**EURING Eurasian-African Bird Migration Project**

**Report**

to the Convention of Migratory Species (CMS)

on

**Migratory Connectivity**

Provided by

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**Abstract**

**1.** Migratory connectivity is defined as the linkage among individuals between the periods and areas where they spend different phases of their annual life cycle. The strength of migratory connectivity thus represents the extent to which individuals mixed in different seasons. Within the framework of the CMS/EURING Eurasian-African Bird Migration Atlas, we investigated the patterns and strength of migratory connectivity in 137 bird species through the analysis of ring recoveries. First, we filtered ringing encounters collected over more than a century in the European-African migration system according to spatiotemporal and condition-specific criteria. Then, we quantified the strength of migratory connectivity between individuals and between arbitrarily pre-defined breeding and non-breeding regions.

**2.** The strength of migratory connectivity was highly variable across species, but most exhibited significant connectivity. Amongst them, connectivity was mainly due to clustering, suggesting that migration strategies also vary at the intraspecific level, with most species geographically splitting into distinct migratory populations. Resident species showed stronger migratory connectivity than partial migrants, which in turn showed stronger connectivity than full migrant species. Most likely, geographical and ecological differences between species contributed to explaining the strength of migratory connectivity more than phylogenetic relatedness.

**3.** Our work also provided useful methodological insights to advise future analyses. A sensitivity analysis showed that migratory connectivity between individuals can be estimated reliably on small samples (30 individuals) and considering different encounter conditions (i.e., alive recaptures or dead recoveries). Furthermore, migratory connectivity between individuals was generally consistent with that estimated between pre-defined regions, though the two metrics should be better suited for different contexts.

**4.** Our analysis showed that ringing data are an excellent tool to investigate migratory connectivity. In quantifying and describing the strength and patterns of migratory connectivity across European birds, we hope that our work will improve the understanding of avian migration and, from a more practical point of view, will assist in bird conservation and management at the population level.

**Introduction**

Migratory connectivity refers to the degree to which individuals stay together while moving to the geographical areas where they spend different phases of their annual life cycle (Webster et al.- 2002). Various definitions of migratory connectivity have been proposed in the scientific literature, depending upon whether connectivity is considered as a property of individuals, populations, areas, or periods of the annual cycle (Salomonsen 1955, Webster et al. 2002, Boulet and Norris 2006, Marra et al. 2006, Rundel et al. 2013, Veen 2013). The concept of migratory connectivity thus extends also to the degree of mixing among individuals during different stages of their annual life cycle (Boulet and Norris 2006, Rundel et al. 2013). This is particularly relevant because focusing not only on the geographical but also on the temporal component of migratory connectivity allows extending this concept to the species that do not perform proper migratory movements. This has a large practical relevance, as birds show uninterrupted graduation of migratory movements (from strictly sedentary to fully migratory) not only between different species but also between populations of the same species and even within the same population (Newton 2008). Thus, studies aiming at investigating the degree of migratory connectivity to a wide range of species or to species where geographical populations differ in their migration behaviour may be in the condition to apply this concept also to populations that do not migrate or show mixed migratory strategies (see e.g. Ambrosini et al. 2016).

In consideration of the aims shared by the CMS/EURING Migration Atlas, we performed migratory connectivity analyses on species breeding or resident within the Palearctic-African migration system. We thus extended the concept of migratory connectivity also to species, populations or individuals that do not perform proper migratory movements.

We performed two different analyses of migratory connectivity. The first one assessed the connectivity of individuals between their breeding and their non-breeding ranges (hereafter, "individual connectivity"). The second measured the connectivity between populations within pre-defined breeding and non-breeding regions (hereafter, "area connectivity"). We first applied robust data filtering to all species in the EURING databank and then selected for the analyses those species with a minimum amount of data (see the data filtering paragraph below for details). For individual connectivity (**Section 1**), we followed the method proposed by Ambrosini et al. (2009), while for the area connectivity (**Section 2**), we followed the method proposed by Cohen et al. (2018). Detailed results of both analyses are provided in the report of each species.

We then summarized the results of individual connectivity in a meta-analysis (**Section 3**)that allowed disclosing some ecological processes that drive the different strengths of migratory connectivity observed in the different species. Importantly, one of the aspects we investigated was the migratory behaviour that we defined based on the same dataset used for assessing migratory connectivity (see methods reported in Section 3). This procedure thus does not imply any arbitrary a priori classification of species into resident, partially migratory or fully migratory (see above), but simply reflects the behaviour of the same populations/individuals used for assessing the strength of migratory connectivity.

**Data filtering procedure**

First, we selected from the EURING Data Bank (EDB) those species having at least 500 records during winter (December-February). This results in a first set of 137 species. Datasets of ringing records included information on encounter conditions and data accuracy that allowed a robust data selection (e.g. Ambrosini et al. 2016). Indeed, we discarded records where:

***a.*** "use for atlas” was FALSE i.e. records that did not satisfy a preliminary check for data accuracy conducted by EURING.

***b.*** “condition” was 3, 4, 5 or 6 i.e. birds that were not found freshly dead or birds that were in poor condition or had an accident when ringed or alive and probably healthy but taken into captivity;

***c.*** “manipulated” was C, F, T, M or H i.e. birds that were kept for more than 13 h during ringing or birds that have been moved or held extensively during ringing or those hand-reared;

***d.*** “moved” was 2, 4 or 6 i.e. birds that were moved unintentionally by man or other agency, or intentionally by man, or moved by water e.g. found on the shoreline;

***e.*** “date accuracy” was 4, 5, 6, 7, 8 i.e. birds for which the dates of ringing and/or recovery were not recorded accurately to the nearest 1 week for both the ringing and the finding date;

***f.*** “coordinates accuracy” was 6, 7, 8 or 9 i.e. birds for which the place of ringing and/or recovery were not recorded accurately to the nearest 100 km for both the ringing and the finding place.

Then, we selected data by applying temporal masking. According to Cramp (1998), we identified species-specific periods corresponding to an “extended” breeding period (B), a “focal” breeding period (FB) and the non-breeding period (NB) (i.e. wintering). An exception was made for *Turdus merula*, for which we considered different periods than those reported by Cramp (1998), which were referred mainly to British populations, particularly for the start of the non-breeding period (Santos 1982, Olios 1995, Main 2002, Andreotti et al. 2010). All species-specific periods we used are reported in Table S1. Records in the FB period or the NB period were retained. In addition, we retained those records in the B period if individuals were caught at the nest (catching method = "N") or if they were aged as “pullus, unable to fledge” (age by scheme = 1). The rationale was that records in the focal breeding and non-breeding periods should correspond to individuals encountered during stationary periods, while individuals encountered at nest were at their breeding grounds. Thus records satisfying either condition should regard individuals at their breeding site.

Furthermore, we selected data by performing spatial masking. For each species, we used the latest, distribution maps provided by BirdLife International (2019 and. discarded records in the FB and B periods laying outside the species-specific breeding range or outside the range where a species is classified as “resident” (i.e. present all year round). We also discarded records in the NB period laying outside the species-specific non-breeding (“wintering”) range or outside the range where a species is classified as resident.

After the above steps, we retained only records of those individuals having at least one observation in both the breeding and the non-breeding periods. Whenever an individual had more than one observation during the breeding or non-breeding periods, we retained the earliest to minimise age bias in data selection.

Finally, we manually discarded some data that were outside the Palearctic-African migration system (e.g. 21 individuals of *Sterna hirundo* that were recovered either in Australia or in the South Atlantic Ocean during the non-breeding period).

All the steps were implemented in a script in R 3.6.2. Data filtering resulted in the removal of 58% - 99% records, depending on the species (mean ± standard error: 92.7 ± 0.7%; N=137), and produced species-specific datasets with numbers of individuals ranging from 20 to 36,506 (mean ± standard error: 2,708 ± 480; N=137).

**Section 1 – Migratory connectivity between individuals**

*1.1 Procedure for the analyses*

We assessed individual migratory connectivity following Ambrosini et al. (2009), using an R function specifically implemented for such purpose. The number of individuals of each of the 137 species in Table S1 was at least N = 20, which has been considered a sufficient sample size (Ambrosini et al. 2009). The analyses were performed as follows:

***a.*** Using individual geographical positions, we calculated two matrices of great-circle (i.e. orthodromic) distances. The first matrix included the distances among individuals in the breeding grounds and the second matrix included the distances among the corresponding individuals in the non-breeding grounds.

***b.*** We calculated the Mantel correlation coefficient (*rM*) between the two distance matrices, and we assessed the relevant 95% confidence interval through 999 bootstrap replicates. We also tested the significance of the Mantel correlation coefficient using a one-tailed permutation test (H0: *rM* = 0; H1: *rM* > 0; 999 permutations). We used a one-tailed test because negative values of the Mantel correlation coefficient are not plausible when referring to migratory connectivity (Ambrosini et al. 2009, Cohen et al. 2018).

***c.*** Whenever the significance of the Mantel test was *P* ≤ 0.1, we performed a k-means cluster analysis on the distance matrices obtained by combining the breeding and non-breeding distance matrices (see Ambrosini et al. 2009 for details) for each pre-defined number of clusters ranging from 2 to 9, and we calculated the relevant intensity of clustering using the overall average silhouette width (*oasw*; Rousseeuw 1987). We used a 0.1 threshold to explore also cases where the Mantel test was marginally non-significant. We then assessed the best number of clusters as that showing the maximum *oasw*. Whenever the maximum *oasw* was < 0.5, indicating a weak or null clustering structure, the analysis stopped, and migratory connectivity was considered to occur from pattern transference. In contrast, if the *oasw* was ≥ 0.5 (i.e., there was a substantial or strong clustering structure in the data), migratory connectivity was considered to be due to clustering. In this case, individuals were assigned to the corresponding cluster.

***d.*** Whenever each cluster identified in step *c* included N < 20 individuals, the analysis stopped. Otherwise, the procedure repeated steps *a*-*d* for each cluster identified in point *c*, to identify sub-clusters up to the fourth level of clustering.

Occasionally, all individuals in a cluster were reported in the same location in either the breeding or the non-breeding grounds (i.e. same latitude and longitude). In these cases, which occurred only in a few species and at the third or fourth levels of clustering, the analysis could not be run because the migratory connectivity is not defined when distances among individuals are always null (Ambrosini et al. 2009).

*1.2 Effect of sample size on migratory connectivity analysis*

We performed simulations by rarefying the overall sample of individuals, to assess whether our estimates of migratory connectivity were affected by sample size. In particular, we were mainly interested in evaluating the robustness of our results when the sample size was small, particularly when N < 100. One aim was to assess on a large set of species the minimum number of individuals above which the analysis can be considered robust. Indeed, the threshold of N = 20 suggested by Ambrosini et al. (2009) was based on simulations. Thus, we rarefied the sample of records of each species to nine decreasing levels, which were arbitrarily set for each group of species with a similar sample size (Table 1). We investigated the potential effects of decreasing sample size on the Mantel correlation coefficient (*rM*), the power of the Mantel permutation test (i.e., the relative frequency of analyses showing significant connectivity, if the analysis on the whole sample of that species was significant) and - whenever the connectivity was significantly positive - on the best number of clusters as well as on the strength of the clustering structure (i.e. on the *oasw* value).

We performed three different types of simulations. The first extracted a simple random sample of individuals from the overall dataset of each species. The second and the third types of simulations were performed with a stratified sampling of individuals. In both cases, the strata were represented by countries to account for the fact that the number of ring encounters for a species may largely vary geographically due to variation in the sampling effort. Indeed, in these cases, we used subsampling strategies where the sampling probability was inversely proportional to the number of observations in each country. Thus, stratified sampling assigned a greater weight of observations recorded in countries with a lower number of records, testing the validity of connectivity analysis in situations with spatially unbalanced sampling. Since the analyses necessitate two records of the same individuals, this procedure was repeated twice, by assigning probabilities based first on the number of records at each country during the breeding period, and second on the number of records at each country during the non-breeding period. In all cases the, sampling of individuals from the original dataset occurred without replacement. For each simulation type, at each level of sample size, we simulated 100 different datasets and performed the connectivity analyses. Simulations were implemented in a script in R 3.6.2.

Our simulations generally showed that the power of the Mantel test decreased under a power of 0.8 below 30 individuals, for *c*. 75% species considered. At the same sample size, for *c*. 75% species the strength of connectivity only differed by a negligible extent (*c*. ± 0.05) from that estimated using all data. Simulations thus showed that 30 individuals may allow a robust migratory connectivity analysis in most cases. We thus suggest using this value as a threshold for running migratory connectivity analyses using the Mantel test, instead of 20, as initially indicated (Ambrosini et al. 2009). Exceptions exist, however, so this point must be carefully investigated for each species (see species-specific reports). We note that this threshold is quite low, suggesting that the method is robust, and allows running the analyses on a quite large number of species.

**Table 1**. The nine, arbitrarily defined levels at which the original sample size was rarefied, for each group of species with similar sample size. For species with a sample size between 20 and 39 individuals (8 species), no simulation was performed.

|  |  |
| --- | --- |
| Original sample size (no. individuals) | Levels (no. individuals) at which sample size was rarefied |
| ≥ 1,000 | 750; 500; 250; 100; 80; 60; 40; 30; 20 |
| 500 - 999 | 250; 150; 100; 80; 60; 50; 40; 30; 20 |
| 100 - 499 | 95; 90; 80; 70; 60; 50; 40; 30; 20 |
| 50 - 99 | 45; 42; 40; 37; 35; 32; 30; 25; 20 |
| 30 - 49 | 29; 28; 27; 26; 25; 24; 23; 22; 20 |

*1.3 Effect of encounter type on migratory connectivity analysis*

Ringing data are affected by a large spatial heterogeneity in sampling effort, which is particularly strong when live recaptures are considered, while dead recoveries are generally less affected (Korner-Nievergelt et al. 2010). To check whether the inclusion of both live recaptures and dear recoveries may have affected our results, we re-ran the analyses separately for individuals whose second (most recent) encounter was either a dead recovery or a live recapture.

For each species with at least 20 individuals from both live recaptures and dead recoveries (N = 104 species), we ran separate connectivity analyses on the ‘live’ and ‘dead’ datasets with the same procedure as above and compared the two bootstrap distributions (N = 999 replicates) of the Mantel correlation coefficients. We then counted the number of records in the bootstrap distribution of *rM* coefficients from the dead dataset that were within the range of values of the bootstrap distribution of *rM* coefficients from the live dataset, and *vice versa*. By dividing the sum of these numbers for the overall number of bootstrap replicates (2,000 replicates, including the *rM* values from the original datasets) we obtained a measure of the “overlap” between the two bootstrap distributions that we used to assess the significance of the difference between *rM* values from dead recoveries and live recaptures of a species. These analyses were run on all records for a species and the results are shown in the report of each species. To summarize the results of these analyses on all species, we compared the Fisher z-transformed *rM* values obtained from the analyses of live recaptures and dead recoveries a linear mixed model including the encounter type as a predictor (reference level: live) and the species as a random grouping factor. The random part of the model also included a random intercept and slope for encounter type. This model parametrization allowed a paired comparison within species similar to that of a paired-sample design (Zuur et al. 2009). The model was also weighed for the inverse of the variance of the response variable (calculated from the bootstrapped 95% confidence interval of the z-transformed *rM* values) to account for the precision of the *rM* estimate.

Overall, in 62 species over 104, the difference between the *rM* coefficients from the dead and alive datasets was not significant. However an overall comparison between *rM* values achieved from live recaptures and dead recoveries across all species having both types of analyses showed that the encounter type did not influence the degree of connectivity (mean ± standard error, dead recoveries: *rM* = 0.79 ± 0.11, alive recaptures: *rM* = 0.90 ± 0.13; mixed model coefficients: intercept = 0.37 ± 0.11, *z* = 3.23, *P* = 0.001; slope = 0.06 ± 0.16, *z* = 0.43, *P* = 0.665; random intercept variance: <0.0001; random slope variance: <0.0001).

The non-significant difference in this analysis thus indicated that the two datasets give generally consistent results and can therefore be combined.

**Section 2 – Migratory connectivity between areas**

*2.1 Procedure for the analyses*

For each species, we assessed migratory connectivity between regions following Cohen et al. (2018), using the R function *calcMC* (package MigConnectivity; Hostetler and Hallworth 2018). Such analysis requires establishing *a priori* breeding and non-breeding regions. We therefore arbitrarily defined 15 regions encompassing the European and African continents (Europe: 8 regions, Africa: 7 regions). European regions corresponded to those used in the CMS/EURING Migration Atlas. We assigned each encounter to the corresponding region. At-sea encounters were assigned to the nearest region because they were very close to the coast in all cases (details not shown). For each species, encounters during the breeding season were assigned to breeding regions and encounters during the non-breeding season to non-breeding regions. Importantly, regions in Europe and North Africa may be included both in the breeding and non-breeding regions, particularly for residents and short-distance migrants.

As the analysis also required a species-specific abundance of individuals in each breeding region, we used national abundances provided by BirdLife International (2015) and pooled them in each pre-defined region. Since national abundances were reported as the minimum and maximum estimates of breeding pairs, we averaged them and multiplied the average number of breeding pairs by two, to get the estimated number of adults. As France was part of three different pre-defined European regions, we assumed that the different abundance of each species in the three parts of France was proportional to the relative range extent of each species in each part of France. For *Athene noctua*, the abundance in the UK was not available, so we used the estimate reported by Newson et al. (2008). For *Aix galericulata* and *Branta canadensis*, for which national abundances were not provided by BirdLife International (2015), we used those reported by Banks et al. (2008). For four species showing breeding or resident encounters in West Africa or North Africa, abundance in such regions was provided by various sources (*Falco tinnunculus*: Cramp et al. 1998; *Larus audouinii*: Cramp et al. 1998, Burger et al. 2020; *Platalea leucorodia*: Matheu et al. 2020; *Sterna caspia*: Cuthbert et al. 2020). For *Scolopax rusticola* and *Tetrao urogallus*, since the available estimates regarded the numbers of calling/lekking males, we estimated the number of mature individuals using a multiplicative factor (2.2 and 2.7, respectively) assessed based on the available information on the sex ratio and the proportion of calling/lekking males (*S. rusticola*: Hodless et al. 2008, 2009, Machado et al. 2008, Faragó et al. 2002, *T. urogallus*: Helle et al. 1999). For 10 species whose encounters in breeding grounds were also recorded across West Africa, North Africa and/or the Arabian peninsula (where these species occasionally occur in resident or breeding populations), there was no available information on the abundance in such regions. Thus, we ran different analyses by setting abundances in those regions to 100, 1,000 and 10,000 individuals, to test the robustness of results to different levels of putative abundance. Since connectivity (*MC*) did not differ using the three values (Wilcoxon paired test; 100 vs 1,000: W = 17, z = 1.36, *P* = 0.17; 100 vs 10,000: W = 18, z = 1.57, *P* = 0.11; 1,000 vs 10,000: W = 22, z = 1.35, *P* = 0.18), we report only the results assuming an abundance of 1,000 individuals in those regions.

The analyses were performed as follows:

***a.*** We calculated the mean geographical position (centroid) of individuals in each region and used them to calculate two matrices of great-circle (i.e. orthodromic) distances among centroids. The first matrix included distance among breeding regions and the second matrix included distances among non-breeding regions.

***b.*** We calculated the transition probabilities, i.e. the proportion of individuals migrating from each breeding region to each non-breeding region as the proportion of individuals encountered in one breeding region that were re-encountered in one non-breeding region.

***c.*** Whenever individuals occurred in more than one breeding and non-breeding region, we calculated the *MC* coefficient using the two distance matrices and transition probabilities, following the equation reported by Cohen et al. (2018), and adjusted the coefficient by the overall abundance of individuals in all breeding regions (*adjusted MC*).

***d.*** Whenever individuals occurred in either one breeding or non-breeding region, the *MC* coefficient was assumed to be null (*MC* = 0; R. Ambrosini, unpublished results), and whenever individuals occurred only in one breeding and one non-breeding region, the MC coefficient was assumed to be 1 (*MC* = 1; Ambrosini, unpublished results).

Figure 1 illustrates the cases of species showing weak connectivity and strong clustering (e.g. *Hirundo rustica*), strong connectivity and strong clustering (e.g. *Cygnus cygnus*), moderate connectivity and weak clustering (e.g. *Bucephala clangula*), and no connectivity (e.g. *Turdus iliacus*). Migratory connectivity maps and detailed results of the analyses for all the 137 species analysed can be downloaded from specific pages on the Atlas website. Here, we present the results of a comparison between the levels of migratory connectivity estimated with the methods of Ambrosini et al. (2009) and Cohen et al. (2018). Albeit values of the strength of migratory connectivity estimated with the two methods are used to measure either migratory connectivity between individuals or between areas (Ambrosini et al. 2009; Cohen et al. 2018), a comparison of their values is important from a methodological point of view, as both *rM* and *MC* are correlation coefficients, under particular circumstances their values are identical, and only comparisons based on simulations have been conducted to date (see Cohen et al. 2018). Comparison based on empirical data may thus provide useful insights into whether the two methods offer consistent estimates of migratory connectivity.

*2.2 Consistency of migratory connectivity between individuals and between areas*

To compare the estimates of migratory connectivity obtained by examining population mixing between pre-defined areas in the European-African migration system with those obtained by considering migratory connectivity between individuals, we used data for all the analysed species (N = 137). First, we assessed the Pearson correlation coefficient between the two measurements and tested if the correlation was significant. Second, because correlation may not be appropriate to test replicability, we also tested the repeatability between the two estimates of migratory connectivity through the intraclass correlation coefficient (*ICC*; Shrout and Fleiss 1979).

Estimates of migratory connectivity between individuals and between pre-defined areas showed good concordance and replicability, both for *MC* estimated using relative abundance (*r* = 0.761, *P* < 0.0001; *ICC* = 0.732) and for that based on absolute abundance (*r* = 0.761, *P* < 0.0001; *ICC* = 0.732).

**C:\Users\Acer\Desktop\Figure 1.tif**

**Figure 1**: Migratory connectivity maps of illustrative bird species showing (a) weak connectivity and strong clustering (e.g. *Hirundo rustica*); (b) strong connectivity and strong clustering (e.g. *Cygnus cygnus*); (c) moderate connectivity and weak clustering (e.g. *Bucephala clangula*); (d) no connectivity (e.g. *Turdus iliacus*). The grey lines connect individual breeding sites and non-breeding destinations, while differently coloured kernel contours depict geographical populations identified by the cluster analysis (solid contour: breeding, dotted contour: non-breeding). Species breeding, non-breeding and resident ranges are also shown according to BirdLife International (2019).

**Section 3 – *Phylogenetic comparative meta-analysis of the strength of migratory connectivity***

*3.1 Statistical methods*

We investigated the difference in the strength of migratory connectivity between resident, partial or full migrant species and between passerines and non-passerines. We only retained species having ≥ 30 individuals sampled, because a lower sample size may not provide reliable estimates of migratory connectivity (see our results based on simulations, above) and discarded the introduced *Aix galericulata* and *Branta canadensis*. The final dataset thus included 129 species. We classified each species as resident, partial or full migrant by examining the first level clusters (hereafter simply clusters) identified by the migratory connectivity analysis or by examining the whole species if the species did not show a clustering structure (*oasw* < 0.5) or showed non-significant connectivity. In particular, we implemented a classification based on the inspection of the overall spatial pattern of individual positions observed in the non-breeding stationary range (i.e. after migration), relative to that found in the breeding range, i.e. before migration. For each cluster or species, we first calculated the 95% minimum convex polygon (MCP) of individual locations in the breeding period (breeding MCP) and the 95% MCP of the same individual locations in the non-breeding stationary period (non-breeding MCP). We then overlapped the breeding and non-breeding MCPs of a cluster and classified those clusters where the overlap was more than 75% of the area of the breeding MCP as migratory. Clusters were classified as migratory otherwise. Such classification should be able especially to distinguish sedentary or non-migratory clusters showing a general tendency of dispersal from those showing actual migration patterns. MCP has been used to quantify the population spread of birds in the breeding and non-breeding grounds (e.g. Blackburn et al. 2017, Burgess et al. 2020) and we should note that, in our case, the increase in MCP extent with increasing sample size (Burgess et al. 2020) would not affect the classification outcome because both the MCPs include exactly the same number of individuals. We then further inspected clusters classified as migratory by calculating the (great-circle) distance migrated by each individual. If the migration distance of at least 25% of individuals in a cluster was 0 km, we classified that cluster as partially migratory, and as fully migratory otherwise.

Following the aforementioned classification of clusters, we classified species including only resident clusters as resident (N = 42 species), species including both resident and fully migratory clusters or at least one partially migratory cluster as partial migrants (N = 24 species), and species including only migratory clusters as full migrants (N = 63 species). Clearly, those species that did not show significant connectivity or a clustering structure were classified based on the same analyses above run on all the individuals of that species.

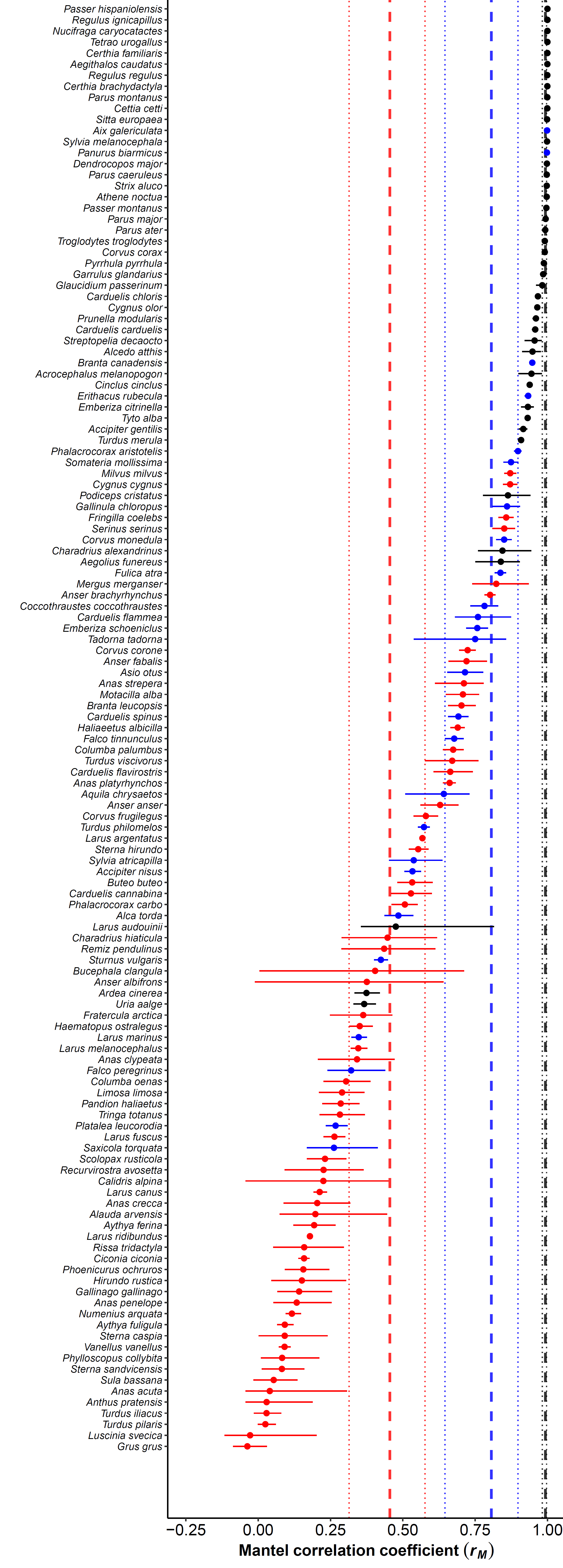
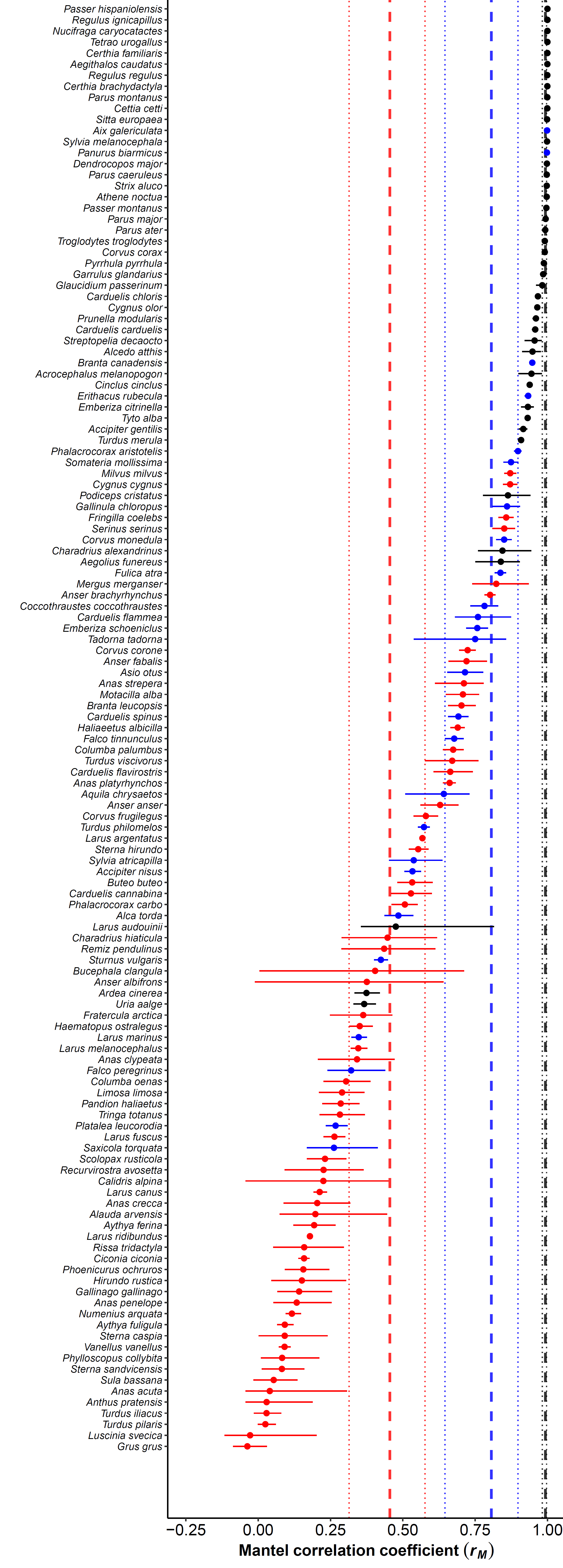
We then conducted a phylogenetic meta-analysis using the *metafor* R package (Viechtbauer 2010). Because *rM* values represent correlation coefficients, they were transformed into *Zr* using Fisher transformation. We fitted a phylogenetic mixed model where the variance components of the random part allow calculating how much variance is attributable to the phylogeny (phylogenetic hereditability, *H2*) while accounting for the fixed effects included in the model (note that *H2* is equivalent to Pagel’s λ; see Nakagawa and Santos 2012, for details). *H2* was calculated as the ratio between the variance due to phylogeny and all the variance components in the model (Nakagawa and Santos 2012). We accounted for phylogeny through a 50% majority rule-consensus tree built using 10,000 bird phylogenies (Hackett et al. 2008) retrieved from [www.birdtree.org](http://www.birdtree.org) (Rubolini et al. 2015). In the model, we included as fixed effects (i.e. moderators) whether the species was resident, partial migrant or full migrant (categorical, entered in the analysis as two binary moderators), whether it was a passerine or non-passerine (binary moderator), as well as the body mass of a species (continuous moderator, in grams). All moderators were also scaled. As a preliminary exploration of the data suggested heterogeneity of variance in *Zr* values both between resident, partial and full migrants and between passerines and non-passerines, we allowed for heterogeneity of variance between these groups by entering them as inner variables in the random part of the model and setting a diagonal covariance structure for the variance-covariance matrix. This allowed the model to estimate different variances for each level of these predictors. We also weighted *Zr* values by the inverse of their sampling variance (equal to *N* − 3, where *N* is the number of individuals sampled). Degrees of freedom were calculated with the containment method that offers better control of the Type I error rate and produces confidence intervals with closer-to-nominal coverage rates (<https://wviechtb.github.io/metafor/reference/index.html>). The model was fitted using REML and the statistical significance was assessed using t-values.

*3.2 Phylogenetic comparative meta-analysis*

Residents showed the highest levels of migratory connectivity, partial migrants intermediate levels, and full migrants the lowest values (Figure 2; Table 2). Post-hoc tests indicated that the differences between all levels were significant (|t124| ≥ 3.706, PFDR ≤ 0.001). Moreover, we detected a significantly positive effect of body mass on the strength of migratory connectivity, while the difference between passerine and non-passerine species was not significant (Table 1). The same model re-fitted by centring all moderators shows that migratory connectivity was generally positive and significantly larger than zero across all species (coef = 1.345 ± 0.117 SE, t124 = 11.505, P < 0.001, corresponding to *rM* = 0.873, 95% CI: 0.805 – 0.918). Hereditability was almost null (*H2* = 0.008), and a model considering the same predictors but not the phylogeny fitted the data similarly (LRT = 2, *df* = 1, P = 0.085).

**Table 2.** Results of the phylogenetic meta-analytic mixed model of the strength of migratory connectivity across species. The significance of the moderators was assessed by a likelihood ratio test. The coefficients (for continuous moderators) or the marginal means (for categorical moderators) are reported together with the relative standard errors. Marginal means are also converted into *rM* values and the relative 95% confidence interval.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Moderator** | **LRT** | ***df*** | **P** | **Level** | **Coef.** | **SE** | ***rM*** | **95% CI** |
| Migration | 59.96 | 2 | < 0.001 | Resident | 2.796 | 0.237 | 0.993 | 0.981 – 0.997 |
| behaviour |  |  |  | Partial migrant | 0.969 | 0.124 | 0.748 | 0.620 – 0.838 |
|  |  |  |  | Full migrant | 0.516 | 0.076 | 0.474 | 0.349 – 0.583 |
| Body mass | 4.96 | 1 | 0.026 |  | 0.104 | 0.042 |  |  |
| Passerine | 3.26 | 1 | 0.071 | Passerine | 1.500 | 0.166 | 0905 | 0.825 – 0.950 |
|  |  |  |  | Non-passerine | 1.234 | 0.121 | 0.844 | 0.759 – 0.900 |



**Figure 2**. Forest plot showing the strength of migratory connectivity (*rM* values and their 95% CIs) across the 129 species included in the comparative meta-analysis (black: residents; blue: partial migrants; red: full migrants). Dashed lines depict marginal means estimated by the phylogenetic model, dotted lines their 95% CIs.

**Conclusions**

Our analysis assessing the strength of migratory connectivity for 137 bird species in the European-African migration system provided some useful methodological insights to advise future analyses of migratory connectivity based on ringing encounters, but also offered a tool to assist in the conservation and management of European birds by describing migratory connectivity patterns accurately, as well as it started to shed light on the ecological drivers of avian migratory connectivity.

First, we demonstrated that ringing encounters are an excellent tool to estimate migratory connectivity. Indeed, a threshold of 30 individuals having one encounter in both the breeding and non-breeding grounds was sufficient to obtain reliable estimates of migratory connectivity for about 75% of the species analysed, and alive and dead encounters generally provided consistent estimates of migratory connectivity, albeit exceptions exist and must be carefully considered species by species. Our estimates of migratory connectivity between individuals and between pre-defined areas, the two metrics currently available to quantify bird population mixing between breeding and non-breeding grounds, showed good agreement across species. Cohen et al. (2018) indeed suggested that under ideal conditions (without grouping error and with sampling proportional to relative abundances) *rM* and *MC* are identical. We confirm that the two methods generally agree in estimating migratory connectivity, at least based on our empirical comparison of the results on 137 species in the European-African migration system. However, we also stress that the two methods are conceptually different and should be better suited for different situations, e.g. depending on whether migratory connectivity should be quantified between target areas or between individuals.

Earlier research called for gaining knowledge on how birds mix between breeding and non-breeding grounds to assist the conservation of European migrants (Beresford et al. 2019). Our analysis was able to identify species-specific patterns of migratory connectivity accurately, thus providing a critical tool that can be used to inform conservation and management strategies on target species on a case-by-case basis. Overall, the strength of migratory connectivity in the European-African bird migration system showed high interspecific variability, but almost all (*c*. 92%) of the species analysed exhibited significant connectivity. Amongst them, migratory connectivity was mainly due to clustering (*c*. 77% species), whereas few species showed connectivity from pattern transference, suggesting that migration strategies also vary at the intraspecific level, with most species showing geographically distinct migratory populations. In a nutshell, our comparative analysis thus suggests that individuals of the analysed species tended, on average, to maintain their reciprocal positions when relocating between breeding and non-breeding grounds or during breeding and non-breeding periods. However, resident species showed stronger migratory connectivity than both partial and full migrants, and larger species tended to show stronger connectivity. Previous studies have shown that migratory connectivity decreases with migration distance (Finch et al. 2018, Somveille et al. 2021). Most likely, our full migrant species were those experiencing longer migration distances, which may explain their weaker connectivity. Additionally, larger species are those that live longer. A longer lifespan, in turn, promotes the social transmission of migratory routes and helps maintain their knowledge across generations (Teitelbaum et al. 2016, Foss-Grant et al. 2018), which may have promoted a higher population mixing in smaller species. We also found the absence of a phylogenetic signal in the strength of migratory connectivity, and no significant difference between passerines and non-passerines. Thus, phylogenetic relatedness between species did not seem to play a role in shaping migratory connectivity. Rather, our comparative analysis suggested that geographical predictors or social life-history traits are more likely to affect how birds redistribute between breeding and non-breeding periods and grounds.

From a theoretical point of view, this analysis shows that the concept of migratory connectivity can be easily extended also in the temporal dimension, i.e. in analysing how individuals re-distribute during different stages of their annual life-cycle, thus allowing including in the analyses also species or populations with mixed migration strategies and also resident species.

In quantifying and describing the strength and patterns of migratory connectivity across European bird species, we hope that our analysis will improve our understanding of avian migration and, more generally, of the geographical links between individuals during different periods of their annual life-cycle and, from a more practical point of view, will facilitate bird conservation and management at the population level.

**References**

Ambrosini, R., Cuervo, J. J., du Feu, C., Fiedler, W., Musitelli, F., Rubolini, D., Sicurella, B., Spina, F., Saino, N., & Møller, A. P. (2016). Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin *Erithacus rubecula*: a continent‐wide analysis. *Journal of Animal Ecology*, 85, 749-760.

Ambrosini, R., Møller, A.P., & Saino, N. (2009) A quantitative measure of migratory connectivity. *Journal of Theoretical Biology*, 257, 203-211.

Andreotti, A., Pirrello, S., Tomasini, S., & Merli, F. (2010) I tordi in Italia. *ISPRA Rapporti* 123/2010: 1-153.

Banks, A.N., Wright, L., Maclean, I.M., Hann, C., & Rehfisch, M.M. (2008). Review of the status of introduced non-native waterbird species in the area of the African-Eurasian Waterbird Agreement: 2007 update. British Trust for Ornithology.

Beresford, A.E., Sanderson, F.J., Donald, P.F., Burfield, I.J., Butler, A., Vickery, J.A., et al. (2019). Phenology and climate change in Africa and the decline of Afro‐Palearctic migratory bird populations. *Remote Sensing in Ecology and Conservation*, 5, 55-69.

BirdLife International (2015) *European Red List of Birds*. Office for Official Publications of the European Communities.

BirdLife International & Handbook of the Birds of the World (2019) *Bird species distribution maps of the world*. Version 2019.1. Available at http://datazone.birdlife.org/species/requestdis.

Boulet, M., & Norris, D.R. (2006). Introduction: the past and present of migratory connectivity. Ornithological Monographs, 61, 1-13.

Burger, J., Gochfeld, M., Garcia, E.F.J., & Sharpe, C.J. (2020). Audouin's Gull (*Ichthyaetus audouinii*), version 1.0. In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, & E. de Juana, Editors). Cornell Lab of Ornithology.

Burgess, M.D., Finch, T., Border, J.A., Castello, J., Conway, G., Ketcher, M., et al. (2020). Weak migratory connectivity, loop migration and multiple non‐breeding site use in British breeding Whinchats *Saxicola rubetra*. *Ibis*, 162, 1292-1302.

Cohen, E.B., Hostetler, J.A., Hallworth, M.T., Rushing, C.S., Sillett, T.S., & Marra, P.P. (2018). Quantifying the strength of migratory connectivity. *Methods in Ecology and Evolution*, 9, 513-524.

Cramp, S. (1998) *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford University Press.

Cuthbert, F.J., & Wires, L.R. (2020). Caspian Tern (*Hydroprogne caspia*), version 1.0. In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, & E. de Juana, Editors). Cornell Lab of Ornithology.

Faragó, S., László, R., & Bende, A. (2012). Consequences of Eurasian Woodcock (*Scolopax rusticola*) hunting on the population in Hungary. *International Scientific Conference on Sustainable Development & Ecological Footprint*, March 26-27, 2012, Sopron, Hungary

Finch, T., Butler, S.J., Franco, A.M., Cresswell, W. (2017). Low migratory connectivity is common in long‐distance migrant birds. *Journal of Animal Ecology*, 86, 662-673.

Foss-Grant, A., Bewick, S., Fagan, W.F. (2018). Social transmission of migratory knowledge: quantifying the risk of losing migratory behavior. *Theoretical Ecology*, 11, 257-270.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C., Braun, E.L., Braun, M.J., et al. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, 320, 1763–1768.

Helle, P., Kurki, S., & Lindén, H. (1999). Change in the sex ratio of the Finnish capercaillie *Tetrao urogallus* population. *Wildlife Biology*, 5, 25-31.

Hoodless, A.N., Inglis, J.G., Doucet, J.P., & Aebischer, N.J. (2008). Vocal individuality in the roding calls of Woodcock *Scolopax rusticola* and their use to validate a survey method. *Ibis*, 150, 80-89.

Hoodless, A.N., Lang, D., Aebischer, N.J., Fuller, R.J., & Ewald, J.A. (2009). Densities and population estimates of breeding Eurasian Woodcock *Scolopax rusticola* in Britain in 2003. *Bird Study*, 56, 15-25.

Hostetler, J.A., & Hallworth, M.T. (2018). *MigConnectivity: estimate strength of migratory connectivity for migratory animals*. R package version 0.3.0. Available at https://github.com/SMBC-NZP/MigConnectivity.

Korner‐Nievergelt, F., Sauter, A., Atkinson, P.W., Guélat, J., Kania, W., Kéry, M., et al. (2010). Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. *Journal of Avian Biology*, 41, 8-17.

Machado, A.L., Ferrand, Y., Gossmann, F., Silveira, A.M., & Gonçalves, D. (2008). Application of a roding survey method to the sedentary Eurasian Woodcock *Scolopax rusticola* population in Pico Island, Azores. *European Journal of Wildlife Research*, 54, 205-214.

Main, I. (2002) Seasonal movements of Fennoscandian Blackbirds *Turdus merula*. *Ringing & Migration,* 21, 65-74.

Marra, P.P., Norris, D.R., Haig, S.M., Webster, M., & Royle, J.A. (2006). Migratory connectivity. In: *Connectivity conservation* (K. . Crooks, & M. Sanjayan, Editors), pp. 157-183. Cambridge University Press.

Matheu, E., del Hoyo, J., Christie, D.A., Garcia, E.F.J., Kirwan, G.M., & Boesman, P.F.D. (2020). Eurasian Spoonbill (*Platalea leucorodia*), version 1.0. In: *Birds of the World* (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, & E. de Juana, Editors). Cornell Lab of Ornithology.

Nakagawa, S., Santos, E.S. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26, 1253-1274.

Newson, S.E., Evans, K.L., Noble, D.G., Greenwood, J.J.D., & Gaston, K.J. (2008). Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *Journal of Applied Ecology*, 45, 1330-1338.

Newton, I. (2008). The migration ecology of birds. Academic Press.

Olioso, G. (1995). La migration prenutiale des especes du genre *Turdus* en Provence. Analyse des repreises de bagues. *Fauna de Provence (C.E.E.P.)*, 16, 73-85.

Rousseeuw, P.J. (1987) Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*, 20, 53-65.

Rubolini, D., Liker, A., Garamszegi, L.Z., Møller, A.P., & Saino, N. (2015). Using the BirdTree. org website to obtain robust phylogenies for avian comparative studies: a primer. *Current Zoology*, 61, 959-965.

Rundel, C.W., Wunder, M.B., Alvarado, A.H., Ruegg, K. C., Harrigan, R., Schuh, A., et al. (2013) Novel statistical methods for integrating genetic and stable isotope data to infer individual-level migratory connectivity. *Molecular Ecology*, 22, 4163-4176.

Salomonsen, F. (1955). The evolutionary significance of bird migration. *Biologiske Meddelelser*, 22, 1-62.

Santos, T. (1982) Migracion e invernada de zorzales y mirlos (genero *Turdus*) en la Peninsula Iberica. Tesi doctoral. Ed. de la Universidad Complutense, Madrid, Spain.

Shrout, P.E., & Fleiss, J.L. (1979). Intraclass correlations: uses in assessing rater reliability. *Psychological Bulletin*, 86, 420.

Somveille, M., Bay, R.A., Smith, T.B., Marra, P.P., & Ruegg, K.C. (2021). A general theory of avian migratory connectivity. *Ecology Letters*, 24, 1848-1858.

Teitelbaum, C.S., Converse, S.J., Fagan, W.F., Böhning-Gaese, K., O’Hara, R.B., Lacy, A.E., & Mueller, T. (2016). Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nature Communications*, 7, 1-7.

Veen, T. (2013) Unraveling migratory connectivity: the next level. *Molecular Ecology*, 22, 4144-4146.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S., & Holmes, R.T. (2002). Links between worlds. Unraveling migratory connectivity. *Trends in Ecology & Evolution*, 17, 76-83.

Zuur, A.F., Ieno, E. N., Walker, N., Saveliev A.A., & Smith, G.M. (2009) Mixed effect models and extensions in ecology with R. Springer.

Table S1: phenological phases used for the analysis of migratory connectivity. Timing is expressed as month-week (e.g. 4-2 is the second week of April). Each period includes both the start and the end week reported in the table.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **EURING\_CODE** | **SCIENTIFIC\_NAME** | **Breeding** | | **Focal breeding** | | **Non-breeding** | |
|  |  | **start** | **end** | **start** | **end** | **start** | **end** |
| 00090 | *Podiceps cristatus* | 2-3 | 9-1 | 5-3 | 7-3 | 12-3 | 1-4 |
| 00360 | *Calonectris diomedea* | 5-4 | 10-3 | 5-4 | 7-4 | 12-3 | 1-2 |
| 00460 | *Puffinus puffinus* | 4-4 | 10-3 | 5-2 | 6-4 | 11-1 | 1-2 |
| 00520 | *Hydrobates pelagicus* | 5-4 | 11-2 | 6-2 | 7-4 | 1-1 | 2-4 |
| 00710 | *Sula bassana* | 4-2 | 11-1 | 6-2 | 7-4 | 12-1 | 1-4 |
| 00720 | *Phalacrocorax carbo* | 2-4 | 10-2 | 4-3 | 6-2 | 12-1 | 1-2 |
| 00800 | *Phalacrocorax aristotelis* | 2-3 | 10-1 | 4-3 | 6-4 | 12-1 | 1-1 |
| 01220 | *Ardea cinerea* | 3-3 | 8-2 | 4-1 | 6-2 | 12-1 | 1-2 |
| 01340 | *Ciconia ciconia* | 4-2 | 8-2 | 5-3 | 7-4 | 12-1 | 1-4 |
| 01440 | *Platalea leucorodia* | 4-1 | 9-2 | 6-1 | 7-3 | 11-4 | 1-4 |
| 01520 | *Cygnus olor* | 4-2 | 11-2 | 4-4 | 8-4 | 1-1 | 2-4 |
| 01540 | *Cygnus cygnus* | 5-3 | 9-4 | 6-3 | 9-2 | 1-1 | 2-3 |
| 01570 | *Anser fabalis* | 5-3 | 9-1 | 6-1 | 8-3 | 1-1 | 2-4 |
| 01580 | *Anser brachyrhynchus* | 5-2 | 8-4 | 5-3 | 8-2 | 12-1 | 3-2 |
| 01590 | *Anser albifrons* | 6-2 | 9-1 | 6-3 | 8-3 | 1-1 | 2-3 |
| 01610 | *Anser anser* | 3-4 | 8-1 | 4-3 | 7-3 | 12-3 | 1-3 |
| 01660 | *Branta canadensis* | 3-3 | 6-4 | 4-1 | 7-2 | 12-1 | 1-4 |
| 01670 | *Branta leucopsis* | 5-4 | 8-4 | 6-1 | 8-2 | 1-1 | 3-3 |
| 01680 | *Branta bernicla* | 6-2 | 9-1 | 6-4 | 8-2 | 1-1 | 2-4 |
| 01730 | *Tadorna tadorna* | 4-3 | 9-1 | 5-1 | 8-3 | 1-1 | 2-2 |
| 01780 | *Aix galericulata* | 4-3 | 8-1 | 4-4 | 7-3 | 8-2 | 4-2 |
| 01790 | *Anas penelope* | 5-3 | 8-4 | 6-1 | 8-2 | 12-3 | 2-4 |
| 01820 | *Anas strepera* | 4-3 | 8-3 | 5-3 | 7-4 | 12-3 | 2-4 |
| 01840 | *Anas crecca* | 3-4 | 8-2 | 6-1 | 7-3 | 12-3 | 2-2 |
| 01860 | *Anas platyrhynchos* | 2-1 | 11-4 | 5-3 | 7-4 | 12-1 | 1-4 |
| 01890 | *Anas acuta* | 4-1 | 8-3 | 6-1 | 7-4 | 12-3 | 1-4 |
| 01910 | *Anas querquedula* | 4-2 | 8-3 | 5-3 | 7-2 | 11-4 | 1-4 |
| 01940 | *Anas clypeata* | 4-4 | 8-3 | 5-3 | 8-1 | 12-2 | 2-2 |
| 01960 | *Netta rufina* | 4-4 | 8-3 | 5-3 | 8-1 | 12-2 | 2-2 |
| 01980 | *Aythya ferina* | 4-3 | 8-2 | 5-3 | 7-4 | 12-2 | 1-4 |
| 02030 | *Aythya fuligula* | 5-2 | 9-3 | 5-3 | 8-4 | 1-1 | 2-3 |
| 02040 | *Aythya marila* | 5-3 | 9-3 | 5-4 | 8-2 | 12-1 | 2-3 |
| 02060 | *Somateria mollissima* | 4-3 | 9-3 | 5-2 | 8-4 | 12-2 | 2-3 |
| 02120 | *Clangula hyemalis* | 6-1 | 9-1 | 6-3 | 8-4 | 1-1 | 2-4 |
| 02130 | *Melanitta nigra* | 6-2 | 9-3 | 6-3 | 9-1 | 1-1 | 2-3 |
| 02150 | *Melanitta fusca* | 5-4 | 9-1 | 6-4 | 8-4 | 1-1 | 2-4 |
| 02180 | *Bucephala clangula* | 5-2 | 9-2 | 5-3 | 8-3 | 1-1 | 2-2 |
| 02210 | *Mergus serrator* | 5-3 | 9-3 | 6-1 | 8-4 | 1-1 | 2-3 |
| 02230 | *Mergus merganser* | 5-2 | 9-3 | 6-2 | 9-1 | 1-1 | 2-4 |
| 02390 | *Milvus milvus* | 3-4 | 7-4 | 5-3 | 7-2 | 12-1 | 1-4 |
| 02430 | *Haliaeetus albicilla* | 4-2 | 9-2 | 6-1 | 8-4 | 12-3 | 2-1 |
| 02670 | *Accipiter gentilis* | 4-1 | 8-2 | 6-1 | 7-3 | 12-3 | 2-2 |
| 02690 | *Accipiter nisus* | 4-4 | 8-2 | 6-1 | 7-4 | 12-1 | 2-3 |
| **EURING\_CODE** | **SCIENTIFIC\_NAME** | **Breeding** | | **Focal breeding** | | **Non-breeding** | |
|  |  | **start** | **end** | **start** | **end** | **start** | **end** |
| 02870 | *Buteo buteo* | 3-4 | 8-1 | 5-3 | 7-3 | 12-1 | 1-4 |
| 02960 | *Aquila chrysaetos* | 3-1 | 8-2 | 4-2 | 7-4 | 12-2 | 2-4 |
| 03010 | *Pandion haliaetus* | 4-3 | 8-1 | 6-1 | 7-4 | 12-1 | 2-3 |
| 03040 | *Falco tinnunculus* | 3-4 | 8-2 | 6-1 | 7-3 | 12-3 | 2-2 |
| 03200 | *Falco peregrinus* | 5-1 | 8-3 | 5-3 | 7-4 | 11-3 | 2-3 |
| 03260 | *Bonasa bonasia* | 4-3 | 7-4 | 4-4 | 7-2 | 8-1 | 4-2 |
| 03290 | *Lagopus lagopus* | 5-1 | 8-3 | 5-2 | 8-2 | 8-4 | 4-4 |
| 03300 | *Lagopus mutus* | 5-1 | 9-2 | 5-3 | 9-1 | 9-3 | 4-4 |
| 03320 | *Tetrao tetrix* | 4-4 | 7-4 | 5-2 | 7-3 | 8-1 | 4-3 |
| 03350 | *Tetrao urogallus* | 4-3 | 9-2 | 5-3 | 8-2 | 9-3 | 4-2 |
| 03550 | *Alectoris chukar* | 3-4 | 8-4 | 5-1 | 6-4 | 9-1 | 3-3 |
| 03570 | *Alectoris graeca* | 4-1 | 8-3 | 5-3 | 7-1 | 12-1 | 2-4 |
| 03580 | *Alectoris rufa* | 4-4 | 9-2 | 5-3 | 7-4 | 9-3 | 4-3 |
| 03590 | *Alectoris barbara* | 3-4 | 8-4 | 4-3 | 7-4 | 9-1 | 3-3 |
| 03640 | *Francolinus francolinus* | 4-3 | 8-4 | 5-1 | 7-3 | 9-1 | 4-2 |
| 03670 | *Perdix perdix* | 4-2 | 11-4 | 5-1 | 8-2 | 12-1 | 2-4 |
| 03700 | *Coturnix coturnix* | 3-4 | 9-2 | 7-1 | 7-4 | 12-1 | 2-4 |
| 03940 | *Phasianus colchicus* | 3-3 | 9-1 | 4-1 | 6-3 | 9-2 | 3-2 |
| 04070 | *Rallus aquaticus* | 5-1 | 9-1 | 5-3 | 7-2 | 12-3 | 2-2 |
| 04240 | *Gallinula chloropus* | 4-3 | 8-3 | 5-3 | 7-2 | 12-3 | 2-3 |
| 04290 | *Fulica atra* | 2-4 | 10-1 | 5-3 | 8-2 | 12-2 | 2-3 |
| 04330 | *Grus grus* | 4-4 | 9-2 | 5-3 | 7-2 | 12-1 | 2-2 |
| 04500 | *Haematopus ostralegus* | 3-4 | 9-3 | 5-1 | 6-2 | 11-1 | 1-4 |
| 04560 | *Recurvirostra avosetta* | 4-2 | 9-1 | 5-3 | 7-2 | 11-2 | 2-2 |
| 04690 | *Charadrius dubius* | 4-1 | 9-4 | 5-4 | 6-3 | 11-3 | 2-2 |
| 04700 | *Charadrius hiaticula* | 3-4 | 9-3 | 5-3 | 7-4 | 12-1 | 1-4 |
| 04770 | *Charadrius alexandrinus* | 4-2 | 9-1 | 5-4 | 6-4 | 11-3 | 2-2 |
| 04850 | *Pluvialis apricaria* | 5-2 | 9-3 | 6-3 | 7-4 | 1-1 | 2-2 |
| 04860 | *Pluvialis squatarola* | 6-1 | 9-1 | 6-3 | 7-2 | 12-1 | 2-3 |
| 04930 | *Vanellus vanellus* | 3-1 | 9-2 | 4-2 | 6-2 | 12-2 | 1-3 |
| 04960 | *Calidris canutus* | 5-4 | 8-4 | 6-1 | 7-3 | 12-1 | 2-4 |
| 05100 | *Calidris maritima* | 5-3 | 8-4 | 6-3 | 7-4 | 12-1 | 3-4 |
| 05120 | *Calidris alpina* | 5-4 | 8-4 | 6-2 | 7-1 | 11-3 | 3-1 |
| 05170 | *Philomachus pugnax* | 4-4 | 8-3 | 5-3 | 6-3 | 11-3 | 2-2 |
| 05180 | *Lymnocryptes minimus* | 5-4 | 9-2 | 6-2 | 8-2 | 12-2 | 2-2 |
| 05190 | *Gallinago gallinago* | 3-4 | 9-3 | 5-1 | 7-2 | 12-1 | 1-4 |
| 05290 | *Scolopax rusticola* | 3-2 | 10-3 | 5-2 | 8-3 | 12-1 | 2-3 |
| 05320 | *Limosa limosa* | 4-1 | 8-3 | 5-2 | 6-3 | 11-1 | 2-1 |
| 05340 | *Limosa lapponica* | 5-3 | 9-1 | 6-1 | 7-2 | 11-3 | 2-4 |
| 05380 | *Numenius phaeopus* | 5-2 | 9-1 | 6-1 | 7-2 | 11-3 | 2-4 |
| 05410 | *Numenius arquata* | 4-4 | 9-1 | 5-2 | 6-4 | 11-3 | 2-3 |
| 05450 | *Tringa erythropus* | 5-3 | 8-3 | 5-4 | 6-2 | 11-1 | 2-4 |
| 05460 | *Tringa totanus* | 3-4 | 8-3 | 5-1 | 6-2 | 11-1 | 2-2 |
| 05480 | *Tringa nebularia* | 4-4 | 8-3 | 5-3 | 6-3 | 11-1 | 3-2 |
| 05530 | *Tringa ochropus* | 4-2 | 8-3 | 5-3 | 5-4 | 11-1 | 2-4 |
| **EURING\_CODE** | **SCIENTIFIC\_NAME** | **Breeding** | | **Focal breeding** | | **Non-breeding** | |
|  |  | **start** | **end** | **start** | **end** | **start** | **end** |
| 05560 | *Actitis hypoleucos* | 4-3 | 8-4 | 6-1 | 6-3 | 10-4 | 2-4 |
| 05610 | *Arenaria interpres* | 5-3 | 8-3 | 6-2 | 7-1 | 11-2 | 3-2 |
| 05750 | *Larus melanocephalus* | 5-2 | 8-3 | 6-1 | 6-4 | 12-1 | 2-4 |
| 05820 | *Larus ridibundus* | 4-1 | 9-1 | 5-2 | 6-2 | 12-1 | 2-2 |
| 05880 | *Larus audouinii* | 4-3 | 8-3 | 5-1 | 7-4 | 11-3 | 2-2 |
| 05900 | *Larus canus* | 5-3 | 9-1 | 6-1 | 7-2 | 12-2 | 2-2 |
| 05910 | *Larus fuscus* | 4-4 | 9-1 | 6-1 | 6-4 | 12-2 | 1-4 |
| 05920 | *Larus argentatus* | 4-2 | 8-4 | 5-3 | 8-2 | 12-2 | 2-2 |
| 06000 | *Larus marinus* | 4-3 | 8-4 | 5-2 | 8-2 | 12-2 | 2-2 |
| 06020 | *Rissa tridactyla* | 5-2 | 9-2 | 6-1 | 7-4 | 12-1 | 1-4 |
| 06060 | *Sterna caspia* | 5-1 | 8-3 | 5-4 | 7-2 | 12-3 | 2-3 |
| 06110 | *Sterna sandvicensis* | 4-4 | 7-4 | 5-2 | 6-4 | 12-1 | 1-2 |
| 06150 | *Sterna hirundo* | 5-2 | 9-2 | 6-3 | 7-2 | 11-2 | 3-1 |
| 06160 | *Sterna paradisaea* | 5-2 | 8-4 | 6-2 | 7-3 | 11-3 | 2-3 |
| 06240 | *Sterna albifrons* | 5-2 | 9-1 | 6-1 | 7-2 | 11-2 | 3-1 |
| 06340 | *Uria aalge* | 4-4 | 8-1 | 5-1 | 7-2 | 12-1 | 1-4 |
| 06360 | *Alca torda* | 4-3 | 8-2 | 5-2 | 7-2 | 11-1 | 2-2 |
| 06540 | *Fratercula arctica* | 4-1 | 8-4 | 4-3 | 7-4 | 10-2 | 3-2 |
| 06650 | *Columba livia* | 2-1 | 12-4 | 2-3 | 12-2 | 1-1 | 1-4 |
| 06680 | *Columba oenas* | 4-3 | 10-4 | 5-1 | 8-2 | 12-1 | 1-4 |
| 06700 | *Columba palumbus* | 2-3 | 12-1 | 5-2 | 8-3 | 12-2 | 2-2 |
| 06840 | *Streptopelia decaocto* | 5-1 | 10-1 | 6-1 | 7-3 | 12-1 | 2-1 |
| 06870 | *Streptopelia turtur* | 5-1 | 10-1 | 6-1 | 7-3 | 12-1 | 2-1 |
| 07350 | *Tyto alba* | 2-4 | 12-1 | 4-1 | 10-4 | 12-2 | 2-3 |
| 07510 | *Glaucidium passerinum* | 4-3 | 7-4 | 4-4 | 7-2 | 12-2 | 2-4 |
| 07570 | *Athene noctua* | 3-3 | 8-3 | 4-2 | 7-4 | 8-4 | 3-2 |
| 07610 | *Strix aluco* | 2-3 | 7-1 | 2-4 | 6-3 | 7-4 | 2-2 |
| 07670 | *Asio otus* | 2-4 | 7-4 | 6-3 | 7-2 | 12-3 | 2-3 |
| 07700 | *Aegolius funereus* | 2-4 | 8-3 | 5-1 | 7-4 | 12-1 | 2-4 |
| 07950 | *Apus apus* | 5-2 | 8-4 | 6-2 | 7-2 | 11-2 | 2-4 |
| 07980 | *Apus melba* | 4-3 | 8-2 | 5-4 | 7-2 | 12-4 | 1-4 |
| 08310 | *Alcedo atthis* | 4-3 | 10-1 | 6-1 | 7-2 | 12-2 | 2-4 |
| 08480 | *Jynx torquilla* | 5-1 | 8-4 | 6-1 | 7-2 | 11-3 | 2-4 |
| 08760 | *Dendrocopos major* | 4-3 | 7-3 | 5-1 | 7-1 | 11-2 | 2-4 |
| 09760 | *Alauda arvensis* | 3-3 | 8-4 | 5-1 | 7-4 | 12-1 | 1-3 |
| 09810 | *Riparia riparia* | 4-4 | 8-4 | 6-1 | 6-4 | 12-1 | 2-3 |
| 09920 | *Hirundo rustica* | 4-4 | 10-2 | 6-1 | 6-4 | 12-3 | 1-4 |
| 10010 | *Delichon urbica* | 4-4 | 10-2 | 6-1 | 6-4 | 12-3 | 1-4 |
| 10110 | *Anthus pratensis* | 3-4 | 8-4 | 5-3 | 6-2 | 12-1 | 1-4 |
| 10140 | *Anthus spinoletta* | 4-1 | 8-1 | 5-1 | 7-4 | 12-2 | 2-4 |
| 10170 | *Motacilla flava* | 4-4 | 8-4 | 6-1 | 7-3 | 11-1 | 2-4 |
| 10200 | *Motacilla alba* | 4-1 | 8-2 | 6-1 | 7-3 | 11-3 | 1-4 |
| 10480 | *Bombycilla garrulus* | 6-1 | 7-4 | 6-3 | 7-2 | 12-1 | 2-4 |
| 10500 | *Cinclus cinclus* | 2-4 | 9-1 | 6-1 | 8-2 | 11-1 | 1-4 |
| 10660 | *Troglodytes troglodytes* | 3-4 | 8-3 | 5-4 | 7-4 | 12-3 | 3-2 |
| **EURING\_CODE** | **SCIENTIFIC\_NAME** | **Breeding** | | **Focal breeding** | | **Non-breeding** | |
|  |  | **start** | **end** | **start** | **end** | **start** | **end** |
| 10840 | *Prunella modularis* | 3-1 | 9-2 | 6-1 | 8-2 | 11-3 | 2-3 |
| 10990 | *Erithacus rubecula* | 3-1 | 7-3 | 5-2 | 6-4 | 11-3 | 2-3 |
| 11040 | *Luscinia megarhynchos* | 4-4 | 7-1 | 5-4 | 6-3 | 10-1 | 3-3 |
| 11060 | *Luscinia svecica* | 4-4 | 8-2 | 6-2 | 7-4 | 12-1 | 1-4 |
| 11210 | *Phoenicurus ochruros* | 4-3 | 7-4 | 5-1 | 7-1 | 11-3 | 2-3 |
| 11220 | *Phoenicurus phoenicurus* | 4-3 | 8-1 | 6-1 | 7-2 | 12-1 | 2-2 |
| 11370 | *Saxicola rubetra* | 4-4 | 7-4 | 6-2 | 7-2 | 11-4 | 2-4 |
| 11390 | *Saxicola torquata* | 4-2 | 8-2 | 6-1 | 7-4 | 11-4 | 1-3 |
| 11460 | *Oenanthe oenanthe* | 3-1 | 8-2 | 5-2 | 7-2 | 11-3 | 2-2 |
| 11870 | *Turdus merula* | 2-4 | 9-2 | 5-2 | 7-2 | 12-1 | 2-2 |
| 11980 | *Turdus pilaris* | 4-4 | 8-4 | 5-2 | 8-1 | 12-2 | 2-3 |
| 12000 | *Turdus philomelos* | 2-4 | 9-1 | 5-3 | 8-2 | 11-2 | 2-3 |
| 12010 | *Turdus iliacus* | 4-4 | 8-1 | 6-2 | 7-2 | 12-2 | 2-3 |
| 12020 | *Turdus viscivorus* | 3-3 | 7-3 | 4-4 | 6-4 | 11-2 | 2-2 |
| 12200 | *Cettia cetti* | 6-1 | 8-4 | 6-3 | 8-2 | 11-1 | 4-4 |
| 12360 | *Locustella naevia* | 4-3 | 9-1 | 6-1 | 7-3 | 11-3 | 2-2 |
| 12380 | *Locustella luscinioides* | 4-2 | 7-3 | 4-3 | 7-2 | 11-3 | 2-1 |
| 12410 | *Acrocephalus melanopogon* | 4-4 | 8-2 | 6-1 | 7-4 | 12-2 | 2-2 |
| 12430 | *Acrocephalus schoenobaenus* | 5-1 | 9-1 | 6-3 | 7-3 | 11-3 | 2-2 |
| 12500 | *Acrocephalus palustris* | 5-1 | 9-1 | 6-3 | 7-3 | 11-3 | 2-2 |
| 12510 | *Acrocephalus scirpaceus* | 5-2 | 9-2 | 6-3 | 7-2 | 11-3 | 2-3 |
| 12530 | *Acrocephalus arundinaceus* | 5-3 | 8-4 | 6-2 | 7-3 | 11-3 | 2-4 |
| 12590 | *Hippolais icterina* | 5-1 | 8-1 | 6-3 | 7-3 | 12-1 | 2-3 |
| 12600 | *Hippolais polyglotta* | 5-1 | 8-4 | 6-3 | 7-2 | 12-1 | 2-3 |
| 12670 | *Sylvia melanocephala* | 3-3 | 7-2 | 5-1 | 5-4 | 1-1 | 2-2 |
| 12740 | *Sylvia curruca* | 4-4 | 8-3 | 6-3 | 7-2 | 11-2 | 2-2 |
| 12750 | *Sylvia communis* | 5-1 | 8-4 | 6-4 | 7-2 | 12-2 | 2-3 |
| 12760 | *Sylvia borin* | 4-4 | 8-3 | 6-3 | 7-2 | 11-2 | 2-2 |
| 12770 | *Sylvia atricapilla* | 4-3 | 8-1 | 6-3 | 7-2 | 12-1 | 1-3 |
| 13080 | *Phylloscopus sibilatrix* | 5-2 | 7-4 | 6-1 | 7-2 | 12-1 | 3-2 |
| 13110 | *Phylloscopus collybita* | 4-4 | 8-1 | 6-1 | 7-2 | 11-4 | 2-3 |
| 13120 | *Phylloscopus trochilus* | 5-1 | 8-1 | 5-3 | 7-3 | 11-2 | 3-3 |
| 13140 | *Regulus regulus* | 4-3 | 8-3 | 6-1 | 7-3 | 12-1 | 2-3 |
| 13150 | *Regulus ignicapillus* | 4-2 | 8-2 | 5-3 | 7-4 | 12-3 | 1-4 |
| 13350 | *Muscicapa striata* | 5-2 | 8-4 | 7-1 | 7-2 | 12-1 | 3-2 |
| 13480 | *Ficedula albicollis* | 4-4 | 7-2 | 5-4 | 6-3 | 11-3 | 2-3 |
| 13490 | *Ficedula hypoleuca* | 4-4 | 8-1 | 5-3 | 7-3 | 12-1 | 2-4 |
| 13640 | *Panurus biarmicus* | 3-3 | 7-1 | 4-3 | 6-3 | 12-1 | 2-3 |
| 14370 | *Aegithalos caudatus* | 4-2 | 9-1 | 5-2 | 8-1 | 11-2 | 3-3 |
| 14420 | *Parus montanus* | 4-3 | 8-1 | 5-3 | 6-1 | 12-1 | 3-1 |
| 14610 | *Parus ater* | 4-2 | 7-4 | 4-4 | 6-3 | 10-3 | 2-4 |
| 14620 | *Parus caeruleus* | 4-1 | 7-3 | 5-1 | 6-1 | 12-1 | 1-4 |
| 14640 | *Parus major* | 3-2 | 7-4 | 5-1 | 6-1 | 12-1 | 1-4 |
| 14790 | *Sitta europaea* | 3-4 | 7-3 | 5-1 | 6-2 | 11-1 | 3-3 |
| 14860 | *Certhia familiaris* | 3-4 | 7-4 | 5-1 | 6-4 | 12-1 | 2-4 |
| **EURING\_CODE** | **SCIENTIFIC\_NAME** | **Breeding** | | **Focal breeding** | | **Non-breeding** | |
|  |  | **start** | **end** | **start** | **end** | **start** | **end** |
| 14870 | *Certhia brachydactyla* | 3-4 | 7-4 | 4-3 | 7-2 | 8-1 | 3-3 |
| 14900 | *Remiz pendulinus* | 4-4 | 8-3 | 5-1 | 6-4 | 12-3 | 1-4 |
| 15150 | *Lanius collurio* | 5-1 | 8-1 | 5-3 | 7-3 | 12-1 | 3-2 |
| 15390 | *Garrulus glandarius* | 3-4 | 7-4 | 6-2 | 6-4 | 11-2 | 3-3 |
| 15490 | *Pica pica* | 3-4 | 8-4 | 4-4 | 6-4 | 9-1 | 3-3 |
| 15570 | *Nucifraga caryocatactes* | 2-4 | 7-4 | 4-1 | 5-4 | 11-1 | 2-3 |
| 15600 | *Corvus monedula* | 4-2 | 6-3 | 4-4 | 6-1 | 11-3 | 2-2 |
| 15630 | *Corvus frugilegus* | 3-1 | 5-3 | 4-2 | 5-1 | 12-1 | 2-2 |
| 15670 | *Corvus corone* | 4-1 | 6-2 | 5-1 | 5-4 | 11-4 | 2-2 |
| 15720 | *Corvus corax* | 1-4 | 8-4 | 4-1 | 6-3 | 9-1 | 1-3 |
| 15820 | *Sturnus vulgaris* | 4-2 | 6-2 | 5-1 | 6-1 | 12-1 | 1-4 |
| 15920 | *Passer hispaniolensis* | 3-1 | 10-4 | 5-3 | 8-3 | 12-1 | 2-4 |
| 15980 | *Passer montanus* | 4-1 | 9-2 | 4-4 | 8-2 | 11-3 | 3-3 |
| 16360 | *Fringilla coelebs* | 4-3 | 7-2 | 5-4 | 6-3 | 12-1 | 2-3 |
| 16380 | *Fringilla montifringilla* | 5-2 | 7-3 | 6-2 | 7-1 | 11-3 | 2-3 |
| 16400 | *Serinus serinus* | 4-1 | 8-2 | 5-1 | 7-3 | 11-2 | 2-3 |
| 16440 | *Serinus citrinella* | 3-1 | 9-1 | 4-3 | 6-4 | 11-4 | 2-4 |
| 16490 | *Carduelis chloris* | 4-4 | 7-2 | 5-3 | 7-1 | 12-1 | 2-4 |
| 16530 | *Carduelis carduelis* | 5-1 | 8-4 | 5-4 | 8-1 | 12-2 | 2-4 |
| 16540 | *Carduelis spinus* | 4-3 | 8-3 | 5-3 | 7-4 | 12-3 | 2-2 |
| 16600 | *Carduelis cannabina* | 4-3 | 8-4 | 5-3 | 7-4 | 11-3 | 2-2 |
| 16620 | *Carduelis flavirostris* | 4-1 | 8-3 | 5-3 | 7-4 | 12-3 | 2-3 |
| 16630 | *Carduelis flammea* | 4-3 | 7-4 | 5-3 | 7-2 | 12-3 | 2-3 |
| 17100 | *Pyrrhula pyrrhula* | 4-3 | 8-3 | 5-2 | 7-3 | 12-1 | 2-3 |
| 17170 | *Coccothraustes coccothraustes* | 4-2 | 8-4 | 4-3 | 8-3 | 12-2 | 1-4 |
| 18570 | *Emberiza citrinella* | 4-3 | 8-2 | 5-3 | 7-4 | 11-3 | 3-2 |
| 18770 | *Emberiza schoeniclus* | 5-1 | 7-3 | 5-3 | 7-1 | 11-3 | 2-2 |