Original Article

Interactive effects of fearfulness and geographical location on bird population trends

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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), and this adaptation may improve their population trends. We analyzed population trends of common breeding birds in relation to flight initiation distance 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 flight initiation distance and geographical location on trends after accounting for confounding and interactive effects; instead, flight initiation distance and location interacted to generate complex spatial patterns of population trends. Trends were more positive for fearful populations northward, westward, and (marginally) toward the center 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 nonlethal 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, whereas species with short FIDs had increasing populations even when controlling statistically for potentially confounding effects. However, a study on population trends in the United Kingdom 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 1960s 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, although 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 et al. (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 9 locations from 8 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 toward 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 nonurban populations (Cuervo and Møller 2013). Data for the 2 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 midpoint 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 2 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 0 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 midpoint 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 center was larger than the distance to the nearest limit) and negative values central populations (the distance to the range center 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 et al. 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 et al. (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 et al. (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 (Cuervo and Møller 2013; Díaz et al. 2013), geographical trends could be partly due to phylogenetic effects. To control for such relationships, we used phylogenetic generalized least square regression 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 were 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 [SDs]), 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, whereas there were no data on brain size for 9 species (Supplementary Appendix). 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 ($r = 0.45 \pm 0.04$ [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 3 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 and Figure 1). FID–trend relationships were more positive northward, westward, and (marginally) toward the center of distribution areas (Table 1 and Figure 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 et al. 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 et al. 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

Table 1

Relationships between population trends of European birds (response variable) and geographical location (latitude, longitude, and marginality) and fearfulness (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, which was, however, not significant ($\lambda = 0.000$, $\chi^2 = -0.012$, $P = 1.000$)

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 × latitude	0.005 (0.002)	2.29	0.023	0.13
FID × longitude	−0.004 (0.002)	−2.27	0.024	0.12
FID × marginality	−0.003 (0.002)	−1.76	0.079	0.10

The full model (no removal of nonsignificant terms was done, as recommended by Forstmeier and Schielzeth 2011) had the statistics $F = 4.73$, df = 12, 329, adjusted $r^2 = 0.11$, $P < 0.0001$. Effect sizes are Pearson's product–moment correlation coefficients. df, degrees of freedom; SE, standard error.
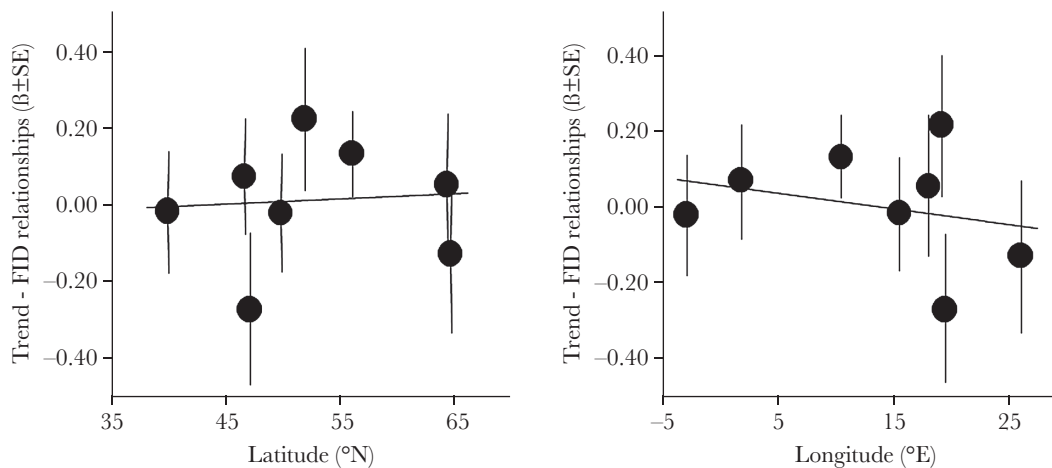
Figure 1
Latitudinal and longitudinal variations in standardized regression coefficients (β ± SE) between population trends of European birds (residuals from a multiple regression between log-transformed trends, migration distance, body mass, relative brain mass, farmland habitat, marginality, and either longitude or latitude) and fearfulness (FID, log-transformed). Lines are best-fit regressions.

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 et al. 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 southernmost 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 poleward (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 has also been documented, especially for farmland birds (Donald et al. 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 not only 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 nonlinear 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 et al. 2008; Reif 2013). Here, we found evidence consistent with this general trend, with farmland species showing more negative population trends than nonfarmland 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 et al. 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 not only on levels of risk (abundance and identity of predators and other sources of risk, such as humans) but also on potential fitness benefits (i.e., 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 easternmost edges of breeding distributions. Further studies including fine-grained estimates of FID, trends, and secondary influences on them (e.g., 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.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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APPENDIX A. SUPPLEMENTARY MATERIAL

1   **APPENDIX A. SUPPLEMENTARY MATERIAL**

2   Information on bird species, country, population trend, mean FID (m),

3   migration distance (°latitude), body mass (g), latitude and longitude of the

4   population/country, marginality of the population within the species

5   breeding range, relative brain size and farmland habitat. Relative brain

6   size is residuals from a log-log phylogenetically corrected regression of

7   brain mass on body mass. See Material and methods for sources and

8   details. Nomenclature and basic phylogeny follows Thuiller et al. (2011).

9

Species	Country	Popul. trend	FID (m)	Migration distance (° 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									