Character displacement within the breeding area questions reinforcement in *Ficedula* flycatchers

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Abstract

At present, studies of reinforcement should be focused on demonstrating how often this process occurs in nature and how important it is for speciation. Here we study the character displacement within the breeding area in the Pied Flycatcher to check the validity of the reinforcement in *Ficedula* flycatchers. We used point-referenced spatial data and a random forest to find the most important explanatory factors of the character displacement, and to reconstruct the phenotypic structure of the populations. The environmental temperature, and not the distance to sympatry, were proven to better describe the geographic pattern of the mean breeding plumage colour of the Pied Flycatcher populations. We conclude that ecologically distinct adaptations drive the morphological differentiation of the Old World flycatchers, and not reinforcement.

Keywords: character displacement, reinforcement, phenotypic structure, random forest, *Ficedula* flycatchers, pied flycatcher, collared flycatcher

Introduction

Reinforcement (Dobzhansky 1937) is the process of enhancing reproductive isolation directly controlled by natural selection to cancel maladaptive hybridization between nascent species living together in the same territory (in sympatry). Often reinforcement is considered as one of the ways to complete the speciation process (Lewontin 1974; Servedio 2004). Scientific acceptance of the theory at the time of its appearance was very high, but in the eighties, it fell drastically (Noor 1999). To date, however, doubts about the existence of reinforcement have been resolved both by theoretical studies and by the identification of such cases in nature (Noor 1999; Servedio and Noor 2003; Butlin and Smadja 2018). Now researchers would change the focus of reinforcement studies to show how often this process occurs in nature and how important it is for speciation (Servedio

and Noor 2003). Therefore, we are addressing to answer these questions by the case study of the character displacement (Brown and Wilson 1956) within the breeding area in the Pied Flycatcher (*Ficedula hypoleuca*).

After the publication of Sætre et al. (Saetre et al. 1997), relationships between the Pied Flycatcher and the Collared Flycatcher (*F. albicollis*) had come to be considered one of the examples of reinforcement, although similar ideas were expressed several times before (Kral et al. 1988; Alatalo et al. 1990a; Lundberg and Alatalo 1992; Alatalo et al. 1994). The Pied Flycatcher breeding range is many times larger than the one of the Collared Flycatcher (Fig. 1). Most of the Pied Flycatcher breeding area does not overlap with the one of the Collared Flycatcher (allopatric populations), while most of the Collared Flycatcher breeding range coincides with the breeding area of the Pied Flycatcher (Fig. 1). Where the ranges of these two species of flycatchers overlap (areas of sympatry, for example, in Central and Eastern Europe), males with a brown colouration of breeding plumage (brown morph) predominate in populations of the Pied Flycatcher. This colouration is very similar to that of females of this species. In the allopatric area (for example, in Fennoscandia), contrastingly coloured males with a black and white colour of the breeding plumage (black morph) predominate in populations of the Pied Flycatcher (Fig. 1 A and B). Such a biographical pattern of the morph ratio in the Pied Flycatcher is fundamental to the assumption that the character displacement within the breeding area of the species is the result of reinforcement (Saetre et al. 1997). However, the coupling of a high proportion of brown males with areas of sympatry in the Pied Flycatcher is revealed only for European populations, without analysing the phenotypic structure of those populations that breed in the most eastern European and the Asian part of the species breeding range (for example, in the European part of Russia to the Ural Mountains and further to Western Siberia, Fig. 1C).

In parallel with the publication of Sætre et al. (Saetre et al. 1997), it was nevertheless noted that the authors' conclusions indeed are based on limited material. "Both the phylogeny and the data on mate choice are based on limited sampling. The case for reinforcement will be more secure when the generality of the preferences has been established, and when a more complete picture of the biogeographic history of the flycatchers is available", wrote R. K. Butlin and T. Tregenza (Butlin and Tregenza 1997). However, these comments were not considered in the following studies (Noor 1999; Servedio and Noor 2003).

In this paper, we decided to follow the opinion of R. K. Butlin and T. Tregenza and conduct a biogeographic study of flycatchers on the largest material that we can obtain for analysis today. Specifically, we checked whether there is a relationship between the

prevailing breeding plumage colour in males and the remoteness of the Pied Flycatcher population from the breeding area of the Collared Flycatcher. To do this, we collected all the data known to us about the phenotypic structure of all populations of the Pied Flycatcher currently studied. We managed to find information for 41 populations. In addition, we analysed zoological collections from 11 museums. This allowed us to further evaluate the phenotypic structure of another 38 metapopulations of the Pied Flycatcher. To check whether the distance from the nesting area of the Collared Flycatcher may have an impact on the phenotypic structure of the Pied Flycatcher, we used a random forest as spatial predictions framework (Hengl et al. 2018). The extensive data sampling and spatial analyses usage largely distinguish our work from similar attempts, in which limited sampling and the linear regression models were used for these purposes (Laaksonen et al. 2015).

Material and Methods

Basic methodological approach

We used point-referenced spatial data and a random forest for spatial predictions framework (RFsp) (Hengl et al. 2018) to find (1) the most important predictor variables highly related to the mean colour score of the males' breeding plumage of the Pied Flycatcher populations (response variable), and (2) a good parsimonious prediction model of the response variable for any point of the breeding range of the Pied Flycatcher. The RFsp was chosen because it can obtain equally accurate and unbiased predictions as other methods of spatial analysis (generalized linear model, different versions of kriging, geographically weighted regression) (Čeh et al. 2018; Hengl et al. 2018). The RFsp is thought to be advantageous over the other spatial analyses for the purpose of this research, as the former needs no rigid statistical assumptions about the distribution and stationarity of the target variable, it is more flexible towards incorporating, combining and extending covariates of different types, and information overlap (multicollinearity) and over-parameterization is not a problem for RFsp (Hengl et al. 2018). The distances from "observation points" to the border of the breeding area of the Collared Flycatcher and geographical coordinates (latitude and longitude) of "observation points" are used as explanatory variables, thus incorporating geographical proximity and geographical connection effects into the prediction process (Hengl et al. 2018). The "observation points" are *F. hypolueca* population "centres" for which the mean breeding plumage colour score was obtained (see below). We used the average daily maximum temperature and its variability (standard deviation) as general climatic characteristics of the population habitat. We put thermal characteristics into the model as alternative explanatory variables, thus contrasting them with the distance to the sympatry area during the prediction process. We

used thermal characteristics in the analysis because it was shown that there is a low air temperature depression of the advertising behaviour of brown males in the Pied Flycatcher (Ilyina and Ivankina 2001; Kerimov et al. 2014), and this can lead to an increase in the proportion of black males in the reproductive part of the Pied Flycatcher population in cold spring years (Kerimov et al. 2014). Additionally, the basal metabolic rate (the amount of energy per unit time that an individual must spend to keep the body functioning at rest) and fledgling production of the males' morphs in the *F. hypoleuca* flycatcher were shown to be dependent on the ambient temperature (Sirkia et al. 2010; Kerimov et al. 2014).

Data collection and preparation

Step I. As a source of temperature data, we used The National Centers for Environmental Prediction (NCEP) / National Center for Atmospheric Research (NCAR) Reanalysis data set R-1, and NCEP / Department of Energy (DOE) Reanalysis II data set R-2 (Kalnay et al. 1996; Kanamitsu et al. 2002). The NCEP/NCAR R-1 and NCEP/DOE R-2 are high-quality, well-documented, freely available state-of-the-art gridded reanalysis data sets with global coverage of many relevant atmospheric variables spanning 1957 to present and 1979 to present, respectively (Kemp et al. 2012). Data for many variables are available at 17 pressure levels ranging from 1000 to 10 mb. Other variables describe conditions either at or near the surface. These data have a spatial resolution of 2.5 x 2.5 degrees and a temporal resolution of 6 h (00, 06, 12, 18 h UTC). We used the **RNCEP** package (version 1.0.8) of functions (Kemp et al. 2012) in the open-source R language to access required temperature data. First, using the *NCEP.gather* function from the **RNCEP** package, we loaded surface temperature data (variable air.sig995 in data set) from April to May for each year in the interval spanning 1980 to 2015 for an area between 35- and 72-degrees north latitude and between -10- and 93-degrees longitude thus covering the breeding areas of the two species of flycatchers. Then using the *NCEP.restrict* function, we cut the interval from April 1 to April 14 and from May 16 to May 31, leaving the period from April 15 to May 15 for all loaded years. Finally, using the *NCEP.aggregate* function, we calculated the mean and standard deviation (SD) of daily maximum temperature for all loaded years, obtaining a point pattern of mean temperatures and SDs for the entire loaded area with a spatial resolution of 2.5 x 2.5 degrees of latitude x longitude. Similarly, we calculated the SD of the maximum daily temperature for May 1 for all years (the rendered thermal data map, see Fig. 2.). The latter assessment of variability mostly characterizes the repeatability or the predictability of temperature between years, and the former SD includes both inter-annual and intra-annual (inter-seasonal) variability, that is, a change in temperature from April 15 to May 15. Inter-seasonal temperature changes will be significantly higher for the continental climate than for the temperate climate. The selected interval spanning 1980 to

2015 seems to be sufficient both for obtaining an unbiased estimate of average temperatures and for a satisfactory assessment of its variability. The selected date interval, which lasts from April 15 to May 15, covers the period of birds' arrival from African wintering grounds, pairing and the beginning of reproduction in most of the populations of considered species of flycatchers. Since the key principle of geography is that “everything is related to everything else, but near things are more related than distant things” (Miller 2004), the climatic characteristics of earlier or later periods or months (March or June, for example) will be highly correlated with the chosen one. Temporal and spatial autocorrelations of temperature data are well-founded and documented facts in modern science, for example, see (Di Cecco and Gouhier 2018). Our goal was not to understand the temperature of which the nesting period determines the phenotypic composition of the population to a greater degree (causation task); this is a task for other studies. We evaluated which variable better predicts the values of the response variable (correlation task). And in this sense, temporal and spatial autocorrelations of the temperatures are not a nuisance for us, but a feature that improves our approach, since it allows a rather arbitrary choice of the period for calculating thermal estimates.

Step II. We were looking for any articles studying the Pied Flycatcher that mentioned the phenotypic structure of this species. Seven variants (types or morphs) were initially identified in the variability range of the male breeding plumage colour in the Pied Flycatcher (Drost 1936). The value 1 of this scale was assigned to the bright coloured black and white males, and the value 7 assigned to the brown coloured males. Accordingly, it is easy to calculate the average colour score of the population, which will describe well the proportion of males of different morphs. The closer the average colour score is to 1, the greater number of black males there are, the blacker is the population as a whole and vice versa; the closer to 7, the greater number of brown males in the population, the browner is the population. In most of the publications, the mean colour score is given, therefore in our work we also used this indicator as the main descriptor of the phenotypic structure. We were able to find information about the phenotypic structure of the Pied Flycatcher for 41 populations (or metapopulations) (Table S1). For each, we found the nearest well-recognized geographical point. Usually it was nearest settlement to which the studied bird population was attributed by the author(s). We found the geographic coordinates in the QGIS program for this point. This geographic point was the "observation point" for those populations whose data on the phenotypic structure were obtained from publications. We used data from the same author (or the same group of authors) for one territory from only one most recent publication. If for the same territory (or a close region) we found data from different authors, then we used all such data in the calculations.

Step III. The Pied Flycatcher studies in the western part of the breeding range were carried out much more often than in the eastern part resulting in a shifted distribution of observation points (Table S1). To compensate for data bias, we examined the collections of the following museums: [1] Siberian Zoological Museum of the Institute of Systematics and Ecology of the Siberian Branch of the Russian Academy of Sciences (Novosibirsk), [2] Collection of the Department of Biogeography of the Faculty of Geography of the M. V. Lomonosov Moscow State University (Moscow), [3] State Museum of Nature of the Kharkiv National V.N. Karazin University (Kharkiv), [4] Zoological Museum of Kyiv National Taras Shevchenko University (Kiev), [5] Zoological Museum of Lviv National I. Frank University (Lviv), [6] Zoological Museum of the Belarusian State University (Minsk), [7] Zoological Museum of the M. V. Lomonosov Moscow State University (Moscow), [8] Zoological Museum of the National Academy of Sciences of Ukraine (Kiev), [9] Zoological Museum of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), [10] Kirov City Zoological Museum (Kirov), [11] Kaunas Zoological T. Ivanauskas Museum (Kaunas), [12] Museum of Natural History of Tartu University (Tartu).

We examined the bird skin collection and determined the colour type of bird skins in museums [1] – [9]. Data on the colour type of 17 males were kindly provided by V. N. Sotnikov from [10]. We received digital photographs of 12 and 11 bird skins from [11] and [12], respectively, for subsequent colour typing. In total, we examined 471 birds' skins, of which 39 skins were excluded because some of them were clearly taken from migratory birds (autumn migration), and for some of them we could not accurately determine the location. Finally, we got colour types for 432 bird skins from museums [2] – [12] (no skin from museum [1] was included in the final data set; see Data S1). For each skin, the geographic coordinate was determined in the QGIS, based on the description of the place where the birds were caught written on the label.

Since the spatial resolution of temperature data was 2.5 x 2.5 degrees of a geographic coordinate, we used polygons of that size to form "populations" (small area populations) (Fig. S4). The minimum sample for a population was 5 individuals, because this number is enough to calculate the mean deviating by less than 1 point of the colour score (a pre-specified error bound) with a probability of 0.95 from the population total mean in a sample of 366 individuals with a standard deviation 1.13 (the population total mean sample size and the standard deviation were estimated in step II). If fewer individuals fell into some 2.5 x 2.5 degrees polygon, we included such individuals in the nearest polygons defined by the QGIS. Such individuals should not be located from the polygons in which they were included at a distance greater than 1.25 degrees (Fig. S4). After this procedure, there were still individuals that did not form populations or were not included in a population. In such

remaining cases, we gradually increased the size of the buffer from the geographical position of the individual, while the areas thus obtained began to overlap. If overlapping areas included 5 or more individuals, then we also considered them as the population for which the mean colour score was calculated (large area populations) (Fig. S4). We were unable to include 14 individuals in any of the populations using any of the above methods (Fig. S4). The "observation point" for populations formed by the skins from museum collections was calculated as the mean coordinate of all population components in QGIS (i.e. the centre of mass, and not the centroid which is the geometric centre of the population) (Fig. S4). We thus obtained 39 populations or observation points (Table S2).

As mentioned, not only breeding, but also migratory birds can get into museum collections. Also, the skin of birds can be collected purposefully of the same type or colour. It is relatively easy to separate autumn migrants by the bird life calendar and the plumage colouring (before the autumn migration, birds moult completely, and the colour of the post breeding plumage is quite different from the colour of the breeding one). However, in our opinion, it is impossible to separate spring migrants from local breeders. Thus, this problem was ignored by us, because we were unable to find criteria and procedures for cleaning the sample that would not lead to significant data loss. We found signs of directional collection of black males in only one case (the small standard deviation, a difference in the mean breeding plumage score from neighbouring populations) (Table S2). For one area in the sample of 6 individuals, there were five males with a colour score 2 and one male with a colour score 3. Such a ratio of morphs is almost impossible to obtain with a random selection method even in dark populations. This observation point was excluded from the analysis (Table S2).

Step IV. For two species of *F. hypoleuca* and *F. albicollis* flycatchers, we downloaded the distribution data (digitized georeferenced maps in geodatabase file format for use in GIS mapping software compiled by BirdLife International and Handbook of the Birds of the World) from BirdLife International (2018) IUCN Red List for birds, http://www.birdlife.org (downloaded from the site on 09.09.2018 using QGIS). We revealed that the bird findings from the Kola Peninsula, and from the northernmost and easternmost parts of the *F. hypoleuca* breeding area in Western Siberia, do not fall into the BirdLife International reproductive range of *F. hypoleuca*. To adjust the range of *F. hypoleuca*, we georeferenced in QGIS the species breeding area from the publication of Sirkia et al. (Sirkia et al. 2015). The final breeding range of *F. hypoleuca* basically contained the BirdLife International data, but the north-western borders were extended to the north and east to the coast of the Kola Peninsula, to the north of Western Siberia coinciding with the border from Sirkia et al.

(Sirkia et al. 2015) for this region, and to the very east of Western Siberia thus including data from museum collections for the area.

We did not include the Spanish (Iberian) and north-western African Atlas Flycatcher in the range of *F. hypoleuca* (Fig. 1). The birds of these territories are well isolated from other European *F. hypoleuca* populations (they can occur in one territory during a migration only), and they are phenotypically closer to each other (Corso et al. 2015; Potti et al. 2016). The Iberian form seems to be intermediate between the African form and *F. hypoleuca* in morphology (Sangster et al. 2004). It is recommended that the Atlas Flycatcher *F. speculigera* should be separated from the Pied Flycatcher *F. hypoleuca* as a species, and the Iberian form should be considered as subspecies *F. hypoleuca iberiae* of *F. hypoleuca* (Sangster et al. 2004). Sometimes, Iberian birds are also distinguished as a separate species (Potti et al. 2016). In both *F. speculigera* and *F. h. iberiae*, the colour of the breeding plumage in males is mainly black-and-white, and its variability is much less than among birds from the rest of Europe (Corso et al. 2015).

We also corrected the north-eastern boundary of the *F. albicollis* breeding range (Moscow is not included in the nesting range of this species), using Vabishchevich and Formozov (Vabishchevich and Formozov 2010) georeferenced distribution data. Southern Sweden, the islands of Öland, Gotland and Saaremaa were also excluded from the final *F. albicollis* breeding range due to the recent expansion of the species over the Baltic Sea thus following Laaksonen et al. (Laaksonen et al. 2015) (Fig. 1).

Step V. All data obtained in the previous steps were entered QGIS for their final assembly. For each *F. hypoleuca* observation point, the distance in kilometres to the boundary of the *F. albicollis* range was calculated (Fig. 1). If the observation point fell inside the *F. albicollis* range, the distance got negative values. Binding of the *F. hypoleuca* observation point to the thermal characteristics of the territory was carried out using the method of the nearest neighbour (the nearest point-referenced values of the thermal characteristics of the territory were chosen), as well as by Inverse Distance Weighted (IDW) interpolation using the 4 nearest points. We used the GRASS 7 *v.surf.idw* algorithm for surface interpolation from point-referenced data by the IDW interpolation for which region the *cellsize* was set to 2.5 (according with the spatial resolution of the temperature data), the power parameter was set to 3, and the number of interpolation points was set to 4. Then we used the point sampling tool to assign the interpolated value to the population observation point.

Thus, our initial model consisted of one response variable (the mean breeding plumage colour of *F. hypoleuca* males in the population) and 9 predictors: *Y* - latitude, *X* - longitude, *cf.dist* - distance to the border of the *F. albicollis* range, *mt* - mean maximum

daily temperature of the nearest temperature referenced point, *mt.idw* - IDW interpolated mean maximum daily temperature, *sd* - standard deviation of the maximum daily temperature from April 15 to May 15 spanning 1980 to 2015 of the nearest temperature referenced point, *sd.idw* - IDW interpolated standard deviation of the maximum daily temperature from April 15 to May 15 spanning 1980 to 2015, *sd.1d* - standard deviation of the maximum day temperature for May 1 spanning 1980 to 2015 of the nearest temperature referenced point, and finally *sd.1d.idw* - IDW interpolated standard deviation of the maximum day temperature for May 1 spanning 1980 to 2015.

Spatial data analysis

We used the open-source R software environment for statistical computing and graphics (version 3.5.0) under an integrated development environment for R - RStudio (RStudio Desktop version 1.1.447) to analyse data assembled on step V. For regression tasks we used the **ranger** package (version 0.10.1) as an implementation of the random forests (Wright and Ziegler 2017). To obtain the most accurate predictions, the random forest parameters need to be optimised (Probst et al. 2018). To configure the parameters of the random forest, we used the **tuneRanger** (version 0.3) package (Probst et al. 2018) which allows model-based optimization for tuning strategy and the three parameters *min.node.size*, *sample.fraction* and *mtry* tuning at once. Out-of-bag predictions were used for evaluation. To evaluate the best *num.trees* parameter, we used the **caret** (version 6.0-80) package. We used a *trainControl* function from the package to set the resampling method to *10*-fold cross-validation procedure. Validation was done by calculating the root mean squared error (RMSE). Thus, the initial model, which included all 9 predictors, was calculated with the following parameters of the random forest: *min.node.size*=8, *sample.fraction*=0.79, *mtry*=2, *num.trees*=250, *splitrule* = "variance", *importance*="impurity", *num.threads*=4, *verbose*=FALSE, *respect.unordered.factors*=TRUE, *replace*=FALSE, *keep.inbag*=TRUE. We obtained the coefficient of determination for the whole model (R^2) equal to 0.73 (out-of-bag predictions), and the mean squared error (MSE) equal to 0.24 (out-of-bag prediction error). To build the most parsimonious prediction model of the response variable, i.e. to reduce the number of predictors with minimal impact on the response variable, we conducted a nested cross-validation procedure using the **caret** package. We estimated the 10-fold cross-validated prediction performance of models with a sequentially reduced number of predictors ranked by variable importance (the variables with the lowest variable importance values was sequentially excluded from the models) in 100 repetitions (Fig. 3). In our case the variable importance was measured as the variance of the responses (Fig. 3C). Validation of the models was done by calculating the RMSE (Fig. 3A). The cross-validation procedure reduced 4 of 9 predictors (including the distance

to the *F. albicollis* breeding area), and the final model performance increased slightly, but statistically significantly (Fig. 3A, B). Thus, the final model included only 5 predictors listed below: *Y*, *X*, *mt*, *sd*, *sd.1d*. After excluding 4 predictors from the model, we again conducted the above procedure for the parameter's optimization of the random forest. The final model was calculated with the following parameters: *min.node.size*=11, *sample.fraction*=0.787, *mtry*=2, *num.trees*=250, *splitrule* = "variance", *importance*="impurity", *num.threads*=4, *verbose*=FALSE, *respect.unordered.factors*=TRUE, *replace*=FALSE, *keep.inbag*=TRUE. The R^2 for the whole final model is 0.75, and the MSE is 0.23. To predict the mean breeding plumage colour score of males in the *F. hypoleuca* within the entire breeding range (to calculate out of sample data), we used the *predict.ranger* function in the **ranger** package with the final random forest model. The values of all 5 predictors obtained in step 1 for the area between 35- and 72-degrees north latitude and between -10- and 93-degrees longitude were used. We calculated the standard error of the predictions using the infinitesimal jack-knife for bagging methodology (Wager et al. 2014) as it implemented in the **ranger** package (Fig. 4, Fig. S2).

Data visualization

To visualize the results of spatial analysis, we transformed point-referenced data into raster surface data in the QGIS. For this, we used the GRASS 7 *v.surf.idw* algorithm for surface interpolation from point-referenced data by the IDW interpolation (region *cellsize* was set to 2.5, power parameter was set to 3, and number of interpolation points was set to 4). To improve the spatial resolution of raster data and to improve the visualization effect, we used the SAGA Resampling algorithm with upscaling and downscaling IDW interpolation. We changed the *cellsize* parameter to obtain the most acceptable visualization effect (usually, the parameter value was equal or less than 0.1). To draw all the other graphs, we used the **ggplot2** (Wickham 2016) (version 3.0.0) package in R. Final processing of the vector-based drawings was carried out in Inkscape™: Open Source Scalable Vector Graphics Editor (version 0.92.3), and the raster-based drawings was done in GNU Image Manipulation Program (GIMP) (version 2.10.4).

Modelling the influence of the *F. albicollis* flycatcher on the population phenotypic structure of the *F. hypoleuca* flycatcher

In the QGIS program, we modelled a hypothetical phenotypic structure of the *F. hypoleuca* populations, as if only one single factor was acting on the distance from the *F. albicollis* breeding range. This simulation was carried out only for visualization and was not used in statistical treatment. First, we transformed the *F. albicollis* range into a raster using the SAGA rasterize data/nodata algorithm, and then modelled the distance effect from the

borders using the *r.grow.distance* algorithm with the cell size parameter set to 1. The final visualization was done using the above data visualization methods (Fig. S3).

H. Löhrl data processing

The figure 2 given on page 271 of the H. Löhrl publication in Bonner Zoologische Beiträge (Löhrl 1965) was georeferenced in QGIS. We have downloaded freely accessible The Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) from the EarthExplorer site (https://earthexplorer.usgs.gov/) for the south-west of Germany and adjacent territories. We used the point sampling tool in QGIS to assign the terrain elevation values to the H. Löhrl observation points for further processing in R (Fig. 5).

Results

A simple graphical analysis of the relationship between the mean colour score and the predictors showed that there are obvious non-linear dependencies in the data structure, including the dependence of the response variable on the distance from the observation point to the sympatry area (Fig. S1). In this regard, the use of linear models cannot be considered as a quite adequate method of analysing such data (Laaksonen et al. 2015).

The thermal characteristics of the area covering the ranges of the flycatcher species demonstrate a strong, but quite expected pattern of variability. Within the Pied Flycatcher distribution area, there is a pronounced south-north gradient of average daily maximum temperatures (Fig. 2). It is particularly pronounced between Central and Eastern Europe on the one hand and Fennoscandia on the other. The variability and predictability of thermal characteristics has a more complex geographic pattern, although in general there is a tendency to increase unpredictability eastward (an increase in the climate continentality as one moves deeper into Eurasia) (Fig. 2).

We used a spatially explicit approach to achieve two main objectives. Firstly, for the purposes of interpretation, we found the most important variables highly related to the population mean colour score of the males' breeding plumage of the Pied Flycatcher (response variable). Secondly, we found the smallest number of variables enough for a good parsimonious prediction of the mean colour score of the males' breeding plumage for any point of the breeding range of the Pied Flycatcher.

The random forest regression has shown that the distance to the breeding area of the Collared Flycatcher is of minimal importance for predicting the phenotypic structure of the Pied Flycatcher populations (Fig. 3). The average daily maximum temperature during the breeding season and its variability are associated with the predominant male colour morph in each population of the species (Fig. 3). Latitude and longitude also affect the phenotypic structure of the Pied Flycatcher populations (Fig. 3). This may indicate that we

did not include any other important variables associated with the geographical location of the population in the study.

Model predictions show that the predominance of black morphs in males is observed in the Pied Flycatcher populations nesting in areas with a predictably colder environment (Fennoscandia and the British Isles) (Fig. 4, Fig. S2). Brown-coloured males predominate in populations nesting in a relatively warm and/or very unstable climate. Populations with a predominance of brown morphs form the entire southern region of the breeding range of the Pied Flycatcher, including the most Eastern European part and the Western Siberian part. Moreover, the populations in which the average values of the colour score reach maximum values (more brown morphs in the population) are outside the breeding range of the Collared Flycatcher – these are central and northern Germany, and the Netherlands (Fig. 4). In sympatry, the phenotypic structure of the Pied Flycatcher populations also changes (Fig. 4), and these changes have a much more complex spatial pattern compared to what one would assume if the mere presence/absence of another species would influence the phenotypic structure of sympatric populations (Fig. S3).

Discussion

The study of the mechanisms of speciation in the Old World flycatchers of the genus *Ficedula*, unfortunately, recalls the very case when the cart was putted before the horse. Acceptance of reinforcement as the main factor of speciation in the *Ficedula* flycatchers and as the mechanism of maintaining intraspecific variability in one of them (Saetre and Saether 2010) occurred even though the biogeographic pattern of phenotypic structure was not revealed for the whole breeding area of the interacted species, and the generality of the female preferences for male breeding plumage was not established.

Surprisingly, data on the mainly brown coloration of the males' breeding plumage of the Pied Flycatcher in Western Siberia were available in the scientific literature (Johansen 1954). Apparently, this information was not widely known. This fact alone would be enough to cast doubt on the generality of the coupling between the character displacement and the areas of sympatry. Now we can say with high certainty that no convincing evidence of the coincidence of the character displacement and the sympatry areas of the flycatchers exist (Fig. 4). Our studies persuasively show that the geographic pattern of variability of the mean colour score of males' breeding plumage in the Pied Flycatcher is much more complicated and cannot be caused solely by interspecific interactions (Fig. 1, Fig. 4 and Fig. S3). For example, the shift of male breeding plumage colouration occurs in the sympatry, but also in the allopatry in most eastern parts of the breeding range of the Pied Flycatcher up to the eastern distribution boundaries in Western Siberia, that is, the most remote populations from the areas of sympatry (Fig. 1 and Fig. 4).

It is crucially important that if reinforcement is inferred from displacement in a secondary male sexual character, the displacement must be detectable by females; and females should use these characters for a mate choice (Howard 1993; Noor 1999). In addition to the publication of Sætre et al. (Saetre et al. 1997), some other studies reveal that a female preferably chooses a black male in allopatric populations of the Pied Flycatcher (Roskaft and Jarvi 1983; Saetre et al. 1994; Dale and Slagsvold 1996). However, there are also several studies done by independent researchers about different allopatric populations in which no clear benefits for black morphs in mate choice were found (Alatalo et al. 1986; Alatalo et al. 1990b; Potti and Montalvo 1991; Lehtonen et al. 2009; Sirkia and Laaksonen 2009). This indicates that the generality of the female preferences for male breeding plumage in the Pied Flycatcher also cannot be considered a fully proven phenomenon.

We think that if the female perceives the male breeding plumage colour as a cue to select a mate, this male trait is not the main one for mate choice or not used at all. For example, it was recently shown that the intensity of the advertising behaviour of free-living males of the Pied Flycatcher is modified by ambient air temperatures in the Moscow Region population (Russia, European part). Black males can maintain a high intensity of advertising behaviour at both low and high temperatures. However, brown males are able to attract females effectively only at higher air temperatures, and at low temperatures reduce dramatically the intensity of advertising behaviour (Ilyina and Ivankina 2001; Kerimov et al. 2014). Quite similar results were obtained in the experiments in the Tomsk population (Russia, Western Siberia) of the Pied Flycatcher. It was shown that females choose black males at low ambient temperatures merely because they are more active (Kerimov et al. 2014). Moreover, it was possible to demonstrate that this mechanism influences the morph ratio in the reproductive part of the population – in years with a cold spring, more black males enter the reproductive part of the Tomsk population, apparently due to the temperature-related depression of the brown males' advertising behaviour (Kerimov et al. 2014). In the literature, there is also evidence that the ambient temperature can affect the reproductive success and the energetics of the morphs. The reproductive output of black males was shown to be the highest when it was cold during egg-laying but warm during the nestling period, whereas the fledgling production of brown males was highest when it was continuously warm (Sirkia et al. 2010). Brown males increase a basal metabolic rate (BMR; the amount of energy per unit time that an individual must spend to keep the body functioning at rest) under the influence of low ambient temperatures, and black males, on the contrary, retain the same level of BMR in a very wide range of daily temperatures (Kerimov et al. 2014). It is likely that the opposed results of earlier studies of female morph preferences could be obtained because the temperature dependence of the

males' energetics and behaviour was not considered. To date, data from Sætre et al. (Saetre et al. 1997) remain the only "strong" evidence of reinforcement (Saetre and Saether 2010) (all others are not an exclusive prerogative of reinforcement) (Noor 1999; Butlin and Smadja 2018). Therefore, the replication of the experiments of Sætre et al. (Saetre et al. 1997) to check the female preferences is necessary on a more extensive material, considering the new information about the dependence of the males' advertising behaviour on ambient temperatures.

The coupling of males' breeding plumage colour variability with weather characteristics in the Pied Flycatcher was noted in one of the first studies devoted to this issue. Löhrl (Löhrl 1965) described a very interesting picture of the spatial segregation of male morphs of the Pied Flycatcher and the Collared Flycatcher. He showed that in south-west Germany brown and black males of the Pied Flycatcher are separated from each other spatially, as well as from the Collared Flycatcher (Fig. 5). Brown males occupied the forests of the lowest lands, the Collared Flycatcher occupied the forests at medium height above sea level, and the black males nested in the highest mountain forests. Such a clear spatial segregation between two species and morphs cannot be explained by a simple interference competition over nest cavities, where the collared flycatcher is a winner (Saetre and Saether 2010). This habitat segregation on such a spatial scale can only be the result of an active habitat choice. Indeed, there is experimental evidence for species-specific habitat preferences in two flycatcher species in their hybrid zone (Adamik and Bures 2007).

All these data can be regarded as evidence considering that the evolution of the plumage colour in the Pied Flycatcher is not driven by reinforcement but is the result of the adaptation of black males to the conditions of higher mountains forests, and brown ones – to the conditions of lower-altitude forests. Then the distribution of brown and black populations of the Pied Flycatcher along the modern breeding area is a projection of adaptations to different ecological subniches that the species have developed in refugia during the last glaciation (*F. albicollis* in Italy, and *F. hypolueca* on the Iberian Peninsula) and their subsequent evolution (Saetre and Saether 2010).

It is very likely that the initial stages of the *F. hypolueca* species formation took place in the relatively higher-altitude conditions of the north of the Iberian Peninsula refuge during Quaternary ice ages (for the European paleoenvironments and maximum extent of ice, for example, see (Tzedakis et al. 2013). Further, as the glaciation receded, the *F. hypolueca* began to expand earlier along its current range, since there are no physical obstacles in this refugium like the Alps in the north of the Apennine Peninsula. Probably, as a result of this expansion, an adaptation to breeding in lower-altitude forests evolved,

marked by the brown colour of the male breeding plumage. The expansion of the *F. albicollis* from its Italian refuge could be limited to the Alps for some time. As a result, when *F. albicollis* began to spread over its existing range, it encountered the brown *F. hypolueca* populations that had spread a little bit earlier. In contact zones the species effectively diverged to different ecological niches, although the *F. albicollis* remained a more stenobiont species (Qvarnstrom et al. 2010). At present, the species are so well segregated ecologically that there may be no competition for microhabitats and nesting sites between them (Walankiewicz et al. 1997; Adamik and Bures 2007; Czeszczewik et al. 2012). Therefore, it seems very likely that the black *F. hypolueca* populations have never shared the same habitats with the *F. albicollis* throughout the entire evolutionary history of these species! Thus, at present the British Isles and Fennoscandia are inhabited by black males preadapted to higher-altitude forests (ancestral state), and the southern and eastern parts of the Pied Flycatcher range are inhabited by brown males adapted to lower-altitude forests (newly evolved state). Thus, there is a clear ecological background for the evolution of the breeding plumage colour in the Pied Flycatcher males as an alternative for reinforcement including ecological adaptation, niche differentiation, and ecological character displacement.

In theoretical studies it was noted that in order to attribute mate choice patterns to reinforcement it was necessary that the character displacement must not have occurred for other, especially ecological reasons (Howard 1993; Noor 1999). This requirement is one where many studies have failed (Howard 1993; Noor 1999), and the reinforcement in *Ficedula* flycatchers seems to have to fill their numbers.

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Data and materials availability: All data and software are available in the main text, the supplementary materials, and on the internet sites for purposes of reproducing the results or extending the analysis.

Software and data sources:

Quantum GIS Development Team. 2013. QGIS Geographic Information System. Open Source Geospatial Foundation Project. https://qgis.org

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

RStudio Team. 2016. RStudio: Integrated Development for R. RStudio, Inc. Boston, MA. http://www.rstudio.com/.

Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) Reanalysis data set R-1. URL http://www.cpc.ncep.noaa.gov/products/wesley/reanalysis.html

Environmental Prediction (NCEP)/Department of Energy (DOE) Reanalysis II data set R-2. URL http://www.cpc.ncep.noaa.gov/products/wesley/reanalysis2/index.html

Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010). the EarthExplorer. URL https://earthexplorer.usgs.gov/

Species distribution data compiled by BirdLife International and Handbook of the Birds of the World from BirdLife International (2018) IUCN Red List for birds. URL http://www.birdlife.org

Literature Cited

Adamik, P. and S. Bures. 2007. Experimental evidence for species-specific habitat preferences in two flycatcher species in their hybrid zone. Naturwissenschaften 94:859-863.

Alatalo, R. V., D. Eriksson, L. Gustafsson, and A. Lundberg. 1990a. Hybridization between Pied and Collared Flycatchers - Sexual selection and speciation theory. J Evolution Biol 3:375-389.

Alatalo, R. V., L. Gustafsson, and A. Lundberg. 1994. Male coloration and species recognition in sympatric flycatchers. P R Soc B 256:113-118.

Alatalo, R. V., A. Lundberg, and C. Glynn. 1986. Female pied flycatchers choose territory quality and not male characteristics. Nature 323:152-153.

Alatalo, R. V., A. Lundberg, and J. Sundberg. 1990b. Can female preference explain sexual dichromatism in the pied flycatcher, Ficedula hypoleuca. Anim Behav 39:244-252.

Anorova, N. S. 1977. Colour morphs of the Pied Flycatcher males breeding on south Moscow area. Bulletin of Moscow Society of Naturalists. Biological series 82:10-18.

Belskii, E. A. and A. G. Lyakhov. 2004. Breeding plumage coloration in Ficedula hypoleuca (Passeriformes, Muscicapidae) males from the Middle Urals. Zool Zh 83:1468-1475.

Bijlsma, R. G. and C. Both. 2014. Bonte Vliegenvangers Ficedula hypoleuca broedend in natuurlijke holtes: verschillen met nestkastbewoners. Drentse Vogels 28:114-125.

Brown, W. L. and E. O. Wilson. 1956. Character displacement. Systematic Zoology 5:49-64.

Butlin, R. K. and C. M. Smadja. 2018. Coupling, reinforcement, and speciation. The American Naturalist 191:155-172.

Butlin, R. K. and T. Tregenza. 1997. Is speciation no accident? Nature 387:551.

Čeh, M., M. Kilibarda, A. Lisec, and B. Bajat. 2018. Estimating the performance of random forest versus multiple regression for predicting prices of the apartments. ISPRS International Journal of Geo-Information 7:168.

Corso, A., O. Janni, M. Viganò, and L. Starnini. 2015. Atlas Pied Flycatcher: variability of identification characters. Dutch Birding 37:141-160.

Curio, E. 1959. Beiträge zur Populationsökologie des Trauerschnäppers (Ficedula h. hypoleuca Pallas). Zoologische Jahrbücher 87:185-230.

Czeszczewik, D., I. Ruczynski, K. Zieba-Schraven, J. Wisniewska, and W. Walankiewicz. 2012. The Pied and the Collared Flycatcher do not compete for microhabitats in the Bialowieza Forest. Belg J Zool 142:133-137.

Dale, S. and T. Slagsvold. 1996. Mate choice on multiple cues, decision rules and sampling strategies in female pied flycatchers. Behaviour 133:903-944.

Di Cecco, G. J. and T. C. Gouhier. 2018. Increased spatial and temporal autocorrelation of temperature under climate change. Sci Rep-Uk 8:14850.

Dobzhansky, T. 1937. Genetics and the Origin of Species.-New York, Columbia Univ. Press. Columbia University Press, New York.

Drost, R. 1936. Über das Brutkleid männlicher Trauerfliegenfanger, Muscicapa hypoleuca. Vogelzug 6:179-186.

Eggenberger, H. 1964. Über die Farbtypen der männlichen Trauerschnäpper, Ficedula hypoleuca, in der Ostschweiz. Ornithologische Beobachter 61:95-99.

Glutz von Blotzheim, U. N. and K. M. Bauer (eds). 1993. Ficedula hypoleuca (Pallas 1764) Trauerfliegenschnäpper, Trauerschnäpper. Pp. 165-263 in Handbuch der Vögel

Mitteleuropas. Bd. 13/1: Passeriformes (4. Teil). Muscicapidae - Paridae. . AULA-Verlag, Wiesbaden.

Grinkov, V. G. 1997. Male plumage variation in the pied flycatcher (Ficedula hypolleuca Pall.) and its relation with offspring quality. Possibility of phenotype diversity maintenance by disruptive selection. Dokl Akad Nauk+ 356:138-140.

Haverschmidt, F. 1973. Waarnemingen aan een populatie Bonte Vliegenvangers Ficedula hypoleuca. Limosa 46:1-20.

von Haartman, L. 1985. The biological significance of the nuptial plumage of the male Pied Flycatcher. Pp. 34-60 *in* V. D. Ilyichev, and V. M. Gavrilov, eds. ACTA XVIII Congressus Internationalis Ornithologici, Moscow, August 16-24, 1982. "Nauka", Moscow.

Hengl, T., M. Nussbaum, M. N. Wright, G. B. M. Heuvelink, and B. Gräler. 2018. Random forest as a generic framework for predictive modeling of spatial and spatio-temporal variables. Peerj 6:e5518.

Howard, D. J. 1993. Reinforcement: Origin, dynamics, and fate of an evolutionary hypothesis. Pp. 46–69 *in* R. G. Harrison, ed. Hybrid zones and the evolutionary process. Oxford University Press, New York.

Ilyina, T. A. and E. V. Ivankina. 2001. Seasonal variation of vinging activity and relative effect of the advertising behaviour of males with different plumage colour in the Pied Flycatcher Ficedula hypoleuca. Acta Ornithol 36:85-89.

Ivankina, E. V., A. B. Kerimov, V. G. Grinkov, and A. V. Bushuev. 2007. Structural and functional aspects of variation of the breeding plumage ornamentation in the male Pied Flycatcher Ficedula hypoleuca (Aves : Passeriformes). Zh Obshch Biol 68:278-295.

Johansen, H. 1954. Die Vogelfauna Westsibiriens. J Ornithol 95:64-111.

Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G. White, J. Woollen, Y. Zhu, M. Chelliah, W. Ebisuzaki, W. Higgins, J. Janowiak, K. C. Mo, C. Ropelewski, J. Wang, A. Leetmaa, R. Reynolds, R. Jenne, and D. Joseph. 1996. The NCEP/NCAR 40-Year Reanalysis Project. Bulletin of the American Meteorological Society 77:437-472.

Kanamitsu, M., W. Ebisuzaki, J. Woollen, S.-K. Yang, J. J. Hnilo, M. Fiorino, and G. L. Potter. 2002. NCEP–DOE AMIP-II Reanalysis (R-2). Bulletin of the American Meteorological Society 83:1631-1644.

Kemp, M. U., E. Emiel van Loon, J. Shamoun-Baranes, and W. Bouten. 2012. RNCEP: global weather and climate data at your fingertips. Methods Ecol Evol 3:65-70.

Kerimov, A. B., V. G. Grinkov, E. V. Ivankina, T. A. Ilyina, and A. V. Bushuev. 2014. The influence of spring temperature on the intensity of advertising behavior and basal metabolic rate in bright and pale Pied Flycatcher (Ficedula Hypoleuca) Males. Zool Zh 93:1288-1302.

Kral, M., T. Jarvi, and V. Bicik. 1988. Inter-specific aggression between the Collared Flycatcher and the Pied Flycatcher - the selective agent for the evolution of light-colored male Pied Flycatcher populations. Ornis Scand 19:287-289.

Laaksonen, T., P. M. Sirkia, S. Calhim, J. E. Brommer, P. K. Leskinen, C. R. Primmer, P. Adamik, A. V. Artemyev, E. Belskii, C. Both, S. Bures, M. D. Burgess, B. Doligez, J. T. Forsman, V. Grinkov, U. Hoffmann, E. Ivankina, M. Kral, I. Krams, H. M. Lampe, J. Moreno, M. Magi, A. Nord, J. Potti, P. A. Ravussin, and L. Sokolov. 2015. Sympatric divergence and clinal variation in multiple coloration traits of Ficedula flycatchers. J Evolution Biol 28:779-790.

Lehtonen, P. K., C. R. Primmer, and T. Laaksonen. 2009. Different traits affect gain of extrapair paternity and loss of paternity in the pied flycatcher, Ficedula hypoleuca. Anim Behav 77:1103-1110.

Lewontin, R. C. 1974. The genetic basis of evolutionary change. Columbia University Press New York.

Löhrl, V. H. 1965. Zwei regional und ökologisch getrennte Formen des Trauerschnäppers (Ficedula hypoleuca) in Südwestdeutschland. Bonner Zoologische Beiträge 16:268 - 283.

Lundberg, A. and R. V. Alatalo. 1992. The Pied Flycatcher. T & AD Poyser Ltd., London.

Miller, H. J. 2004. Tobler's first law and spatial analysis. Annals of the Association of American Geographers 94:284-289.

Noor, M. A. F. 1999. Reinforcement and other consequences of sympatry. Heredity 83:503-508.

Nyholm, N. E. I. and H. E. Myhrberg. 1983. Breeding area fidelity of the pied flycatcher Ficedula hypoleuca at Ammarnäs, Swedish Lapland. Ornis Fennica 60:22-27.

Potti, J., J. L. Copete, C. Gutierrez-Exposito, and C. Camacho. 2016. Morphological and sexual traits in Atlas and Iberian Pied Flycatchers Ficedula hypoleuca speculigera and F-h. iberiae: a comparison. Bird Study 63:330-336.

Potti, J. and S. Montalvo. 1991. Male arrival and female mate choice in Pied Flycatchers Ficedula-Hypoleuca in central Spain. Ornis Scand 22:45-54.

Probst, P., M. Wright, and A.-L. Boulesteix. 2018. Hyperparameters and tuning strategies for random forest. arXiv:1804.03515.

Qvarnstrom, A., A. M. Rice, and H. Ellegren. 2010. Speciation in Ficedula flycatchers. Philos T R Soc B 365:1841-1852.

Ristow, D. 1975. Der Trauerschnäpper (Ficedula hypoleuca) in der Eifel und im Kottenforst bei Bonn. Kilda-Verlag, Greven.

Roskaft, E. and T. Jarvi. 1983. Male plumage color and mate choice of female Pied Flycatchers Ficedula hypoleuca. Ibis 125:396-400.

Roskaft, E., T. Jarvi, N. E. I. Nyholm, M. Virolainen, W. Winkel, and H. Zang. 1986. Geographic variation in secondary sexual plumage color characteristics of the male Pied Flycatcher. Ornis Scand 17:293-298.

Saetre, G. P., S. Dale, and T. Slagsvold. 1994. Female Pied Flycatchers prefer brightly colored males. Anim Behav 48:1407-1416.

Saetre, G. P., T. Moum, S. Bures, M. Kral, M. Adamjan, and J. Moreno. 1997. A sexually selected character displacement in flycatchers reinforces premating isolation. Nature 387:589-592.

Saetre, G. P. and S. A. Saether. 2010. Ecology and genetics of speciation in Ficedula flycatchers. Mol Ecol 19:1091-1106.

Sangster, G., J. M. Collinson, A. J. Helbig, A. G. Knox, and D. T. Parkin. 2004. Taxonomic recommendations for British birds: second report. Ibis 146:153-157.

Servedio, M. R. 2004. The what and why of research on reinforcement. Plos Biol 2:e420-e420.

Servedio, M. R. and M. A. F. Noor. 2003. The role of reinforcement in speciation: theory and data. Annual Review of Ecology, Evolution, and Systematics 34:339-364.

Sirkia, P. M., P. Adamik, A. V. Artemyev, E. Belskii, C. Both, S. Bures, M. Burgess, A. V. Bushuev, J. T. Forsman, V. Grinkov, D. Hoffmann, A. Jarvinen, M. Kral, I. Krams, H. M. Lampe, J. Moreno, M. Magi, A. Nord, J. Potti, P. A. Ravussin, L. Sokolov, and T. Laaksonen. 2015. Fecundity selection does not vary along a large geographical cline of trait means in a passerine bird. Biol J Linn Soc 114:808-827.

Sirkia, P. M. and T. Laaksonen. 2009. Distinguishing between male and territory quality: females choose multiple traits in the pied flycatcher. Anim Behav 78:1051-1060.

Sirkia, P. M., M. Virolainen, and T. Laaksonen. 2010. Melanin coloration has temperature-dependent effects on breeding performance that may maintain phenotypic variation in a passerine bird. J Evolution Biol 23:2385-2396.

Sternberg, H. 1964. Untersuchungen über die Farbtypenzugehörigkeit der männlichen Trauerschnäpper, Ficedula hypoleuca, im Schweizerischen Mittelland. Ornithologische Beobachter 61:90–94.

Sternberg, H., V. G. Grinkov, E. V. Ivankina, T. A. Ilyina, A. B. Kerimov, and A. Schwarz. 2002. Evaluation of the size and composition of nonbreeding surplus in a Pied Flycatcher Ficedula hypoleuca population: Removal experiments in Germany and Russia. Ardea 90:461-470.

Trettau, W. 1952/53. Planberingung des Trauerfliegenschnäppers (Muscícapa hypoleuca) in Hessen. Vogelwarte - Zeitschrift für Vogelkunde 16:89-95.

Trettau, W. and F. Merkel. 1943. Ergebnisse einer Planberingung des Trauerfliegenschnäppers (Muscicapa hypoleuca Pallas) in Schlesien. Vogelzug 14:77-90.

Tzedakis, P. C., B. C. Emerson, and G. M. Hewitt. 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. Trends Ecol Evol 28:696-704.

Vabishchevich, A. P. and N. A. Formozov. 2010. Song variability in Pied Flycatchers Ficedula hypoleuca: impact of the sympatry with Collared Flycatchers F. albicollis. Acta Ornithol 45:189-202.

Vysotsky, V. G. 1995. Coloring of male pied flycatchers and its relationship with other characters. Ornitologiya 26:28-32.

Wager, S., T. Hastie, and B. Efron. 2014. Confidence Intervals for random forests: the jackknife and the infinitesimal jackknife. Journal of machine learning research : JMLR 15:1625-1651.

Walankiewicz, W., C. Mitrus, D. Czeszczewik, and P. M. Jablonski. 1997. Is the Pied Flycatcher Ficedula hypoleuca overcompeted by the Collared Flycatcher Ficedula albicollis in the natural forest of Bialowieza? Acta Ornithol 2:213-217.

Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

Winkel, W., D. Richter, and R. Berndt. 1970. Über Beziehungen zwischen Farbtyp und Lebensalter männlicher Trauerschnäpper (Ficedula hypoleuca). Vogelwelt 91:161-170.

Winkel, W. and D. Winkel. 1984. Polygynie des Trauerschnäppers (Ficedula hypoleuca) am Westrand seines Areals in Mitteleuropa. J Ornithol 125:1-14.

Wright, M. N. and A. Ziegler. 2017. ranger: A fast implementation of random forests for high dimensional data in C++ and R. Journal of Statistical Software 77:17.

Zang, H. 1975. Populationsstudien am Trauerschnäpper (Ficedula hypoleuca) im Bergwald des Harzes als einem suboptimalen Habitat. Vogelwelt 96:161-184.

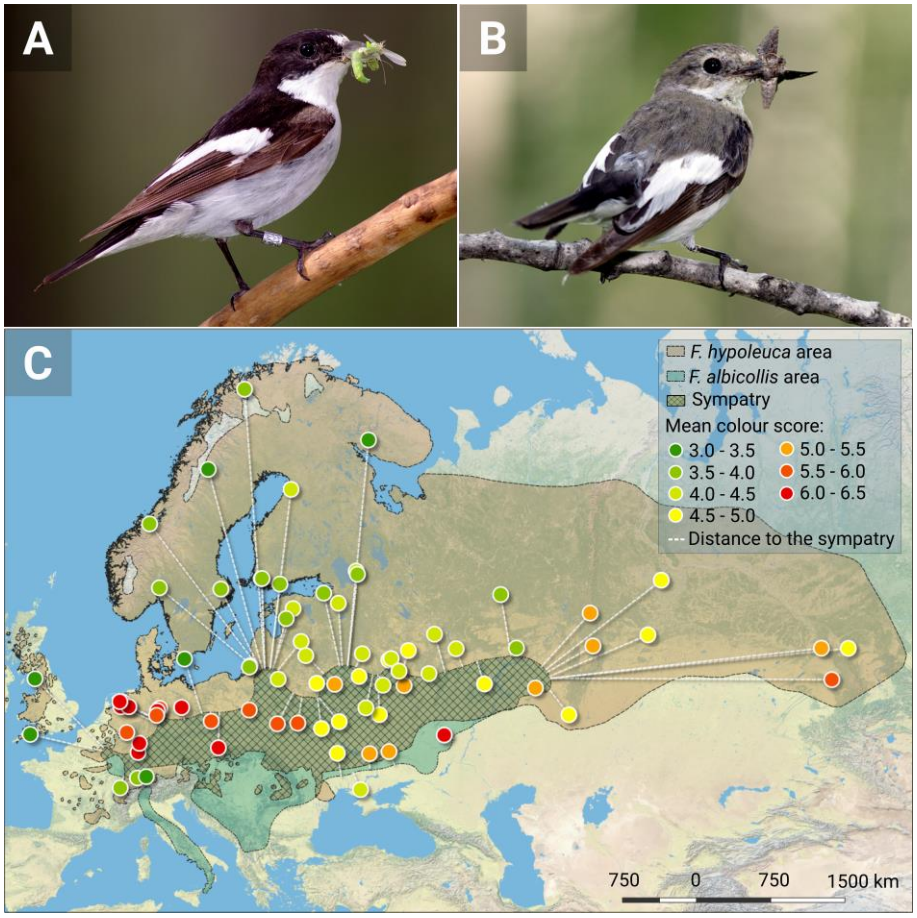

Fig. 1. The variability of the male breeding plumage colour and the mean colour score in populations of the Pied Flycatcher (F. hypoleuca).
(**A**) The contrast-coloured male (black morph). (**B**) The less bright male (brown morph). (**C**) The mean colour score in populations breeding in different parts of the Pied Flycatcher *F. hypoleuca* range. For each observation point, the distance to the border of the Collared Flycatcher *F. albicollis* is shown. Photos (**A**) and (**B**) credits: Vladimir G. Grinkov. Map source: the U.S. National Park Service (NPS) Natural Earth physical map.

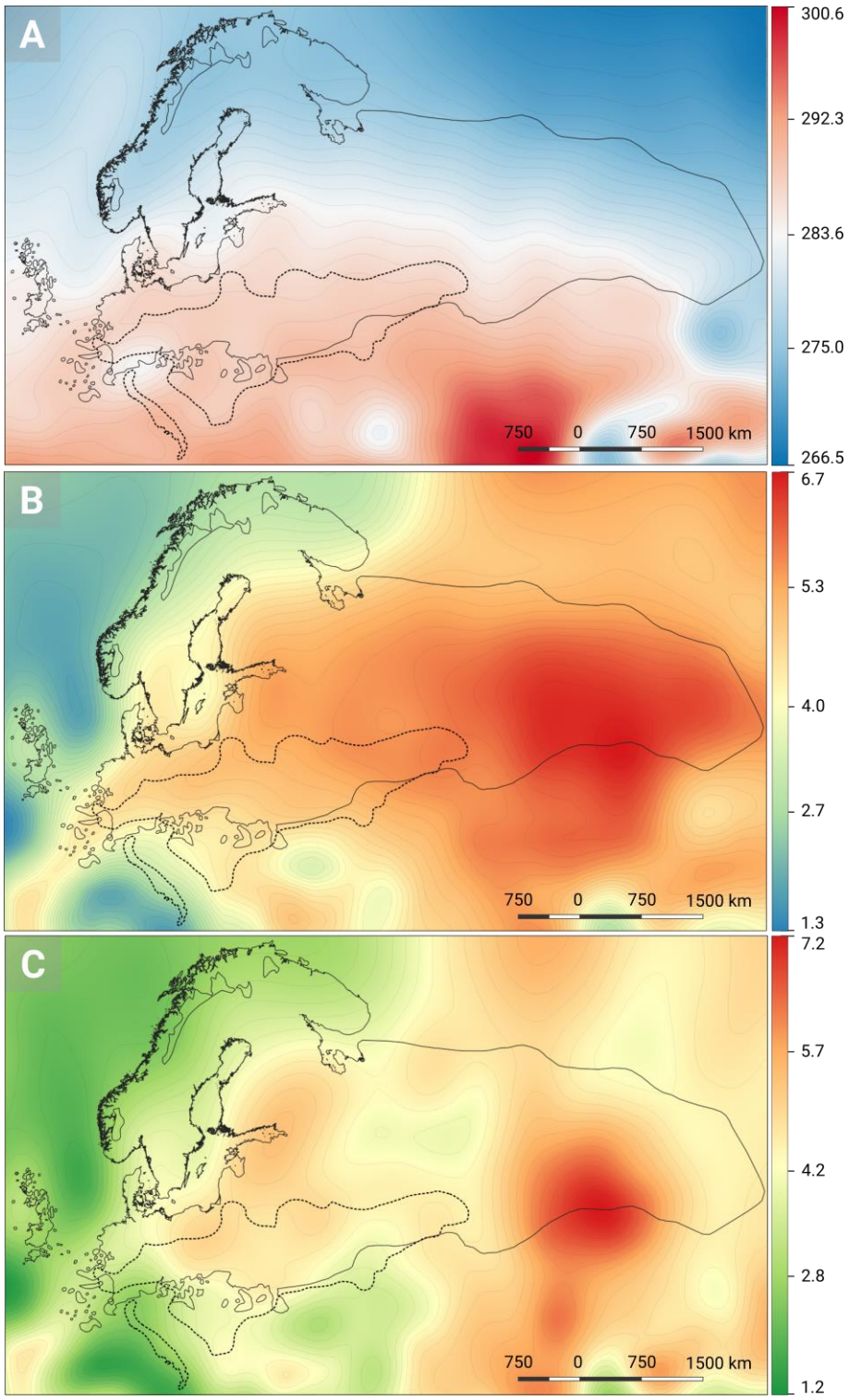

Fig. 2. Thermal characteristics of the territories covered by the breeding ranges of the two species of *Ficedula* flycatchers.

The images show (**A**) the mean daily maximum temperature in Kelvin, (**B**) the standard deviation of the daily maximum temperature, and (**C**) the standard deviation of the maximum temperature on May 1. The *F. hypoleuca* area is drawn with a solid line, the *F. albicollis* area is drawn with a dashed line. Each colour links to the value of the corresponding thermal characteristics (the key is on the right of each image). The hairlines

connect the areas with the same values of the shown characteristic (for example, in the figure (**A)** these are isotherms).

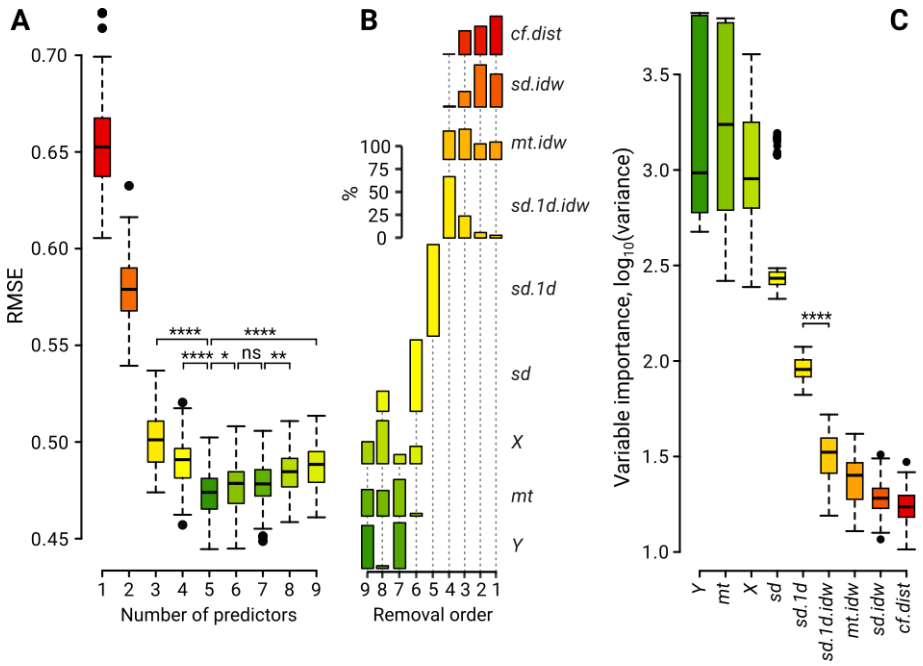

Fig. 3. The results of the 10-fold cross-validation procedure for 100 repetitions. (**A**) Prediction performance of models calculated as the root mean squared error (RMSE) with sequentially reduced number of predictors. (**B**) The removal order of predictors and its frequency in percent (%), showing at what step and how often the predictors obtaining the lowest variable importance value were excluded from the models. (**C**) The variable importance values measured as the variance of the responses are given for all predictors (the variable importance values on the ordinate axis are converted by a decimal logarithm). The figure parts (**A**) and (**C**) show the median (the line across the box), the interquartile range (IQR, the box), the positive and negative 1.5*IQR extension of the IQR (the vertical dotted line). The small black circles represent outliers from the latter range. A horizontal line with downward serifs at the ends connects the compared values for which significance levels of Student's t-test (two-tailed) shown as following: ns for $p > 0.05$; * for $p < 0.05$; ** for $p < 0.01$, and **** for $p < 0.0001$. Variable predictor names are in italics; for a description, please see the material and methods.

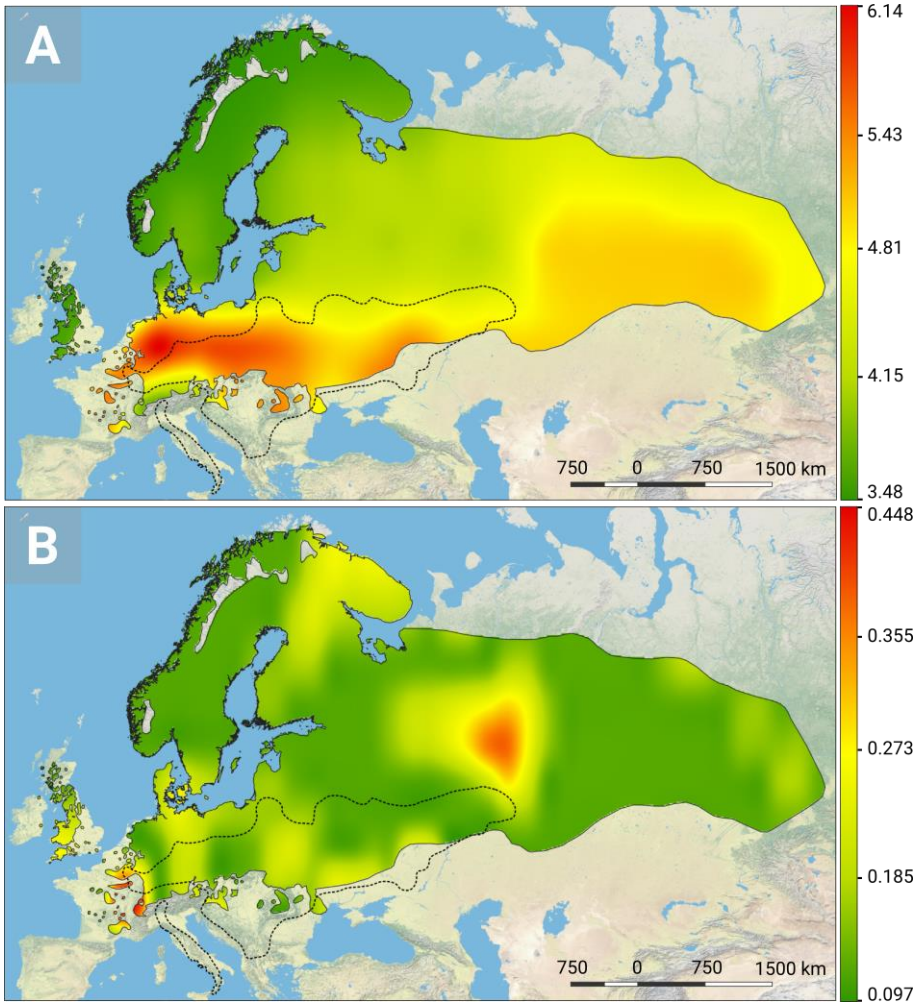

Fig. 4. Reconstruction of the phenotypic structure of the *F. hypoleuca* populations for the entire breeding range.

(**A**) Mean colour score predicted by the final random forest model. (**B**) Accuracy of the predicted values (the standard error of the predictions, see also Fig. S2). In the figure parts, the colour links to the value of the corresponding characteristic shown (the key is on the right of each part).

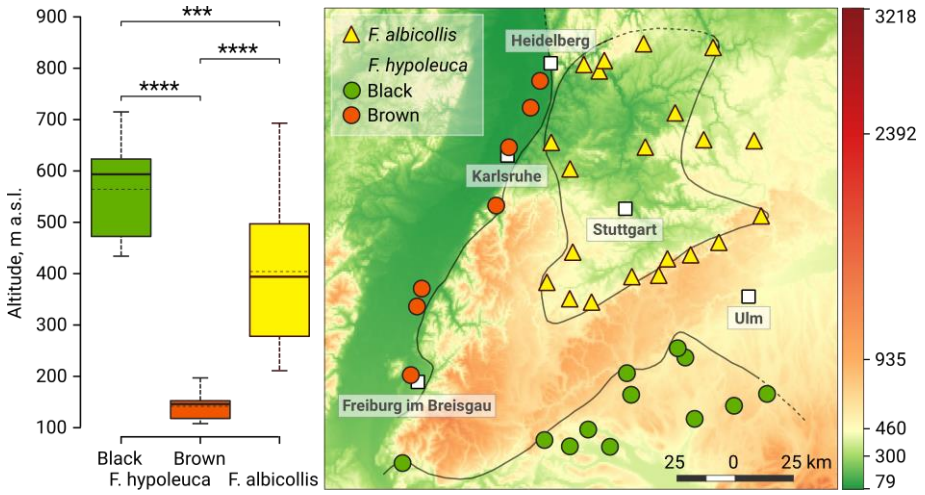

Fig. 5. Small-scale spatial segregation between two species of the *Ficedula* flycatcher in south-west Germany, depending on the elevation above sea level.
Reprocessed data of figure 2 (page 271) of the H. Löhrl publication in Bonner Zoologische Beiträge (Löhrl 1965) are shown. On the map, the colour indicates the height above sea level (altitude) in meters (according to the color rump on the right of the map) and the location of the nests of the two species of *Ficedula* flycatchers. The graph compares the height of the nest locations above sea level. The graph shows the median (the solid line across the box), the mean (the dashed line across the box), the interquartile range (IQR, the box), the positive and negative 1.5*IQR extension of the IQR (the vertical dotted line). A horizontal line with downward serifs at the ends connects the compared values for which the significance levels of Student's t-test (two-tailed) are shown as following: *** for $p < 0.001$, and **** for $p < 0.0001$.

Supplementary Materials.

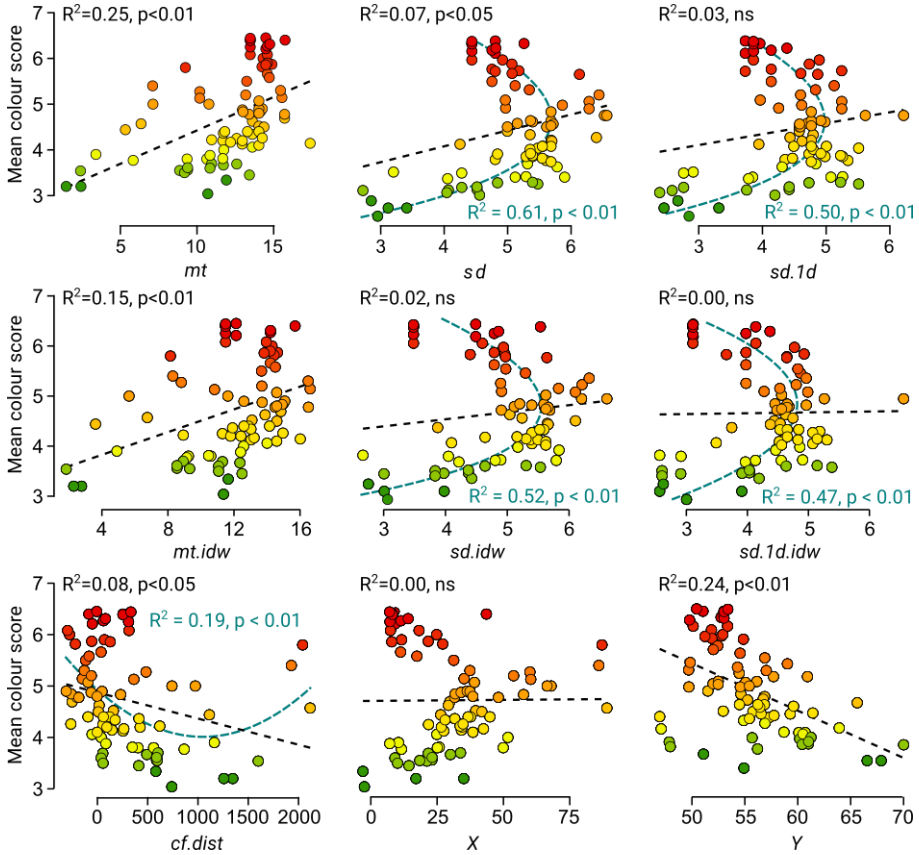

Fig. S1. The relationship between the mean colour score (response variable) and all predictors.

The scatterplots are presented for each predictor separately (the predictor name is written in italics under the x-axis), the linear (black dashed line) and non-linear (blue dashed curve) regressions are drawn; for each regression, the coefficient of determination (R^2) and the significance level are given (indicated in black and blue font, respectively).

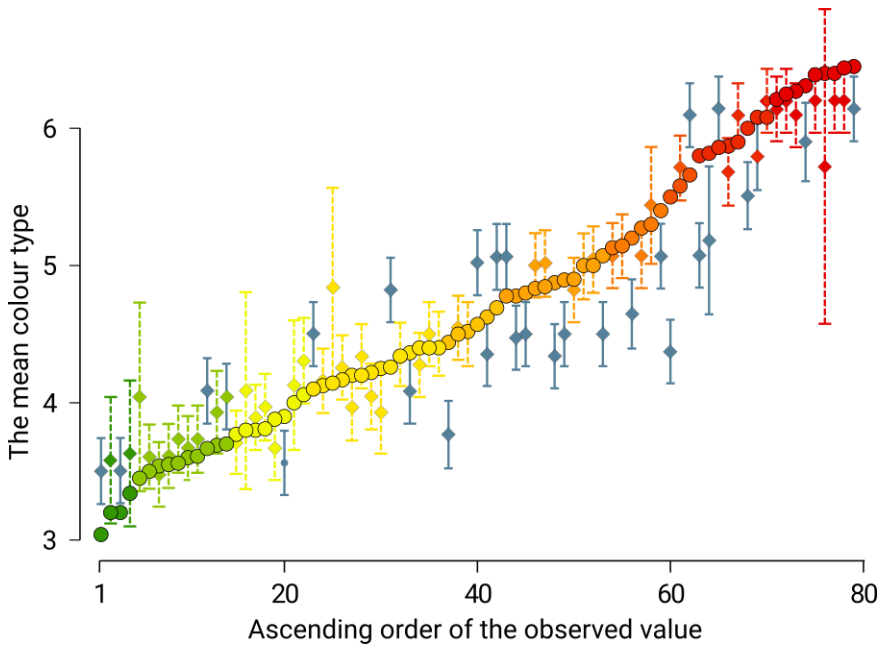

Fig. S2. Comparison of observed and predicted values of mean colour score of male breeding plumage in the *F. hypoleuca* populations.
The observed values are drawn in circles, the corresponding predicted values are drawn in diamonds; for each predicted value, a dashed vertical line indicates a 95% confidence interval (95% CI). Dark blue colour indicates such predictions that do not contain the observed value in the 95% CI.

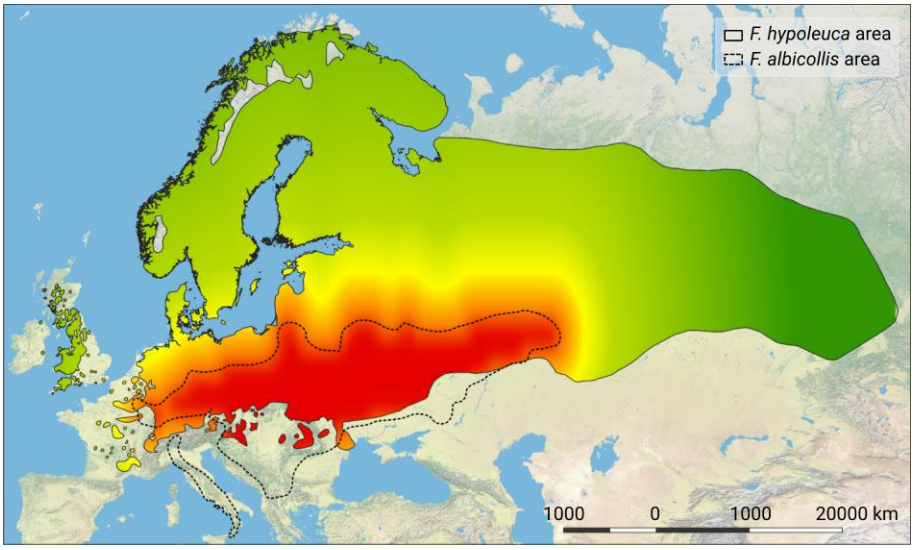

Fig. S3. The hypothetical phenotypic structure of *F. hypoleuca* **populations is drawn as if it was determined by the distance from the nesting range of** *F. albicollis***.**
The transition from red through yellow to green corresponds to a change in the proportions of different morphs in the populations of *F. hypoleuca* from the most frequent brown through the intermediate to the most frequent black, respectively.

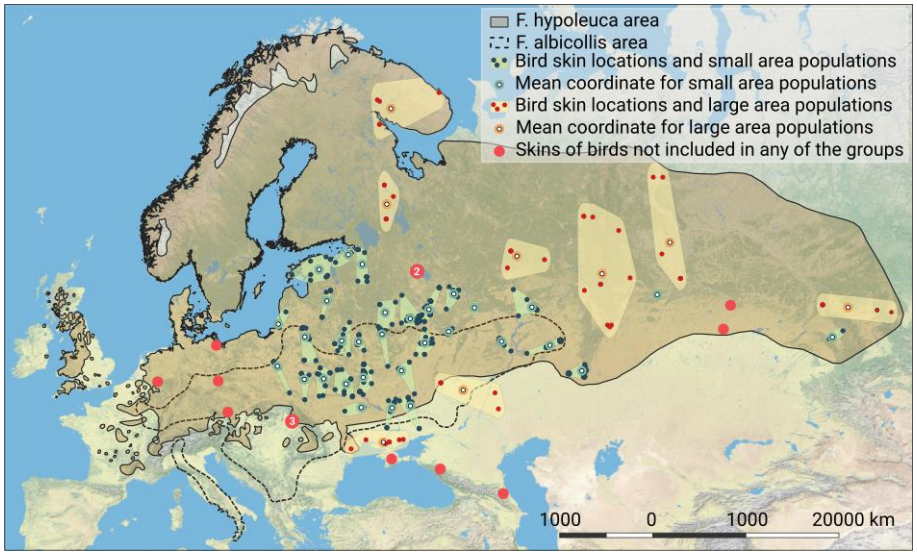

Fig. S4. "Populations" formed from bird skins which were studied in 11 museums. The average population coordinate is the observation point used in the calculations (for summary data, please, see Table S2).

Table S1.

The mean colour of males' breeding plumage in the Pied Flycatcher *Ficedula hypoleuca* populations.

#	Longitude	Latitude	Mean colour type	Sample size	Location	Country	Source
1	17.36	49.64	6.08	50	Moravia-Jeseníky	Czech Republic	Laaksonen et al. 2015; Sirkia et al. 2015
2	24.95	58.15	3.81	73	Kilingi-Nõmme	Estonia	Laaksonen et al. 2015; Sirkia et al. 2015
3	22.16	60.43	3.56	408	Ruissalo	Finland	Laaksonen et al. 2015; Sirkia et al. 2015
4	22.24	60.44	3.61	1207	Turku	Finland	von Haartman 1985
5	24.25	60.14	3.80	117	Siuntio	Finland	Roskaft et al. 1986
6	25.50	65.02	4.44	48	Oulu	Finland	Laaksonen et al. 2015
7	7.09	50.74	5.86	66	Bonn	Germany	Ristow 1975
8	7.29	52.52	6.40	416	Lingen	Germany	Winkel and Winkel 1984
9	7.32	52.53	6.39	806	Lingen	Germany	Handbuch der Vögel Mitteleuropas, 1993
10	8.36	49.30	6.21	42	Harthausen	Germany	Laaksonen et al. 2015; Sirkia et al. 2015
11	8.51	49.96	6.45	49	Mönchbruch, Hessen	Germany	Trettau 1952/53
12	10.43	51.94	5.66	44	Goslar, Harz, Lower Saxony	Germany	Zang 1975
13	10.52	52.25	6.27	536	Braunschweig	Germany	Winkel et al. 1970
14	10.78	52.42	5.90	1583	Wolfsburg, Lower Saxony	Germany	Sternberg et al. 2002
15	13.24	52.49	6.31	15	Berlin, Grunewald	Germany	Curio 1959
16	27.15	55.89	4.34	60	Kraslava	Latvia	Laaksonen et al. 2015; Sirkia et al. 2015
17	9.65	63.33	3.90	166	Songli	Norway	Roskaft et al. 1986
18	10.75	59.92	3.77	72	Oslo	Norway	Laaksonen et al. 2015; Sirkia et al. 2015
19	20.29	69.36	3.54	95	Skibotn	Norway	Laaksonen et al. 2015; Sirkia et al. 2015
20	16.55	51.52	5.58	105	Jemielno, Silesia	Poland	Trettau and Merkel 1943
21	20.83	55.16	3.69	459	Courish spit	Russia	Vysotsky 1995
22	32.80	60.85	4.22	217	Scientific field station "Mayachino"	Russia	Laaksonen et al. 2015; Sirkia et al. 2015
23	32.94	60.68	3.70	93	Ladoga Ornithological Station "Gumbaricy"	Russia	Grinkov 1997
24	33.89	52.45	4.26	110	Bryansky Les Nature Reserve	Russia	Own data
25	35.81	53.98	4.40	NA	Ugra National Park	Russia	Vabishchevich and Formozov 2010
26	36.72	55.70	4.40	1403	Zvenigorod	Russia	Ivankina et al. 2007
27	37.57	54.90	4.80	1631	Moscow region	Russia	Anorova 1977

28	37.60	54.90	4.10	NA	PTS Natural Biosphere Reserve	Russia	Vabishchevich and Formozov 2010
29	59.34	56.49	5.13	376	Ekaterinburg	Russia	Belskii and Lyakhov 2004
30	84.95	56.35	5.40	1770	Tomsk	Russia	Own data
31	13.55	55.67	3.45	54	Vombs fure	Sweden	Laaksonen et al. 2015
32	16.21	65.95	3.20	403	Ammarnäs	Sweden	Nyholm and Myhrberg 1983
33	17.63	59.85	3.55	408	Uppsala	Sweden	Lundberg and Alatalo 1992
34	6.35	46.63	3.88	81	Vaud	Switzerland	Laaksonen et al. 2015; Sirkia et al. 2015
35	8.29	47.39	3.60	34	Aagau-Zürich	Switzerland	Sternberg 1964
36	9.27	47.49	3.50	73	Bischofszell, Thurgau	Switzerland	Eggenberger 1964
37	6.31	52.88	6.44	112	Diever - Doldersum	The Netherlands	Bijlsma and Both 2014
38	6.42	52.52	6.25	77	Ommen	The Netherlands	Haverschmidt 1973
39	6.60	52.86	6.08	440	Drenthe	The Netherlands	Laaksonen et al. 2015; Sirkia et al. 2015
40	-3.73	50.60	3.34	88	East Dartmoor	United Kingdom	Laaksonen et al. 2015; Sirkia et al. 2015
41	-3.20	54.40	3.04	489	Cumbria	United Kingdom	Lundberg and Alatalo 1992

Table S2.

The observation points for "populations" formed by the bird skins from museum collections.

The mean colour type for population with ID 4, indicated in square brackets, was excluded from the analysis (see the materials and methods for the explanation). The column "Populations" contains identifiers of populations, denoted as L-1, L-2, etc. for large populations and S-1, S-2, etc. for small populations, respectively (please also see Fig. S4 and Data S1).

ID	Longitude	Latitude	Mean colour type	Standard deviation	Number of the bird skins	Populations
1	33.29	46.49	4.14	1.46	7	L-1
2	42.67	50.55	6.40	0.89	5	L-2
3	34.17	67.26	3.20	1.10	5	L-3
4	33.68	62.50	[2.17]	0.41	6	L-4
5	49.00	59.54	3.80	1.10	5	L-5
6	59.02	58.47	5.27	1.56	11	L-6
7	67.00	60.35	5.00	1.26	6	L-7
8	87.96	56.34	4.57	0.98	7	L-8
9	20.81	52.30	5.59	1.28	17	S-1
10	20.92	55.24	4.25	1.06	12	S-2
11	23.97	51.35	6.00	1.20	8	S-3
12	24.05	54.37	3.91	0.94	11	S-4
13	26.25	51.40	5.82	1.47	11	S-5
14	26.62	56.76	4.13	1.36	8	S-6
15	25.73	58.73	4.20	1.23	10	S-7
16	28.91	51.01	4.69	1.11	13	S-8
17	28.38	54.10	4.63	1.60	8	S-9
18	29.16	59.63	3.67	0.82	6	S-10
19	30.69	49.23	4.78	1.20	9	S-11
20	30.90	51.50	4.85	1.09	39	S-12
21	30.39	54.04	5.50	0.93	8	S-13
22	30.80	59.05	4.36	1.21	11	S-14
23	34.30	49.21	5.14	1.10	14	S-15
24	33.12	54.55	4.88	1.81	8	S-16
25	33.48	56.00	4.20	1.79	5	S-17
26	36.48	49.36	5.30	1.06	10	S-18
27	35.41	51.98	4.90	1.79	10	S-19
28	36.45	55.60	4.94	1.30	17	S-20
29	38.17	53.95	5.07	1.49	14	S-21
30	38.64	56.21	4.50	1.49	48	S-22
31	40.95	54.73	4.50	1.38	6	S-23
32	41.58	57.21	4.17	0.41	6	S-24

33	44.00	56.32	4.40	1.34	5	S-25
34	47.18	54.06	4.78	1.72	9	S-26
35	52.89	53.79	5.25	1.28	8	S-27
36	50.76	56.36	4.00	1.63	13	S-28
37	56.64	51.97	4.83	1.40	12	S-29
38	65.50	57.17	5.00	1.58	5	S-30
39	86.11	54.34	5.80	1.30	5	S-31

Data S1. The list of bird skins stored in museum collections and used to calculate the mean breeding plumage color score of males in the Pied Flycatcher populations.

Row ID	Bird skin ID	Colour type	Latitude.S-N	Longitude.W-E	Population ID	Museum	Location (transliterated)	Location (translated)
1	R-11766	2	53.849	13.694	N/A	7	Anklam, Pomeraniya	Anklam, Pomerania
2	R-109136	5	52.431	56.991	S-29	7	YUzhnyj Ural, verhov'ya reki Malaya Suren'	Southern Ural, upper reaches of the Malaya Suren river
3	R-109144	3	52.001	57.034	S-29	7	YUzhnyj Ural, Kasmarka	South Ural, Kasmark
4	R-109135	5	52.001	57.034	S-29	7	YUzhnyj Ural, Kasmarka	South Ural, Kasmark
5	R-109145	3	52.001	57.034	S-29	7	YUzhnyj Ural, Kasmarka	South Ural, Kasmark
6	R-29249	4	54.108	54.122	S-27	7	Belebejskij rajon	Belebey district
7	R-109142	6	54.108	54.122	S-27	7	Belebejskij rajon	Belebey district
8	R-107465	5	61.038	60.973	L-6	7	Verhov'ya reki Malaya Sos'va	The upper river Malaya Sosva
9	R-50644	6	61.794	57.923	L-6	7	Verhov'ya Pechory	Upper Pechora
10	R-83501	4	56.235	40.681	S-24	7	Vladimirskaya oblast', selo Nesterkovo	Vladimir region, village Nesterkovo
11	R-60274	6	58.219	62.315	L-6	7	Ekaterinburgskaya oblast'	Yekaterinburg region
12	R-13750	4	57.012	42.003	S-24	7	Ivanovskaya oblast'	Ivanovo region
13	R-51815	4	59.673	66.055	L-7	7	Irtysh, verhov'ya reki Kondy, ozero Orditur (?)	Irtysh, headwaters of the river Konda, Orditur lake (?)
14	R-40007	3	58.669	37.275	N/A	7	Kalininskaya oblast', Ves'egonskij rajon	Kalinin region, Vesyegonsky district
15	R-40006	2	58.669	37.275	N/A	7	Kalininskaya oblast', Ves'egonskij rajon	Kalinin region, Vesyegonsky district
16	R-40008	6	57.123	35.466	S-20	7	Kalininskaya oblast', Lihoslavskij rajon	Kalinin region, Likhoslav district
17	R-88770	2	63.523	33.402	L-4	7	Kareliya	Karelia
18	R-88769	2	63.523	33.402	L-4	7	Kareliya	Karelia
19	R-89750	5	54.788	87.356	S-31	7	Kemerovskaya oblast', Pron'evskij rajon	Kemerovo region, Pronevsky district
20	R-11737	4	57.452	41.499	S-24	7	Kostromskaya oblast', Plyos	Kostroma region, Plyos
21	R-97950	5	56.163	91.389	L-8	7	Krasnoyarskij kraj, Kozul'skij rajon	Krasnoyarsk Territory, Kozulsky District
22	R-41100	4	67.661	32.561	L-3	7	Laplandskij zapovednik	Lapland Reserve
23	7554	4	66.538	32.823	L-3	4	Louhskij rajon, CHyornaya rechka	Loukhsky district, Black River
24	N/A	2	66.538	32.823	L-3	4	Louhskij rajon, CHyornaya rechka	Loukhsky district, Black River
25	R-89460	4	55.727	36.212	S-20	7	Moskovskaya oblast', Arhangel'skoe	Moscow region, Arkhangelsk
26	R-75466	7	55.741	36.501	S-20	7	Moskovskaya oblast', Gluboko-Istrinskij zapovednik	Moscow region, Gluboko-Istrinsky reserve
27	R-36697	2	56.315	38.132	S-22	7	Moskovskaya oblast', Zagorskij rajon	Moscow region, Zagorsky district
28	R-117099	3	55.865	37.836	S-22	7	Moskovskaya oblast', Losinyj ostrov	Moscow region, Losiny island
29	R-60277	4	55.495	36.039	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district
30	R-6028	3	55.495	36.039	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district
31	R-83497	4	55.495	36.039	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district
32	R-83498	4	55.495	36.039	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district
33	R-83500	4	55.495	36.039	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district
34	R-83495	6	55.495	36.039	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district
35	R-83496	7	55.495	36.039	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district
36	R-83499	5	55.495	36.039	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district

37	R-117088	5	55.536	37.066	S-20	7	Moskovskaya oblast', Narofominskij rajon, Aprelevka	Moscow region, Narofominsky district, Aprelevka
38	R-117092	4	55.536	37.066	S-20	7	Moskovskaya oblast', Narofominskij rajon, Aprelevka	Moscow region, Narofominsky district, Aprelevka
39	R-60216	5	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
40	R-60234	4	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
41	R-60212	6	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
42	R-?	6	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
43	R-60226	4	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
44	R-60218	5	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
45	R-60235	7	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
46	R-60239	5	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
47	R-60232	6	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
48	R-60227	3	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
49	R-60221	3	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
50	R-60217	3	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
51	R-60229	5	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
52	R-60233	4	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
53	R-60238	4	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
54	R-60213	4	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
55	R-60236	3	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
56	R-60219	2	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
57	R-60211	4	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
58	R-60222	7	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
59	R-68209	2	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
60	R-60224	3	55.861	38.783	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
61	R-11736	3	55.438	37.565	S-22	7	Moskovskaya oblast', Podol'skij rajon	Moscow region, Podolsky district
62	R-11726	6	55.438	37.565	S-22	7	Moskovskaya oblast', Podol'skij rajon	Moscow region, Podolsky district
63	R-11734	4	55.438	37.565	S-22	7	Moskovskaya oblast', Podol'skij rajon	Moscow region, Podolsky district
64	R-11725	4	55.438	37.565	S-22	7	Moskovskaya oblast', Podol'skij rajon	Moscow region, Podolsky district
65	R-109820	7	55.503	37.305	S-20	7	Moskovskaya oblast', reka Desna	Moscow region, Desna river
66	R-109817	4	55.503	37.305	S-20	7	Moskovskaya oblast', reka Desna	Moscow region, Desna river
67	R-109819	6	55.772	37.432	S-20	7	Moskovskaya oblast', Serebryanyj bor	Moscow region, Serebryanny Bor
68	R-117096	5	54.889	38.114	S-21	7	Moskovskaya oblast', Stupinskij rajon	Moscow region, Stupinsky district
69	R-117095	6	54.889	38.114	S-21	7	Moskovskaya oblast', Stupinskij rajon	Moscow region, Stupinsky district
70	R-11733	4	57.421	27.055	S-6	7	Marienburg, Liflyandiya	Marienburg, Livonia
71	R-11731	2	57.421	27.055	S-6	7	Marienburg, Liflyandiya	Marienburg, Livonia
72	R-11727	6	57.421	27.055	S-6	7	Marienburg, Liflyandiya	Marienburg, Livonia
73	R-11751	4	57.421	27.055	S-6	7	Marienburg, Liflyandiya	Marienburg, Livonia
74	R-93065	4	53.901	27.557	S-9	7	Minskaya oblast'ast'	Minsk region
75	R-60241	4	55.752	37.614	S-22	7	Moskva	Moscow
76	R-60207	4	55.752	37.614	S-22	7	Moskva	Moscow
77	R-60242	4	55.752	37.614	S-22	7	Moskva	Moscow
78	R-11739	6	55.752	37.614	S-22	7	Moskva	Moscow

79	R-116590	7	55.752	37.614	S-22	7	Moskva	Moscow
80	R-117087	4	55.752	37.614	S-22	7	Moskva	Moscow
81	R-60260	3	56.741	38.852	S-22	7	Pereslavl'-Zalesskij	Pereslavl-Zalessky
82	R-60261	7	56.741	38.852	S-22	7	Pereslavl'-Zalesskij	Pereslavl-Zalessky
83	R-60204	4	56.741	38.852	S-22	7	Pereslavskij rajon	Pereslavsky district
84	R-60259	2	56.741	38.852	S-22	7	Pereslavskij rajon	Pereslavsky district
85	R-60205	5	56.741	38.852	S-22	7	Pereslavskij rajon	Pereslavsky district
86	R-60273	3	61.838	56.864	L-6	7	Pechorskij zapovednik (poselok Ilychskij?)	Pechora Nature Reserve (Ilychsky village?)
87	R-50636	4	61.838	56.864	L-6	7	Pechora, dolina reki Ul'n	Pechora, Uln River Valley
88	R-35771	3	55.174	59.654	L-6	7	reka Malyj Syrostan, u Zlatousta	Maly Syrostan river, near Chrysostom
89	R-65543	4	54.834	40.915	S-23	7	Ryazanskaya oblast', Bel'kovskij rajon, selo Aluhtinskie dvoriki	Ryazan region, Belkovsky district, village Alukhtinsky courtyards
90	R-60262	3	54.541	40.859	S-23	7	Ryazanskaya oblast', Izhevskij rajon	Ryazan region, Izhevsky district
91	R-11741	3	54.236	39.011	S-21	7	Ryazanskaya oblast'ast'. Mihalovskij rajon	Ryazan region Michalovsky district
92	R-29254	7	54.231	85.803	S-31	7	Salair, verhov'ya reki CHulysh	Salair, the upper reaches of the river Chulysh
93	R-29255	7	54.231	85.803	S-31	7	Salair, verhov'ya reki CHulysh	Salair, the upper reaches of the river Chulysh
94	R-29247	4	54.231	85.803	S-31	7	Salair, reka Syuhta	Salair, Syukhta River
95	R-29256	6	54.231	85.803	S-31	7	Salair, reka Syuhta	Salair, Syukhta River
96	R-29245	4	56.508	84.973	L-8	7	Tomsk	Tomsk
97	R-29246	5	56.508	84.973	L-8	7	Tomsk	Tomsk
98	R-29252	6	57.167	65.501	S-30	7	Tyumen'	Tyumen
99	R-30168	4	57.167	65.501	S-30	7	Tyumen'	Tyumen
100	R-29251	7	57.167	65.501	S-30	7	Tyumen'	Tyumen
101	R-93314	5	63.934	66.161	L-7	7	Hantymansijskij nacional'nyj okrug, Nizhnyaya Ob'	Khanty-Mansi National District, Lower Ob
102	R-70519	4	56.531	32.861	S-17	7	Central'nyj lesnoj gosudarstvennyj zapovednik	Central Forest State Reserve
103	R-70517	2	56.531	32.861	S-17	7	Central'nyj lesnoj gosudarstvennyj zapovednik	Central Forest State Reserve
104	21358	7	49.132	46.819	L-2	3	EHl'ton	Elton
105	R-15996	6	52.297	56.997	S-29	7	YUzhnyj Ural	Southern Urals
106	R-35772	3	52.297	56.997	S-29	7	YUzhnyj Ural, Aleksandrovka	South Ural, Aleksandrovka
107	R-109146	4	52.001	57.034	S-29	7	YUzhnyj Ural, verhov'ya reki Kasmarka	South Ural, headwaters of the Kasmark
108	R-15994	4	51.551	56.915	S-29	7	YUzhnyj Ural, Ziyanchurinskij rajon	South Ural, Zianchurinsky District
109	R-15993	6	51.551	56.915	S-29	7	YUzhnyj Ural, Ziyanchurinskij rajon	South Ural, Zianchurinsky District
110	R-35773	7	55.166	60.118	L-6	7	YUzhnyj Ural, Turgoyak	South Ural, Turgoyak
111	R-48062	4	57.607	39.858	S-22	7	YAroslavskaya oblast'	Yaroslavskaya oblast
112	R-60271	4	57.607	39.858	S-22	7	YAroslavskaya oblast'	Yaroslavskaya oblast
113	R-60256	6	57.607	39.858	S-22	7	YAroslavskaya oblast'	Yaroslavskaya oblast
114	R-60206	7	56.769	38.761	S-22	7	YAroslavskaya oblast', Pleshcheevo	Yaroslavl region, Plescheevo
115	1462.188	4	54.533	28.531	S-9	6	Belorussiya, Minskaya oblast'ast', Kletnoe	Belarus, Minsk region, Kletnoe
116	1455/639	6	53.834	30.233	S-13	6	Belorussiya, Mogilyovsk, Selec	Belarus, Mogilevsk, Selets
117	1452/1775	6	53.442	31.005	S-13	6	Belorussiya, Propojsk, CHizhenka	Belarus, Propoisk, Chizhenka
118	1454\815	6	55.355	29.299	S-9	6	Belorussiya, Vitebskaya oblast'ast' Obol'	Belarus, Vitebsk region Obol
119	1456\532	7	53.834	30.233	S-13	6	Belorussiya, Mogilyovsk, YUr'evo	Belarus, Mogilevsk, Yuryevo
120	N/A	4	53.834	30.233	S-13	6	Belorussiya, Mogilyovsk, YUr'evo	Belarus, Mogilevsk, Yuryevo

121	1458\601	6	53.834	30.233	S-13	6	Belorussiya, Mogilyovsk,	Belarus, Mogilevsk,
122	1463\35	4	53.417	27.918	S-9	6	Belorussiya, Minskaya oblast'ast', Igumenskij rajon, Gorelec	Belarus, Minsk region, Igumen district, Gorelets
123	1457\458	7	53.701	28.249	S-9	6	Belorussiya, Minskaya oblast'ast', Igumenskij rajon	Belarus, Minsk region, Igumen district
124	1472\731	4	54.889	28.698	S-9	6	Belorussiya, Lepel'skij rajon	Belarus, Lepel district
125	1385	5	54.502	30.405	S-13	6	Vitebskaya oblast', Orshanskij rajon	Vitebsk region, Orsha district
126	1391	2	53.901	27.557	S-9	6	Minskaya oblast'ast', Belopol'sk rajon	Minsk region, Belopolsk district
127	N/A	7	50.351	46.416	L-2	9	Volgogradskaya oblast'ast', Valuevka	Volgograd region, Valuevka
128	1380	5	54.502	30.405	S-13	6	Vitebskaya oblast', Orshanskij rajon	Vitebsk region, Orsha district
129	N/A	5	54.502	30.405	S-13	6	Vitebskaya oblast', Orshanskij rajon	Vitebsk region, Orsha district
130	A5748	4	56.163	91.389	L-8	2	Krasnoyarskij kraj, Kozul'skij rajon	Krasnoyarsk Territory, Kozulsky District
131	A5745	6	54.697	40.849	S-23	2	Okskij zapovednikk	Oksky Reserve
132	A5746	5	54.697	40.849	S-23	2	Okskij zapovednikk	Oksky Reserve
133	A5747	3	54.697	40.849	S-23	2	Okskij zapovednikk	Oksky Reserve
134	N/A	4	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
135	N/A	5	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
136	N/A	4	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
137	N/A	5	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
138	N/A	2	62.917	34.455	L-4	9	Kareliya, Medvezh'ya gora	Karelia, Bear Mountain
139	N/A	6	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
140	N/A	5	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
141	N/A	3	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
142	N/A	4	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
143	N/A	5	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
144	N/A	2	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
145	N/A	4	55.162	20.837	S-2	9	Kurshskaya kosa	Curonian Spit
146	N/A	4	59.717	29.464	S-10	9	Leningradskaya oblast'ast', Novaya burya	Leningrad region, New Storm
147	N/A	3	59.934	30.319	S-14	9	Sankt-Peterburg	St. Petersburg
148	N/A	3	59.934	30.319	S-14	9	Sankt-Peterburg	St. Petersburg
149	N/A	4	59.717	29.464	S-10	9	Leningradskaya oblast'ast', Novaya burya	Leningrad region, New Storm
150	N/A	4	59.717	29.464	S-10	9	Leningradskaya oblast'ast', Novaya burya	Leningrad region, New Storm
151	N/A	2	59.717	29.464	S-10	9	Leningradskaya oblast'ast', Novaya burya	Leningrad region, New Storm
152	N/A	4	59.717	29.464	S-10	9	Leningradskaya oblast'ast', Novaya burya	Leningrad region, New Storm
153	N/A	5	59.934	30.319	S-14	9	Sankt-Peterburg	St. Petersburg
154	N/A	4	57.667	41.031	S-24	9	Kostromskaya oblast', YUr'eveckij rajon	Kostroma region, Yuryevets district
155	N/A	4	57.452	42.125	S-24	9	Ivanovskaya oblast'ast', Kineshnyj rajon	Ivanovo region, Kineshny district
156	N/A	4	67.591	32.833	L-3	9	Kol'skij poluostrov, ozero Imandra	Kola Peninsula, Imandra Lake
157	N/A	3	61.686	33.614	L-4	9	Kareliya, Pryazhinskij rajon	Karelia, Pryazha district
158	N/A	4	59.934	30.319	S-14	9	Sankt-Peterburg	St. Petersburg
159	N/A	2	61.686	33.614	L-4	9	Kareliya, Pryazhinskij rajon	Karelia, Pryazha district
160	N/A	2	61.686	33.614	L-4	9	Kareliya, Pryazhinskij rajon	Karelia, Pryazha district
161	N/A	5	55.752	37.614	S-22	9	Moskva	Moscow
162	N/A	4	55.752	37.614	S-22	9	Moskva	Moscow

163	N/A	4	57.819	58.843	L-6	9	Permskaya oblast'ast', reka Serebryanka	Perm Region, Serebryanka River
164	N/A	4	59.151	30.833	S-14	9	Leningradskaya oblast'ast', Dubovik	Leningrad region, Dubovik
165	N/A	5	57.452	42.125	S-24	9	Ivanovskaya oblast'ast', Kineshnyj rajon	Ivanovo region, Kineshny district
166	N/A	6	54.933	41.401	S-23	9	Ryazanskaya oblast'ast', Kasimovskij rajon	Ryazan region, Kasimov district
167	N/A	3	59.756	31.072	S-14	9	Leningradskaya oblast'ast', Mihajlovskij rajon	Leningrad region, Mikhailovsky district
168	N/A	6	58.017	30.283	S-14	9	Novgorodskaya, oblast', Velesh	Novgorod region, Veles
169	N/A	2	67.976	39.831	L-3	9	Murmanskaya oblast', Iokanga	Murmansk region, Iokanga
170	A5743	5	56.317	44.001	S-25	2	Nizhnij Novgorod	Nizhny Novgorod
171	A5741	3	56.317	44.001	S-25	2	Nizhnij Novgorod	Nizhny Novgorod
172	A5742	6	56.317	44.001	S-25	2	Nizhnij Novgorod	Nizhny Novgorod
173	N/A	5	56.317	44.001	S-25	9	Nizhnij Novgorod	Nizhny Novgorod
174	N/A	3	56.317	44.001	S-25	9	Nizhnij Novgorod	Nizhny Novgorod
175	N/A	6	57.997	31.361	S-14	9	Novgorskaya oblast', Starorussk rajon	Novgorod region, Starorussky district
176	N/A	7	57.819	58.843	L-6	9	Permskaya oblast'ast', reka Serebryanka	Perm Region, Serebryanka River
177	N/A	6	56.682	34.715	S-17	9	Tverskaya oblast', Bernovo	Tver region, Bernovo
178	N/A	6	57.436	56.942	L-6	9	permsk. oblast'ast' kungur	Perm. area kungur
179	N/A	7	51.782	55.107	S-29	9	Orenburg	Orenburg
180	N/A	6	54.975	73.382	N/A	9	Omsk	Omsk
181	N/A	7	58.187	68.243	L-7	9	Tobol'sk	Tobolsk
182	N/A	7	55.051	59.922	L-6	9	YUzhnyj ural, Syrostan	South Ural, Syrostan
183	N/A	5	56.508	84.973	L-8	9	Tomsk	Tomsk
184	N/A	5	53.651	52.448	S-27	9	Orenburgskaya oblast', Buguruslan	Orenburg region, Buguruslan
185	N/A	6	51.782	55.107	S-29	9	Orenburg	Orenburg
186	N/A	6	63.933	65.042	L-7	9	Beryozov (Komi)	Berezov (Komi)
187	N/A	6	58.283	31.315	S-14	9	Il'men'	Ilmen
188	N/A	6	56.508	84.973	L-8	9	Tomsk	Tomsk
189	N/A	7	53.651	52.448	S-27	9	Orenburgskaya oblast', Buguruslan	Orenburg region, Buguruslan
190	N/A	5	57.167	65.501	S-30	9	Tyumen'	Tyumen
191	N/A	5	53.651	52.448	S-27	9	Orenburgskaya oblast', Buguruslan	Orenburg region, Buguruslan
192	N/A	4	53.651	52.448	S-27	9	Orenburgskaya oblast', Buguruslan	Orenburg region, Buguruslan
193	N/A	4	53.651	52.448	S-27	9	Orenburgskaya oblast', Buguruslan	Orenburg region, Buguruslan
194	N/A	3	56.025	93.061	L-8	9	Krasnoyarsk	Krasnoyarsk
195	N/A	3	57.167	65.501	S-30	9	Tyumenskaya, Oblast'ast'	Tyumen region
196	N/A	4	58.187	68.243	L-7	9	Tobol'sk	Tobolsk
197	N/A	4	58.187	68.243	L-7	9	Tobol'sk	Tobolsk
198	N/A	4	58.283	31.315	S-14	9	Il'men'	Ilmen
199	N/A	4	58.283	31.315	S-14	9	Il'men'	Ilmen
200	N/A	3	56.183	51.332	S-28	10	Kirovskaya oblast'ast', Ust'-Lyusa	Kirov region, Ust-Luce
201	N/A	5	59.848	48.284	L-5	10	Kirovskaya oblast'ast', Oparinskij rajon	Kirov region, Oparinsky district
202	N/A	6	56.366	50.998	S-28	10	Kirovskaya oblast', Karakul'naya pristan'	Kirov region, Karakulnaya pier
203	N/A	2	56.366	50.998	S-28	10	Kirovskaya oblast', Karakul'naya pristan'	Kirov region, Karakulnaya pier
204	N/A	3	58.832	47.884	L-5	10	Kirovskaya oblast'ast', Bobrovy	Kirov region, Bobrov
205	N/A	5	59.848	48.284	L-5	10	Kirovskaya oblast'ast', Oparinskij rajon	Kirov region, Oparinsky district
206	N/A	4	56.183	51.332	S-28	10	Kirovskaya oblast'ast', Ust'-Lyusa	Kirov region, Ust-Luce

207	N/A	3	59.848	48.284	L-5	10	Kirovskaya oblast'ast', Oparinskij rajon	Kirov region, Oparinsky district
208	N/A	5	56.183	51.332	S-28	10	Kirovskaya oblast'ast', Ust'-Lyusa	Kirov region, Ust-Luce
209	N/A	6	56.848	50.181	S-28	10	Kirovskaya oblast'ast', Lazorevo	Kirov region, Azorevo
210	N/A	7	56.183	51.332	S-28	10	Kirovskaya oblast'ast', Ust'-Lyusa	Kirov region, Ust-Luce
211	N/A	3	59.332	52.245	L-5	10	Kirovskaya oblast'ast', Ierhnekamskij rajon	Kirov region, Ierhnekamsk district
212	N/A	2	56.366	50.998	S-28	10	Kirovskaya oblast', Karakul'naya pristan'	Kirov region, Karakulnaya pier
213	N/A	3	56.366	50.998	S-28	10	Kirovskaya oblast', Karakul'naya pristan'	Kirov region, Karakulnaya pier
214	N/A	4	57.491	48.582	S-28	10	Kirovskaya oblast'ast', Pizhanskij rajon	Kirov region, Pizhansky district
215	N/A	2	56.183	51.332	S-28	10	Kirovskaya oblast'ast', Ust'-Lyusa	Kirov region, Ust-Luce
216	N/A	4	56.183	51.332	S-28	10	Kirovskaya oblast'ast', Ust'-Lyusa	Kirov region, Ust-Luce
217	N/A	6	55.002	23.838	S-4	11	Kauno, Litva	Kauno, Litva
218	N/A	4	54.928	23.699	S-4	11	Kacergine, Litva	Kacergine, Litva
219	N/A	4	54.966	24.167	S-4	11	Didysis raistas, Litva	Didysis raistas, Litva
220	N/A	4	55.002	23.838	S-4	11	Kauno, Litva	Kauno, Litva
221	N/A	4	54.219	24.564	S-4	11	Varena, Litva	Varena, Litva
222	N/A	4	54.219	24.564	S-4	11	Varena, Litva	Varena, Litva
223	N/A	4	56.051	21.813	S-2	11	Plunges, Platelis	Plunges, Platelis
224	N/A	3	55.702	26.069	S-6	11	Zarasu, Litva	Zarasu, Litva
225	N/A	4	55.702	26.069	S-6	11	Zarasu, Litva	Zarasu, Litva
226	N/A	4	55.702	26.069	S-6	11	Zarasu, Litva	Zarasu, Litva
227	N/A	3	55.002	23.838	S-4	11	Kauno, Litva	Kauno, Litva
228	N/A	7	59.354	27.058	S-7	12	Pussi, Estonia	Pussi, Estonia
229	N/A	3	59.354	27.058	S-7	12	Pussi, Estonia	Pussi, Estonia
230	N/A	4	58.333	26.665	S-7	12	Lemmatsi, Estonia	Lemmatsi, Estonia
231	N/A	4	58.271	26.532	S-7	12	Noo, Estonia	Noo, Estonia
232	N/A	5	58.419	22.551	S-7	12	Saaremaa, Estonia	Saaremaa, Estonia
233	N/A	4	59.498	26.537	S-7	12	Kunda, Estonia	Kunda, Estonia
234	N/A	3	59.246	24.711	S-7	12	Todva, Estonia	Todva, Estonia
235	N/A	3	58.425	24.733	S-7	12	Tori-paikuse, Estonia	Tori-paikuse, Estonia
236	N/A	4	59.166	27.651	S-10	12	Puhatu, Estonia	Puhatu, Estonia
237	N/A	5	58.073	24.726	S-7	12	Parnu	Parnu
238	N/A	4	58.373	26.717	S-7	12	Tartumaa	Tartumaa
239	R-21348	7	51.285	13.848	N/A	7	Bohra Sa	Bohra sa
240	R-107271	3	48.948	15.042	N/A	7	Avstriya, Litsehau	Austria, Litsehau
241	R-76336	2	52.741	23.969	S-4	7	Belovezhskaya Pushcha	Bialowieza Forest
242	R-76337	4	52.741	23.969	S-4	7	Belovezhskaya Pushcha	Bialowieza Forest
243	R-11729	5	51.242	6.792	N/A	7	Vestfaliya	Westphalia
244	8758/12	3	48.955	28.743	S-11	8	Vinnickaya oblast'	Vinnytsia region
245	20746/72	6	51.767	25.515	S-5	8	Volynskaya oblast', Lyubeshovsk. rajon	Volyn region, Lyubeshovsk. area
246	17134/61	7	51.226	24.038	S-3	8	Volynskaya oblast', Lyuboml'sk. rajon	Volyn region, Lyubomlsk. area
247	13950	6	51.499	23.951	S-3	3	Volynskaya oblast', okr. SHacka	Volyn region, env. Shatsk
248	13949	7	51.499	23.951	S-3	3	Volynskaya oblast', okr. SHacka	Volyn region, env. Shatsk
249	13951	5	51.499	23.951	S-3	3	Volynskaya oblast', okr. SHacka	Volyn region, env. Shatsk
250	26215/34	5	51.671	24.529	S-3	8	Volynskaya oblast', Ratnovsk. rajon	Volyn region, Ratnovsk. area

251	27133/41	5	47.661	33.692	S-15	8	Dnepropetrovskaya oblast', Apostolovskij rajon	Dnipropetrovsk region, Apostolovsky district
252	27507/80	5	47.661	33.692	S-15	8	Dnepropetrovskaya oblast', Apostolovskij rajon	Dnipropetrovsk region, Apostolovsky district
253	17011/58	6	47.598	37.495	S-18	8	Doneckaya oblast', Volnovahskij rajon	Donetsk region, Volnovakha district
254	17012/59	5	47.598	37.495	S-18	8	Doneckaya oblast', Volnovahskij rajon	Donetsk region, Volnovakha district
255	14630/50	7	50.253	28.662	S-8	8	ZHitomir	Zhytomyr
256	26481/79	4	50.101	29.634	S-8	8	ZHitomirskaya oblast', Popel'nyanskij rajon	Zhytomyr region, Popelnyan district
257	26480/78	3	50.101	29.634	S-8	8	ZHitomirskaya oblast', Popel'nyanskij rajon	Zhytomyr region, Popelnyan district
258	21252/75	4	50.461	28.674	S-8	8	ZHitomirskaya oblast', CHernyahovskij rajon	Zhytomyr region, Chernyakhovsky district
259	16493/57	7	48.212	22.636	N/A	8	Zakarpatskaya oblast', Beregovskij rajon	Transcarpathian region, Beregovo district
260	16492/56	7	48.212	22.636	N/A	8	Zakarpatskaya oblast', Beregovskij rajon	Transcarpathian region, Beregovo district
261	16490/54	7	48.212	22.636	N/A	8	Zakarpatskaya oblast', Beregovskij rajon	Transcarpathian region, Beregovo district
262	35463/99	4	46.692	35.153	L-1	8	Zaporozhskaya oblast', Akimovskij rajon	Zaporozhye region, Akimov district
263	19884/68	5	46.722	35.628	L-1	8	Zaporozhskaya oblast', Priazovskij rajon	Zaporizhia region, Priazovsky district
264	7551	4	45.961	29.483	L-1	4	Izmail'skaya oblast'ast'	Izmail region
265	7546	5	50.436	30.521	S-12	4	Kiev	Kiev
266	8759/13	3	50.436	30.521	S-12	8	Kiev	Kiev
267	8753/7	6	50.436	30.521	S-12	8	Kiev	Kiev
268	8754/8	6	50.436	30.521	S-12	8	Kiev	Kiev
269	8764/18	4	50.436	30.521	S-12	8	Kiev	Kiev
270	8763/17	5	50.436	30.521	S-12	8	Kiev	Kiev
271	8757/11	5	50.436	30.521	S-12	8	Kiev	Kiev
272	41195/105	5	50.226	30.904	S-12	8	Kievskaya oblast', Borispol'skij rajon, Voronkov	Kiev region, Boryspil district, Voronkov
273	20659/98	4	51.367	29.448	S-8	8	Kievskaya oblast', Polesskij rajon, Vil'cha	Kiev region, Polessky district, Vilcha
274	20662/70	4	51.367	29.448	S-8	8	Kievskaya oblast', Polesskij rajon, Vil'cha	Kiev region, Polessky district, Vilcha
275	20660/86	5	51.367	29.448	S-8	8	Kievskaya oblast', Polesskij rajon, Vil'cha	Kiev region, Polessky district, Vilcha
276	8784/38	6	51.367	29.448	S-8	8	Kievskaya oblast', Polesskij rajon, Vil'cha	Kiev region, Polessky district, Vilcha
277	8778/32	7	53.225	50.173	S-27	8	Kujbyshevskaya oblast'	Kuybyshev region
278	R-60255	7	52.121	35.095	S-19	7	Kurskaya oblast', Dmitriev-L'govskij	Kursk region, Dmitriev-Lgovsky
279	R-60257	6	52.121	35.095	S-19	7	Kurskaya oblast', Dmitriev-L'govskij	Kursk region, Dmitriev-Lgovsky
280	R-44094	6	52.121	35.095	S-19	7	Kurskaya oblast', Dmitriev-L'govskij	Kursk region, Dmitriev-Lgovsky
281	R-60254	2	52.121	35.095	S-19	7	Kurskaya oblast', Dmitriev-L'govskij	Kursk region, Dmitriev-Lgovsky
282	R-60253	3	52.121	35.095	S-19	7	Kurskaya oblast', Dmitriev-L'govskij	Kursk region, Dmitriev-Lgovsky
283	R-44098	5	52.121	35.095	S-19	7	Kurskaya oblast', Dmitriev-L'govskij	Kursk region, Dmitriev-Lgovsky
284	R-44097	3	52.121	35.095	S-19	7	Kurskaya oblast', Dmitriev-L'govskij	Kursk region, Dmitriev-Lgovsky
285	R-60251	7	52.121	35.095	S-19	7	Kurskaya oblast', Dmitriev-L'govskij	Kursk region, Dmitriev-Lgovsky
286	7547	5	50.436	30.521	S-12	4	okrestnosti Kieva, ZHukov ostrov	outskirts of Kiev, Zhukov island
287	7548	4	50.436	30.521	S-12	4	okrestnosti Kieva, Irnen'	surroundings of Kiev, Irnen
288	7555	5	50.436	30.521	S-12	4	okrestnosti Kieva, Pushcha-Vodica	outskirts of Kiev, Puscha-Voditsa
289	13138	4	49.592	34.549	S-15	3	Poltava	Poltava
290	13132	7	49.592	34.549	S-15	3	Poltava	Poltava
291	13131	4	49.592	34.549	S-15	3	Poltava	Poltava

292	13130	6	49.592	34.549	S-15	3	Poltava	Poltava
293	13129	5	49.592	34.549	S-15	3	Poltava	Poltava
294	13128	6	49.592	34.549	S-15	3	Poltava	Poltava
295	13126	4	49.592	34.549	S-15	3	Poltava	Poltava
296	13135	4	49.867	34.727	S-15	3	Poltavskij uezd, Get'manshchina	Poltava County, Hetman
297	13137	4	48.945	34.108	S-15	3	Poltavskij uezd, Kovan'chino, r. Vorskla	Poltava County, Kovankino, r. Vorskla
298	13139	7	48.945	34.108	S-15	3	Poltavskij uezd, Kovan'chino, r. Vorskla	Poltava County, Kovankino, r. Vorskla
299	13143	6	48.945	34.108	S-15	3	Poltavskij uezd, Kovan'chino, r. Vorskla	Poltava County, Kovankino, r. Vorskla
300	13141	4	49.751	35.196	S-18	3	Poltavskij uezd, reka Kolomak	Poltava County, Kolomak River
301	13142	5	49.759	33.89	S-15	3	Poltavskij uezd, reka CHornen'ka	Poltava County, Chornya River
302	17133/60	4	51.701	25.765	S-5	8	Rovenskaya oblast', Zarechnenskij rajon, Ostrovsk	Rivne region, Zarechnensky district, Ostrovsk
303	8783/37	7	50.883	26.451	S-5	8	Rovenskaya Oblast', Kostopol'skij rajon	Rivne Region, Kostopil Region
304	8775/29	7	50.883	26.451	S-5	8	Rovenskaya Oblast', Kostopol'skij rajon	Rivne Region, Kostopil Region
305	21339	4	52.301	33.798	S-16	3	Sumskaya oblast', Seredinogubskij rajon, Staraya guba	Sumy region, Seredinogubsky district, Old Bay
306	21354	5	53.152	38.131	S-21	3	Tul'skaya oblast', Efremovskij rajon	Tula region, Efremovsky district
307	R-75278	3	53.924	37.691	S-21	7	Tul'skaya oblast', Novosil'skij rajon	Tula region, Novosilsky district
308	R-116306	3	54.351	38.263	S-21	7	Tul'skaya oblast', Venevskij rajon	Tula region, Venevsky district
309	R-75279	7	53.924	37.691	S-21	7	Tul'skaya oblast'ast', Novosil'skij rajon	Tula region, Novosilsky district
310	R-75276	6	53.924	37.691	S-21	7	Tul'skaya oblast'ast', Novosil'skij rajon	Tula region, Novosilsky district
311	R-11753	5	54.192	46.974	S-26	7	Ul'yanovskaya oblast', Karsunskij rajon	Ulyanovsk region, Karsunsky district
312	R-11755	2	54.192	46.974	S-26	7	Ul'yanovskaya oblast', Karsunskij rajon	Ulyanovsk region, Karsunsky district
313	R-11763	3	54.192	46.974	S-26	7	Ul'yanovskaya oblast', Karsunskij rajon	Ulyanovsk region, Karsunsky district
314	R-11762	5	53.789	47.511	S-26	7	Ul'yanovskaya oblast', Pronzino	Ulyanovsk region, Pronzino
315	R-11756	6	54.192	46.974	S-26	7	Ul'yanovskaya oblast', Karsunskij rajon	Ulyanovsk region, Karsunsky district
316	R-11750	3	54.192	46.974	S-26	7	Ul'yanovskaya oblast', Karsunskij rajon	Ulyanovsk region, Karsunsky district
317	R-11759	6	54.192	46.974	S-26	7	Ul'yanovskaya oblast', Karsunskij rajon	Ulyanovsk region, Karsunsky district
318	R-11760	6	54.192	46.974	S-26	7	Ul'yanovskaya oblast', Karsunskij rajon	Ulyanovsk region, Karsunsky district
319	21348	6	49.992	36.206	S-18	3	Har'kov, Lozoven'ki	Kharkov, Lozovenki
320	21350	7	49.992	36.206	S-18	3	Har'kov, Pomerki	Kharkov, Pomerki
321	13145	6	49.638	36.636	S-18	3	Har'kovskaya oblast'	Kharkov region
322	13146	4	49.638	36.636	S-18	3	Har'kovskaya oblast'ast'	Kharkiv region
323	21352	5	49.702	36.352	S-18	3	Har'kovskaya oblast', Zmievskij rajon, Severnyj Donec	Kharkiv region, Zmievsky district, Northern Donets
324	21351	6	49.702	36.352	S-18	3	Har'kovskaya oblast', Zmievskij rajon, Severnyj Donec	Kharkiv region, Zmievsky district, Northern Donets
325	21349	4	49.992	36.206	S-18	3	Har'kov, Pomerki	Kharkov, Pomerki
326	19395/66	3	46.511	33.978	L-1	8	Hersonskaya oblast', CHaplinskij rajon, Askaniya-nova	Kherson region, Chaplinsky district, Askania-Nova
327	8770/24	3	46.371	33.541	L-1	8	Hersonskaya oblast', CHaplinskij rajon, CHaplinka	Kherson region, Chaplinsky district, Chaplinka
328	19394/65	3	46.511	33.978	L-1	8	Hersonskaya oblast', CHaplinskij rajon, Askaniya-nova	Kherson region, Chaplinsky district, Askania-Nova

329	37780/97	5	51.135	30.964	S-12	8	CHernigovskaya oblast', Kozeleckij rajon, Samojlovka	Chernihiv region, Kozelets district, Samoilovka
330	8760/14	4	51.042	31.888	S-12	8	CHernigovskaya oblast', Nezhinskij rajon, Nezhin	Chernihiv region, Nezhinsky district, Nezhin
331	8749/3	2	51.812	31.091	S-12	8	CHernigovskaya oblast', Repkinskij rajon	Chernihiv region, Repkinsky district
332	8765/19	5	51.812	31.091	S-12	8	CHernigovskaya oblast', Repkinskij rajon	Chernihiv region, Repkinsky district
333	8756/10	5	51.812	31.091	S-12	8	CHernigovskaya oblast', Repkinskij rajon	Chernihiv region, Repkinsky district
334	8752/6	3	51.812	31.091	S-12	8	CHernigovskaya oblast', Repkinskij rajon	Chernihiv region, Repkinsky district
335	8755/9	3	51.812	31.091	S-12	8	CHernigovskaya oblast', Repkinskij rajon	Chernihiv region, Repkinsky district
336	8762/16	4	51.812	31.091	S-12	8	CHernigovskaya oblast', Repkinskij rajon	Chernihiv region, Repkinsky district
337	8748/2	5	51.812	31.091	S-12	8	CHernigovskaya oblast', Repkinskij rajon	Chernihiv region, Repkinsky district
338	8751/5	5	51.918	30.965	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Vir	Chernihiv region, Repkinsky district, Vir
339	8781/35	7	51.918	30.965	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Vir	Chernihiv region, Repkinsky district, Vir
340	8772/26	7	51.967	30.931	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Vir	Chernihiv region, Repkinsky district, Vir
341	8773/27	6	51.967	30.931	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Vir	Chernihiv region, Repkinsky district, Vir
342	8747/1	4	51.967	30.931	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Vir	Chernihiv region, Repkinsky district, Vir
343	8792/46	5	51.967	30.931	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Vir	Chernihiv region, Repkinsky district, Vir
344	8767/21	6	51.967	30.931	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Klubovka	Chernihiv region, Repkinsky district, Klubovka
345	8766/20	4	51.951	30.949	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Brekhunovka	Chernihiv region, Repkinsky district, Brehunovka
346	8750/4	5	51.918	30.965	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Vir	Chernihiv region, Repkinsky district, Vir
347	8793/47	5	51.918	30.965	S-12	8	CHernigovskaya oblast', Repkinskij rajon, Vir	Chernihiv region, Repkinsky district, Vir
348	21171/74	4	51.903	31.857	S-12	8	CHernigovskaya oblast', SHCHorskij rajon, Borovichi	Chernihiv region, Shchorsky district, Borovichi
349	R-60265	7	54.911	32.875	S-16	7	Smolensk. oblast'	Smolensk. region
350	R-60266	7	54.911	32.875	S-16	7	Smolensk. oblast'	Smolensk. region
351	R-60264	7	54.911	32.875	S-16	7	Smolensk. oblast'	Smolensk. region
352	R-60267	4	54.911	32.875	S-16	7	Smolensk. oblast'	Smolensk. region
353	R-60268	6	55.215	34.301	S-17	7	Smolenskaya oblast', Vyazemskij rajon	Smolensk region, Vyazemsky district
354	21344	3	55.066	32.686	S-17	3	Smolenskaya oblast', YArcevskij uezd	Smolensk region, Yartsevo district
355	N/A	4	52.715	25.349	S-4	6	Belorussiya, Ivacevichsk. rajon	Belarus, Ivatsevichsky. area
356	N/A	5	52.051	27.932	S-8	6	Belorussiya, Gomel'sk. ZHitkovichsk. rajon. Hvoensk	Belarus, Gomel. Zhitkovichsk. area. Hvoensk
357	1459/109	6	53.139	29.227	S-9	6	Belorussiya, Bobrujsk	Belarus, Bobruisk
358	1474\1645	4	54.783	33.413	S-16	6	Smolenskaya oblast', Dorogobuzhskij rajon, Aleksino	Smolensk region, Dorogobuzh district, Aleksino
359	1460\2990	3	54.783	33.413	S-16	6	Smolenskaya oblast', Dorogobuzhskij rajon, Aleksino	Smolensk region, Dorogobuzh district, Aleksino
360	N/A	4	51.782	23.639	S-3	6	Brestskaya oblast'ast', Leninskij rajon, Dubeckaya	Brest region, Leninsky district, Dubetskaya
361	N/A	3	51.832	26.999	S-5	6	Brestskaya oblast', Stolinskij rajon, Koshara-ol'm	Brest region, Stolin district, Koshara-olm
362	N/A	4	52.741	23.969	S-4	6	Belovezhskaya Pushcha	Bialowieza Forest

363	N/A	7	51.782	23.639	S-3	6	Brestskaya oblast'ast', Leninskij rajon, Dubeckaya	Brest region, Leninsky district, Dubetskaya
364	1388	6	52.443	30.978	S-12	6	Gomel'	Gomel
365	1392	4	52.065	28.383	S-8	6	Mozyrskij rajon, Mordvin	Mozyr District, Mordvin
366	1397	7	51.832	26.999	S-5	6	Brestskaya oblast', Stolinskij rajon, Koshara-ol'm	Brest region, Stolin district, Koshara-olm
367	1387	6	51.832	26.999	S-5	6	Gomel'skaya oblast'	Gomel region
368	1378	5	52.443	30.978	S-12	6	Gomel'	Gomel
369	1394	7	52.443	30.978	S-12	6	Gomel'	Gomel
370	1384	4	52.443	30.978	S-12	6	Gomel'	Gomel
371	1383	5	52.443	30.978	S-12	6	Gomel'	Gomel
372	1386	5	52.443	30.978	S-12	6	Gomel'	Gomel
373	1377	5	52.443	30.978	S-12	6	Gomel'	Gomel
374	2306	4	52.033	27.848	S-8	6	Gomel'skaya oblast', ZHitkovich rajon, Ozerany	Gomel region, Zhitkovich district, Ozeryan
375	N/A	7	49.837	24.034	S-3	5	L'vov	Lviv
376	N/A	7	50.101	25.732	S-5	5	Ternopol', Kremenec	Ternopil, Kremenets
377	N/A	7	52.626	20.385	S-1	9	Pol'sha, Plon'sk	Poland, Plonsk
378	N/A	6	50.597	27.607	S-8	9	ZHitomirskaya oblast', Novograd	Zhytomyr region, Novograd
379	N/A	5	50.436	30.521	S-12	9	Kiev	Kiev
380	N/A	6	52.626	20.385	S-1	9	Pol'sha, Plon'sk	Poland, Plonsk
381	N/A	4	49.267	30.932	S-11	9	CHerkasska oblast', Lysnyanskij rajon, Pochapicy	Cherkassk region, Lysnyansky district, Pochapitsy
382	N/A	7	49.267	30.932	S-11	9	CHerkasska oblast', Lysnyanskij rajon, Pochapicy	Cherkassk region, Lysnyansky district, Pochapitsy
383	N/A	5	52.231	20.996	S-1	9	Varshava	Warsaw
384	N/A	6	52.231	20.996	S-1	9	Varshava	Warsaw
385	N/A	5	49.267	30.932	S-11	9	CHerkasska oblast', Lysnyanskij rajon, Pochapicy	Cherkassk region, Lysnyansky district, Pochapitsy
386	N/A	7	52.626	20.385	S-1	9	Pol'sha, Plon'sk	Poland, Plonsk
387	N/A	5	49.267	30.932	S-11	9	CHerkasska oblast', Lysnyanskij rajon, Pochapicy	Cherkassk region, Lysnyansky district, Pochapitsy
388	N/A	4	49.267	30.932	S-11	9	CHerkasska oblast', Lysnyanskij rajon, Pochapicy	Cherkassk region, Lysnyansky district, Pochapitsy
389	N/A	7	46.694	31.236	L-1	9	Odesskaya oblast', Koblast'evo	Odessa region, Koblastievo
390	N/A	7	52.231	20.996	S-1	9	Varshava	Warsaw
391	N/A	7	52.231	20.996	S-1	9	Varshava	Warsaw
392	N/A	4	52.184	25.849	S-5	9	Pinsk, vyzhlovichi	Pinsk, Vyzhlovichi
393	N/A	4	52.231	20.996	S-1	9	Varshava	Warsaw
394	N/A	4	52.231	20.996	S-1	9	Varshava	Warsaw
395	N/A	5	52.231	20.996	S-1	9	Varshava	Warsaw
396	N/A	5	50.049	29.633	S-8	9	ZHitomirirskaya oblast', Popel'nyanskij rajon, Mohnachka	Zhytomyr region, Popelnyan district, Mokhnachka
397	N/A	4	52.231	20.996	S-1	9	Varshava	Warsaw

398	N/A	6	52.184	25.849	S-5	9	Pinsk, vyzhlovichi	Pinsk, Vyzhlovichi
399	N/A	4	52.231	20.996	S-1	9	Varshava	Warsaw
400	N/A	7	52.231	20.996	S-1	9	Varshava	Warsaw
401	N/A	6	50.279	36.943	S-19	9	Har'kovskaya oblast'ast', Volchanskij rajon	Kharkiv region, Volchansky district
402	N/A	4	49.267	30.932	S-11	9	CHerkasska oblast', Lysnyanskij rajon, Pochapicy	Cherkassk region, Lysnyansky district, Pochapitsy
403	N/A	5	49.267	30.932	S-11	9	CHerkasska oblast', Lysnyanskij rajon, Pochapicy	Cherkassk region, Lysnyansky district, Pochapitsy
404	N/A	6	49.267	30.932	S-11	9	CHerkasska oblast', Lysnyanskij rajon, Pochapicy	Cherkassk region, Lysnyansky district, Pochapitsy
405	N/A	6	52.231	20.996	S-1	9	Varshava	Warsaw
406	N/A	7	52.231	20.996	S-1	9	Varshava	Warsaw
407	N/A	5	50.346	22.236	S-1	9	Galiciya	Galicia
408	N/A	4	52.231	20.996	S-1	9	Varshava	Warsaw
409	N/A	7	50.148	26.182	S-5	9	Ternopol'sk oblast', Kremenskij rajon, Surazh	Ternopil region, Kremensky district, Surazh
410	N/A	3	54.911	32.875	S-16	9	Smolenskaya oblast'	Smolensk region
411	N/A	4	52.601	36.349	S-19	9	Orlovskaya oblast', Karachaevskij rajon	Oryol region, Karachay district
412	N/A	5	51.097	40.041	L-2	9	Voronezhskaya oblast'ast', Bobrovskij rajon	Voronezh region, Bobrovsky district
413	N/A	4	55.788	49.173	S-28	9	Kazan'	Kazan
414	N/A	5	53.934	39.101	S-21	9	Ryazanskaya oblast'ast', Mihajlovskij rajon, Nyuhovec	Ryazan region, Mikhailovsky district, Nyukhovets
415	N/A	4	53.924	37.691	S-21	9	Tul'skaya oblast'ast', Novosil'skij rajon.	Tula region, Novosilsky district.
416	N/A	4	53.152	38.131	S-21	9	Tul'skaya oblast', Efremovskij rajon	Tula region, Efremovsky district
417	N/A	6	51.097	40.041	L-2	9	Voronezhskaya oblast'ast', Bobrovskij rajon	Voronezh region, Bobrovsky district
418	N/A	6	53.934	38.801	S-21	9	Granica Tula-Ryazan'	Border Tula-Ryazan
419	N/A	7	53.934	38.801	S-21	9	Granica Tula-Ryazan'	Border Tula-Ryazan
420	N/A	7	51.097	40.041	L-2	9	Voronezhskaya oblast'ast', Bobrovskij rajon	Voronezh region, Bobrovsky district
421	R-3840	6	45.20	34.29	N/A	7	Krym	Crimea
422	R-6128	4	55.31	35.42	S-20	7	Moskovskaya oblast', Mozhajskij rajon	Moscow region, Mozhaisky district
423	R-11728	6	57.32	26.57	S-6	7	Liflyandiya, Marienburg, Volkskij uezd	Livonia, Marienburg, Volk County
424	R-11761	7	53.39	48.30	S-26	7	Ul'yanovskaya oblast', Gremyachij klyuch	Ulyanovsk region, Gremyachy key
425	R-11767	6	56.53	74.22	N/A	7	Tobol'skaya oblast', v 12 verstah ot goroda Tara	Tobolsk region, 12 versts from the city of Tara
426	R-15995	6	52.00	56.55	S-29	7	YUzhnyj Ural, Ziyangurinskij	South Ural, Zyangurinsky
427	R-24065	4	44.35	40.06	N/A	7	Majkop	Maykop
428	R-60210	7	55.41	38.13	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
429	R-60228	6	55.41	38.13	S-22	7	Moskovskaya oblast', Noginskij rajon	Moscow region, Noginsk district
430	R-60258	6	56.45	38.41	S-22	7	YAroslavskaya oblast', Ozero Pleshchevo	Yaroslavl region, Lake Pleschevo
431	R-75277	7	53.16	37.11	S-21	7	Tul'skayaoblast', Novosil'skij rajon	Tula region, Novosilsky district
432	R-102886	3	42.24	47.45	N/A	7	Dagestan, Izberbashskij rajon, selo Utamysh	Dagestan, Izberbash district, village Utamysh

Colour type	Drost's colour score value
Latitude.S-N	Latitude
Longitude.W-E	Longitude
Location (transliterated)	Place of bird detection indicated on tag (transliterated)
Location (translated)	Place of bird detection indicated on tag (machine translation)
Population ID	Population IDs formed by the bird skins; labled as L-1, L-2, etc. for large populations and S-1, S-2, etc. for small populations, respectively (please also see Fig. S4 and Table S2). N/A - skins of birds not included in any population.
Museum	Museum identifier:
	[2] Collection of the Department of Biogeography of the Faculty of Geography of the M. V. Lomonosov Moscow State University (Moscow)
	[3] State Museum of Nature of the Kharkiv National V.N. Karazin University (Kharkiv)
	[4] Zoological Museum of Kyiv National Taras Shevchenko University (Kiev)
	[5] Zoological Museum of Lviv National I. Frank University (Lviv)
	[6] Zoological Museum of the Belarusian State University (Minsk)
	[7] Zoological Museum of the M. V. Lomonosov Moscow State University (Moscow)
	[8] Zoological Museum of the National Academy of Sciences of Ukraine (Kiev)
	[9] Zoological Museum of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg)
	[10] Kirov City Zoological Museum (Kirov)
	[11] Kaunas Zoological T. Ivanauskas Museum (Kaunas)
	[12] Museum of Natural History of Tartu University (Tartu)