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2 **Interactive effects of fearfulness and geographical location on the**

3 **population trends of breeding birds**

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Abstract

Animal populations are currently under pressure from multiple factors that include land use and climate change. They may adapt to such effects by reducing the distance at which they flee from humans (i.e., flight initiation distance, FID), consequently modifying 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 larger-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, eastwards and (marginally) towards the centre of distribution areas, and more negative for fearless populations toward the south, west, 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.

Introduction

Human disturbance of wild organisms is a common cause of concern in a world with a rapidly increasing human population (e.g. Wong and Candolin 2012; Ehrlich and Ehrlich 2013). Such effects of disturbance include release of stress hormones (e.g. Wingfield and Ramenofsky 1999), increased metabolic rate (e.g. Belanger and Bédard 1990), reduction in foraging activity (e.g. Madsen 1998a, b), disturbance from hunting (e.g. Madsen 1988a, b) and non-lethal effects of predation (e.g. 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 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 that is a cause of frequent disturbance. Parallel latitudinal trends in FID and raptor abundance (Díaz et al. 2013) suggest that birds also adjust their behavior in response to natural levels of disturbance by predators.

Burger (1981), Burger & Gochfeld (1981) and several others noticed that human disturbance at seabird colonies linked to escape behavior and FID could result in altered habitat use and reduced reproductive performance. Therefore, FID can be a useful tool in conservation including assessment of levels of disturbance and susceptibility to disturbance (e. g. Madsen, 1995, 1998a, b; Weston et al. 2012). The population consequences of FIDs can be investigated by

86 relating population trends to FID (Møller 2008b). We should expect species with

87 long FIDs for their body size to show declining population trends because such

88 species should be more prone to get disturbed by humans. Among 56 species of

89 birds, FID accounted for 33% of the variance in population trends in Denmark,

90 with effect sizes ranging from 0.36 to 0.58 in different analyses. Therefore,

91 species with long FIDs for their body size had declining populations while

92 species with short FIDs had increasing populations even when controlling

93 statistically for potentially confounding effects. Thaxter et al. (2010) analyzed

94 population trends in the UK in relation to predictors that included FID recorded

95 in Denmark, but found no significant relationship between FID and population

96 trends. This raises the question whether population trends and FID should

97 originate from the same geographic location to make analyses meaningful.

98   Many national and international monitoring programs tally population

99 trends of organisms as diverse as birds, mammals, butterflies and bumblebees. In

100 particular, birds have been popular targets for monitoring since the 1960's in

101 many countries in Europe, and population trends based on European continent-

102 wide monitoring have been published since 1980 (European Bird Census Council,

103 http://www.ebcc.info/index.php?ID=509). According to these data, while many

104 species have increased in distribution and abundance, a majority, at least in

105 specific habitats such as farmland, have shown a clear decline. Although humans

106 either directly or indirectly play a major role in determining long-term population

107 trends of birds in Europe (Reif 2013), the underlying mechanisms remain poorly

108 understood. In addition, population trends vary intraspecifically. Cuervo and

109 Møller (2013) found stronger increases in northern populations and greater

110 fluctuations in marginal populations, somewhat expected from influences of

111 global warming on climatic niches (Hampe and Petit 2005), and Donald et al.

112 (2001) and Reif et al. (2011) showed longitudinally varying trends. Reif et al.

113 (2011) also showed an interesting difference in the effect of relative brain size on

114 trends at both sides of the iron curtain, consistent with the differences in land-use

115 intensity across Europe. These intriguing and varying patterns, and the need to

116 optimize conservation priorities, mean that there are good reasons to investigate

117 patterns of population trends at different spatial scales in an attempt to elucidate

118 the underlying mechanisms including the potential effects of FID.

119   The objectives of this study were to test whether population trends were

120 related to FID, and whether these influences varied across the European

121 continent. If spatial changes in FID could partially compensate for the main

122 effects of factors of global change on trends, we predicted significant interactions

123 between FID and latitude, longitude and marginality on trends. We also tested

124 whether previously established predictors of population trends such as farmland

125 habitat, migration distance, body mass or brain mass affected the relationship

126 between population trend and FID. Overall, geographical variation in the

127 relationships between trends and recent responses of organisms to changes in the

128 level of human activities will help to understand our impact on wild populations

129 of animals and eventually to reduce such impacts.

130

131 **Materials and methods**

132   We recorded FID for a total of 159 species during the breeding seasons

133 2009-2010 at nine locations from eight countries along a wide latitudinal gradient

134 across Europe, from Finland in the north to Spain in the south, by using a

135 standard procedure developed by Blumstein (2006). These data are reported in

136 Díaz et al. (2013). In brief, we walked at ordinary walking speed towards a bird

137 recording the distance from the bird when we started walking, the distance at

138 which the birds initiated escape, and the bird's height in the vegetation. This

139 information was used to estimate FID. In order to account for the height at which

140 individuals were perched, FID was calculated as the Euclidean distance between

141 the approaching human and the focal bird (which equals the square-root of the

142 sum of the squared flight distance and the squared height in the vegetation).

143 Observers wore neutrally colored clothes and behaved as normal pedestrians.

144 FID was measured by a number of trained observers and therefore data were

145 pooled for analysis. We used the FID estimates for rural populations in each

146 location (that consisted of paired rural and urban sites; Díaz et al. 2013), because

147 the population size estimates used to assess trends for each country are mostly

148 based on data coming from non-urban populations (Cuervo and Møller 2013).

149 Data for the two Spanish sites were averaged to obtain a single country-level

150 estimate.

151 We obtained from Cuervo and Møller (2013) the population trends for

152 breeding birds in all European countries for which we had information on FID:

153 Finland, Norway, Denmark, Poland, Czech Republic, Hungary, France and

154 Spain. Available population size estimates for each bird species and country were

155 regressed on years, and the slope of this regression was used as a proxy for

156 population trend (Cuervo and Møller 2013).

157 Latitude and longitude of bird populations in each country were estimated

158 as the coordinates of the mid-point between the northernmost and the

159 southernmost, and between the easternmost and the westernmost, mainland points

160 of the breeding range of every country, excluding islands except for Denmark.

161 Marginality of each bird population was estimated using the distance (L) in

162 degrees between the breeding population latitude and the northernmost or the

163 southernmost (the one that resulted in a shorter distance) limits of the breeding

164 distribution range of the species and the distance (C) in degrees between the

165 population latitude and the latitude of the mid-point between the northernmost

166 and the southernmost limits of the breeding distribution range of the species

167 according to the equation $\log_{10}(C+1) - \log_{10}(L+1)$, with positive values

168 representing marginal populations and negative values central populations. These

169 values were transformed by adding the absolute value of the most negative

170 number and dividing by the largest value resulting from the previous addition, to

171 ensure that marginality estimates ranged from 0 (central population) to 1

172 (marginal population; see Cuervo and Møller 2013 for details).

173   Bird population trends have previously been shown to be systematically

174   affected by body size, migration distance, farmland habitat and relative brain size

175   (reviews in Møller 2008a, Møller et al. 2008, Reif 2013). We extracted

176   information on mean body mass of adult birds of each species from Cramp &

177   Perrins (1977-1994). Migration distances (mean of the northernmost and the

178   southernmost latitudes of the breeding distribution range minus the corresponding

179   mean for the wintering distribution range) were taken from Møller et al. (2008).

180   Farmland habitat was coded as 1 (species depending on arable and/or mixed

181   farmland) or 0 (species depending on other habitat types) following Appendix 2

182   in Tucker and Evans (1997). Relative brain sizes were the residuals of a log-log

183   phylogenetically corrected regression of brain mass on body mass based on a

184   sample of 567 bird species (Møller 2008a); brain mass data were obtained from

185   Iwaniuk and Nelson (2002), Møller and Erritzøe (2014), Galván and Møller

186   (2011) and Garamszegi et al. (2002).

187   We $\log_{10}$-transformed FID, population trend and migration distance before

188   analyses. Within-species repeatability of FID and trends across Europe was

189   computed following Lessells and Boag (1987), and differences between them and

190   the null hypothesis of zero repeatability were tested following Becker (1984).

191   Significant repeatabilities imply statistical dependence of estimates for the same

192   species in different countries, a fact that will bias results based on

193   phylogenetically-structured databases (Garamszegi and Møller 2010). As species

194   occupy a variable number of study locations and countries (Cuervo and Møller

195   2013, Díaz et al. 2013), geographical trends could be partly due to phylogenetic

196   effects. To control for such relationships we used phylogenetic generalized least

197   square regression (PGLS) models implemented in R (see Díaz et al. 2013 for a

198   similar approach). After estimating the phylogenetic scaling parameter lambda

199   (λ), we calculated the phylogenetically corrected partial correlations between the

200   variables of interest. Different populations of the same species were considered

201   as polytomies with a constant small genetic distance of $1 \cdot 10^{-10}$ between them. We

202 used the R script and the edited phylogeny supplied as Supplementary Files S1

203 and S2 in Díaz et al. (2013), but using the function *pglm3.3.r* instead of the

204 *pglm3.1.r* to fit type III (orthogonal) models. The dependent variable was the

205 population trend, confounding variables were farmland habitat, migration

206 distance, body size and relative brain size, and predictors FID, latitude, longitude,

207 marginality, and the first-order interaction between FID and geographical

208 variables. Predictors were computed from the corresponding input variables

209 ($\log_{10}$FID and geographical variables) by standardizing them (i.e., by subtracting

210 sample means and dividing by standard deviations), in order to allow direct

211 comparison of effect sizes (computed from *P* values of t-tests according to Lipsey

212 and Wilson 2001) and to make main effects biologically interpretable even when

213 involved in interactions (Schielzeth 2010). The magnitude of associations

214 between trends and predictor variables was estimated as their effect sizes,

215

216 **Results**

217   We collected data on mean FID and on recent population trends from 338

218 populations of 129 bird species. Data on farmland habitat, body size and

219 migration distance were available for all them, while there were no data on brain

220 size for 9 species (Supplementary Table 1). Both FID and trends were

221 significantly repeatable within species ($F_{1, 209} = 3.08$, $P < 0.001$ and $F_{1, 209} = 1.45$,

222 $P = 0.009$, respectively). FID was significantly more repeatable than population

223 trends ($r = 0.45 \pm 0.04$ (SD) *vs.* $r = 0.15 \pm 0.05$; $t_{338} = 4.0$, $P < 0.001$; Becker

224 1984); in other words, geographical variation within species was larger for

225 population trends than for mean fearfulness as reflected by FID.

226   Log-transformed population trends were significantly related to $\log_{10}$FID

227 ($F_{1, 337} = 7.96$, $P = 0.005$, $r^2 = 0.02$), but not to latitude ($F_{1, 337} = 0.00$, $P = 0.967$,

228 $r^2 = 0.00$), longitude ($F_{1, 337} = 0.40$, $P = 0.530$, $r^2 = 0.00$) or marginality ($F_{1, 337} =$

229 0.62, $P = 0.432$, $r^2 = 0.00$). The relationship vanished, however, after correcting

230 for significant effects of farmland habitat, migration distance and body mass

231   (effect sizes from 0.14 to 0.16), while also accounting for phylogenetic effects

232   (Table 1). Trends were more negative for farmland birds, long-distance migrants

233   and smaller species (Table 1). Relative brain size showed no significant effects

234   on population trends, which did not show significant geographical trends either

235   (Table 1). However, FID showed significant interactive effects with latitude,

236   longitude and marginally, with effect sizes ranging from 0.10 to 0.13 (Table 1,

237   Fig. 1). FID-trend relationships were more positive northwards, eastwards and

238   (marginally) towards the centre of distribution areas (Table 1, Fig. 2). These

239   interactions implied that trends were more negative for fearless populations

240   toward the south, west, and the margins of distribution ranges.

241

242   **Discussion**

243   Many different factors have been proposed to account for population

244   trends of birds (reviewed in Reif, 2013). These variables range from migration

245   and the perils of living under different climate regimes (Hjort and Lindholm,

246   1978; Baillie et al., 1992; Sanderson et al., 2006; Reif, 2011), relative brain mass

247   that facilitates the ability to cope with changing environments (Shultz et al., 2005;

248   Møller et al., 2008; Reif et al., 2011), thermal range and hence the ability to cope

249   with changing climatic conditions (Jiguet et al., 2007), the number of broods with

250   species producing more broods doing better (Julliard et al., 2004), and body mass

251   with large sized species with smaller total populations having negative population

252   trends (Bennett and Owens, 2002).

253   Geographical variation in trends within breeding ranges of species are also

254   to be expected due to geographical changes in the suitability of environmental

255   conditions (the niche variation hypothesis; Brown 1984), in the intensity of global

256   change drivers (Hampe and Petit 2005, Reif et al. 2011, Tryjanowski et al. 2011)

257   or both (Díaz et al. 1998). Cuervo and Møller (2013) have recently shown that

258   changes in population size of breeding birds in Europe are the strongest at the

259   margins of the breeding distribution, but are particularly negative at the southern-

260 most range margins, where increasing temperatures may render environmental

261 conditions for maintenance of viable populations the most difficult. Climate

262 change has affected the distribution of many species, and range margins have on

263 average moved pole-wards (e.g. Chen et al., 2011). Longitudinal variation due to

264 differences in land-use intensity between Western and Eastern Europe have also

265 been documented, especially for farmland birds (Donald et al. 2001). However,

266 we did not find evidence for direct effects of these variables after accounting for

267 effects of third variables and their interactions. We hypothesized that effects of

268 longitude would be stronger towards the west where agriculture and forestry is

269 more industrialized than in the east. In fact, Reif et al. (2011) suggested that the

270 iron curtain dividing industrialized Western Europe from more extensive land use

271 in Eastern Europe as one factor accounting for spatial heterogeneity in population

272 trends, together with relative brain mass. Here we found no evidence of an effect

273 of relative brain mass on population trends contrary to previous reports (Shulz et

274 al. 2005; Thaxter et al. 2010; Reif et al. 2011). We hypothesize that these

275 differences among studies may arise from the inclusion of different predictors and

276 their interactions, but also from inclusion of multiple countries that differ in

277 significant predictors of population trends.

278   Bird species breeding on farmland displayed the steepest declines. This is

279 probably a consequence of agriculture having become ever more industrialized

280 and intensified and thereby disproportionately negatively affecting farmland

281 specialists (Fuller et al., 1995; Chamberlain et al., 2000; Møller et al., 2008; Reif,

282 2013). Here we found evidence consistent with this general trend with farmland

283 species showing strong population declines. Migration has been predicted to

284 affect population trends because migrants are affected negatively by land-use and

285 climate change in their breeding range, during migration and in their winter

286 quarters (Hjort and Lindholm, 1978; Baillie et al., 1992; Sanderson et al., 2006;

287 Møller et al. 2008; Reif, 2013). Here we found a negative effect of migration

288 distance on population trends, when accounting for the effects of the remaining

289 variables.

290   We hypothesized that population trends would be negatively related to

291 FID, as reported by Møller (2008a) for European birds. We found an overall

292 main effect of FID in this study, that however vanished when considering

293 phylogenetic and interactive effects with geographical location. This fact suggests

294 that the observed geographical variation in trends would in fact be the net result

295 of complex interactions between spatial variation in many factors proposed to

296 drive populations trends (Reif, 2103). Our results showed that fearfulness of bird

297 populations (i.e., long FIDs) enhanced population trends where such trends were

298 already less negative (northern and eastern European populations ; Cuervo and

299 Møller 2013, Tryjanowski et al. 2011), but this relationship reversed at more

300 stressful extremes of spatial gradients, such as southern, western and marginal

301 locations. We interpret these interactions as implying that we cannot assess

302 predictors by considering solely their main effects. We are unaware of any

303 previous studies investigating such interaction effects as predictors of population

304 trends. Finally, we note that the effect of FID remained after inclusion of body

305 mass as a predictor of population trends. Large species are generally more

306 threatened than small species (Bennett and Owens 2002). However, large species

307 also have longer FID than small species. Therefore, we conclude that species

308 with a relatively long FID and hence species that are easily disturbed by humans

309 show declining population trends, especially at low latitudes and eastern and

310 marginal locations of their breeding distribution ranges, where tolerance to

311 disturbance would be positively selected.

312   In conclusion, we have analyzed for the first time how geographical

313 patterns of population trends of birds in Europe are related to natural and man-

314 made geographical variation in environmental factors such as climate, predation

315 risk and land use, and how they interact with a measure of the tolerance of birds

316 to human disturbance. Overall we found that proneness to risk-taking as

317 estimated by short FIDs enhanced population resilience to disturbance in a

318 changing world, as more tolerant individuals will reduce the costs associated with

319 escape behaviors (Cooper and Blumstein 2014). In contrast, bird species and

320 populations less tolerant of frequent disturbance, by humans or wild and domestic

321 predators would perform worse, especially at the southern-most edges of

322 breeding distributions.

323

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479 **Legends to figures**

480

481 **Fig. 1.** Relationship between population trends of European birds and fearfulness

482 (flight initiation distance, FID, log-transformed), and latitude (left), longitude

483 (right) and marginality (bottom). Trend data are the residuals from a multiple

484 regression between log-transformed trends, migration distance, body mass,

485 relative brain mass and farmland habitat. Planes represent best-fitted multiple

486 regression models. Filled symbols are located above the planes and open symbols

487 below.

488

489 **Fig. 2**. Latitudinal and longitudinal variation in standardized regression

490 coefficients (ß±SE) between population trends of European birds (residuals from

491 a multiple regression between log-transformed trends, migration distance, body

492 mass, relative brain mass and farmland habitat) and fearfulness (flight initiation

493 distance, FID, log-transformed). Lines are best-fit regressions.

494   **Fig. 1**

495
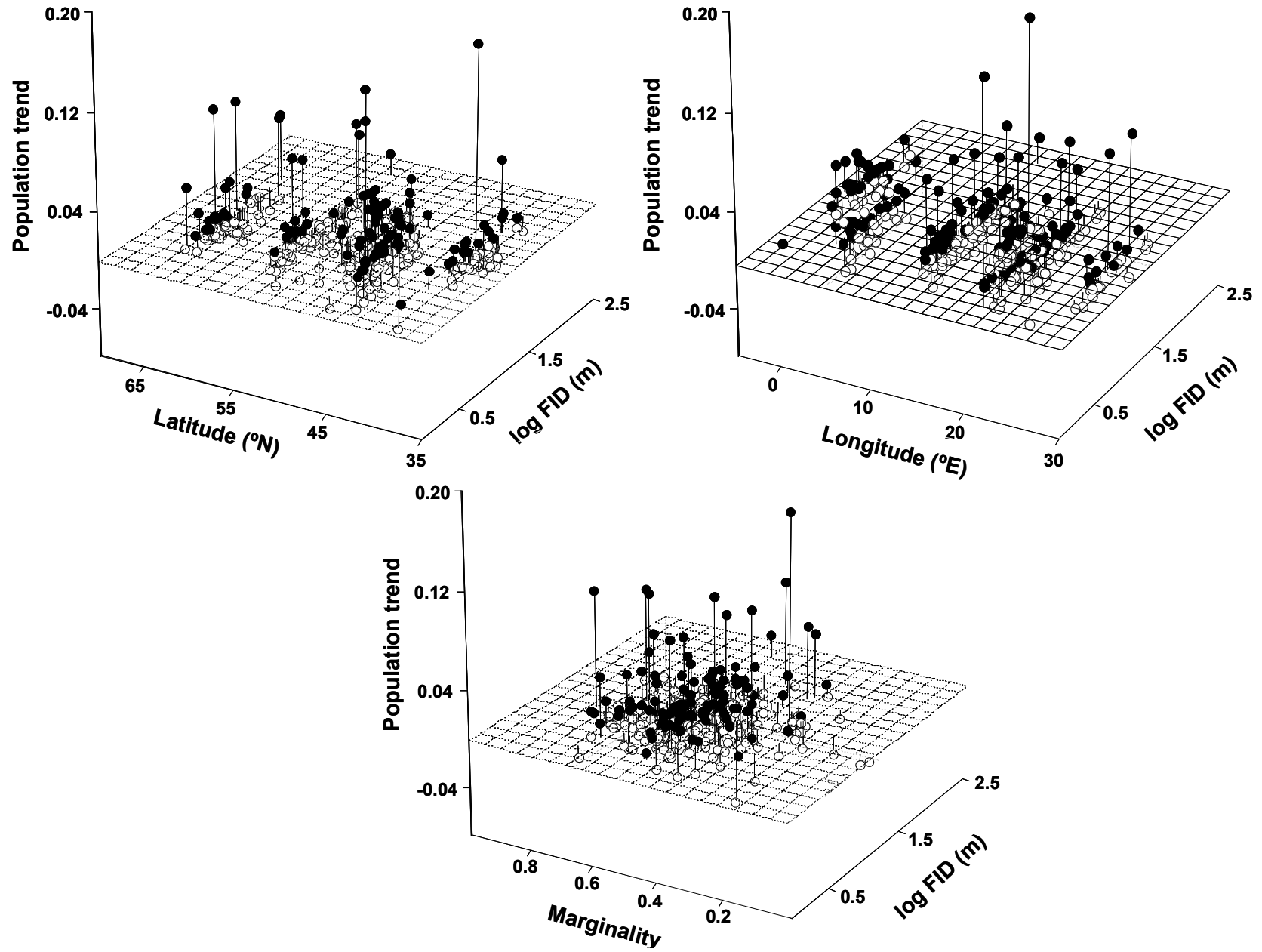
496   **Fig. 2.**
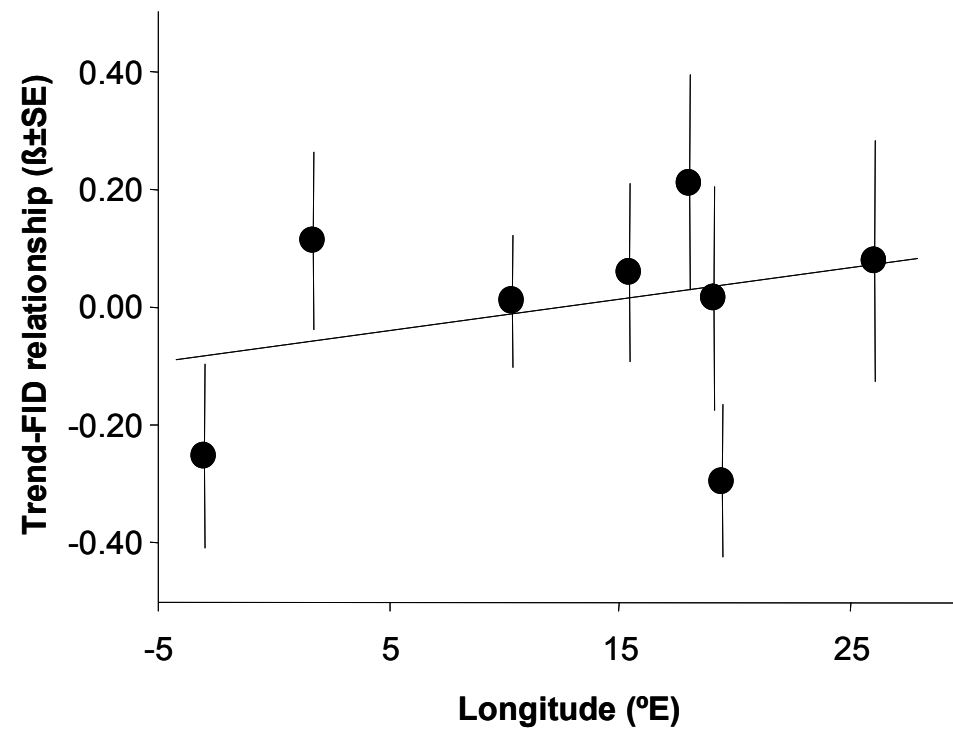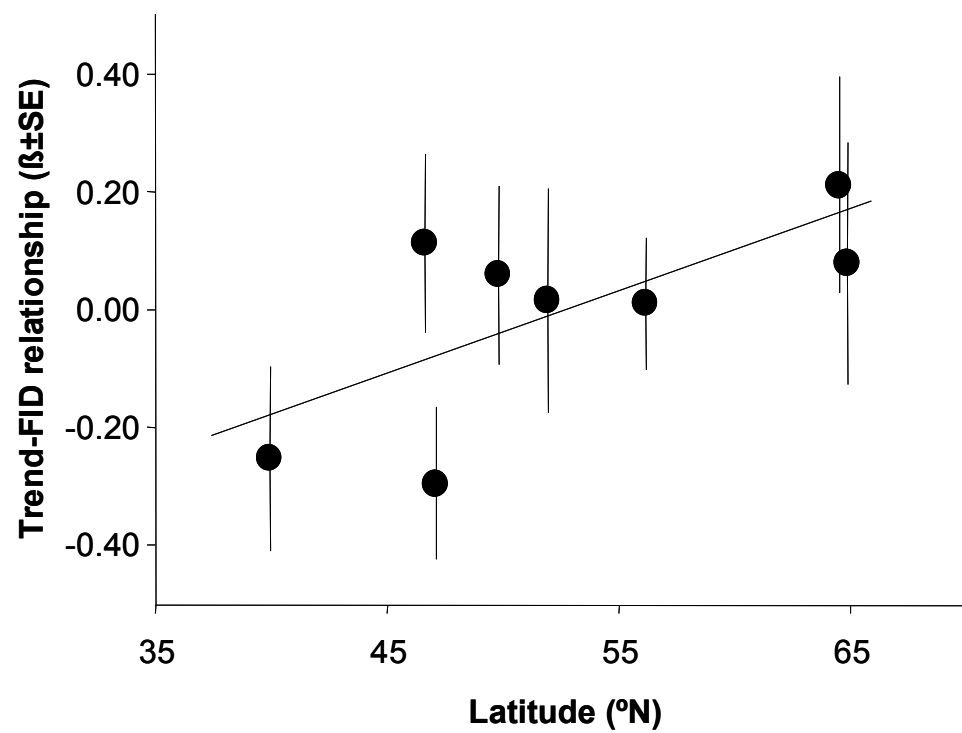
497   **Table 1.** Relationships between population trends of European birds (response variable) and geographical location (latitude,

498   longitude and marginality) and fearfulness (flight initiation distance, FID), after accounting for effects of farmland habitat,

499   migration distance, body mass and relative brain size on trends and correcting for the effect of the phylogenetic structure of

500   the data set, that was, however, not significant ($\lambda = 0.000$, $\chi^2 = -0.012$, $P = 1.000$). The full model (no removal of non-

501   significant terms as recommended by Forstmeier and Schielzeth 2010) had the statistics $F = 4.73$, d.f. = 12, 329, adjusted $r^2 =$

502   0.11, $P < 0.0001$. Effect sizes are Pearson's product-moment correlation coefficients.

503

504

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

505