

Research Article

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Improving national bird population estimates in Europe: insights from comparisons with atlas abundance data

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Summary

In Europe, population estimates of breeding birds are produced nationally and are periodically compiled at EU or pan-European scales. Until now, no other source was available to explore the robustness of these estimates. In this study, we compared population sizes reported in the latest edition of the European Red List of Birds (ERLoB) with those produced using data from the second European Breeding Bird Atlas (EBBA2) to assess their consistency and determine parameters behind variability in population estimates that deserve further attention in the future. In general, European population estimates derived from summing local abundance data from EBBA2 were similar to those obtained from ERLoB, although for some species they differed considerably, particularly in those distributed mainly in southern Europe. National population estimates from EBBA2 also did not differ markedly from those in ERLoB. However, we found that EBBA2 provided larger national population sizes than ERLoB for widespread species, suggesting that spatial information is more relevant for properly assessing their population size than for localised species. Our analysis also showed that, in general, population estimates based on robust methodological protocols (e.g. complete counts, statistical inference) contributed to reducing differences between ERLoB and EBBA2 values. Interestingly, EBBA2 and ERLoB estimates were quite similar for species classified in Europe as “Threatened” or “Near Threatened”, whereas the values for “Least Concern” species were consistently different between these two sources. Our results indicate which type of species would benefit from additional efforts to improve national population estimates and their consistency across countries, issues that are of paramount importance for guiding conservation strategies in Europe.

Introduction

Reliable information on the number of individuals in bird populations is essential in ecology and conservation, and often has important legal implications at national and international levels (Brouwer et al. 2003; Callaghan et al. 2021; Robinson et al. 2022). Academic institutions, NGOs, and governmental bodies in many countries have developed their own strategies to estimate population sizes for birds and other taxonomic groups. However, this has often proven challenging. Choosing the best methodology depends on many factors, such as the availability of field data based on appropriate survey techniques and/or the selection of robust analytical protocols and technical capacities (Buckland et al. 2008; Taylor and Pollard 2008; Thompson 2002; Thogmartin 2010). As a result, robust protocols to estimate national population sizes are not always well developed and documented, and outcomes have limitations (Hewson et al. 2018; Jiguet et al. 2016; Murgui et al. 2011; Nagy et al. 2022; Newson et al. 2005).

In Europe, national population sizes for all breeding bird species have been collated in several publications since the 1990s. The first estimates were compiled in the framework of the first European Bird Census Council (EBCC) atlas (EBBA1), which was mainly based on data from the 1980s and early 1990s (Hagemeijer and Blair 1997) and were also published by BirdLife International as a basis for identifying Species of European Conservation Concern (SPECs) (Tucker and Heath 1994). Some of these estimates were updated in the late 1990s to help set thresholds for identifying Important Bird Areas – now Important Bird and Biodiversity Areas – (IBAs) in Europe (BirdLife International and EBCC 2000). Since then, European population estimates have been updated three times, and used when applying International Union for Conservation of Nature (IUCN) Red List criteria at regional scale to produce the European Red List of Birds (ERLoB)

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(BirdLife International 2004, 2015, 2021). The 2021 update was based on estimates reported to the European Commission by EU Member States under Article 12 of the EU Birds Directive for the period 2013–2018, with equivalent data provided by national experts in non-EU countries (BirdLife International 2021).

Beyond the initial aims of determining SPEC and ERLoB categories, population estimates are used in Europe for multiple purposes of great relevance for conservation. For instance, the EU and European bird population trends and derived multi-species indicators produced by the Pan-European Common Bird Monitoring Scheme (PECBMS) are generated by weighting national trends by national population estimates (Brlík *et al.* 2021; Gregory *et al.* 2008). Population estimates are also important for determining countries' responsibilities for species conservation by considering the international significance of national populations (BirdLife International 2017; Eaton *et al.* 2015; Keller and Bollmann 2004). Identifying priority sites for conservation also relies heavily on understanding the national or international importance of local populations: the quantitative criteria by which sites may qualify as IBAs, Key Biodiversity Areas (KBAs), Ramsar sites or Special Protection Areas (SPAs) include thresholds, such as supporting 1% of the population of threatened or migratory species (Donald *et al.* 2019).

Bird atlases represent a valuable source of data on species' distribution and local abundance for estimating population sizes (Herrando *et al.* 2008; Musgrove 2013; Robertson *et al.* 1995; Strebel *et al.* 2020; Szabo *et al.* 2012). Until recently, information about the variation in species' abundance across Europe was only patchily available, and despite efforts to tackle this (e.g. EBBA1), the goal of presenting comparable data at a continental scale has proven challenging (Hagemeijer and Blair 1997). The second European Breeding Bird Atlas (EBBA2) (Keller *et al.* 2020) covered a huge geographical area for breeding bird species. It collected information on the number of breeding birds of each species per atlas square of 50 × 50 km during 2013–2017, roughly the same period used for the latest population update in Europe in the context of ERLoB (BirdLife International 2021). The resulting maps provide a geographical pattern of abundance across species' ranges and thus also represent a suitable data set for deriving population estimates.

EBBA2 and ERLoB are thus the only two comprehensive, large-scale efforts aiming at providing quantitative information on breeding bird numbers in Europe. While EBBA2 produced a detailed estimation of species abundance in each 50 × 50 km square within each country, ERLoB aggregated national population estimates to produce European population estimates. In this study, we aimed to investigate whether population estimates based on abundance data from EBBA2 differ from those reported for ERLoB, and how any differences could potentially be used to improve population estimates in Europe in the future. We compared ERLoB- and EBBA2-derived population estimates to identify species for which European population sizes differ, and explored whether these differences varied according to the species' European threat level, the extent of their distribution, and their particular range within Europe. Since population estimates are produced at national level, we then attempted to determine if different parameters (i. number of 50 × 50 km squares occupied by the species; ii. level of species threat; iii. methodology reported for the estimation; iv. country) helped to explain such differences between EBBA2 and ERLoB. First, we expect that since the amount of information, expertise, and capacity varies strongly among European countries, differences between ERLoB and EBBA2 population estimates will substantially vary between countries. Second, as threatened species generally receive more attention and considerable information has already been

compiled across their ranges, we expect national population estimates from EBBA2 and ERLoB to be more similar for threatened than for non-threatened species. Third, as robust estimation protocols should integrate spatially explicit data on abundance in the calculation process, we expect national population estimates based on such protocols (e.g. complete surveys or statistically robust estimates) to be more similar, whereas less robust estimates (especially those based on expert assessment) are expected to differ more between EBBA2 and ERLoB. Finally, since the protocol used for assessing population size involves unequivocally a higher number of estimates in EBBA2 (one value for each of the squares in which the species occurs) than in ERLoB (only a single value per country), we hypothesise that the larger the distribution of a species, the higher the difference between the two data sources.

Methods

Data sources

ERLoB, coordinated by BirdLife International (2021), compiled population estimates from all European countries for the period 2013–2018 and assessed the threat status for species' populations in Europe using IUCN Red List criteria (IUCN 2012). EBBA2, coordinated by EBCC and its network of partner organisations (Keller *et al.* 2020), collected information on the distribution and abundance of bird species in each square of 50 × 50 km (hereafter "50-km square") in Europe, mostly during the period 2013–2017. The geographical coverage of these two projects was essentially the same, though only ERLoB included Greenland and only EBBA2 included the European part of Kazakhstan. Both projects used the same taxonomic list (HBW and BirdLife International 2019) and population unit (breeding pairs, with very few exceptions), which greatly facilitated comparisons between them. National coordinators reported minimum and maximum numbers of birds at country level in ERLoB and at 50-km square level in EBBA2 (see Figure 1A and C). ERLoB estimates at national level were based on one of the following methods, ranked from higher to lower quality: (1) complete survey or a statistically robust estimate; (2) based mainly on extrapolation from a limited amount of data; (3) based mainly on expert assessment with very limited data (BirdLife International 2021; DG Environment 2017). In EBBA2, three main protocols were used to estimate abundance per 50-km square: direct count, statistical inference, or expert assessment (Keller *et al.* 2020). Direct count refers to cases in which all nests are detected and counted in the field, which is often the case for colonial breeders such as pelicans, auks, cormorants, and gulls, or localised species nesting in prominent trees or on cliffs such as some raptors. Statistical inference refers to a set of different techniques aimed at extrapolating local densities to the whole area of study, usually taking into account the distribution of the species or its habitats, as well as detection probability. Direct counts and statistical inferences are considered of higher quality than expert assessments, which refer to intuitive evaluations by fieldworkers or specialists. In a few countries and for a minority of species, national coordinators did not provide information on abundance (both for ERLoB and EBBA2).

Data treatment

We compiled population estimates for 482 native breeding bird species (89% of the total number of native breeders in EBBA2) and 48 countries. Kazakhstan and Greenland were not included because

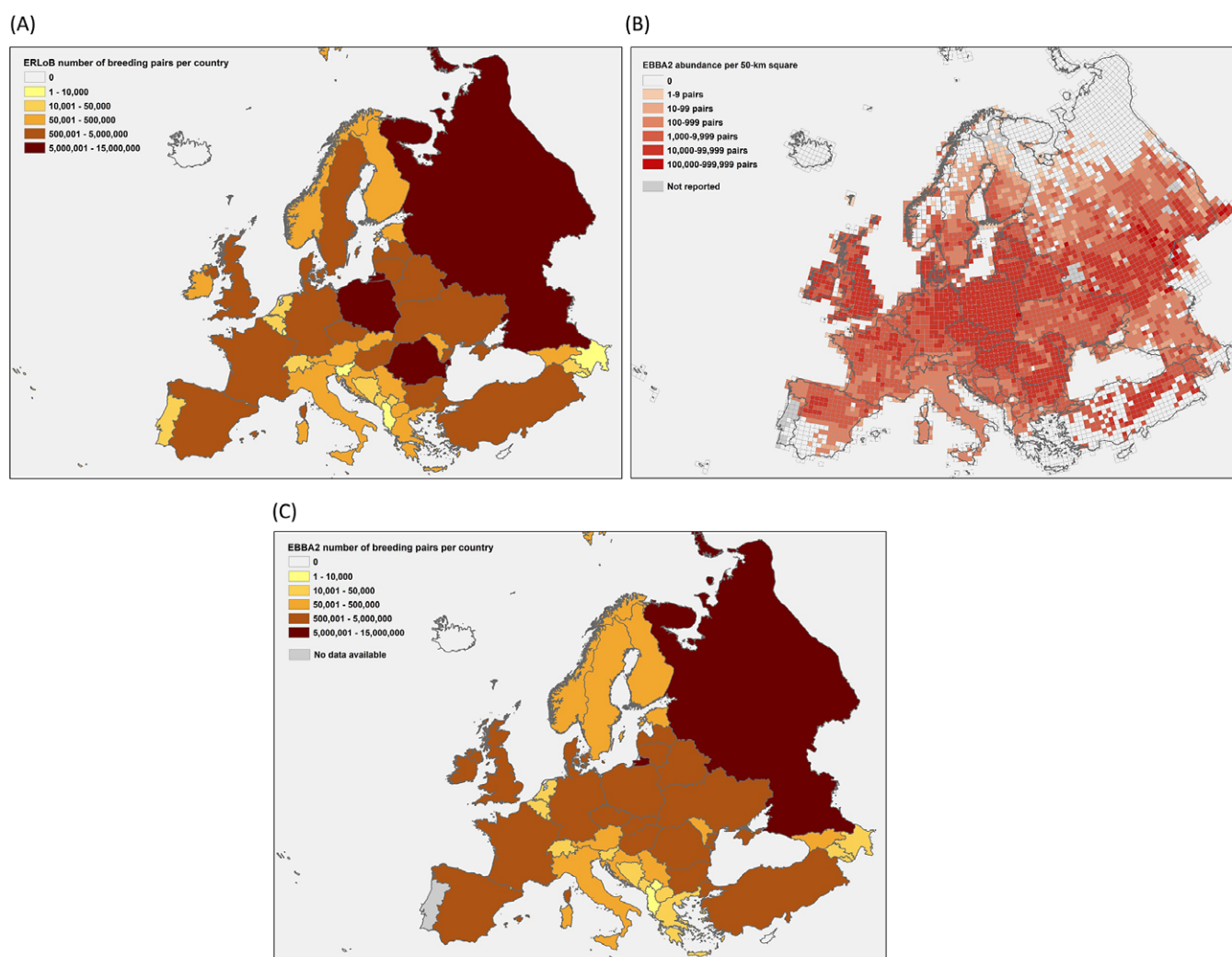


Figure 1. Population estimates (number of breeding pairs) for the Eurasian Skylark *Alauda arvensis* for European countries: (A) ERLob; (B) EBBA2 abundance estimates per 50-km square; (C) sum of EBBA2 abundances for all 50-km squares per country. Note that (B) is an intermediate product used to generate (C), i.e. EBBA2 population estimates, which are used for the comparison with (A), i.e. ERLob population estimates. Regarding EBBA2, note that when more than 50% of the squares occupied by the species in a country had no 50-km data on abundance (not reported), the overall population estimate was not assessed (see grey squares across Portugal in map B and the resulting missing population estimate for that country in map C). When this percentage was lower than 50%, the average number of breeding pairs per 50-km square in the country was used as an estimation for the squares missing an abundance value, and thus a total population for the country could be estimated (see few grey squares in Finland or European Russia in maps B and the resulting estimation of the population for these countries in map C).

information was not available for both projects. Both in ERLob and EBBA2, national coordinators reported a minimum and a maximum value for the estimation of bird population sizes. For example, Switzerland reported a minimum of 25,000 and a maximum of 30,000 breeding pairs of Eurasian Skylarks *Alauda arvensis* for ERLob (BirdLife International 2021). In general, such intervals of values are derived from different sources of uncertainty, typically from confidence errors in statistical calculations of population size or interannual variation in observed numbers of breeding birds (often the population does not refer to a single year but to a period of various consecutive years), or both. A unique value of population size for ERLob was calculated as the geometric mean of the minimum and maximum values at country level, e.g. 27,386 pairs for the Eurasian Skylark in Switzerland (see Figure 1A). Similarly, for EBBA2, population size was computed as the sum of the geometric means of the minimum and maximum reported for 50-km squares (see Figure 1B and C). In total, 9,098

combinations of country and species had population estimates for EBBA2 and ERLob (see Figure 1 for more details).

To assess how differences in country-based estimates were influenced by the robustness of the method used to calculate them, we first needed to harmonise and simplify the original categories (see above) to make them comparable between EBBA2 and ERLob. For that, we differentiated expert assessment (low quality) from the other types of estimations (higher quality). First, we assigned “0” to method “Expert assessment” and “1” to the other methods for both EBBA2 and ERLob, separately. Then, we generated a variable that summed up these values for EBBA2 and ERLob methods, to give an overall indication of the robustness of the method used in calculating estimates for EBBA2 and ERLob. Finally, values were converted into the following three categories: (1) low (value = 0; when expert assessment was used for both the estimation of EBBA2 and ERLob); (2) medium (value = 1; when for instance expert assessment was used in ERLob for a particular species and country, but

statistical inference or direct count was used in EBBA2 for the same species and country, or vice versa; high (value = 2; when neither EBBA2 nor ERLoB used expert assessment but another method of higher quality for the estimation of population size).

Continental analysis

To compare the ERLoB and EBBA2 estimates at the European scale and determine the level of consistency between them, we summed up estimates from all countries in which the species was reported in each project. For species and countries where the EBBA2 population estimate could not be assessed (e.g. Eurasian Skylark in Portugal; see Figure 1C), that species was not included. This resulted in a total of 320 native species for which this comparison was conducted.

The difference among estimates was calculated for each species using the following formula:

$$Dif.est.Eu_i = \left(\sum EBBA2.est_{i,c} - \sum ERLoB.est_{i,c} \right) / \left(\sum EBBA2.est_{i,c} + \sum ERLoB.est_{i,c} \right) / 2$$

where EBBA2.est are the estimates for each species *i* for each country *c*, and ERLoB.est are the estimates for each species *i* for each country *c*.

This corresponds to the relative difference between EBBA2 and ERLoB estimates, normalised by dividing by the mean to give a homogeneous distribution among countries and species. Using the relative difference between EBBA2 and ERLoB allowed us to

determine whether EBBA2 estimates were higher or lower than the ERLoB ones, and to do it in a comparable manner for both common and scarce species. Positive values correspond to estimates higher in EBBA2 than in ERLoB, and negative values where EBBA2 values were lower.

Next, we modelled the relative difference in population estimates as a function of: (1) the European distribution, calculated as the number of 50-km squares where the species was found in Europe as a whole in EBBA2 (subtracting squares in the European part of Kazakhstan) to give an indication of how widespread species are (i.e. the higher the number of squares, the more widespread is the species; hereafter number of occupied squares “no.occ.sq”); (2) level of threat in Europe, divided in three different categories: “Least Concern” (LC), “Near Threatened” (NT) and “Threatened” (including VU: “Vulnerable”, EN: “Endangered”, and CR: “Critically Endangered”). Species Red List categories were obtained from the latest ERLoB update (BirdLife International 2021).

The model structure used for this analysis included the interaction between “no.occ.sq” and “threat”. We applied a simple linear regression model using the R *stats* package (R Core Team 2022). There were no random effects involved because there was only one value per species.

Finally, relative differences in species estimates were grouped using the k-means clustering method (Hartigan and Wong 1979; MacQueen 1967) with the R *stats* package (R Core Team 2022). As a first step, we plotted the absolute differences in population estimates with a histogram to check whether different clusters could be identified. Before performing k-means clustering, we used the “set.

Table 1. Results of the 18 candidate models explaining relative differences in species population size estimates at the country level evaluated based on their *Akaike information criterion* (AIC) values: *k* is the number of parameters estimated in the model, AIC the AIC values, and Δ_i the AIC differences compared with the most parsimonious model (model ID 2). The base model in this case corresponds to model ID 18, where only the random effects are included. “occ” refers to species occupancy in number of 50-km squares in EBBA2, “method” is the robustness of method used to estimate species population sizes (categorised as high, medium, and low, see Methods), and “threat” is the level of species threat in ERLoB (categorised as Least Concern, Near Threatened, and Threatened)

Model ID	Model structure	<i>k</i>	AIC	Δ_i
2	~ occ * method + occ * threat + (1 species) + (1 country)	13	17648.18	0.00
1	~ occ * method * threat + (1 species) + (1 country)	21	17651.73	3.08
5	~ occ * method + threat + (1 species) + (1 country)	11	17652.60	4.22
8	~ occ * method + (1 species) + (1 country)	9	17719.32	6.69
3	~ method * threat + method * occ + (1 species) + (1 country)	15	17723.54	10.91
6	~ occ * threat + method + (1 species) + (1 country)	11	17729.23	16.60
14	~ threat + method + (1 species) + (1 country)	8	17731.96	19.33
11	~ occ + threat + method + (1 species) + (1 country)	9	17733.82	21.19
17	~ method + (1 species) + (1 country)	6	17735.14	22.51
4	~ method * threat + threat * occ + (1 species) + (1 country)	15	17736.56	23.93
13	~ occ + method + (1 species) + (1 country)	7	17736.76	24.13
10	~ method * threat + (1 species) + (1 country)	12	17738.82	26.19
9	~ occ * threat + (1 species) + (1 country)	9	17739.91	27.28
7	~ occ + threat * method + (1 species) + (1 country)	13	17740.70	28.07
16	~ threat + (1 species) + (1 country)	6	17742.73	30.10
12	~ occ + threat + (1 species) + (1 country)	7	17744.62	31.99
18	~ (1 species) + (1 country)	4	17746.23	33.60
15	~ occ + (1 species) + (1 country)	5	17747.89	35.26

seed()” function to guarantee that the same random values were produced each time. This is because the k-means clustering algorithm starts with *k* randomly selected centroids, and this way we could ensure reproducible results. Three different clusters were automatically generated based on threshold value, and the algorithm assigned each observation (species) to a particular group according to whether differences between ERLoB and EBBA2 estimates were large, small or not discernible (cluster means 1.441, 0.664, and 0.195, respectively).

After that, we used ordinal regression to test for differences between groups in terms of: (1) species’ European breeding range category (based on EBBA2 and classifying species as mainly found in the north (N), north-east (NE), north-west (NW), south (S), south-east (SE), south-west (SW), east (E) or west (W) of Europe, or other); (2) whether species were generalists or specialists according to the main habitat preferences reported in EBBA2 (Keller et al. 2020); (3) the taxonomic–functional categories of species as in ERLoB (BirdLife International 2021). As our predictors, we considered all model combinations among the three previously mentioned variables (i.e. species’ range, species’ main habitat preferences, and species’ taxonomic–functional categorisation), without including interactions. We defined our clusters as a factor variable with ordered levels (i.e. not discernible, small or large differences between ERLoB and EBBA2 estimates) and used it as our response variable. The candidate models were evaluated according to their parsimony based on their Akaike information criterion (AIC) values (Burnham and Anderson 2002). Analysis of variance (ANOVA) tests were performed to identify the significant effects of the model predictors using the R *car* package (Fox and Weisberg 2019). Ordinal regressions were performed using the MASS package (Venables and Ripley 2002). See Supplementary material Appendix S1 for an explanation on how the three different predictors were defined, and Figure S1 for an example of species’ attribution to their main European breeding range.

Country-based analysis

For this analysis, we included all combinations of country and species for which estimates had been calculated (e.g. Eurasian Skylark included for all countries except Portugal; see Figure 1B). Our species pool consisted of a total of 482 native species for which EBBA2 and ERLoB estimates were available for at least one country.

We used the relative differences between country-level estimates EBBA2-ERLoB as our response variable (hereafter “Dif.est.c”), also normalised by dividing by the mean.

As predictors, we included: (1) extent of distribution of the species in the country (i.e. occupancy, hereafter “occ”), calculated as the proportion of 50-km squares in which the species was found in the country; (2) robustness of method (hereafter “method” with three levels, defined as a factor; see previous section for an explanation of how this variable was created); (3) level of species threat (hereafter “threat” with three levels, defined as a factor). In this case, the most complex model structure included a triple interaction between “occ”, “method”, and “threat”, with two random effects of “species” and “country” (model ID 1 in Table 1). We applied a linear effects mixed model using the R package *lme4* (Bates et al. 2015). All model combinations were again evaluated based on their AIC values.

Results

Continental analysis

Among the 320 species in the clustering analysis, more than half (180, 56.3%) had very similar European population estimates in both EBBA2 and ERLoB, with a negligible normalised difference value of <0.43 (threshold value for “not discernible” cluster; Figure 2). Another third (107 species, 33.4%) differed by a small amount (values between 0.43 and 1.05; threshold value for “small”

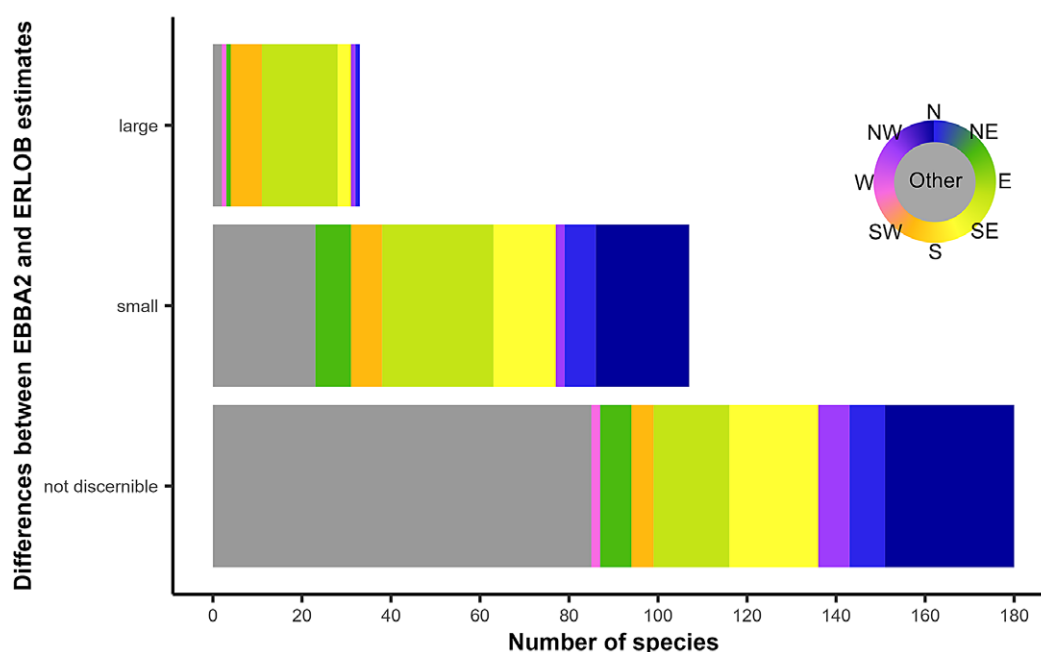


Figure 2. Results of the clustering analysis performed with the k-means method at the European scale. Species were classified in three different groups with ordered levels (i.e. not discernible, small, and large differences between ERLoB and EBBA2 estimates; cluster means 1.441, 0.664, and 0.195, respectively) and categorised in their main breeding range categories along the European gradient: north (N), north-east (NE), north-west (NW), south (S), south-east (SE), south-west (SW), east (E) or west (W). Species widespread across Europe or located in non-adjacent quarters were classified as “other” (see Figure S1 for more details).

Table 2. Results of the best-fit model according to *Akaike information criterion* (AIC) (model ID 2) in the country-based analysis. Parameters include main terms (“occ”, “method” and “threat”) as well as two interaction terms: occ:method and occ:threat. “occ” refers to species occupancy in 50-km squares, whereas “method” is the robustness of method used to estimate species population sizes (categorised as high, medium, and low). In this case, “low” (less accurate method) and Least Concern species have been defined as reference levels to assess for differences between categories in these two variables.

Parameters	Estimate	SE	<i>t</i>	<i>P</i>
(Intercept)	−0.115	0.056	−2.040	0.041
area.occ	0.002	0.001	3.880	<0.001
method_medium	0.081	0.037	2.191	0.028
method_high	0.216	0.048	4.456	<0.001
threat_nearthreatened	0.047	0.069	0.674	0.501
threat_threatened	0.181	0.050	3.641	<0.001
area.occ:method_medium	−0.002	0.001	−4.010	<0.001
area.occ:method_high	−0.003	0.001	−4.205	<0.001
area.occ:threat_nearthreatened	−0.001	0.001	−1.238	0.216
area.occ:threat_threatened	−0.003	0.001	−2.702	0.007

cluster; Figure 2), while the remaining 10.3% (33 species) differed by a large amount (value of >1.05; threshold value for “large” cluster; Figure 2). Among the 140 species (44%) with small or large differences, more than 70% had higher population estimates in ERLoB ($n = 99$) than in EBBA2 ($n = 41$) (Appendix S2). Examples of species with particularly large differences are White-winged Snowfinch *Montifringilla nivalis* (LC), Red-legged Partridge *Alectoris rufa* (NT), and Little Bustard *Tetrax tetrax* (VU), with much higher estimates in ERLoB; Cory’s Shearwater *Calonectris borealis* (LC), Yellow-breasted Bunting *Emberiza aureola* (CR), and Black-bellied Sandgrouse *Pterocles orientalis* (EN), with much higher estimates in EBBA2. The full list of species with their estimated European populations shows a high variety of cases (see Appendix S2).

The linear regression model including the interaction between “no.occ.sq” and “threat” revealed a significant difference in population estimates at the continental scale between Threatened and Least Concern species, the latter defined as contrast, i.e. reference level (Threatened species: $b = 0.237$, $SE = 0.119$, $t = 1.995$, $P = 0.047$). In general, the differences between EBBA2 and ERLoB estimates were smaller for Threatened species than for Least Concern species. There were no significant differences in estimates between Near Threatened and Least Concern species. Differences were also non-significant between Near Threatened and Threatened species. Similarly, the extent of the species distribution (widespread vs localised) at a continental scale did not have any effect on the differences between EBBA2 and ERLoB estimates.

The results from the clustering analysis revealed that the model including species’ range category as the only predictor was ranked highest. Although the model including information on habitat (generalists vs specialists) and species’ range category was ranked as the second most parsimonious model (difference in AIC compared with the top ranked model $\Delta_i < 2$), there were no significant differences among the three clusters for the habitat variable ($b = 0.229$, $SE = 0.283$, $t = 0.809$, $P = 0.418$). However, this

analysis revealed a considerable number of species with a southern European distribution (ranges S, SE, and SW) with large differences in population size estimates (Figure 2). These accounted for more than 80% of species within the large difference cluster, in contrast to <1% of species with a northern distribution (N, NE, and NW) (Figure 2). Southern species also dominated the cluster with small differences between EBBA2 and ERLoB estimates (43%) compared with northern species (28%). The number of species with southern and northern distributions was very similar in the cluster with no differences between estimates (23% and 24%, respectively). Species classified as “other” were highly abundant in that cluster as well (47%) (Figure 2). The ordinal regression model only revealed significant differences among clusters between species with SE ($b = 1.283$, $SE = 0.415$, $t = 3.091$, $P = 0.002$), SW ($b = 1.594$, $SE = 0.564$, $t = 2.826$, $P = 0.005$), and “other” ($b = 1.073$, $SE = 0.393$, $t = 2.731$, $P = 0.006$) distributions compared with species with S distributions (defined as a reference level).

Country-based analysis

The model including “occ”, “method”, “threat” and the interaction terms between “occ:method” and “occ:threat” was the top ranked model (difference in AIC of the top ranked model $\Delta_i > 2$ compared with the rest of the models) (Table 1). In the top ranked model, all main terms were positively associated with the relative differences in estimates (Table 2), whereas the two interaction terms were negatively associated with the relative differences in estimates (Table 2). The percentage of variance in relative difference in estimates explained by the random effects of species and country was around 20% (marg $R^2 = 0.007$, cond $R^2 = 0.221$), and most of it was explained by country (Figure 3).

Across all 48 countries, there was no evidence that EBBA2 population estimates were systematically higher or lower than ERLoB population estimates. Considering species’ distribution, EBBA2 estimates were usually higher than ERLoB estimates for widespread species, whereas for localised species EBBA2 estimates tended to be lower than those in ERLoB (Figure 4A). In general, the smallest differences between EBBA2 and ERLoB estimates were found at an intermediate gradient of occupancy of a species within a given country (species occurring in c.60% of the 50-km squares in a country) (Figure 4A).

In general, population estimates based on robust methodological protocols (e.g. direct counts, statistical inference) were consistently more similar between ERLoB and EBBA2 than those based on less robust methods (e.g. expert assessment) (Table 2, Figure 4B). This was more evident for widespread species when both EBBA2 and ERLoB were based on such methods (highly robust) than when only one of them used robust methods (moderately robust) (Table 2, Figure 4B). Expert assessments therefore provided higher EBBA2 estimates than ERLoB for widespread species, but the opposite for localised species.

For Threatened species, estimates were similar between EBBA2 and ERLoB, especially in the case of widespread species (Figure 4C). Least Concern species, on the other hand, showed substantial differences along the occupancy gradient, with EBBA2 tending to provide higher estimates than ERLoB for widespread species, and vice versa (Figure 4C). Importantly, differences in estimates for Threatened species generally seemed not to depend on the method used.

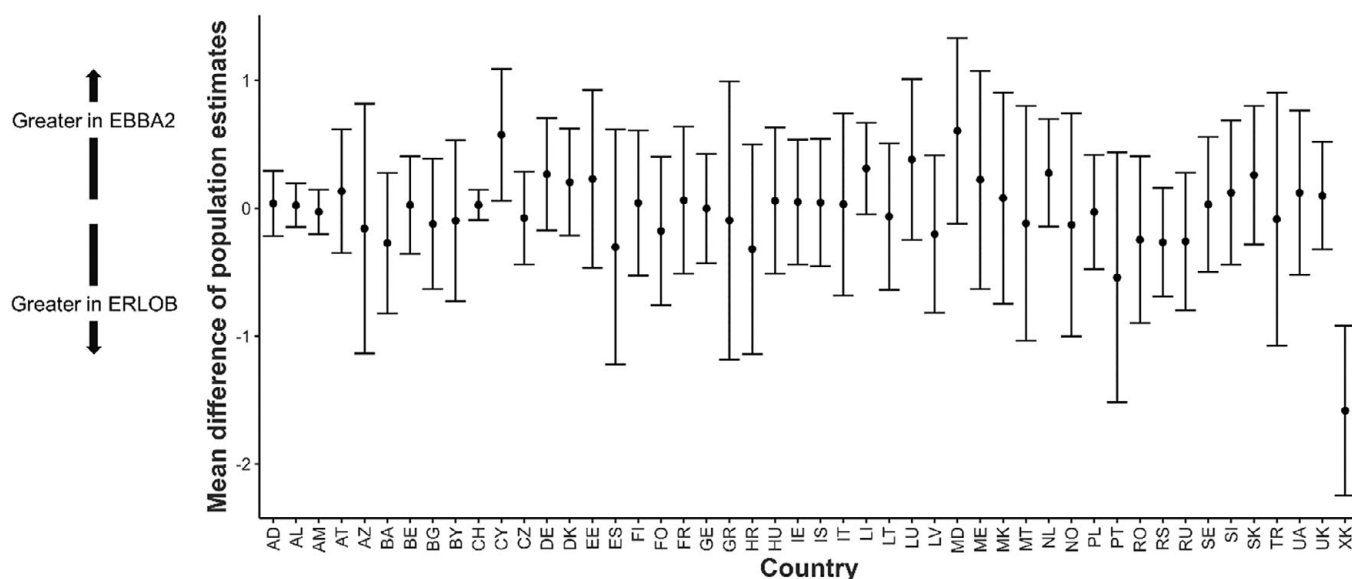


Figure 3. Mean of the difference between the EBBA2–ERLOB estimates for each country, with its standard deviation. The difference between the EBBA2–ERLOB estimates for each country is the normalised difference in national estimates of population sizes for 482 bird species by country ($n = 48$). Countries are assigned a two-letter code following the ISO Alpha-2 code. The 0 value on the y-axis means that there are no differences between EBBA2 and ERLOB estimates.

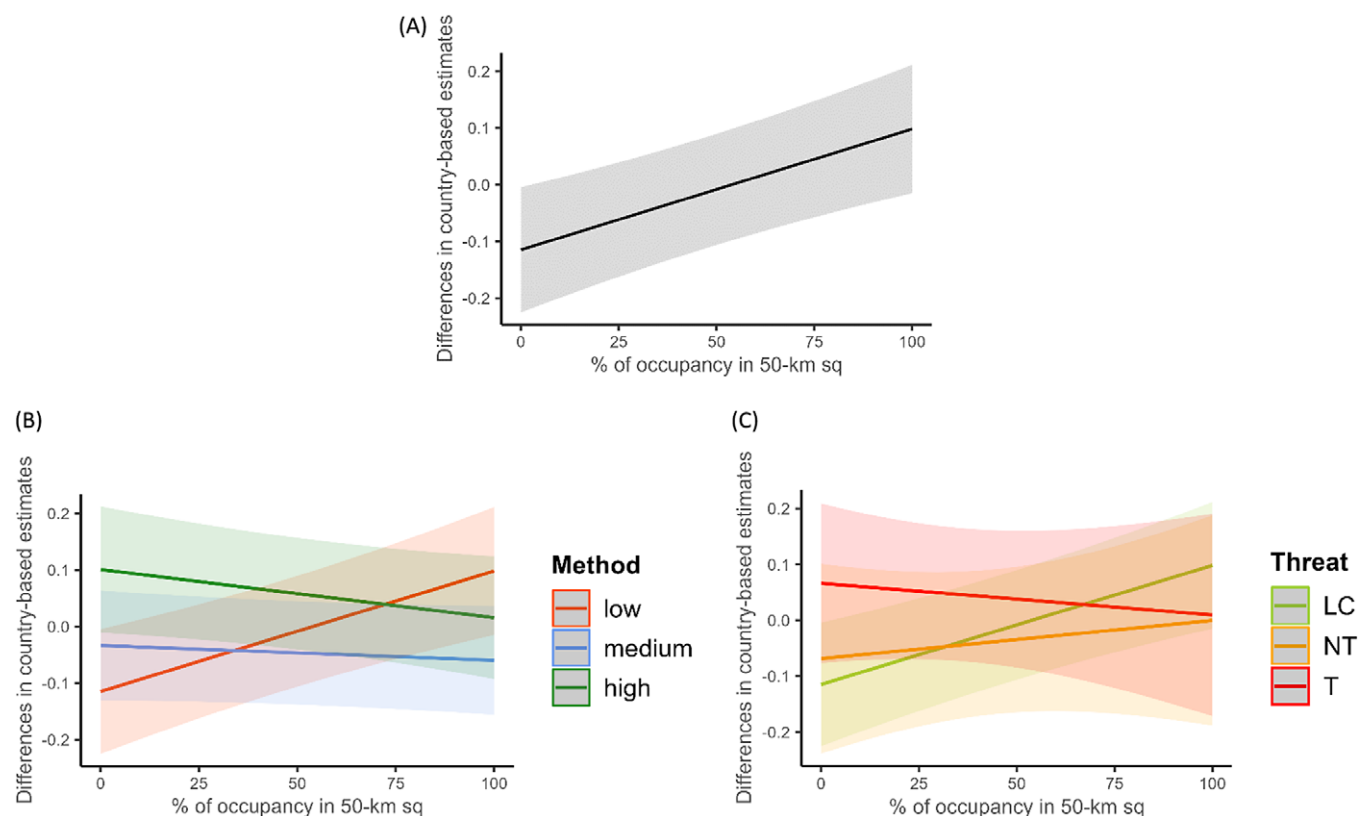


Figure 4. Predicted values of relative differences in country-based estimates for: (A) main term percentage of occupancy in 50-km squares; (B) interaction term between the robustness of method used to estimate species population sizes (categorised as high, medium, and low; see Methods section) and species occupancy in 50-km squares; (C) interaction term between the threat category of species (defined as Least Concern, Near Threatened, and Threatened) and occupancy in 50-km squares. Panels show the gradient of occupancy from localised (left) to widespread species (right). Positive differences in estimates mean that EBBA2 estimates were higher than those of ERLOB, while negative values indicate higher estimates for ERLOB (see Figure 3).

Discussion

Estimating bird population sizes over large territories is a very complex issue for most species, especially as there is no way of objectively determining what is the real population value. Considering this unavoidable limitation, this study assumed that when several estimates are available, the more similar they are to each other means they are probably closer to the real population size. Given this complexity, we conducted several analyses with the aim of providing tools to contribute towards the progressive improvement of national (and thereby continental) population estimates.

We examined differences between population estimates from two sources of information: ERLoB, which compiles population estimates produced at national level and does not explicitly document the use of spatial information on abundance in the process of generating such estimates; EBBA2, which focuses on the distribution and abundance of breeding birds in each 50-km square across Europe. By doing this comparison, we have been able to better understand some of the key drivers behind variability in population estimation, and to identify which types of species require further efforts to improve their population estimates in Europe.

We found a substantial number of species with differences in the European population estimates between the two projects. Often these differences related to how the information has been aggregated or calculated for specific species. We identified several factors contributing to the differences at both European and national scales, as discussed below.

At a continental scale, we did not find a general effect of the extent of occupancy on differences between EBBA2 and ERLoB estimates. The effect of threat status, however, indicated that population estimates for Least Concern species varied more widely than those for Threatened species. This could be explained by the fact that many Threatened species receive more attention and there is considerable structured, well-referenced information compiled across their ranges. Despite these interesting results, the proportion of variance explained by this model, which included the interaction between occupancy (number of 50-km squares) and the level of species threat, was very low. This indicates that other factors related to species traits that affect survey methods (e.g. diurnal vs nocturnal, territorial vs colonial, etc.) could influence the differences in population estimates at a continental scale.

With regard to species' range, the cluster analysis revealed that species with southern ranges dominated the group of species with the largest differences in population size estimates between ERLoB and EBBA2. This result highlights the importance of improving population estimates in southern Europe, especially for Least Concern species concentrated in that region (see "LC" species with "range" south (S), south-east (SE), and south-west (SW) in [Appendix S2](#); [Appendix S1](#) lists the countries in these categories). Although there are some exceptions, in general monitoring and atlas work is not widely developed in southern Europe, particularly in the south-east. The majority of the 18 countries in this region (see [Appendix S1](#)) have no national atlases or monitoring schemes, although some have started common bird monitoring in the context of international collaborative initiatives ([EBCC 2024](#)). Consequently, capacities to robustly estimate population sizes are relatively low. In addition, the diversity of landscapes and habitats in the Mediterranean, Macaronesian, Anatolian, Black Sea, Steppic, and southern Alpine regions relates to heterogeneity in bird distribution and abundance ([Keller et al. 2020](#)), which could make the estimation of population sizes even more complex than in other regions. Investment in monitoring and atlas work through local

ornithological organisations, supported at national or international levels, is thus highly recommended to improve population estimates in an area holding many species that do not breed elsewhere in Europe ([Keller et al. 2020](#)).

The country-scale analysis was particularly relevant because the official estimates compiled by ERLoB are developed at national level. This analysis revealed that the extent of occupancy and the level of robustness in methods used for producing population estimates were the strongest predictors overall. For widespread species, EBBA2 estimates were generally higher than those in ERLoB, but lower for localised species. This is consistent with our hypothesis, as spatial information is more relevant for a proper assessment of population size for widespread than for localised species. It should be noted that even if spatial information on abundance is known to have been used by some countries when providing national population estimates for ERLoB (e.g. in particular cases where abundance information has been used for national atlases; e.g. [Knaus et al. 2018](#)), this information is not always properly used and/or documented in the sources of their population estimates for ERLoB (or the reported data by EU countries under Article 12 of the Birds Directive). We therefore advocate for the assessment of spatially explicit information on abundance that complements the processes conducted so far for producing official population estimates for the whole of the country. In this context, EBBA2 and national atlases represent a very valuable source of information.

In terms of method robustness, we found that the use of robust methodological protocols (e.g. direct counts, statistical inference) had a significant effect in reducing differences between EBBA2 and ERLoB estimates compared with less robust protocols based solely on expert assessment. This was especially true for widespread species when both EBBA2 and ERLoB reported their estimates being generated by robust methods. Importantly, differences in estimates for Threatened species generally seemed not to depend on the method used, which could be associated with higher quality information (i.e. high number of local studies, better field data and analytical protocols) for this particular group of species. Similarly, for Threatened species, small differences between EBBA2 and ERLoB population sizes were found compared with Least Concern species, especially in the case of widespread species. This result is again consistent with the hypothesis that Threatened species have similar estimates regardless of the source, and matches the result found at the continental scale. For Least Concern species, EBBA2 tended to provide higher estimates than ERLoB for widespread species, which suggests that information on distribution is critical to understanding differences found for this particular group of species. Directly mapping absolute abundance through spatially explicit models or combining some local abundance data with fine-scale distribution models of relative abundance are two approaches that have proven useful in generating robust population estimates for widespread species. Indeed, countries with bird atlases that have developed either spatially explicit models of absolute abundance ([Gedeon et al. 2014](#); [Knaus et al. 2018](#)) or fine-scale distribution models of relative abundance ([Balmer et al. 2013](#); [Sovon Vogelonderzoek Nederland 2018](#)) tend to be amongst those with smaller differences between EBBA2 and ERLoB ([Figure 3](#)). Conversely, countries that have not produced a national atlas ([EBCC 2022](#)) are often amongst those with the highest inconsistencies between the EBBA2 and ERLoB estimates ([Figure 3](#)).

The fact that 20% of the variance in the country-level analysis was explained by the random effects of the best-fit model, and that most of it was accounted for by the variable "country", supports the

hypothesis that the difference between EBBA2 and ERLoB national population size estimates is strongly related to country. This supports our hypothesis that ERLoB and EBBA2 population estimates differ substantially within countries due to strong variations in the amount of information, expertise, and capacities among European countries. Similar to the analysis performed at a continental scale, the proportion of variance explained by the best-fit model was very low, and so other factors may also explain differences in population estimates at a country level. For instance, in some countries, differences could be small because the same people and institutions compiled and provided the data, using a common approach for both EBBA2 and ERLoB. The information on who was involved in these two processes of reporting data for these projects is difficult to track and, consequently, has not been incorporated in our analyses. Finally, it is important to note that our analyses do not incorporate information on the uncertainty of population estimates, which may have a significant impact on studies that compare different population sizes (Bird et al. 2021; Robinson et al. 2022).

Protocols that aim to incorporate information on species' distribution when deriving bird population estimates have been developed at subnational, national, and global levels (e.g. Franch et al. 2021; Knaus et al. 2018). These multi-scale approaches may provide another opportunity to check for consistency in population estimates, but caution is required, as large differences can indicate underlying misconceptions in the overall approach, analytical biases, or simply lack of robust data. For example, Callaghan et al. (2021) attempted to estimate global bird population sizes by modelling the relationship between eBird reporting rates and independent estimates and extrapolating globally, but failed to account for extreme uncertainty and unquantifiable biases (Robinson et al. 2022). This generated unreliable population estimates, such as 2.7 million individuals of Balearic Shearwater *Puffinus mauretanicus* (Callaghan et al. 2021) compared with c.3,000 breeding pairs in both ERLoB and EBBA2 (see Appendix S2). To conclude, the main messages of this study are: (1) comparisons between population estimates may provide useful information on how to improve estimates; (2) estimates based on robust methods are better than expert-based assessments; (3) non-threatened species require better estimates; (4) harmonising protocols between countries is desirable; (5) southern European countries in particular seem to require more effort on monitoring and analyses. Reliable national population estimates are crucial for producing the essential regional, continental, and global bird population estimates required to address current conservation challenges.

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