubecula (L.)	13	13	23 III	28 IV	0.21	0.2	pas
71	Picus canus J.F. Gmel.	12	13	8 III	11 IV	0.23	0.2	oth
72	Pernis apivorus (L.)	8	13	25 IV	3 V	-	-	bop
73	Cuculus canorus L.	12	12	24 IV	3 V	0.55	0.5	oth
74	Falco subbuteo L.	11	12	18 IV	3 V	0.35	0.4	bop
75	<i>Sterna hirundo</i> L.	3	12	16 IV	3 V	-	-	wat
76	Anser albifrons (Scop.)	1	12	8 III	8 III	-	-	wat
77	Phylloscopus trochilus (L.)	11	11	14 IV	5 V	0.29	0.3	pas
78	Sitta europaea (L.)	11	11	7 III	19 IV	0.15	0.2	pas
79	Motacilla cinerea Tunst.	10	10	9 III	3 V	0.11	0.1	pas
80	Loxia curvirostra L.	6	8	15 III	28 IV	-	-	pas
81	Spatula querquedula (L.)	2	8	16 III	16 III	-	-	wat
82	Circus pygargus (L.)	6	7	12 IV	28 IV	-	-	bop
83	Lanius excubitor L.	6	6	7 III	21 IV	-	-	pas
84	Curruca communis Lath.	6	6	19 IV	5 V	-	-	pas
85	Poecile palustris (L.)	5	6	17 III	31 III	-	-	pas
86	Turdus torauatus L	5	6	29 III	21 IV	-	-	pas
87	Buteo lagonus (Pont.)	5	5	8 III	23 III	_	_	bon
88	Nucifraga carvocatactes (I)	5	5	7 III	25 III 2 V	_	_	nas
89	Sylvia atricanilla (I_)	5	5	19 IV	$\frac{2}{5}$ V	_	_	pus
90	Pandion haliaetus (I_)	<u></u>	5 4	6 IV	21 IV	_	_	bon
01	Phasianus colchicus I			15 III	6 IV	_	_	oth
02	I musiumus concincus L.	1	4	20 III	20 III	-	-	wot
92 02	Corvus corrig I	1	4	10 IV	10 W	-	-	wal
93 04	Emboriza soloconiclus (I)	2	2 2	Q 111	16 11	-	-	pas
74 05	Emberiza schoenicius (L.)	2	2 2	0 III 15 III	10 III 25 IV	-	-	pas har
7J 04	A capthia flamma (L.)		2 2	13 III 0 III	23 I V 0 111	-	-	bop
70 07	Acaninis jiammea (L.)		3	0 III 2 V	8 III 2 M	-	-	pas
9/	Crex crex (L.)		3	3 V	3 V	-	-	wat

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98	Dendrocopos leucotos (Bechst.)	2	2	29 III	30 III	-	-	oth
99	Larus canus L.	2	2	30 III	28 IV	-	-	wat
100	Milvus migrans (Bodd.)	2	2	11 IV	19 IV	-	-	bop
100	Passer domesticus (L.)	2	2	8 III	30 III	-	-	pas
102	Regulus ignicapilla (Temm.)	2	2	30 III	28 IV	-	-	pas
103	Anas crecca L.	1	1	6 IV	6 IV	-	-	wat
104	Certhia familiaris L.	1	1	16 III	16 III	-	-	pas
105	Dryobates minor (L.)	1	1	15 III	15 III	-	-	oth
106	Emberiza calandra L.	1	1	1 V	1 V	-	-	pas
107	Falco columbarius L.	1	1	9 III	9 III	-	-	bop
108	Merops apiaster L.	1	1	1 V	1 V	-	-	oth
109	Milvus milvus (L.)	1	1	29 III	29 III	-	-	bop
110	Oriolus oriolus (L.)	1	1	2 V	2 V	-	-	pas
111	Phoenicurus phoenicurus (L.)	1	1	28 IV	28 IV	-	-	pas
112	<i>Riparia riparia</i> (L.)	1	1	18 IV	18 IV	-	-	pas
113	Streptopelia decaocto (Friv.)	1	1	8 III	8 III	-	-	pig
114	<i>Curruca curruca</i> (L.)	1	1	24 IV	24 IV	-	-	pas
115	Tringa totanus (L.)	1	1	10 IV	10 IV	-	-	wat
116	Troglodytes troglodytes (L.)	1	1	8 III	8 III	-	-	pas
117	Upupa epops L.	1	1	25 IV	25 IV	-	-	oth