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

aDepartment of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (BGC-MNCN-CSIC), c/Serrano 115bis, E-28006 Madrid, Spain, bDepartment of Evolutionary Ecology, Museo Nacional de Ciencias Naturales, CSIC, c/José Gutiérrez Abascal 2, E-28006 Madrid, Spain, dDepartment of Zoology and Laboratory of Ornithology, Palacky University, 17 listopadu 50, CZ-77146 Olomouc, Czech Republic, eCypresvej 1, DK-9700 Broderslev, Denmark, fDepartamento de Zoologia, Facultad de Ciencias, Universidad de Granada, Campus Fuente Nueva, E-18071 Granada, Spain, gNature Inventory and EIA-Services, Arctic Centre, University of Lapland, PO Box 122, Arktikum house, Pohjoisranta 4, 96100-Rovaniemi, Finland, hEcology Research Group, Hungarian Academy of Sciences, Hungarian Natural History Museum, Eötvös Loránd University, Pázmány Péter sétány 1/c, H-1117 Budapest, Hungary, iBehavioral Ecology Group, Department of Systematics, Zoology and Ecology, Eötvös Loránd University, Pázmány Péter sétány 1/c, H-1117 Budapest, Hungary, jDepartment of Plant Pathology, Corvinus University of Budapest, Ménesi út 44, H-1118 Budapest, Hungary, kDepartment of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, PL-60-625 Poznań, Poland, and kLaboratoire d’Ecologie, Systématique et Evolution, CNRS UMR 8079, Université Paris-Sud, Bâtiment 362, F-91405 Orsay Cedex, France

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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 promiscuity to disturbance by humans and animals alike
is the flight initiation distance (FID): the distance at which an ani-
mal 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 continu-
ing to feed and/or rest, FID constitutes an instantaneous mea-
sure 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 den-
sities, which are a cause of frequent disturbance. Parallel latitudi-
nal 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 Diaz 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 conser-
vation including assessment of levels of disturbance and susceptibil-
The population consequences of FIDs can be investigated by relat-
ing population trends to FID (Moller 2008). We should expect spe-
cies 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 sta-
tistically for potentially confounding effects. However, a study on pop-
ulation trends in the United Kingdom in relation to predictors that
included FID recorded in Denmark did not find significant relation-
ship between FID and population trends (Thaxter et al. 2010). This
raises the question whether population trends and FID should origin-
ate from the same geographic location to make analyses meaningful.

Many national and international monitoring programs tally pop-
ulation trends of organisms as diverse as birds, mammals, butter-
flies, 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 mechan-
isms remain poorly understood. In addition, population trends
vary across the distribution range of species. Cuervo and Moller
(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
2003), and Donald et al. (2001) and Reif et al. (2011) showed longi-
tudinally varying trends. Reif et al. (2011) also showed an interest-
ing 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 differ-
ent spatial scales in an attempt to elucidate the underlying mecha-
isms, 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 par-
tially compensate for the main effects of factors of global change on
trends, we predicted significant interactions between FID and lati-
tude, longitude, and marginality on trends. We also tested whether
previously established predictors of population trends such as farm-
land habitat, migration distance, body mass, or brain mass affected
the relationship between population trend and FID. Overall, eluci-
dating 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 seas-
sons 2009–2010 at 9 locations from 8 countries along a wide latitudi-
nal 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 Diaz 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 ini-
tiated escape, and the bird’s height in the vegetation. This informa-
tion 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 color-
ed 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 (Diaz et al.
2013), because the population size estimates used to assess trends for
each country are mostly based on data coming from nonurban popu-
lations (Cuervo and Moller 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 Moller (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 Moller 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

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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. \( G \) 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 Moller 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 Moller 2008; Moller 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 Moller 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 (Moller 2008); brain mass data were obtained from Garamszegi et al. (2002), Iwanik and Nelson (2002), Galván and Moller (2011), and Moller and Erritzoe (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 Moller 2010). As species occupy a variable number of study locations and countries (Cuervo and Moller 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 (\( \lambda \)), 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 pgml3.3.r instead of the pgml3.1.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 (Schiezeth 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 (\( F_{1,295} = 3.08, P < 0.001 \) and \( F_{1,295} = 1.45, P = 0.009 \), respectively). FID was significantly more repeatable than population trends \( (r = 0.45 \pm 0.04 \text{ [SD]} \) vs. \( r = 0.15 \pm 0.05; t_{337} = 4.0, P < 0.001; \) 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; Moller 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 (Diaz...
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

### Table 1

<table>
<thead>
<tr>
<th>Source</th>
<th>Estimate (SE)</th>
<th>t</th>
<th>P</th>
<th>Effect size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Farmland</td>
<td>−0.008 (0.003)</td>
<td>−2.50</td>
<td>0.013</td>
<td>0.14</td>
</tr>
<tr>
<td>Migration distance</td>
<td>−0.006 (0.002)</td>
<td>−2.71</td>
<td>0.007</td>
<td>0.15</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.018 (0.006)</td>
<td>2.93</td>
<td>0.004</td>
<td>0.16</td>
</tr>
<tr>
<td>Relative brain size</td>
<td>−0.014 (0.010)</td>
<td>−1.46</td>
<td>0.147</td>
<td>0.08</td>
</tr>
<tr>
<td>FID</td>
<td>0.000 (0.002)</td>
<td>0.16</td>
<td>0.876</td>
<td>0.01</td>
</tr>
<tr>
<td>Latitude</td>
<td>−0.002 (0.002)</td>
<td>−1.07</td>
<td>0.286</td>
<td>0.06</td>
</tr>
<tr>
<td>Longitude</td>
<td>0.003 (0.002)</td>
<td>1.50</td>
<td>0.134</td>
<td>0.08</td>
</tr>
<tr>
<td>Marginality</td>
<td>0.001 (0.002)</td>
<td>0.38</td>
<td>0.706</td>
<td>0.02</td>
</tr>
<tr>
<td>FID × latitude</td>
<td>0.005 (0.002)</td>
<td>2.29</td>
<td>0.023</td>
<td>0.13</td>
</tr>
<tr>
<td>FID × longitude</td>
<td>−0.004 (0.002)</td>
<td>−2.27</td>
<td>0.024</td>
<td>0.12</td>
</tr>
<tr>
<td>FID × marginality</td>
<td>−0.003 (0.002)</td>
<td>−1.76</td>
<td>0.079</td>
<td>0.10</td>
</tr>
</tbody>
</table>

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.
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; Möller 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 Möller (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 whereas such trends were already less negative, as in northern European populations (Cuervo and Möller 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, will 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.behco.oxfordjournals.org/

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**REFERENCES**


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