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Catchment-scale habitat selection in stream-dwelling bird species: the Grey Wagtail *Motacilla cinerea* and White-throated Dipper *Cinclus cinclus* in the Beskid Żywiecki Mts (S Poland)

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Abstract: The Grey Wagtail *Motacilla cinerea* and White-throated Dipper *Cinclus cinclus* are closely associated with the running waters and inhabit fast-flowing streams. However, catchment-scale habitat preferences of these stream-dwelling species remain poorly recognized. The aim of this study was to assess species breeding habitat selection with respect to the topography and habitat type in the Beskid Żywiecki Mts (S Poland). The habitat characteristics increasing the probability of occurrence of the Grey Wagtail were increasing altitude, north-westerly aspect, gentler slope and decreasing distance from roads; in the case of the White-throated Dipper, they were gentler slope and decreasing distances from both roads and built-up areas and northerly aspects. While White-throated Dippers preferred watercourses that crossed open habitats (meadows, farmlands and early successional stages of forest) and avoided watercourses flowing through coniferous and mixed forest stands, Grey Wagtails showed no clear preferences for forest stands. Although the observed preference for man-made structures could be an artefact (since infrastructure tends to be concentrated in stream valleys), both species preferred locations where the stream gradient is gentler. Such sites, with local accumulations of larger volumes of water, create habitat suitable for aquatic invertebrates serving as the main food source of both studied species. As hydro-engineering works and forest management in adjacent terrestrial areas may change the character of watercourses and water quality (oxygenation and acidification), preservation of naturally flowing watercourses is important for conservation of stream-dwelling bird species.

Key words: species distribution, water-related birds, topography, mountains, the Carpathians

Wybiórczość siedliskowa ptaków związanych z potokami w skali zlewni: pliszka górska *Motacilla cinerea* i pluszcz *Cinclus cinclus* w Beskidzie Żywieckim. Abstrakt: Pliszka górska *Motacilla cinerea* i pluszcz *Cinclus cinclus* zasiedlając szybko płynące rzeki i strumienie należą do gatunków ściśle związanych z ciekami. Jednak preferencje siedliskowe ptaków wykorzystujących górskie cieki pozostają słabo rozpoznane w skali zlewni. Celem pracy była ocena preferencji siedliskowych pliszki górskiej i pluszcza w warunkach Beskidu Żywieckiego w odniesieniu do topografii terenu i typu siedliska. Cechami siedliska zwiększającymi prawdopodobieństwo występowania pliszki górskiej były rosnąca wysokość nad poziomem morza, ekspozycja północno-zachodnia i łagodniejsze nachylenie stoków, a także malejąca odległość od dróg; w przypadku pluszcza były to łagodniejsze nachylenie stoku oraz malejące odległości od dróg i obszarów zabudowanych, a także północne ekspozycje. Pluszcze preferowały cieki przecinające siedliska otwarte (łąki, pola uprawne i wczesne stadia sukcesyjne lasów), unikając cieków płynących przez drzewostany iglaste i mieszane. Natomiast pliszki górskie nie wykazywały wyraźnych preferencji względem typu drzewostanu otaczającego cieki. Stwierdzona preferencja przez pliszkę górską i pluszcza struktur tworzonych przez człowieka (drogi i zabudowa) może być jednak artefaktem, gdyż infrastruktura zwykle bywa skoncentrowana w dolinach. Badane gatunki preferowały miejsca, w których spadek strumienia jest łagodniejszy, co zapewne ma związek z możliwością gromadzenia się większych objętości wody i tworzenia siedlisk odpowiednich dla bezkręgowców stanowiących główne źródło pożywienia obu badanych gatunków. Ponieważ prace hydro-inżynieryjne i gospodarka leśna na przyległych obszarach lądowych mogą zmieniać charakter cieków i jakość wody (natlenienie i zakwaszenie), zachowanie naturalnie płynących wód jest istotne dla ochrony gatunków ptaków związanych z wodami górskimi.

Słowa kluczowe: rozmieszczenie gatunku, ptaki wodne, topografia, góry, Karpaty

Mountain watercourses host a unique community of organisms owing to the highly specific physicochemical and trophic conditions of the water (Hughes & Noss 1992, Allan & Flecker 1993). White-throated Dipper *Cinclus cinclus* (hereafter: Dipper) and Grey Wagtail *Motacilla cinerea* are typical stream-dwelling bird species of the Palaearctic. Both have narrow habitat requirements (stenotopic), and streams with clear, fast-flowing water are of key importance to both as a breeding and foraging habitat. Because they react immediately to degradation of habitats and water pollution, these birds are good biological indicators, allowing for reliable assessments of changes in the environment (Vickery 1991, Del Guasta 2003). The key factor determining the occurrence of Dippers and Grey Wagtails is the natural character of watercourses and the greatest threat to them is therefore posed by the transformation of riverine and riparian environments (Ciach 2016a, 2016b).

Human activities, such as water supply management, floodplain regulation, environmental changes within catchment areas (urbanization, deforestation, fertilization), as well as climate changes and events (often extreme in character) have led to the habitat degradation and loss of biological diversity of riverine ecosystems (Nilsson & Dynesius 1994, Wyżga et al. 2008, Figarski & Kajtoch 2015). Regulation of watercourses, and hydro-engineering works like riverbank reinforcement, embankment and dam construction, the removal of gravel and wood from river beds, and stream gradient reduction, can radically alter their character: microhabitat structure is simplified and the natural hydrological dynamics change (Johnson 1992, Malmqvist & Rundle 2002). However, the impact of human activities on natural habitats in high-mountain regions is limited. As less accessible mountainous areas may still have a topography with naturally flowing watercourses that are not seriously affected by the human activities, local land characteristics may govern the occurrence of certain species and determine species distributions.

Studies of Dippers and Grey Wagtails carried out in the Polish Carpathians and the Sudetes have dealt mainly with the regional abundance and distribution of these birds (Dziuba 2006, Czapulak et al. 2008b, Ledwoń et al. 2009, Cichocki & Mielczarek 2011). This work assessed habitat selection of the Dipper and Grey Wagtail with respect to the catchment characteristics, i.e. topography of streams and the nature of the terrestrial habitats they cross. We aimed to identify those sites in mountain ranges that are most suitable for the occurrence of the studied stream-dwelling bird species.

Methods

Study area

The study was conducted in the Beskid Żywiecki Mountains. These consist of several ranges, with the Wielka Racza (1 236 m asl) and the Pilsko (1 557 m asl) dominating the area (Kondracki 2000). The Beskid Żywiecki Mountains are composed of flysch rocks. The dominant plant communities include fertile Carpathian beech forest *Dentario glandulosae-Fagetum* in the lower subalpine zone, fir-spruce forest *Abieti-Piceetum* in the middle subalpine zone, and the upper subalpine acidophilous Carpathian spruce forest *Plagiothecio-Piceetum* (Holeksa & Szwagrzyk 2004a, 2004b, Szwagrzyk & Holeksa 2004). However, forestry management practices have given rise to far-reaching changes in the region's woodland communities: an introduced the Norway Spruce *Picea abies* has become dominant in many places. In recent years, however, these extensive artificial spruce stands have seriously deteriorated in quality.

The hydrographic network of the Beskid Żywiecki Mountains consists of two main rivers – the Soła and the Koszarawa – and their numerous tributaries, the total length of these watercourses being 673.4 km. The source of most of them lie at high altitudes, sometimes above 1 400 m asl (GUGiK 2013). The streams have steep gradients and many cascades. The majority of riverbeds are natural, although parts have been regulated, especially through the building of weirs and the reinforcement of riverbanks, along which communication routes are often located. The study area included the Beskid Żywiecki Mountains Special Protection Area PLB240002 (Important Bird Area PL127), covering the western part of the Beskid Żywiecko-Orawski Mountains. It also largely overlaps with the Beskid Żywiecki Mountains Special Area of Conservation PLH240006.

Methods and data analyses

Data on species distribution were taken from a survey of breeding birds conducted in the Beskid Żywiecki Mountains Special Protection Area (36 962 ha) in 2008. Three surveys were carried out in mid-April to mid-May, mid-May to mid-June, and mid-June to late July, all of which covered breeding season of the Grey Wagtail and Dipper in the Carpathians (Cramp 1998, Ciach & Sikora 2015). All observations were marked on a 1:25 000 scale map and the localities of birds recorded during all three surveys were used to identify breeding territories (Ciach et al. 2009). According to D'Amico & Hemery (2003), three visits are required to detect Dippers on linear territories and to identify the whole breeding population. Crowther et al. (2018) identified territory size and territory limits in the winter and in the breeding season with two visits. To study the upper and lower extents of the territory of American Dippers *Cinclus mexicanus*, Feck & Hall (2004) conducted several visits, while Chen & Wang (2010) to determine the boundaries of territories of the Brown Dipper *Cinclus pallasii* with at least one marked individual. For the Grey Wagtail, at least two visits are recommended to survey the breeding population (Ciach & Sikora 2015, Cichocki et al. 2023). However, specific recommendations on the methodology for delimiting the territories are not available for the species. Borders of neighbouring territories were identified on the basis of simultaneous observations of birds displaying territorial behaviour. The survey revealed 35 Dipper territories and 203 Grey Wagtail territories.

The centre of each Dipper and Grey Wagtail breeding territory was specified as the centre of mass (barycentre) of a polygon, set from three observation points. For two observations, the middle point of the distance between them was taken as the centre of a breeding area. For a single observation of a nest, family, pair, or an individual indicating occupation of a territory, the point of observation was taken as the centre of the breeding territory. Observations of birds flying over the area were not included in the territory mapping. Methods based on a large number of observations applied for accurate determination of territory limits or frequency of territory use, e.g. kernel density estimation, concave/convex polygons, are difficult to apply in population studies. As the delineation of territories is not based on individually marked birds recorded during multiple visits or tracked with telemetry, the method adopted in this study is, to some extent, an approximation of the locations of the territories. As the precision of estimation of the center of breeding territory based on low number of records is limited, conducted analyses were restricted to the basic catchment characteristics. As the territories identified referred to confirmed, probable or possible breeding events, the information on the breeding category was not included in the analyses.

The results of the bird survey were combined with numerical spatial data – a digital elevation model (DEM), a topographical database (GUGiK 2014), and CORINE Land Cover 2006 (CLC) (GIOŚ 2006) – in order to determine habitat variables for both Dipper and Grey Wagtail territories and the random points. For every point in the Dipper and Grey Wagtail territories and a comparative layer of random points, the following variables were determined: (a) topography, (b) urbanization and (c) habitat characteristics (Table 1). Measurements were taken in 203 Grey Wagtail territories, in 35 Dipper territories and at 203 randomly selected points (Fig. 1). Coordinates of the random points in a number equal to the number of Grey Wagtail territories were generated within the linear layer of hydrographic network of the study area (KZGW 2009) using QGIS software (QGIS Development Team 2013). As the Grey Wagtails and Dippers co-occur and their ranges overlap in the spatial scale of the Carpathians (Ciach 2016a, Ciach 2016b), the same set of random points was used to characterize habitat preferences of both studied species. Topographical parameters were determined using QGIS software (QGIS Development Team 2013) from the digital elevation model (DEM) with the pixel size of approximately

Table 1. Habitat variables measured in Grey Wagtail *Motacilla cinerea* and White-throated Dipper *Cinclus cinclus* territories and at random points in the Beskid Żywiecki Mts (southern Poland)
Tabela 1. *Zmienne siedliskowe mierzone w terytoriach pliszki górskiej i pluszcza oraz w punktach losowych w Beskidzie Żywieckim. (1) – zmienne, (2) – jednostki, (3) – źródło danych, (4) – topografia, (5) – wysokość, (6) – spadek, (7) – wystawa, (8) – urbanizacja, (9) – odległość od dróg, (10) – odległość od terenów zabudowanych, (11) – charakterystyka siedlisk, (12) – wielkość płatu siedliska, (13) – typ siedliska, (14) – m n.p.m., (15) – stopnie, (16) – typ pokrycia terenu*

Variables (1)	Unit (2)	Data source (3)
	Topography (4)	
Altitude (5)	m asl (14)	Digital Elevation Model (DEM) (CODGiK 2010)
Slope (6)	degrees (15)	
Aspect (7)	degrees	
	Urbanization (8)	
Distance from roads (9)	m	Topographical Database (GUGiK 2008)
Distance from built-up areas (10)	m	
	Habitat characteristics (11)	
Habitat patch size (12)	ha	CORINE Land Cover 2006 (GIOŚ 2006)
Type of vegetation (13)	land cover type (16)	

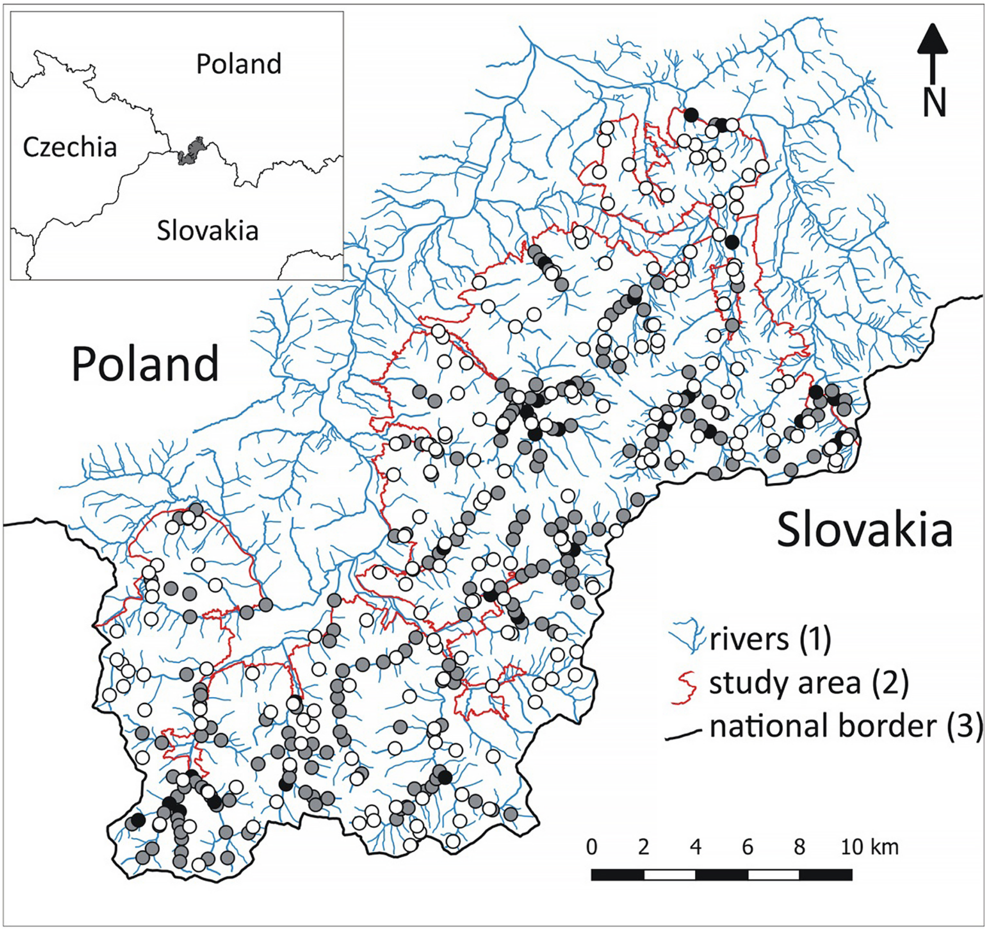

Fig. 1. Distribution of White-throated Dipper *Cinclus cinclus* (black circles) and Grey Wagtail *Motacilla cinerea* territories (grey circles) and random points (open circles) in the Beskid Żywiecki Mts (southern Poland)

Rys. 1. *Rozmieszczenie terytoriów pluszcza (czarne kółka) i pliszki górskiej (szare kółka) oraz punktów losowych (białe kółka) w Beskidzie Żywieckim. (1) – rzeki, (2) – granica terenu badań, (3) – granica państwa*

80 × 80 m (CODGiK 2010). Altitudes, slopes and aspects (Table 1) were derived from the DEM raster layers for each of centre of Dipper and Grey Wagtail territories and the random points. Urbanization proxies (distance from roads and distance from built-up areas) were taken from the Topographical Database available in the Geoportal resources (GUGiK 2013) by using the Geoxa Viewer software (CGIS 2011). The shortest distances from the central points of the species' territories and random points to the axes of roads and built-up areas was measured. The road network was defined as consisting of paved and dirt roads, as well as foot and cycle paths, while built-up areas were defined as land covered with buildings (GUGIK 2008).

Habitat characteristics (habitat type and patch size) were taken from CLC model (GIOŚ 2006). The global CLC includes 44 classes of land cover (there are 31 such classes in Poland), distinguished on the basis of satellite photographs that has spatial accuracy of approximately 20 × 20 m. To characterize territories of the studied species, the layers with the territories and random points were spatially joined with the CLC layers. Six types of habitats overlapped with territories of the studied species: built-up areas, open habitats (arable fields, meadows, crops, farmlands), deciduous forests, coniferous forests, mixed forests and forests subject to change. This last category includes copses, early successional stages, and also disturbed habitats, where tree stands have disintegrated as a consequence of natural disasters.

In the first step, descriptive statistics of habitat variables in Grey Wagtail and White-throated Dipper territories were calculated and compared with values obtained at random points. Since the data distribution of the variables differed from normality (Shapiro-Wilk W test, $P < 0.05$), differences in the variables were analysed with the non-parametric Mann-Whitney U test. The χ^2 test was used to analyse the differences in the slope aspect and the type of habitat available and that actually utilized. A minimum probability level of $P < 0.05$ was considered significant. Owing to the dichotomous nature of the dependent variable (0 – random site, 1 – Dipper/Grey Wagtail site), a generalized linear model (GLM) with binomial distribution was used to determine habitat characteristics predicting the probability of Dipper/Grey Wagtail occurrence. Akaike's information criterion (AIC) was used to select model best describing the probability of species occurrence (Burnham & Anderson 2002). The model with the lowest AIC was presented, for which GLM was run to visualise strength and direction of the relationship between the species occurrence and variables indicated in the best describing model (Nagelkerke pseudo-R^2 was calculated for each presented model). Prior to the modelling procedure, co-linearity between variables was inspected using Pearson's correlation matrix and aspect data (degrees) were cosine-transformed. The statistical procedures were performed in STATISTICA 13 software (TIBCO Software 2017).

Results

The Grey Wagtail has a wide range of vertical occurrence, its territories being located between 398 m and 1 235 m asl (Table 2). However, 74.4% of pairs (N=203) were found in the altitude range from 600 to 900 m asl (Fig. 2). The Dipper's range of vertical occurrence is smaller: its territories were sited between 394 m and 904 m asl (Table 2). However, 82.9% of pairs (N=35) were found at altitudes from 600 to 900 m asl (Fig. 2).

In the Beskid Żywiecki Mountains Grey Wagtails selected breeding localities with a gentler slope and situated at a shorter distance from roads compared to the random points (Table 2). The species preferred localities with a north and westerly aspects (χ^2 =15.67; P=0.028), avoiding those with a north-easterly or south-easterly aspect (Fig. 3). The total of 59.1% of the Grey Wagtails territories was located on slopes with northerly, north-westerly or westerly aspects (Fig. 3). Dippers selected localities with a gentler slope, situated at shorter distances from built-up areas and from roads compared to the random points (Table 2). The aspect of the species territories differed from that of the random points (χ^2 =59.51; P<0.000) and the total of 77.1% of territories was located on slopes with northerly, north-westerly or north-easterly aspects (Fig. 3).

Both the Grey Wagtail and Dipper territories covered a wide spectrum of habitats and were situated in all six habitat types (Fig. 4). The proportions of particular types of habitats within the Grey Wagtail territories and at random points did not differ (χ^2 =7.01; P=0.22). However, higher than expected proportion of the species territories was located in watercourses that cross forests subject to change, i.e. early successional stages and

Table 2. Median, quartiles and ranges of habitat variables in Grey Wagtail *Motacilla cinerea* (N=203) and White-throated Dipper *Cinclus cinclus* (N=35) territories and at random points (N=203) in the Beskid Żywiecki Mts (southern Poland). The same set of random points was used to characterize habitat preferences of both studied species and tests refer to differences between Grey Wagtail territories and random points and Dipper territories and random points. Quartiles – percentiles 25% – 75%, Z_c – value of the Mann-Whitney U test approximation

***Tabela 2.** Mediany, kwartyle i zakresy zmiennych siedliskowych w terytoriach pliszki górskiej (N=203) i pluszcza (N=35) oraz w punktach losowych (N=203) w Beskidzie Żywieckim. Do określenia preferencji siedliskowych obu badanych gatunków wykorzystano ten sam zestaw punktów losowych, a testy odnoszą się do różnic między terytoriami pliszki górskiej i punktami losowymi oraz terytoriami pluszcza i punktami losowymi. Objaśnienia zmiennych przedstawione są w Tabeli 1, (1) – punkty losowe, (2) – pliszka górska, (3) – pluszcz, (4) – mediana, (5) – kwartyle (percentyle 25% – 75%), (6) – zakres, Z_c – wartość aproksymacji testu U Manna-Whitneya*

Variables	median (4)	quartiles (5)	range (6)	Z_c	P
	random points (1)				
Altitude	743.0	613–870	403–1164		
Slope	9.9	6.1–14.9	0.3–29.2		
Distance from roads	37.0	17–83	2–715		
Distance from built-up areas	416.0	159–929	0–2623		
Habitat patch size	283.0	99–14 831	25–14 831		
	Grey Wagtail (2)				
Altitude	741.0	646–835	398–1 235	–0.57	0.567
Slope	8.3	5.9–12.4	0.9–22.1	2.42	0.016
Distance from roads	19.0	11–38	0–300	5.57	0.000
Distance from built-up areas	328.0	75–931	0–2 729	1.35	0.177
Habitat patch size	250.0	80–14 831	25–14 831	0.00	0.999
	White-throated Dipper (3)				
Altitude	692.0	622–761	394–904	1.52	0.129
Slope	7.1	5.1–13.2	0.9–18.3	2.35	0.019
Distance from roads	19.0	13–29	3–96	3.62	0.000
Distance from built-up areas	182.0	50–518	0–1368	2.69	0.007
Habitat patch size	250.0	109–14 831	34–14 831	0.27	0.786

disturbed patches, where tree stands have disintegrated as a result of natural disasters (χ^2 =4.73; P=0.030) (Fig. 4). The types of habitats within the Dipper territories and at random points differed (χ^2 =17.65; P=0.003). The species preferred watercourses that cross open habitats, i.e. meadows, farmlands (χ^2 =7.71; P=0.005), and forests subject to change (χ^2 =7.05; P=0.008), avoiding watercourses within coniferous (χ^2 =5.33; P=0.021) and mixed woodland (χ^2 =4.33; P=0.037) (Fig. 4).

The highest rank model describing the probability of Grey Wagtail occurrence (AIC=523.5; R^2_N =0.15) consisted of four habitat variables: altitude, slope, aspect and distance from roads (Table 3). The subsequent best describing model (AIC=524.8; R^2_N =0.15) included variable additional to above listed: distance from built-up areas. The model best describing the probability of Dipper occurrence (AIC=183.5; R^2_N =0.15) consisted of two habitat variables: distance from built-up areas and distance from roads (Table 3). The subsequent best describing model (AIC=184.5; R^2_N =0.13) consisted of single habitat variables: distance from roads.

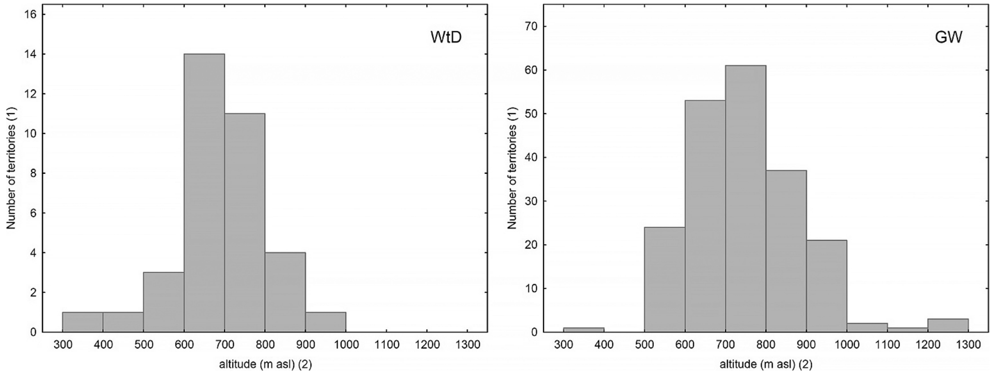

Fig. 2. Distribution of White-throated Dipper *Cinclus cinclus* (WtD – left figure) and Grey Wagtail *Motacilla cinerea* (GW – right figure) territories in relation to altitude in the Beskid Żywiecki Mts (southern Poland)
Rys. 2. *Rozmieszczenie terytoriów pluszcza (WtD – lewy rysunek) i pliszki górskiej (GW – prawy rysunek) w zależności od wysokości nad poziomem morza w Beskidzie Żywieckim. (1) – liczba terytoriów, (2) – wysokość w metrach nad poziomem morza*

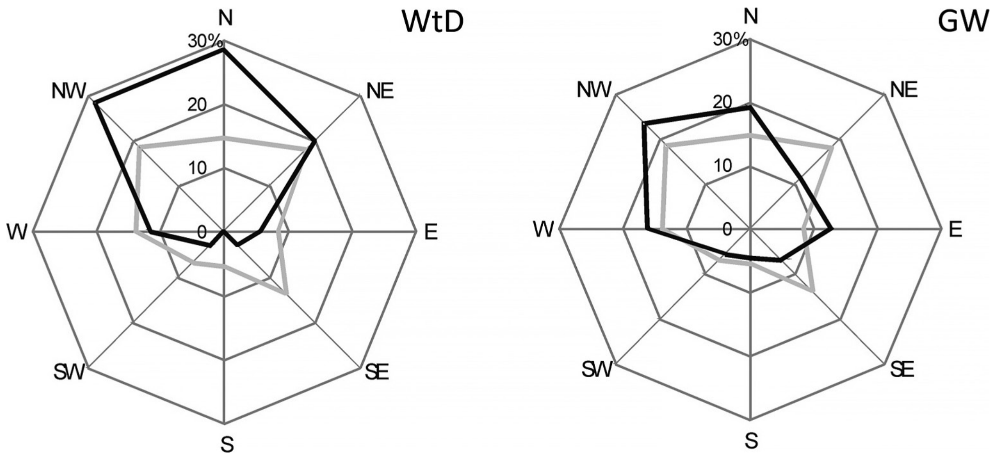

Fig. 3. Slope aspect in White-throated Dipper *Cinclus cinclus* (WtD – left figure, black line) and Grey Wagtail *Motacilla cinerea* (GW – right figure, black line) territories and at random points (grey lines) in the Beskid Żywiecki Mts (southern Poland)
Rys. 3. *Wystawa stoku w terytoriach pluszcza (WtD – lewy rysunek, czarna linia) i pliszki górskiej (GW – prawy rysunek, czarna linia) oraz w losowych punktach (szare linie) w Beskidzie Żywieckim*

Discussion

Habitat characteristics

The results of this study indicate that in the Beskid Żywiecki the altitude range from 600 to 900 m asl, where deciduous low-alpine forest is dominant, is the most frequently occupied by Grey Wagtails and Dippers. At higher altitudes these birds breed less frequently, and above the tree line do not breed at all. This altitudinal distribution may be explained by the fact that at high altitudes streams carry only small amounts of water and

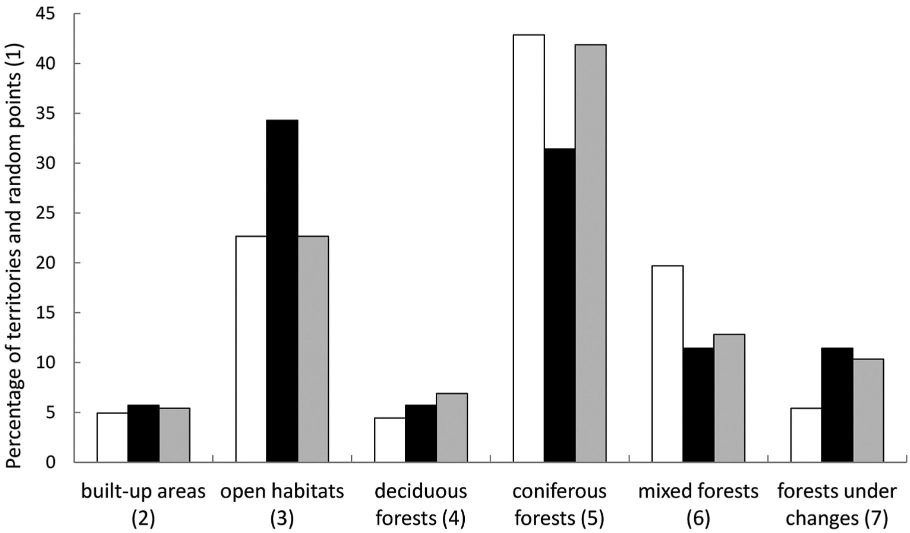

Fig. 4. Percentage of White-throated Dipper *Cinclus cinclus* (black bars) and Grey Wagtail *Motacilla cinerea* (grey bars) territories and random points (open bars) in the six habitat types under consideration in the Beskid Żywiecki Mts (southern Poland)

Rys. 4. *Procentowy udział (1) terytoriów pluszcza (czarne słupki) i pliszki górskiej (szare słupki) oraz punktów losowych (białe słupki) w sześciu wyróżnionych typach siedlisk w Beskidzie Żywieckim. (2) – tereny zabudowane, (3) – siedliska otwarte, (4) – lasy liściaste, (5) – lasy iglaste, (6) – lasy mieszane, (7) – lasy będące w stanie zmian*

Table 3. Generalized linear model describing the relationship between the presence of Grey Wagtail *Motacilla cinerea* and White-throated Dipper *Cinclus cinclus* and the habitat characteristics of the landscape in the Beskid Żywiecki Mts (southern Poland)

Tabela 3. *Uogólniony model liniowy opisujący zależność między występowaniem pliszki górskiej i pluszcza a charakterystyką siedlisk w krajobrazie Beskidu Żywieckiego. Objaśnienia zmiennych przedstawione są w Tabeli 1, (1) – ocena, (2) – błąd standardowy, (3) – statystyka Walda, (4) – wyraz wolny, (5) – pliszka górska, (6) – pluszcz*

Variables	Estimate (1)	SE (2)	Wald's Stats (3)	P
Grey Wagtail (5)				
Intercept (4)	–0.846	0.547	2.4	0.122
Altitude	0.003	0.001	10.0	0.002
Aspect	0.029	0.146	0.0	0.844
Slope	–0.044	0.023	3.7	0.054
Distance from roads	–0.013	0.003	23.5	0.000
White-throated Dipper (6)				
Intercept (4)	–0.576	0.332	3.0	0.082
Distance from roads	–0.023	0.008	8.0	0.005
Distance from built-up areas	–0.001	0.000	2.6	0.104

have narrow beds. Such watercourses do not therefore provide enough invertebrates, like the larvae of stoneflies Plecoptera, mayflies Ephemeroptera or caddisflies Trichoptera (Mikulski 1974), which serve as the main prey items of Grey Wagtail and Dipper (Santamarina 1993, Horváth 2002). Moreover, river bed erosion is greater at high altitudes; the rock and organic materials carried by the water accumulate at the bottom only in the lower sections of rivers where the current is slower, forming suitable habitats for the benthos organisms (Mikulski 1974). Apart from the presence of nesting sites, the occurrence of stream-dwelling bird species is closely associated with the availability of adequate prey, and food shortages resulting from changes in the trophic conditions of the river, adversely affect growth and body weight (Moreno-Rueda & Rivas 2007).

The slope of the surrounding terrain has a significant impact on the amount of water in the stream and influences the shape of its bed. For this reason, both Grey Wagtails and Dippers preferred locations with a gentler gradient, where larger volumes of water accumulate in the stream bed and rock debris is deposited; this in turn influences the composition and abundance of the benthos (Castella et al. 2001). The macroinvertebrates that the two species feed on have high oxygen requirements and are typical rheobionts, i.e. they inhabit fast-flowing streams, the speed of the current being governed by the slope gradient (Mikulski 1974). Consequently, the selection of a suitable gradient should be a trade-off between the sufficient oxygenation of the water and the accumulation of a suitable volume of water and the deposition of rock and organic materials at the bottom enabling the development of macrobenthos.

The results of this work indicate that Grey Wagtails preferred a north-western aspect. The reason for this may be the specific soil, climate and vegetation conditions, which are conducive to the high and stable humidity (Hutchins et al. 1976, Fu & Rich 2002). Since the locally prevailing winds are westerlies (Lorenc 2005), a western aspect also receives greater rainfall. Also, water evaporates more slowly from northern slopes than from southern ones, so in these conditions the soil generally acquires a structure promoting water retention (Gutiérrez-Jurado et al. 2013). Consequently, north-western slopes are characterized by slower evaporation and increased water retention contributing to the maintenance of a higher humidity in habitats, which in turn causes fewer fluctuations in the water levels of watercourses (Zawadzki 1999). Thus, stabilization of the water flow, i.e. the reduction of low water levels and absence of periodic dry phases, especially in the case of small streams, may determine the use of watercourses by Grey Wagtails. Continuous water flow in streams of temperate climatic zone may be a future challenge owing to water abstractions, climate change and land use transitions, constituting a threat for biodiversity of water systems (Datry et al. 2014, Messager et al. 2021).

The Dipper preferred open localities, avoiding sections of streams/rivers passing through coniferous and mixed woodland. This may be related to the acidification of water and soil by spruce needles, which leads to changes in trophic conditions and the composition and abundance of macrobenthos (Ormerod et al. 1985, Ormerod et al. 1986, Tyler & Ormerod 1991, Vickery 1991, 1992). The lack of a similar dependence in the Grey Wagtail may be associated with its broader foraging niche: it can forage also in non-aquatic habitats (Cramp 1998), so presumably it is not so dependent on water quality. On the other hand, the Dipper's preference for areas with forest disturbances may be due to the accumulation of coarse wood debris in the stream bed in such places, which increases the diversity of microhabitats within the stream and may cause larger volumes of water to accumulate there. The habitat preferences of both species may also be influenced by the type of vegetation growing on the riverbanks (Hajzlerová & Reif 2014).

Forests, particularly in montane conditions, are essential for the maintenance of appropriate water conditions and water quality (Norton & Fisher 2000, Sliva & Williams 2001). The water-conservational influence of forest habitats lies first of all in prolonging the residence time of water in the drainage area; in addition, it improves the self-purification of water, slows down runoff and regulates the transport of rock debris. These services are best provided by multi-storey mixed forest stands of older age, growing on soils with a well-developed soil profile containing a rich layer of humus. Moreover, the presence of permanent forest cover in the vicinity of streams influences the water chemistry (Staaf & Olsson 1994, Olsson et al. 1996).

The impact of human on mountain watercourses

Grey Wagtails and Dippers use buildings (bridges, dams, rock rolls) as nesting sites (Czapulak et al. 2008a, Ledwoń et al. 2009). Such sites are less frequently subject to pressure from terrestrial predators, to which these structures hinder or prevent access. The present results indicate that both species occurred in the vicinity of roads. This could have been an artefact, however, since the presence of human infrastructure depends on land suitability for development. Both species inhabit streams of the studied area, in the valleys of which buildings and transport infrastructure are located. Human-made constructions in montane valleys, particularly in narrow ones, are often built in the immediate vicinity of watercourses. Any positive impact of built-up areas must be therefore treated with caution, in terms of the specificity of the study area, where, with increasing size of the valley, concentrations of buildings and the density of road networks are greater. Presumably, of greater importance to these species in a given area is the nature of the watercourse, i.e. its width, slope, flow rate and oxygenation, rather than the presence of man-made structures.

The regulation of watercourses can have deleterious consequences for benthic macroinvertebrates (benthos), constituting the food of stream-dwelling avian species. Some watercourses in the Beskid Żywiecki Mts have been much transformed by the construction of weirs and bank reinforcement. By simplifying the microhabitat structure and changing the natural hydrological dynamics, such structures lead to ecological degradation and reduce the biodiversity of riverine ecosystems (Nilsson & Dynesius 1994, Wyżga et al. 2008, Figarski & Kajtoch 2015). The alteration of flow regimes is the most serious threat to the environment and populations of riverine ecosystems (Sparks 1995, Ward et al. 1999). As a result of regulation, shortened rivers with a broad, shallow bed lose the character of mountain streams and become similar to lowland rivers, in which the accumulation of material carried along with the water prevails (Bucała & Radecki-Pawlik 2011). The river bottoms are then mostly sandy, and therefore unstable, conditions that are unfavourable to invertebrates. Transformed riverbeds may also be subject to the rapid succession of vegetation.

In conclusion, the distribution of Dippers and Grey Wagtails in catchment-scale of mountain areas depends on the local topography. Slope and aspect, by determining the physical parameters of a watercourse, have a direct impact on stream-dwelling species. Both these factors, along with habitats a watercourse crosses, create favourable habitats by contribution to the physicochemical and biological quality of the water. Hydro-engineering works in streams and forest management in adjacent areas, which may change the natural character of watercourses and water quality, may impact the occurrence of stream-dwelling species.

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