Interactive effects of fearfulness and geographical location on bird population trends

Mario Díaz[a], José Javier Cuervo[b], Tomas Grim[c], Einar Flensted-Jensen[d], Juan Diego Ibáñez-Álamo[e], Jukka Jokimäki[f], Gábor Markó[g,h,i], Piotr Tryjanowski[j] and Anders Pape Møller[k]

[a]Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (BGC-MNCN-CSIC), c/Serrano 115bis, E-28006 Madrid, Spain, [b]Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales, CSIC, E-28006 Madrid, Spain, [c]Palacky University, Department of Zoology and Laboratory of Ornithology, CZ-77146 Olomouc, Czech Republic, [d]Cypresvej 1, DK-9700 Brønderslev, Denmark, [e]Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain, [f]Nature Inventory and EIA-services, Arctic Centre, University of Lapland, P. O. Box 122, FI-96101 Rovaniemi, Finland, [g]Ecology Research Group, Hungarian Academy of Sciences, Hungarian Natural History Museum, Eötvös Loránd University, Pázmány Péter sétány 1/c, H-1117 Budapest, Hungary, [h]Eötvös Loránd University, Behavioral Ecology Group, Department of Systematics, Zoology and Ecology, Pázmány Péter sétány 1/c, H-1117 Budapest, Hungary, [i]Department of Plant Pathology, Corvinus University of Budapest, Ménesi út 44, H-1118 Budapest, Hungary, [j]Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, PL-60-625 Poznań, Poland, [k]Laboratoire d'Ecologie, Systématique et Evolution, CNRS UMR 8079, Université Paris-Sud, Bâtiment 362, F-91405 Orsay Cedex, France

Address correspondence to M. Díaz. E-mail Mario.Diaz@ccma.csic.es

Short title: Population trends and fearfulness

ABSTRACT

Animal populations are currently under pressure from multiple factors that include human land use and climate change. They may compensate for such effects by reducing, either by habituation or by natural selection, the distance at which they flee from humans (i.e., flight initiation distance, FID), and this adaptation may improve their population trends. We analyzed population trends of common breeding birds in relation to FID and geographical location (latitude, longitude, and marginality of the breeding distribution) across European countries from Finland in the north to Spain in the south, while also considering other potential predictors of trends like farmland habitat, migration, body size and brain size. We found evidence of farmland, migratory and smaller-sized species showing stronger population declines. In contrast, there was no significant effect of relative brain size on population trends. We did not find evidence for main effects of FID and geographical location on trends after accounting for confounding and interactive effects; instead, FID and location interacted to generate complex spatial patterns of population trends. Trends were more positive for fearful populations northwards, westwards and (marginally) towards the centre of distribution areas, and more negative for fearless populations toward the south, east, and the margins of distribution ranges. These findings suggest that it is important to consider differences in population trends among countries, but also interaction effects among factors, because such interactions can enhance or compensate for negative effects of other factors on population trends.

Key-words: breeding birds, flight initiation distance, latitude, longitude, marginality of distribution.

INTRODUCTION

Human disturbance of wild organisms is a common cause of concern in a world with a rapidly increasing human population (Wong and Candolin 2012; Ehrlich and Ehrlich 2013). Such effects of disturbance include release of stress hormones (Wingfield and Ramenofsky 1999), increased metabolic rate (Belanger and Bédard 1990), reduction in foraging activity (Madsen 1998a; 1998b), displacement from preferred foraging and roosting sites and changes in diurnal rhythms (Madsen and Fox 1995) and non-lethal effects of predation (Abrams 1991). These factors on their own and in combination may have effects on the condition of animals and hence on their reproduction and survival prospects. A common behavioral measure of proneness to disturbance by humans and animals alike is the flight initiation distance (FID): The distance at which an animal takes flight when approached by a potential predator (Cooper and Blumstein 2015). Because all animals continuously have to weigh the risk of falling prey to a predator by fleeing too late when approached against the benefits of staying put and hence continuing to feed and/or rest, FID constitutes an instantaneous measure of this individual trade-off. Cooke (1980) noticed that urban birds had much shorter flight distances than rural populations of the same species, and that this difference depended on body size, the difference being larger in small species with high metabolism. This change in behavior between urban and rural habitats allowed birds to coexist with humans even at high human population densities, which are a cause of frequent disturbance. Parallel latitudinal trends in FID and raptor abundance in paired urban and rural sites suggest that birds, besides responding to human presence, also adjust their behavior in response to natural levels of disturbance by predators (see Díaz et al. 2013 and references therein).

It has been noticed that human disturbance at seabird colonies linked to escape behavior and FID could result in altered habitat use and reduced reproductive performance (Burger 1981; Burger and Gochfeld 1981). Therefore, FID can be a useful tool in conservation including assessment of levels of disturbance and susceptibility to disturbance (Madsen 1995; 1998a; 1998b;

Weston et al. 2012). The population consequences of FIDs can be investigated by relating population trends to FID (Møller 2008). We should expect species with long FIDs for their body size to show declining population trends because such species should be more prone to get disturbed by humans. Among 56 species of birds, FID accounted for 33% of the variance in population trends in Denmark, with effect sizes ranging from 0.36 to 0.58 in different analyses. Therefore, species with long FIDs for their body size had declining populations while species with short FIDs had increasing populations even when controlling statistically for potentially confounding effects. However, a study on population trends in the UK in relation to predictors that included FID recorded in Denmark did not find significant relationship between FID and population trends (Thaxter et al. 2010). This raises the question whether population trends and FID should originate from the same geographic location to make analyses meaningful.

Many national and international monitoring programs tally population trends of organisms as diverse as birds, mammals, butterflies and bumblebees. In particular, birds have been popular targets for monitoring since the 1960's in many countries in Europe, and population trends based on European continent-wide monitoring have been published since 1980 (European Bird Census Council, http://www.ebcc.info/index.php?ID=509). According to these data, while many species have increased in distribution and abundance, a majority, at least in specific habitats such as farmland, have shown a clear decline. Although humans either directly or indirectly play a major role in determining long-term population trends of birds in Europe (Reif 2013), the underlying mechanisms remain poorly understood. In addition, population trends vary across the distribution range of species. Cuervo and Møller (2013) found stronger increases in northern populations and greater fluctuations in marginal populations, somewhat expected from influences of global warming on climatic niches (Hampe and Petit 2005), and Donald, Green and Heath (2001) and Reif et al. (2011) showed longitudinally varying trends. Reif et al. (2011) also showed an interesting difference in the effect of relative brain size on trends at both sides of the iron curtain, consistent with the differences in land-use intensity across Europe. These intriguing and varying patterns, and the need to optimize conservation priorities, mean that there are good reasons to investigate patterns of population trends at different spatial scales in an attempt to elucidate the underlying mechanisms, including the potential effects of FID.

The objectives of this study were to test whether population trends were related to FID, and whether these influences varied across the European continent. If spatial changes in FID could partially compensate for the main effects of factors of global change on trends, we predicted significant interactions between FID and latitude, longitude and marginality on trends. We also tested whether previously established predictors of population trends such as farmland habitat, migration distance, body mass or brain mass affected the relationship between population trend and FID. Overall, elucidating geographical variation in the relationships between trends and recent responses of organisms to changes in the level of human activities will help us to understand our impact on wild populations of animals and eventually to reduce such impacts.

METHODS

We recorded FID for a total of 159 species during the breeding seasons 2009-2010 at nine locations from eight countries along a wide latitudinal gradient across Europe, from Finland in the north to Spain in the south, by using a standard procedure developed by Blumstein (2006). These data are reported in Díaz et al. (2013). In brief, we walked at ordinary walking speed towards a bird recording the distance from the bird when we started walking, the distance at which the birds initiated escape, and the bird's height in the vegetation. This information was used to estimate FID. In order to account for the height at which individuals were perched, FID was calculated as the Euclidean distance between the approaching human and the focal bird (which equals the square-root of the sum of the squared flight distance and the squared height in the vegetation). Observers wore neutrally colored clothes and behaved as normal pedestrians. FID was measured by a number of trained observers and therefore data were pooled for analysis. We used the FID estimates for rural populations in each location, which consisted of paired rural and urban sites (Díaz et al. 2013), because the population size estimates used to assess trends for each country are mostly based on data coming from non-urban populations (Cuervo and Møller 2013). Data for the two Spanish sites were averaged to obtain a single country-level estimate.

Population trends for breeding birds in all European countries for which we had information on FID (Finland, Norway, Denmark, Poland, Czech Republic, Hungary, France and Spain) were obtained from Cuervo and Møller (2013). Available population size estimates for each bird species and country were regressed on years, and the slope of this regression was used as a proxy for population trend. We used time series of 7-27 years gathered until 2004-2008 depending on countries and species (see Cuervo and Møller 2013 for details and a full discussion of the quality of trend estimates).

Latitude and longitude for each country were estimated as the coordinates of the mid-point between the northernmost and the southernmost, and between the easternmost and the westernmost, mainland points of every country, excluding islands except for Denmark. Latitude and longitude for each country were considered the latitude and longitude for all bird populations in that particular country regardless of the actual distribution of every species within the country. Marginality of each bird population was estimated by comparing two distances (in degrees): L is the distance between the population (i.e., the country) latitude and the northernmost or the southernmost (the one that resulted in a shorter distance) limits of the breeding distribution range of the species. L was set to zero in the few cases in which the country latitude index was more southern than the southernmost limit of the species range or more northern than the northernmost limit of the species range. C is the distance between the population latitude and the latitude of the mid-point between the northernmost and the southernmost limits of the breeding distribution range of the species. Marginality was computed as $\log_{10}(C+1) - \log_{10}(L+1)$, with positive values representing marginal populations (the distance to the range centre was larger than the distance to the nearest limit) and negative values central populations (the distance to the range centre was smaller than the distance to the nearest limit). These values were transformed by adding the absolute value of the most negative number and dividing by the largest value resulting from the previous addition, to ensure that marginality estimates ranged from 0 (central population) to 1 (marginal population; see Cuervo and Møller 2013 for details).

Bird population trends have previously been shown to be systematically affected by body size, migration distance, farmland habitat and relative brain size (reviews in Møller 2008; Møller, Rubolini and Lehikoinen 2008; Reif 2013). We extracted information on mean body mass of adult birds of each species from Cramp and Perrins (1977-1994). Migration distances (mean of the northernmost and the southernmost latitudes of the breeding distribution range minus the corresponding mean for the wintering distribution range) were taken from Møller, Rubolini and Lehikoinen (2008). Farmland habitat was coded as 1 (species depending on arable and/or mixed farmland) or 0 (species depending on other habitat types) following Appendix 2 in Tucker and Evans (1997). Relative brain sizes were the residuals of a log-log phylogenetically corrected regression of brain mass on body mass based on a sample of 567 bird species (Møller, 2008); brain mass data were obtained from Garamszegi, Møller and Erritzøe (2002), Iwaniuk and Nelson (2002), Galván and Møller (2011) and Møller and Erritzøe (2014).

We $\log_{10}$-transformed FID, population trend and migration distance before analyses. Within-species repeatability of FID and trends across Europe was computed following Lessells and Boag (1987), and differences between them and the null hypothesis of zero repeatability were tested following Becker (1984). Significant repeatabilities imply statistical dependence of estimates for the same species in different countries, a fact that will bias results based on phylogenetically-structured databases (Garamszegi and Møller 2010). As species occupy a variable number of study locations and countries (Díaz et al. 2013; Cuervo and Møller 2013), geographical trends could be partly due to phylogenetic effects. To control for such relationships we used phylogenetic generalized least square regression (PGLS) models implemented in R (Díaz et al. 2013). After estimating the phylogenetic scaling parameter lambda (λ), we calculated the phylogenetically corrected partial correlations between the variables of interest. Different populations of the same species were considered as polytomies with a constant small genetic distance of 10^{-10} between them. We used the R script and the edited phylogeny supplied as Supplementary Files S1 and S2 in Díaz et al. (2013), but using the function *pglm3.3.r* instead of the *pglm3.1.r* to fit type III (orthogonal) models. We used the phylogeny reported in Thuiller et al. (2011). The dependent variable was the population trend, confounding variables were farmland habitat, migration distance, body size and relative brain size, and predictors FID, latitude, longitude, marginality, and the first-order interaction between FID and geographical variables. Predictors were computed from the corresponding input variables ($\log_{10}$FID and geographical variables) by standardizing them (i.e., by subtracting sample means and dividing by standard deviations), in order to allow direct comparison of effect sizes (Pearson's product-moment correlation coefficients computed from *P* values of t-tests according to Lipsey and Wilson 2001) and to make main effects biologically interpretable even when involved in interactions (Schielzeth 2010).

RESULTS

We collected data on mean FID and on recent population trends from 338 populations of 129 bird species. Data on farmland habitat, body size and migration distance were available for all of them, while there were no data on brain size for 9 species (Appendix A). Both FID and trends were significantly repeatable within species ($F_{1, 209} = 3.08$, $P < 0.001$ and $F_{1, 209} = 1.45$, $P = 0.009$, respectively). FID was significantly more repeatable than population trends (r =

0.45 ± 0.04 (SD) *vs.* $r = 0.15 \pm 0.05$; $t_{338} = 4.0$, $P < 0.001$; Becker 1984); in other words, geographical variation within species was larger for population trends than for mean fearfulness as reflected by FID.

Log-transformed population trends were significantly related to $\log_{10}$FID ($F_{1, 337} = 7.96$, $P = 0.005$, $r^2 = 0.02$), but not to latitude ($F_{1, 337} = 0.00$, $P = 0.967$, $r^2 = 0.00$), longitude ($F_{1, 337} = 0.40$, $P = 0.530$, $r^2 = 0.00$) or marginality ($F_{1, 337} = 0.62$, $P = 0.432$, $r^2 = 0.00$) when predictor effects were analyzed one by one. The relationship with FID vanished, however, after correcting for significant effects of farmland habitat, migration distance and body mass (effect sizes for these three confounding variables ranged from 0.14 to 0.16), while also accounting for phylogenetic effects (Table 1). Trends were more negative for farmland birds, long-distance migrants and smaller species (Table 1). Relative brain size showed no significant effects on population trends, which did not show significant geographical trends either (Table 1). However, FID showed significant interactive effects with latitude and longitude, and marginally-significant interactive effects with marginality, with effect sizes ranging from 0.10 to 0.13 (Table 1, Fig. 1). FID-trend relationships were more positive northwards, westwards and (marginally) towards the centre of distribution areas (Table 1, Fig. 1). These interactions implied that trends were more negative for fearless populations toward the south, east, and the margins of distribution ranges.

DISCUSSION

Many different factors have been proposed to account for population trends of birds (reviewed in Reif 2013). These variables range from migration and the perils of living under different climate regimes (Hjort and Lindholm 1978; Baillie and Peach 1992; Sanderson et al. 2006; Reif 2013), relative brain mass that facilitates the ability to cope with changing environments (Shultz et al. 2005; Møller, Rubolini and Lehikoinen 2008; Reif et al. 2011), thermal range and hence the ability to cope with changing climatic conditions (Jiguet et al.

2007, 2010), the number of broods with species producing more broods doing better (Julliard, Jiguet and Couvet 2004), and body mass with large sized species with smaller total populations having negative population trends (Bennett and Owens 2002).

Geographical variation in trends within breeding ranges of species are also expected due to geographical changes in the suitability of environmental conditions (the niche variation hypothesis; Brown 1984), in the intensity of global change drivers (Hampe and Petit 2005; Reif et al. 2011; Tryjanowski et al. 2011) or in both (Díaz et al. 1998). It has been suggested that population responses of birds to environmental gradients may be highly species-specific, even precluding broad generalizations (Taper, Böhning-Gaese and Brown 1995); however, Cuervo and Møller (2013) have recently shown that changes in population size of breeding birds in Europe are the strongest at the margins of the breeding distribution, but are particularly negative at the southern-most range margins, where increasing temperatures may render environmental conditions for maintenance of viable populations the most difficult. Climate change has affected the distribution of many species, and range margins have on average moved pole-wards (Chen et al. 2011), and recent work has shown fine-grained effects of climate change on local population trends (Jiguet et al. 2010). Longitudinal variation due to differences in land-use intensity between Western and Eastern Europe have also been documented, especially for farmland birds (Donald, Green and Heath 2001). However, we did not find evidence for direct effects of these variables after accounting for effects of third variables and their interactions. Reif et al. (2011) suggested that longitudinal effects of the iron curtain dividing industrialized Western Europe from more extensive land use in Eastern Europe interacted with relative brain mass to account for spatial heterogeneity in population trends. Here we found no evidence of an effect of relative brain mass on population trends contrary to previous reports (Shultz et al. 2005; Thaxter et al. 2010; Reif et al. 2011). We hypothesize that these differences among studies may arise from the inclusion of different predictors and their interactions, but also from inclusion of multiple countries that differ in significant predictors of population trends. Studies such as this, encompassing the widest ranges of variation of relevant variables available even at the expense of lower precision within ranges, are thus essential to detect non-linear and interactive relationships of geographically-varying conditions on local abundance and trends (e.g. Jiguet et al. 2010; Concepción et al. 2012).

Bird species breeding on farmland displayed the steepest declines. This is probably a consequence of agriculture having become ever more industrialized and intensified and thereby disproportionately negatively affecting farmland specialists (Fuller et al. 1995; Chamberlain et al. 2000; Møller, Rubolini and Lehikoinen 2008; Reif 2013). Here we found evidence consistent with this general trend, with farmland species showing more negative population trends than non-farmland birds. Migration has been predicted to affect population trends because migrants are affected negatively by land-use and climate change in their breeding range, during migration and in their winter quarters (Hjort and Lindholm 1978; Baillie and Peach 1992; Sanderson et al. 2006; Møller, Rubolini and Lehikoinen 2008; Reif 2013). Here we found a negative effect of migration distance on population trends, when accounting for the effects of the remaining variables.

We hypothesized that population trends would be negatively related to FID, as reported by Møller (2008) for European birds. Most recent work indicates that FID can be considered a general measure of the willingness of animals to be involved in risky activities such as foraging and courtship under perceived risky conditions (reviewed in Cooper and Blumstein 2014, 2015). Such willingness to take risks would depend on levels of risk (abundance and identity of predators and other sources of risk, such as humans), but also on potential fitness benefits (ie. it will be worth taking more risks if the expected fitness consequence of the reward is larger, as under food shortage or time-limited conditions), after accounting for species- and population-specific proneness to risk-taking associated with phylogeny, urban habitat or life-history traits such as body size or migratory behavior (Díaz et al. 2013). We found an overall main effect of FID in this study, which however vanished when considering interactive effects with geographical location. This fact suggests that the observed geographical variation in trends would in fact be the net result of complex interactions between spatial variations in many factors proposed to drive population trends (Reif 2013), as well as on the varying effects of risk-taking behaviors on trends. Our results showed that fearfulness of bird populations (i.e., long FIDs) enhanced population trends where such trends were already less negative, as in northern European populations (Cuervo and Møller 2013), or where land use intensity is higher, as in western European countries (Tryjanowski et al. 2011), but these relationships reversed at more stressful extremes of spatial gradients, such as southern and marginal locations. We interpret these interactions as implying that we cannot assess predictors by considering solely their main effects. We are unaware of any previous studies investigating such interaction effects as predictors of population trends.

In conclusion, we have analyzed for the first time how geographical patterns of population trends of birds in Europe, as related to natural and man-made geographical variation in environmental factors such as climate, predation risk and land use, interact with a measure of the tolerance of birds to human disturbance. Overall we found that proneness to risk-taking as estimated by short FIDs enhanced population resilience to disturbance in a changing world, as more tolerant individuals will reduce the costs associated with escape behaviors (Cooper and Blumstein 2014). In contrast, bird species and populations less tolerant of frequent disturbance, by humans or wild and domestic predators, would perform worse, especially at the southern- and eastern-most edges of breeding distributions. Further studies including fine-grained estimates of FID, trends and secondary influences on them (eg. Jiguet et al. 2010) carried out over wide geographical gradients would be needed to ascertain whether these patterns were due to geographical variations in risks, fitness benefits of risk-taking, or both.

ACKNOWLEDGMENTS

Comments by two anonymous referees were very helpful during revision. We thank Martin Flade, Magne Husby, Jaroslaw Krogulec, Robert Kwak, Jiří Reif, Norbert Teufelbauer, Tibor Szép and Dansk Ornithologisk Forening for information on population size estimates. JJC was supported by the Spanish National Research Council (grant EST001196). This paper is a contribution by MD to the project RiskDisp (CGL2009-08430) and to the thematic networks GlobiMed (www.globimed.net) and REMEDINAL III.

APPENDIX A. SUPPLEMENTARY MATERIAL

Information on bird species, country, population trend, mean FID (m), migration distance (ºlatitude), body mass (g), latitude and longitude of the population/country, marginality of the population within the species breeding range, relative brain size and farmland habitat. Relative brain size is residuals from a log-log phylogenetically corrected regression of brain mass on body mass. See Material and methods for sources and details. Nomenclature and basic phylogeny follows Thuiller et al. (2011).

REFERENCES

Abrams PA. 1991. Strengths of indirect effects generated by optimal foraging. Oikos 62:167-176.

Baillie SR, Peach WJ. 1992. Population limitation in Palaearctic-African migrant passerines. Ibis 134:120–132.

Becker WA. 1984. A manual of quantitative genetics. Washington: Pullman Academic Enterprises.

Belanger L, Bédard J. 1990. Energetic cost of man-induced disturbance to staging snow geese. J. Wildl. Manage. 54:36-41.

Bennett PM, Owens IPF. 2002. Evolutionary ecology of birds. Oxford: Oxford Univ. Press.

Blumstein DT. 2006. Developing an evolutionary ecology of fear: How life history and natural history traits affect disturbance tolerance in birds. Anim. Behav. 71:389–399.

Brown JH. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124:255-279.

Burger J, Gochfeld M. 1981. Discrimination of the threat of direct versus tangential approach to the nest by incubating herring and great black-backed gulls. J. Comp. Physiol. Psychol. 95:676–684.

Burger J. 1981. The effect of human activity on birds at a coastal bay. Biol. Conserv. 21:231–241.

Chamberlain DE, Fuller RJ, Bunce RGH, Duckworth JC, Shrubb M. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl. Ecol. 37:771–788.

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024-1026.

Concepción ED, Díaz M, Kleijn D, Báldi A, Batáry P, Clough Y, Gabriel D, Herzog F, Holzschuh A, Knop E, Marshall JP, Tscharntke T, Verhulst J 2012. Interactive effects of landscape context constrains the effectiveness of local agri-environmental management. J. Appl. Ecol. 49:695-705.

Cooke AS. 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. Biol. Conserv. 18:85-88.

Cooper Jr WE, Blumstein DT. 2014. Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. Behav. Ecol. 25:44-52.

Cooper Jr WE, Blumstein DT. 2015. Escaping from predators: An integrative view of escape decisions and refuge use. Cambridge: Cambridge Univ. Press.

Cramp S, Perrins CM (eds) 1977-1994. The birds of the Western Palearctic. Oxford: Oxford Univ. Press.

Cuervo JJ, Møller AP. 2013. Temporal variation in population size of European bird species: Effects of latitude and marginality of distribution. PLoS One 8:e77654.

Díaz M, Carbonell R, Santos T, Tellería JL. 1998. Breeding bird communities in pine plantations of the Spanish plateaux: Biogeography, landscape and vegetation effects. J. Appl. Ecol. 35:562-574.

Díaz M, Møller AP, Flensted-Jensen E, Grim T, Ibáñez-Álamo JD, Jokimäki J, Markó G, Tryjanowski P. 2013. The geography of fear: A latitudinal gradient in anti-predator escape distances of birds across Europe. PloS One 8:e64634.

Donald PF, Green RE, Heath MF. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. B 268:25–29.

Ehrlich PR, Ehrlich AH. 2013. Can a collapse of global civilization be avoided? Proc. R. Soc. B 280:20122845.

Forstmeier W, Schielzeth H. 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav. Ecol. Sociobiol. 65:47-55.

Fuller R J, Gregory RD, Gibbons DW, Marchant JH, Wilson JD, Baillie SR, Carter N. 1995. Population declines and range contractions among lowland farmland birds in Britain. Conserv. Biol. 9:1425-1441.

Galván I, Møller AP. 2011. Brain size and the expression of pheomelanin-based colour in birds. J. Evol. Biol. 24:999-1006.

Garamszegi LZ, Møller AP. 2010. Effects of sample size and intraspecific variation in phylogenetic comparative studies: a meta-analytic review. Biol. Rev. 85:797–805.

Garamszegi LZ, Møller AP, Erritzøe J. 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proc. R. Soc. B 269:961–967.

Hampe A, Petit RJ. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8:461-467.

Hjort C, Lindholm CG. 1978. Annual bird ringing totals and population fluctuations. Oikos 30:387–392.

Iwaniuk AN, Nelson JE. 2002. Can endocranial volume be used as an estimate of brain size in birds? Can. J. Zool. 80:16-23.

Jiguet F, Devictor V, Ottvall R, Van Turnhout C, Van der Jeugd H, Lindström Å. 2010. Bird population trends are linearly affected by climate change along species thermal ranges. Proc. R. Soc. B 277:3601–3608.

Jiguet F, Gadot AS, Julliard R, Newson SE, Couvet D. 2007. Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biol. 13:1672–1684.

Julliard R, Jiguet F, Couvet D. 2004. Common birds facing global changes: What makes a species at risk? Global Change Biol. 10:148 –154.

Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116-121.

Lipsey MW, Wilson DB. 2001. Practical meta- analysis. Applied Social Research Methods Series 39. London: Sage. www.campbellcollaboration.org/escalc/html/EffectSizeCalculator-Home.php

Madsen J. 1995. Impacts of disturbance on migratory waterfowl. Ibis 137:S67–S74.

Madsen J. 1998a. Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of disturbance effects of recreational activities. J. Appl. Ecol. 35:386–397.

Madsen J. 1998b. Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. J. Appl. Ecol. 35:398–417.

Madsen J, Fox AD. 1995. Impacts of hunting disturbance on waterbirds: A review. Wildl. Biol. 1:193-207.

Møller AP. 2008. Flight distance and population trends in European breeding birds. Behav. Ecol. 19:1095–1102.

Møller AP, Erritzøe J. 2014. Predator–prey interactions, flight initiation distance and brain size. J. Evol. Biol. 27:34-42.

Møller AP, Rubolini D, Lehikoinen E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proc. Nat. Acad. Sci. USA 105:16195–16200.

Reif J. 2013. Long-term trends in bird populations: a review of patterns and potential drivers in North America and Europe. Acta Ornithol. 48:1-16.

Reif J, Böhning-Gaese K, Flade M, Schwarz J, Schwager M. 2011. Bird population trends across iron curtain, brain matters. Biol. Conserv. 144:2524–2533.

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ. 2006. Long-term population declines in Afro-Palearctic migrant birds. Biol. Conserv. 131:93–105.

Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients. Met. Ecol. Evol. 1:103–113.

Shultz S, Bradbury RB, Evans KL, Gregory RD, Blackburn TM. 2005. Brain size and resource specialization predict long-term population trends in British birds. Proc. R. Soc. B 272:2305–2311.

Taper ML, Böhning-Gaese K, Brown JH. 1995. Individualistic responses of bird species to environmental change. Oecologia 101:478-486.

Thaxter CB, Joys AC, Gregory RD, Baillie SR, Noble DG. 2010. Hypotheses to explain patterns of population change among breeding bird species in England. Biol. Conserv. 143 2006-2019.

Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araújo MB 2011. Consequences of climate change on the tree of life in Europe. Nature 470:531–534.

Tryjanowski P, Hartel T, Báldi A, Szymański P, Tobolka M, Herzon I, Goławski A, Konvička M, Hromada M, Jerzak L, Kujawa K, Lenda M, Orłowski M, Panek M, Skórka P, Sparks TH, Tworek S,Wuczyński A, Żmihorski M. 2011. Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. Acta Ornithol. 46:1–12.

Tucker GM, Evans MI (comp) 1997. Habitats for birds in Europe. A conservation strategy for the wider environment. Cambridge: BirdLife International.

Weston MA, McLeod EM, Blumstein DT, Guay PJ. 2012. A review of flight-initiation distances and their application to managing disturbance to Australian birds. Emu 112:269-286.

Wingfield JC, Ramenofsky M. 1999. Hormones and the behavioral ecology of stress. In: Stress Physiology in Animals. Balm PHM, editor. Sheffield: Sheffield Academic Press. pp. 1-51.

Wong B, Candolin U. 2012. Behavioural responses to a changing world: Mechanisms and consequences. Oxford: Oxford Univ. Press.

Fig. 1. Latitudinal and longitudinal variation in standardized regression coefficients (ß±SE) between population trends of European birds (residuals from a multiple regression between log-transformed trends, migration distance, body mass, relative brain mass, farmland habitat, marginality, and either longitude or latitude) and fearfulness (flight initiation distance, FID, log-transformed). Lines are best-fit regressions.

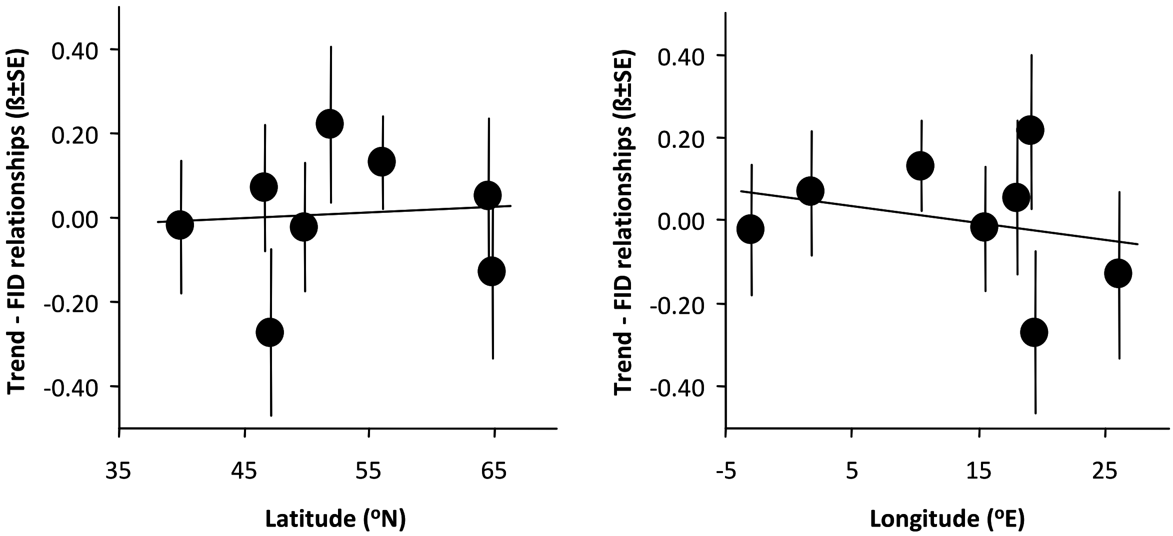

Table 1. Relationships between population trends of European birds (response variable) and geographical location (latitude, longitude and marginality) and fearfulness (flight initiation distance, FID), after accounting for effects of farmland habitat, migration distance, body mass and relative brain size on trends and correcting for the effect of the phylogenetic structure of the data set, that was, however, not significant (λ = 0.000, χ^2 = -0.012, P = 1.000). The full model (no removal of non-significant terms was done, as recommended by Forstmeier and Schielzeth 2011) had the statistics F = 4.73, d.f. = 12, 329, adjusted r^2 = 0.11, P < 0.0001. Effect sizes are Pearson's product-moment correlation coefficients.

Source	estimate (SE)	*t*	*P*	Effect size
Farmland	-0.008(0.003)	-2.50	0.013	0.14
Migration distance	-0.006(0.002)	-2.71	0.007	0.15
Body mass	0.018(0.006)	2.93	0.004	0.16
Relative brain size	-0.014(0.010)	-1.46	0.147	0.08
FID	0.000(0.002)	0.16	0.876	0.01
Latitude	-0.002(0.002)	-1.07	0.286	0.06
Longitude	0.003(0.002)	1.50	0.134	0.08
Marginality	0.001(0.002)	0.38	0.706	0.02
FID x Latitude	0.005(0.002)	2.29	0.023	0.13
FID x Longitude	-0.004(0.002)	-2.27	0.024	0.12
FID x Marginality	-0.003(0.002)	-1.76	0.079	0.10

APPENDIX A. SUPPLEMENTARY MATERIAL

Information on bird species, country, population trend, mean FID (m), migration distance (ºlatitude), body mass (g), latitude and longitude of the population/country, marginality of the population within the species breeding range, relative brain size and farmland habitat. Relative brain size is residuals from a log-log phylogenetically corrected regression of brain mass on body mass. See Material and methods for sources and details. Nomenclature and basic phylogeny follows Thuiller et al. (2011).

Species	Country	Popul. trend	FID (m)	Migration distance (º latitude)	Body mass (g)	Latitude	Longitude	Marginality	Rel. brain size	Farmland
Accipiter nisus	Denmark	0.002	36.14	12.79	204.0	56.16	10.38	0.585	0.464	0
Acrocephalus palustris	Czech Rep.	-0.010	14.14	66.84	12.0	49.80	15.48	0.599	-0.281	0
Acrocephalus palustris	Denmark	0.012	8.76	66.84	12.0	56.16	10.38	0.683	-0.281	0
Acrocephalus schoenobaenus	Denmark	-0.003	6.93	62.10	11.9	56.16	10.38	0.595	-0.357	0
Acrocephalus scirpaceus	Denmark	-0.009	6.59	44.60	11.8	56.16	10.38	0.659	-0.330	0
Aegitahlos caudatus	France	0.000	5.27	0.00	8.8	46.71	1.72	0.489	-0.385	0
Aegithalos caudatus	Spain	-0.010	10.84	0.00	8.8	39.90	-2.99	0.500	-0.385	0
Aegithalos caudatus	Hungary	0.155	6.36	0.00	8.8	47.16	19.51	0.489	-0.385	0
Alauda arvensis	Denmark	-0.008	31.42	13.02	36.4	56.16	10.38	0.581	-0.033	1
Alauda arvensis	Poland	0.017	45.44	13.02	36.4	51.92	19.13	0.533	-0.033	1
Alcedo atthis	France	-0.042	8.54	0.00	32.4	46.71	1.72	0.429	-0.099	0
Alectoris rufa	Spain	0.004	37.08	0.00	477.5	39.90	-2.99	0.732	0.303	1
Anas platyrhynchos	Denmark	0.048	28.76	8.13	1119.0	56.16	10.38	0.579	0.720	0
Anas platyrhynchos	France	0.012	4.81	8.13	1119.0	46.71	1.72	0.533	0.720	0
Anas platyrhynchos	Norway	0.123	11.11	8.13	1119.0	64.56	18.01	0.709	0.720	0
Anas platyrhynchos	Poland	0.014	88.00	8.13	1119.0	51.92	19.13	0.531	0.720	0
Anser anser	Denmark	0.107	180.00	12.28	3464.5	56.16	10.38	0.578	1.080	0
Anthus pratensis	Denmark	-0.027	13.22	15.64	19.3	56.16	10.38	0.595	-0.312	0
Anthus pratensis	Finland	0.002	28.31	15.64	19.3	64.95	26.07	0.730	-0.312	0
Anthus pratensis	Norway	0.001	5.82	15.64	19.3	64.56	18.01	0.722	-0.312	0
Anthus pratensis	Poland	-0.046	32.00	15.64	19.3	51.92	19.13	0.619	-0.312	0
Anthus spinoletta	France	-0.037	7.50	21.27	21.5	46.71	1.72	0.549	-0.237	0
Anthus trivialis	Denmark	-0.013	10.90	47.07	23.4	56.16	10.38	0.587	-0.210	0
Apus apus	Denmark	0.006	38.10	59.39	39.7	56.16	10.38	0.585	-0.205	0
Ardea cinerea	Denmark	0.195	62.08	1.50	1433.0	56.16	10.38	0.330	0.903	0
Ardea cinerea	France	0.049	26.00	1.50	1433.0	46.71	1.72	0.289	0.903	0
Ardea cinerea	Norway	0.207	50.00	1.50	1433.0	64.56	18.01	0.596	0.903	0
Athene noctua	Spain	-0.008	25.73	0.00	168.0	39.90	-2.99	0.439	0.579	1
Aythya fuligula	Denmark	0.015	10.68	17.08	656.5	56.16	10.38	0.603	0.651	0
Buteo buteo	Czech Rep.	0.012	55.26	29.57	806.5	49.80	15.48	0.502	0.896	0
Buteo buteo	Denmark	0.033	60.01	29.57	806.5	56.16	10.38	0.591	0.896	0
Carduelis cannabina	Czech Rep.	-0.011	14.93	4.11	19.0	49.80	15.48	0.547	-0.187	0
Carduelis cannabina	Denmark	-0.011	10.80	4.11	19.0	56.16	10.38	0.635	-0.187	0
Carduelis cannabina	Poland	-0.062	12.89	4.11	19.0	51.92	19.13	0.574	-0.187	0
Carduelis cannabina	Spain	-0.009	18.51	4.11	19.0	39.90	-2.99	0.532	-0.187	0
Carduelis carduelis	Czech Rep.	-0.009	14.95	1.16	15.6	49.80	15.48	0.564	-0.240	0
Carduelis carduelis	Denmark	0.169	10.77	1.16	15.6	56.16	10.38	0.667	-0.240	0
Carduelis carduelis	France	-0.002	11.00	1.16	15.6	46.71	1.72	0.524	-0.240	0

Carduelis carduelis	Spain	-0.022	11.52	1.16	15.6	39.90	-2.99	0.490	-0.240	0
Carduelis carduelis	Hungary	0.032	8.99	1.16	15.6	47.16	19.51	0.530	-0.240	0
Carduelis chloris	Czech Rep.	-0.021	12.98	1.34	27.7	49.80	15.48	0.507	-0.057	0
Carduelis chloris	Denmark	0.036	6.53	1.34	27.7	56.16	10.38	0.581	-0.057	0
Carduelis chloris	Finland	0.253	15.22	1.34	27.7	64.95	26.07	0.730	-0.057	0
Carduelis chloris	France	-0.020	7.65	1.34	27.7	46.71	1.72	0.502	-0.057	0
Carduelis chloris	Spain	0.033	15.92	1.34	27.7	39.90	-2.99	0.518	-0.057	0
Carduelis chloris	Hungary	0.050	18.43	1.34	27.7	47.16	19.51	0.501	-0.057	0
Carduelis chloris	Norway	0.022	5.88	1.34	27.7	64.56	18.01	0.720	-0.057	0
Carduelis chloris	Poland	0.009	15.11	1.34	27.7	51.92	19.13	0.531	-0.057	0
Carduelis flammea	Denmark	-0.001	4.50	9.46	13.1	56.16	10.38	0.622	-0.263	0
Carduelis flammea	Norway	-0.027	12.00	9.46	13.1	64.56	18.01	0.653	-0.263	0
Carduelis spinus	Finland	0.015	10.11	6.83	13.8	64.95	26.07	0.740	-0.272	0
Carpodacus erythrinus	Finland	-0.014	9.44	0.00	13.8	64.95	26.07	0.804	--	0
Certhia brachydactyla	France	0.031	7.12	0.00	9.2	46.71	1.72	0.635	-0.338	0
Certhia brachydactyla	Spain	0.024	11.15	0.00	9.2	39.90	-2.99	0.603	-0.338	0
Certhia familiaris	Denmark	0.015	4.47	0.00	9.2	56.16	10.38	0.582	-0.297	0
Cettia cetti	Spain	0.000	26.84	2.11	14.1	39.90	-2.99	0.564	--	0
Cisticola juncidis	Spain	-0.011	31.89	0.00	8.5	39.90	-2.99	0.337	--	0
Clamator glandarius	Spain	0.185	55.60	4.58	153.5	39.90	-2.99	0.344	0.205	0
Coccothraustes coccothraustes	Czech Rep.	-0.020	22.17	5.07	54.7	49.80	15.48	0.591	0.222	0
Coccothraustes coccothraustes	France	0.038	5.10	5.07	54.7	46.71	1.72	0.551	0.222	0
Coccothraustes coccothraustes	Hungary	0.038	24.00	5.07	54.7	47.16	19.51	0.556	0.222	0
Columba livia	France	0.024	8.00	0.00	261.0	46.71	1.72	0.403	0.303	1
Columba livia	Spain	0.007	30.87	0.00	261.0	39.90	-2.99	0.291	0.303	1
Columba livia	Hungary	0.350	6.00	0.00	261.0	47.16	19.51	0.410	0.303	1
Columba oenas	France	-0.012	17.75	3.45	494.5	46.71	1.72	0.546	0.333	1
Columba palumbus	Czech Rep.	0.028	27.26	2.03	494.5	49.80	15.48	0.521	0.365	1
Columba palumbus	Denmark	0.018	28.17	2.03	494.5	56.16	10.38	0.606	0.365	1
Columba palumbus	Finland	0.024	30.00	2.03	494.5	64.95	26.07	0.812	0.365	1
Columba palumbus	France	0.052	14.43	2.03	494.5	46.71	1.72	0.485	0.365	1
Columba palumbus	Spain	0.011	45.40	2.03	494.5	39.90	-2.99	0.461	0.365	1
Columba palumbus	Hungary	0.008	21.47	2.03	494.5	47.16	19.51	0.490	0.365	1
Columba palumbus	Norway	0.016	7.00	2.03	494.5	64.56	18.01	0.796	0.365	1
Columba palumbus	Poland	0.018	60.41	2.03	494.5	51.92	19.13	0.548	0.365	1
Corvus corax	Denmark	0.293	78.06	0.00	1200.6	56.16	10.38	0.448	1.189	0
Corvus cornix	Czech Rep.	-0.019	13.89	5.71	544.5	49.80	15.48	0.528	0.944	0
Corvus cornix	Denmark	0.011	41.15	5.71	544.5	56.16	10.38	0.579	0.944	0
Corvus cornix	Finland	-0.013	31.69	5.71	544.5	64.95	26.07	0.717	0.944	0
Corvus cornix	Hungary	0.113	24.09	5.71	544.5	47.16	19.51	0.536	0.944	0
Corvus cornix	Norway	0.001	17.30	5.71	544.5	64.56	18.01	0.708	0.944	0
Corvus corone	France	0.001	20.41	5.71	544.5	46.71	1.72	0.537	0.944	0
Corvus frugilegus	Denmark	0.031	46.53	2.32	453.5	56.16	10.38	0.645	0.904	1
Corvus monedula	Denmark	0.000	32.11	0.29	249.0	56.16	10.38	0.635	0.660	1
Corvus monedula	Finland	0.168	60.00	0.29	249.0	64.95	26.07	0.872	0.660	1
Corvus monedula	Spain	-0.030	46.86	0.29	249.0	39.90	-2.99	0.573	0.660	1
Corvus monedula	Poland	0.019	18.23	0.29	249.0	51.92	19.13	0.576	0.660	1
Cuculus canorus	Denmark	-0.010	21.72	49.38	120.5	56.16	10.38	0.562	0.164	0
Cyanopica cyanus	Spain	0.060	56.86	0.00	71.0	39.90	-2.99	0.579	0.314	0
Delichon urbica	Spain	0.026	35.51	44.25	19.6	39.90	-2.99	0.378	-0.262	0
Dendrocopos major	Czech Rep.	0.018	18.56	0.00	89.7	49.80	15.48	0.498	0.405	0
Dendrocopos major	Denmark	0.005	14.20	0.00	89.7	56.16	10.38	0.581	0.405	0
Dendrocopos major	France	0.033	14.00	0.00	89.7	46.71	1.72	0.460	0.405	0
Dendrocopos major	Spain	0.069	58.14	0.00	89.7	39.90	-2.99	0.411	0.405	0
Dendrocopos major	Hungary	-0.014	32.98	0.00	89.7	47.16	19.51	0.466	0.405	0
Dendrocopos major	Norway	0.097	9.85	0.00	89.7	64.56	18.01	0.745	0.405	0
Dendrocopos syriacus	Hungary	0.023	13.99	0.00	76.8	47.16	19.51	0.726	--	0
Dryocopus martius	France	0.069	38.71	0.00	273.0	46.71	1.72	0.517	0.870	0

Dryocopus martius	Poland	0.025	50.16	0.00	273.0	51.92	19.13	0.542	0.870	0
Egretta garzetta	France	0.041	24.50	7.53	532.5	46.71	1.72	0.400	--	0
Emberiza cirlus	Spain	-0.008	15.00	0.48	23.8	39.90	-2.99	0.583	-0.135	1
Emberiza citrinella	Czech Rep.	-0.014	15.54	4.72	26.8	49.80	15.48	0.611	-0.106	1
Emberiza citrinella	Denmark	-0.016	9.79	4.72	26.8	56.16	10.38	0.600	-0.106	1
Emberiza citrinella	Finland	-0.002	10.43	4.72	26.8	64.95	26.07	0.743	-0.106	1
Emberiza citrinella	Norway	-0.023	8.20	4.72	26.8	64.56	18.01	0.734	-0.106	1
Emberiza citrinella	Poland	-0.016	3.08	4.72	26.8	51.92	19.13	0.597	-0.106	1
Emberiza schoeniclus	Czech Rep.	0.001	28.07	10.52	18.8	49.80	15.48	0.510	-0.167	0
Emberiza schoeniclus	Denmark	-0.008	9.17	10.52	18.8	56.16	10.38	0.575	-0.167	0
Emberiza schoeniclus	Norway	-0.022	8.00	10.52	18.8	64.56	18.01	0.705	-0.167	0
Emberiza schoeniclus	Poland	0.026	36.51	10.52	18.8	51.92	19.13	0.527	-0.167	0
Erithacus rubecula	Czech Rep.	-0.001	16.71	5.00	16.4	49.80	15.48	0.510	-0.196	0
Erithacus rubecula	Denmark	0.006	8.91	5.00	16.4	56.16	10.38	0.585	-0.196	0
Erithacus rubecula	France	0.023	5.19	5.00	16.4	46.71	1.72	0.503	-0.196	0
Erithacus rubecula	Norway	-0.001	5.47	5.00	16.4	64.56	18.01	0.727	-0.196	0
Erithacus rubecula	Spain	0.015	2.24	5.00	16.4	39.90	-2.99	0.519	-0.196	0
Falco tinnunculus	Czech Rep.	-0.003	50.58	5.60	174.5	49.80	15.48	0.228	0.570	1
Falco tinnunculus	Denmark	0.019	28.35	5.60	174.5	56.16	10.38	0.294	0.570	1
Falco tinnunculus	France	-0.040	6.32	5.60	174.5	46.71	1.72	0.290	0.570	1
Falco tinnunculus	Spain	-0.012	115.49	5.60	174.5	39.90	-2.99	0.350	0.570	1
Falco tinnunculus	Hungary	-0.007	25.00	5.60	174.5	47.16	19.51	0.284	0.570	1
Ficedula hypoleuca	Denmark	-0.034	5.39	43.00	14.4	56.16	10.38	0.583	-0.364	0
Ficedula hypoleuca	Finland	0.013	6.59	43.00	14.4	64.95	26.07	0.726	-0.364	0
Ficedula hypoleuca	Norway	-0.019	7.07	43.00	14.4	64.56	18.01	0.718	-0.364	0
Fringilla coelebs	Czech Rep.	-0.010	13.62	5.54	24.2	49.80	15.48	0.499	-0.126	0
Fringilla coelebs	Denmark	0.011	9.39	5.54	24.2	56.16	10.38	0.571	-0.126	0
Fringilla coelebs	Finland	-0.002	8.50	5.54	24.2	64.95	26.07	0.710	-0.126	0
Fringilla coelebs	France	-0.003	6.55	5.54	24.2	46.71	1.72	0.500	-0.126	0
Fringilla coelebs	Spain	0.047	17.26	5.54	24.2	39.90	-2.99	0.515	-0.126	0
Fringilla coelebs	Norway	0.008	7.30	5.54	24.2	64.56	18.01	0.701	-0.126	0
Fringilla coelebs	Poland	0.002	8.76	5.54	24.2	51.92	19.13	0.522	-0.126	0
Fulica atra	Denmark	0.010	19.87	3.32	732.5	56.16	10.38	0.158	0.484	0
Galerida cristata	Spain	-0.013	36.40	0.00	44.7	39.90	-2.99	0.417	0.033	1
Gallinago gallinago	Denmark	-0.028	25.83	7.05	106.5	56.16	10.38	0.279	0.117	0
Gallinago gallinago	Finland	-0.009	54.15	7.05	106.5	64.95	26.07	0.542	0.117	0
Gallinula chloropus	Denmark	-0.015	20.00	0.00	348.5	56.16	10.38	0.400	0.296	0
Gallinula chloropus	France	0.018	10.32	0.00	348.5	46.71	1.72	0.263	0.296	0
Garrulus glandarius	Czech Rep.	0.041	39.15	0.00	161.7	49.80	15.48	0.484	0.605	0
Garrulus glandarius	Denmark	0.001	20.95	0.00	161.7	56.16	10.38	0.564	0.605	0
Garrulus glandarius	France	0.030	11.16	0.00	161.7	46.71	1.72	0.446	0.605	0
Garrulus glandarius	Hungary	0.011	27.87	0.00	161.7	47.16	19.51	0.452	0.605	0
Grus grus	Poland	0.051	100.00	39.10	4541.5	51.92	19.13	0.572	1.246	1
Haematopus ostralegus	Denmark	-0.009	40.01	21.39	531.0	56.16	10.38	0.587	0.583	0
Haematopus ostralegus	Norway	-0.010	19.00	21.39	531.0	64.56	18.01	0.714	0.583	0
Hippolais icterina	Denmark	-0.034	7.76	71.34	13.3	56.16	10.38	0.601	-0.293	0
Hippolais polyglotta	Spain	0.028	16.57	30.63	11.5	39.90	-2.99	0.619	--	0
Hirundo rustica	Czech Rep.	-0.007	15.63	42.34	19.1	49.80	15.48	0.482	-0.269	1
Hirundo rustica	Denmark	-0.008	10.15	42.34	19.1	56.16	10.38	0.561	-0.269	1
Hirundo rustica	Finland	-0.013	11.18	42.34	19.1	64.95	26.07	0.712	-0.269	1
Hirundo rustica	Poland	0.007	10.77	42.34	19.1	51.92	19.13	0.507	-0.269	1
Lanius collurio	Czech Rep.	0.046	21.31	64.73	30.7	49.80	15.48	0.554	0.008	1
Lanius collurio	Denmark	-0.011	17.39	64.73	30.7	56.16	10.38	0.639	0.008	1
Lanius collurio	Hungary	0.017	11.91	64.73	30.7	47.16	19.51	0.559	0.008	1
Lanius collurio	Poland	-0.003	35.01	64.73	30.7	51.92	19.13	0.580	0.008	1
Lanius excubitor	Poland	0.072	22.36	4.87	66.9	51.92	19.13	0.555	0.199	1
Lanius excubitor	Spain	-0.044	31.05	4.87	66.9	39.90	-2.99	0.669	0.199	1
Lanius senator	Spain	-0.012	36.12	28.45	36.0	39.90	-2.99	0.575	--	1

Larus argentatus	Denmark	0.019	50.09	22.14	895.0	56.16	10.38	0.673	0.774	0
Larus argentatus	France	0.050	15.10	22.14	895.0	46.71	1.72	0.952	0.774	0
Larus canus	Denmark	-0.009	59.94	13.76	386.5	56.16	10.38	0.671	0.602	1
Larus canus	Norway	-0.024	14.00	13.76	386.5	64.56	18.01	0.729	0.602	1
Larus fuscus	France	0.170	22.00	34.35	817.5	46.71	1.72	0.646	0.726	0
Larus marinus	Denmark	0.220	57.52	7.28	1599.5	56.16	10.38	0.528	0.837	0
Larus ridibundus	Denmark	-0.033	37.75	23.50	280.5	56.16	10.38	0.624	0.453	0
Locustella naevia	Czech Rep.	-0.010	7.22	29.75	12.7	49.80	15.48	0.597	-0.222	1
Loxia curvirostra	Denmark	-0.040	4.74	0.00	40.6	56.16	10.38	0.571	0.173	0
Luscinia luscinia	Denmark	-0.016	15.89	63.10	25.0	56.16	10.38	0.670	-0.125	0
Luscinia megarhynchos	Czech Rep.	0.099	15.52	32.20	20.2	49.80	15.48	0.722	-0.179	0
Luscinia megarhynchos	Spain	0.018	25.87	32.20	20.2	39.90	-2.99	0.560	-0.179	0
Luscinia megarhynchos	Hungary	0.023	10.53	32.20	20.2	47.16	19.51	0.659	-0.179	0
Luscinia megarhynchos	Poland	-0.011	46.01	32.20	20.2	51.92	19.13	0.794	-0.179	0
Merops apiaster	Spain	0.008	94.95	19.86	55.1	39.90	-2.99	0.335	-0.098	1
Miliaria calandra	Denmark	-0.004	10.29	6.40	47.7	56.16	10.38	0.782	0.074	1
Miliaria calandra	Spain	-0.008	24.18	6.40	47.7	39.90	-2.99	0.576	0.074	1
Miliaria calandra	Poland	0.064	31.64	6.40	47.7	51.92	19.13	0.671	0.074	1
Motacilla alba	Czech Rep.	-0.014	18.03	18.13	20.8	49.80	15.48	0.480	-0.250	0
Motacilla alba	Denmark	0.049	11.62	18.13	20.8	56.16	10.38	0.556	-0.250	0
Motacilla alba	Finland	0.000	7.57	18.13	20.8	64.95	26.07	0.699	-0.250	0
Motacilla alba	France	0.002	6.33	18.13	20.8	46.71	1.72	0.445	-0.250	0
Motacilla alba	Spain	-0.019	24.36	18.13	20.8	39.90	-2.99	0.421	-0.250	0
Motacilla alba	Norway	0.026	7.15	18.13	20.8	64.56	18.01	0.690	-0.250	0
Motacilla alba	Poland	0.005	25.56	18.13	20.8	51.92	19.13	0.505	-0.250	0
Motacilla cinerea	Czech Rep.	-0.017	8.00	24.68	17.4	49.80	15.48	0.507	-0.279	0
Motacilla cinerea	Denmark	-0.027	6.87	24.68	17.4	56.16	10.38	0.562	-0.279	0
Motacilla cinerea	France	-0.015	9.07	24.68	17.4	46.71	1.72	0.503	-0.279	0
Motacilla flava	Denmark	-0.027	11.20	40.99	17.5	56.16	10.38	0.562	-0.371	1
Motacilla flava	Finland	-0.036	11.84	40.99	17.5	64.95	26.07	0.709	-0.371	1
Motacilla flava	Poland	-0.030	5.39	40.99	17.5	51.92	19.13	0.509	-0.371	1
Muscicapa striata	Czech Rep.	0.057	15.56	64.40	15.5	49.80	15.48	0.516	-0.292	0
Muscicapa striata	Denmark	0.010	10.08	64.40	15.5	56.16	10.38	0.584	-0.292	0
Muscicapa striata	Finland	-0.004	9.06	64.40	15.5	64.95	26.07	0.729	-0.292	0
Muscicapa striata	Spain	-0.025	21.98	64.40	15.5	39.90	-2.99	0.551	-0.292	0
Numenius arquata	Finland	-0.008	42.07	44.67	725.0	64.95	26.07	0.744	0.595	0
Oriolus oriolus	Spain	0.056	30.34	44.77	68.5	39.90	-2.99	0.485	0.117	0
Oriolus oriolus	Hungary	0.003	24.12	44.77	68.5	47.16	19.51	0.536	0.117	0
Parus ater	Czech Rep.	0.017	12.08	0.00	9.3	49.80	15.48	0.520	-0.264	0
Parus ater	Denmark	-0.009	5.41	0.00	9.3	56.16	10.38	0.605	-0.264	0
Parus ater	France	-0.049	4.00	0.00	9.3	46.71	1.72	0.483	-0.264	0
Parus ater	Spain	0.019	18.49	0.00	9.3	39.90	-2.99	0.456	-0.264	0
Parus caeruleus	Czech Rep.	0.002	10.08	0.00	11.8	49.80	15.48	0.540	-0.200	0
Parus caeruleus	Denmark	0.007	6.61	0.00	11.8	56.16	10.38	0.622	-0.200	0
Parus caeruleus	Finland	0.258	8.00	0.00	11.8	64.95	26.07	0.825	-0.200	0
Parus caeruleus	France	0.033	5.17	0.00	11.8	46.71	1.72	0.537	-0.200	0
Parus caeruleus	Spain	0.027	9.93	0.00	11.8	39.90	-2.99	0.570	-0.200	0
Parus caeruleus	Hungary	0.025	5.94	0.00	11.8	47.16	19.51	0.535	-0.200	0
Parus caeruleus	Norway	0.012	6.09	0.00	11.8	64.56	18.01	0.808	-0.200	0
Parus cristatus	Denmark	-0.013	7.20	0.00	11.2	56.16	10.38	0.636	-0.189	0
Parus cristatus	France	0.005	4.81	0.00	11.2	46.71	1.72	0.603	-0.189	0
Parus major	Czech Rep.	-0.002	10.47	0.00	18.5	49.80	15.48	0.370	-0.073	0
Parus major	Denmark	-0.009	5.46	0.00	18.5	56.16	10.38	0.479	-0.073	0
Parus major	Finland	0.021	8.61	0.00	18.5	64.95	26.07	0.649	-0.073	0
Parus major	France	0.017	4.60	0.00	18.5	46.71	1.72	0.307	-0.073	0
Parus major	Spain	0.013	11.92	0.00	18.5	39.90	-2.99	0.000	-0.073	0
Parus major	Hungary	0.027	7.65	0.00	18.5	47.16	19.51	0.317	-0.073	0
Parus major	Norway	0.003	5.74	0.00	18.5	64.56	18.01	0.639	-0.073	0

Parus major	Poland	-0.009	16.49	0.00	18.5	51.92	19.13	0.408	-0.073	0
Parus montanus	Norway	-0.004	5.61	0.00	11.7	64.56	18.01	0.716	-0.102	0
Parus palustris	Czech Rep.	-0.022	10.60	0.00	11.9	49.80	15.48	0.542	-0.151	0
Parus palustris	Denmark	-0.013	4.03	0.00	11.9	56.16	10.38	0.638	-0.151	0
Parus palustris	France	-0.008	6.60	0.00	11.9	46.71	1.72	0.503	-0.151	0
Passer domesticus	Czech Rep.	-0.026	15.28	0.00	30.4	49.80	15.48	0.435	-0.041	0
Passer domesticus	Denmark	-0.013	4.72	0.00	30.4	56.16	10.38	0.521	-0.041	0
Passer domesticus	Finland	-0.038	16.67	0.00	30.4	64.95	26.07	0.671	-0.041	0
Passer domesticus	France	0.004	4.83	0.00	30.4	46.71	1.72	0.392	-0.041	0
Passer domesticus	Spain	-0.004	19.76	0.00	30.4	39.90	-2.99	0.277	-0.041	0
Passer domesticus	Hungary	-0.004	7.34	0.00	30.4	47.16	19.51	0.398	-0.041	0
Passer domesticus	Norway	-0.008	4.24	0.00	30.4	64.56	18.01	0.662	-0.041	0
Passer domesticus	Poland	-0.027	11.05	0.00	30.4	51.92	19.13	0.463	-0.041	0
Passer montanus	Czech Rep.	-0.009	16.67	3.62	21.7	49.80	15.48	0.378	-0.123	1
Passer montanus	Denmark	0.036	6.35	3.62	21.7	56.16	10.38	0.487	-0.123	1
Passer montanus	Spain	-0.027	13.79	3.62	21.7	39.90	-2.99	0.041	-0.123	1
Passer montanus	Hungary	0.073	8.08	3.62	21.7	47.16	19.51	0.325	-0.123	1
Passer montanus	Poland	-0.051	14.45	3.62	21.7	51.92	19.13	0.415	-0.123	1
Perdix perdix	Denmark	-0.012	24.92	0.00	382.0	56.16	10.38	0.655	0.259	1
Phoenicurus ochruros	Czech Rep.	0.009	15.89	15.83	16.0	49.80	15.48	0.612	-0.254	0
Phoenicurus ochruros	France	0.006	4.12	15.83	16.0	46.71	1.72	0.567	-0.254	0
Phoenicurus ochruros	Hungary	0.061	15.10	15.83	16.0	47.16	19.51	0.573	-0.254	0
Phoenicurus ochruros	Poland	-0.011	22.40	15.83	16.0	51.92	19.13	0.648	-0.254	0
Phoenicurus phoenicurus	Czech Rep.	0.061	19.10	33.93	15.9	49.80	15.48	0.505	-0.321	0
Phoenicurus phoenicurus	Denmark	0.019	12.05	33.93	15.9	56.16	10.38	0.579	-0.321	0
Phoenicurus phoenicurus	Finland	0.020	20.02	33.93	15.9	64.95	26.07	0.725	-0.321	0
Phylloscopus collybita	Czech Rep.	0.010	11.03	22.55	7.7	49.80	15.48	0.507	-0.455	0
Phylloscopus collybita	Denmark	0.168	7.88	22.55	7.7	56.16	10.38	0.581	-0.455	0
Phylloscopus collybita	France	-0.018	5.25	22.55	7.7	46.71	1.72	0.500	-0.455	0
Phylloscopus trochilus	Denmark	-0.020	6.06	68.09	9.4	56.16	10.38	0.617	-0.507	0
Phylloscopus trochilus	Hungary	-0.034	2.00	68.09	9.4	47.16	19.51	0.725	-0.507	0
Phylloscopus trochilus	Norway	-0.011	5.05	68.09	9.4	64.56	18.01	0.725	-0.507	0
Pica pica	Denmark	0.008	37.59	0.00	228.0	56.16	10.38	0.551	0.736	0
Pica pica	Finland	0.002	29.00	0.00	228.0	64.95	26.07	0.694	0.736	0
Pica pica	France	-0.112	15.12	0.00	228.0	46.71	1.72	0.438	0.736	0
Pica pica	Spain	-0.008	38.13	0.00	228.0	39.90	-2.99	0.399	0.736	0
Pica pica	Hungary	0.016	21.46	0.00	228.0	47.16	19.51	0.443	0.736	0
Pica pica	Norway	0.000	13.98	0.00	228.0	64.56	18.01	0.685	0.736	0
Pica pica	Poland	0.022	26.66	0.00	228.0	51.92	19.13	0.499	0.736	0
Picus viridis	France	0.026	17.82	0.00	193.5	46.71	1.72	0.587	0.636	0
Picus viridis	Spain	-0.006	50.24	0.00	193.5	39.90	-2.99	0.657	0.636	0
Pluvialis apricaria	Finland	-0.010	18.00	17.97	175.5	64.95	26.07	0.741	0.314	0
Prunella modularis	Czech Rep.	-0.011	13.56	9.23	19.0	49.80	15.48	0.585	-0.163	0
Prunella modularis	Denmark	-0.018	7.43	9.23	19.0	56.16	10.38	0.594	-0.163	0
Prunella modularis	France	-0.006	4.61	9.23	19.0	46.71	1.72	0.606	-0.163	0
Pyrrhula pyrrhula	Denmark	0.010	7.65	0.00	31.1	56.16	10.38	0.592	-0.058	0
Pyrrhula pyrrhula	Finland	0.061	5.00	0.00	31.1	64.95	26.07	0.738	-0.058	0
Pyrrhula pyrrhula	Norway	-0.042	16.00	0.00	31.1	64.56	18.01	0.729	-0.058	0
Regulus regulus	Denmark	-0.008	5.41	0.00	5.8	56.16	10.38	0.578	-0.446	0
Regulus regulus	France	-0.003	3.24	0.00	5.8	46.71	1.72	0.484	-0.446	0
Regulus regulus	Norway	-0.007	5.11	0.00	5.8	64.56	18.01	0.718	-0.446	0
Riparia riparia	Denmark	-0.020	23.10	42.73	13.2	56.16	10.38	0.572	-0.466	0
Saxicola rubetra	Denmark	-0.040	15.43	34.84	16.6	56.16	10.38	0.602	-0.222	1
Saxicola rubetra	Finland	-0.018	23.09	34.84	16.6	64.95	26.07	0.751	-0.222	1
Saxicola torquata	Hungary	-0.006	15.98	3.98	14.9	47.16	19.51	0.280	--	1
Scolopax rusticola	Finland	0.020	9.00	14.32	309.5	64.95	26.07	0.732	0.388	0
Serinus serinus	Czech Rep.	-0.039	13.94	4.91	12.0	49.80	15.48	0.621	-0.371	0
Serinus serinus	France	-0.033	6.06	4.91	12.0	46.71	1.72	0.574	-0.371	0

Serinus serinus	Spain	-0.025	21.67	4.91	12.0	39.90	-2.99	0.551	-0.371	0
Serinus serinus	Hungary	-0.059	14.14	4.91	12.0	47.16	19.51	0.581	-0.371	0
Serinus serinus	Poland	-0.044	24.04	4.91	12.0	51.92	19.13	0.658	-0.371	0
Sitta europaea	Czech Rep.	0.014	13.39	0.00	23.9	49.80	15.48	0.492	0.017	0
Sitta europaea	France	-0.038	4.92	0.00	23.9	46.71	1.72	0.450	0.017	0
Sitta europaea	Norway	0.025	5.41	0.00	23.9	64.56	18.01	0.788	0.017	0
Streptopelia decaocto	Czech Rep.	0.026	22.42	0.00	201.5	49.80	15.48	0.460	0.157	0
Streptopelia decaocto	Denmark	0.000	26.43	0.00	201.5	56.16	10.38	0.547	0.157	0
Streptopelia decaocto	France	0.077	11.67	0.00	201.5	46.71	1.72	0.418	0.157	0
Streptopelia decaocto	Spain	0.538	23.61	0.00	201.5	39.90	-2.99	0.315	0.157	0
Streptopelia decaocto	Hungary	0.044	10.79	0.00	201.5	47.16	19.51	0.424	0.157	0
Streptopelia decaocto	Poland	0.005	13.31	0.00	201.5	51.92	19.13	0.488	0.157	0
Streptopelia turtur	Czech Rep.	-0.022	27.99	25.90	136.5	49.80	15.48	0.550	0.102	1
Streptopelia turtur	France	-0.006	7.07	25.90	136.5	46.71	1.72	0.509	0.102	1
Streptopelia turtur	Spain	-0.004	97.53	25.90	136.5	39.90	-2.99	0.440	0.102	1
Sturnus unicolor	Spain	0.018	42.70	0.00	90.6	39.90	-2.99	0.728	0.262	1
Sturnus vulgaris	Czech Rep.	0.030	36.44	2.63	80.5	49.80	15.48	0.493	0.235	1
Sturnus vulgaris	Denmark	-0.015	14.31	2.63	80.5	56.16	10.38	0.567	0.235	1
Sturnus vulgaris	France	-0.005	9.75	2.63	80.5	46.71	1.72	0.477	0.235	1
Sturnus vulgaris	Hungary	0.042	13.46	2.63	80.5	47.16	19.51	0.477	0.235	1
Sturnus vulgaris	Norway	-0.016	8.83	2.63	80.5	64.56	18.01	0.697	0.235	1
Sturnus vulgaris	Poland	0.049	31.28	2.63	80.5	51.92	19.13	0.517	0.235	1
Sylvia atricapilla	Czech Rep.	0.074	13.56	19.63	18.9	49.80	15.48	0.476	-0.207	0
Sylvia atricapilla	Denmark	0.044	8.48	19.63	18.9	56.16	10.38	0.557	-0.207	0
Sylvia atricapilla	France	0.013	4.83	19.63	18.9	46.71	1.72	0.438	-0.207	0
Sylvia atricapilla	Spain	0.044	11.47	19.63	18.9	39.90	-2.99	0.373	-0.207	0
Sylvia atricapilla	Hungary	0.056	10.81	19.63	18.9	47.16	19.51	0.443	-0.207	0
Sylvia atricapilla	Norway	0.119	3.16	19.63	18.9	64.56	18.01	0.704	-0.207	0
Sylvia atricapilla	Poland	0.031	11.32	19.63	18.9	51.92	19.13	0.502	-0.207	0
Sylvia borin	Czech Rep.	-0.012	19.10	63.25	19.1	49.80	15.48	0.584	-0.220	0
Sylvia borin	Denmark	-0.014	6.78	63.25	19.1	56.16	10.38	0.598	-0.220	0
Sylvia cantillans	Spain	0.028	5.22	20.82	8.1	39.90	-2.99	0.668	--	0
Sylvia communis	Czech Rep.	0.000	14.70	53.05	14.5	49.80	15.48	0.527	-0.281	1
Sylvia communis	Denmark	0.004	7.54	53.05	14.5	56.16	10.38	0.598	-0.281	1
Sylvia communis	Spain	-0.021	22.94	53.05	14.5	39.90	-2.99	0.570	-0.281	1
Sylvia curruca	Czech Rep.	0.041	17.26	27.79	12.4	49.80	15.48	0.514	-0.296	0
Sylvia curruca	Denmark	-0.022	5.72	27.79	12.4	56.16	10.38	0.590	-0.296	0
Sylvia curruca	Hungary	-0.007	8.55	27.79	12.4	47.16	19.51	0.509	-0.296	0
Sylvia melanocephala	Spain	-0.002	23.22	3.61	13.5	39.90	-2.99	0.660	-0.269	0
Tadorna tadorna	Denmark	0.013	37.71	9.35	1152.0	56.16	10.38	0.638	0.684	0
Tringa hypoleucos	France	-0.021	20.00	44.39	47.8	46.71	1.72	0.527	-0.108	0
Tringa totanus	Denmark	-0.030	29.71	35.28	112.0	56.16	10.38	0.576	0.149	0
Troglodytes troglodytes	Czech Rep.	0.011	10.55	1.34	8.9	49.80	15.48	0.497	-0.312	0
Troglodytes troglodytes	Denmark	0.029	7.51	1.34	8.9	56.16	10.38	0.577	-0.312	0
Troglodytes troglodytes	France	0.012	4.90	1.34	8.9	46.71	1.72	0.461	-0.312	0
Troglodytes troglodytes	Norway	-0.002	3.00	1.34	8.9	64.56	18.01	0.731	-0.312	0
Turdus iliacus	Finland	-0.002	14.05	10.77	62.9	64.95	26.07	0.741	0.133	0
Turdus iliacus	Norway	0.026	4.00	10.77	62.9	64.56	18.01	0.732	0.133	0
Turdus merula	Czech Rep.	0.016	21.51	3.98	95.9	49.80	15.48	0.438	0.284	0
Turdus merula	Denmark	0.015	12.22	3.98	95.9	56.16	10.38	0.524	0.284	0
Turdus merula	France	0.016	8.02	3.98	95.9	46.71	1.72	0.396	0.284	0
Turdus merula	Spain	0.007	21.98	3.98	95.9	39.90	-2.99	0.284	0.284	0
Turdus merula	Hungary	0.012	9.08	3.98	95.9	47.16	19.51	0.402	0.284	0
Turdus merula	Norway	0.015	9.65	3.98	95.9	64.56	18.01	0.665	0.284	0
Turdus merula	Poland	-0.018	22.59	3.98	95.9	51.92	19.13	0.466	0.284	0
Turdus philomelos	Czech Rep.	-0.001	29.03	14.65	70.5	49.80	15.48	0.576	0.196	0
Turdus philomelos	Denmark	-0.004	15.37	14.65	70.5	56.16	10.38	0.596	0.196	0
Turdus philomelos	France	0.034	8.10	14.65	70.5	46.71	1.72	0.595	0.196	0

Turdus pilaris	Czech Rep.	-0.003	29.31	10.77	92.1	49.80	15.48	0.709	0.261	1
Turdus pilaris	Denmark	-0.001	18.14	10.77	92.1	56.16	10.38	0.634	0.261	1
Turdus pilaris	Finland	0.037	20.95	10.77	92.1	64.95	26.07	0.735	0.261	1
Turdus pilaris	Norway	-0.015	8.56	10.77	92.1	64.56	18.01	0.727	0.261	1
Turdus pilaris	Poland	-0.038	5.50	10.77	92.1	51.92	19.13	0.677	0.261	1
Turdus viscivorus	Czech Rep.	0.024	49.90	4.36	117.8	49.80	15.48	0.526	0.313	0
Turdus viscivorus	Denmark	0.018	23.86	4.36	117.8	56.16	10.38	0.602	0.313	0
Turdus viscivorus	France	-0.011	27.00	4.36	117.8	46.71	1.72	0.534	0.313	0
Upupa epops	Spain	0.001	40.43	9.59	67.1	39.90	-2.99	0.339	0.102	0
Vanellus vanellus	Denmark	-0.011	33.99	12.08	218.5	56.16	10.38	0.598	0.326	1

REFERENCE

Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araújo MB 2011. Consequences of climate change on the tree of life in Europe. Nature 470:531–534.