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1 **Flight initiation distance and refuge in urban birds**

2

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25 collected data; FM and YB suggested hypotheses; FM and PM designed and performed  
26 the statistical analysis; FM, PM, DTB and YB wrote the first draft of the manuscript, and all  
27 authors contributed substantially to revisions.

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35

36 **Abstract**

37 Risk-taking in birds is often measured as the flight initiation distance (FID), the distance at  
38 which individuals take flight when approached by a potential predator (typically a human).  
39 The ecological factors that affect avian FID have received great attention over the past  
40 decades and meta-analyses and comparative analyses have shown that FID is correlated  
41 with body mass, flock size, starting distance of the approaching human, density of  
42 potential predators, as well as varying along rural to urban gradients. However,  
43 surprisingly, only few studies (mainly on reptiles and mammals) have explored effects of  
44 different types of refugia and their availability on animal escape decisions.

45 We used Bayesian regression models (controlling for the phylogenetic relatedness of bird  
46 species) to explore changes in escape behaviour recorded in European cities in  
47 relationship to the birds' distance to the nearest refuge and distance fled to the refuge. In  
48 our analyses, we also included information on the type of refuge, built-up and vegetation  
49 cover, starting distance, flock size, urbanization level, and type of urban habitat. We found  
50 that birds preferred tree refuges over artificial and bush refuges. Birds escaped earlier if  
51 the distance to the nearest refuge of any type was longer and if birds fled longer distances  
52 to the refuge. FID was shorter when birds used bushes as refugia or landed on the ground  
53 after flushing compared to using artificial refugia. Similarly, the distance fled to a refuge  
54 was shortest when using bushes, and increased when escaping to artificial substrates and  
55 trees. Birds were more timid in suburban than core areas of cities, cemeteries than parks,  
56 and in areas with higher bush cover but lower cover of built-up areas and trees. Our  
57 findings provide novel information regarding the importance of refuge proximity and type  
58 as factors affecting the escape behaviour of urban birds.

59

60 **Keywords:** birds; escape behaviour; human disturbance; refuge distance; trees; urban  
61 habitats

62

## 63 INTRODUCTION

64 There are three different defensive mechanisms that can be adopted for a prey when  
65 facing a predatory threat: avoiding detection through camouflage, evading the capture by  
66 escaping and trying to deter the predator (Kalb et al., 2019). However, the most common  
67 action for a prey confronting a predatory threat is to escape (Lima and Dill, 1990). An early  
68 escape can reduce foraging efficiency or increase physiological costs, while, on the other  
69 hand, a delayed escape can increase the risk of mortality due to predation (Ydenberg and  
70 Dill, 1986). In birds, fearfulness and willingness to take a risk is frequently estimated as the  
71 flight initiation distance (FID) when an individual bird is approached by a human under  
72 standardized conditions. Across species, FID is typically positively correlated with body  
73 size, perhaps because larger species which live longer and delay their reproduction  
74 minimize mortality due to predation by taking fewer risks (Virkkala and Lehikoinen, 2014;  
75 Wasser and Sherman, 2010), and they take a longer time to get airborne and thus avoid  
76 capture (Fernández-Juricic et al., 2006; Hemmingsen, 1951; Møller, 2008a; Weston et al.,  
77 2012). Finally, the number of birds in a flock can positively affect FID, probably due to  
78 “many eyes” scanning and increased vigilance (Morelli et al., 2019; Pulliam, 1973). The  
79 flock size seems to be more related to FID than to the distance moved during the escape  
80 (Tätte et al., 2018).

81 Among the environmental factors affecting FID, many studies have focused on the  
82 characteristics of habitat related to a degree of urbanization (Samia et al., 2017),  
83 interactions between predators and prey (Møller, 2008b), predator abundance (Díaz et al.,  
84 2022, 2013), level of stress of individuals (Tablado et al., 2021), as well as the time of day  
85 and season when FID is measured (Mikula et al., 2018; Piratelli et al., 2015). FID could be  
86 modulated by food abundance, being shorter in areas with lower food availability (Møller et  
87 al., 2015). Variation in the weather also can affect the escape behaviour, with FIDs

88 expected to decrease with increasing temperature and precipitation (Díaz et al., 2021).  
89 Additionally, some researchers suggested that birds are able to adapt their escape  
90 behaviour strategies to specific characteristics of human-modified habitats, including a  
91 road's speed limit (Legagneux and Ducatez, 2013) or the type and intensity of human  
92 activities (Morelli et al., 2018).

93 Shelter is a key factor regulating many aspects of predator–prey interactions (Berryman  
94 and Hawkins, 2006). Although FID is well-studied in relation to several ecological factors,  
95 and despite that the type and distance to refuge is predicted to affect escape responses  
96 (Cooper and Frederick, 2007; Ydenberg and Dill, 1986), the empirical effects of refuge  
97 characteristics are still poorly known and understood. Most of the studies on the effects of  
98 refuge characteristics on escape behaviour focused on mammals (Bonenfant and Kramer,  
99 1996; Dill and Houtman, 1989) and reptiles (Martín and López, 2003; Zani et al., 2009),  
100 with only sporadic reports on birds (e.g. Blumstein et al., 2004; Hall et al., 2020; Møller,  
101 2012). Although objects used by birds as refuges, including trees, bushes or artificial  
102 structures, are important components of the landscape occupied, no systematic research  
103 was conducted to quantify the main effects of refuge characteristics on FID in European  
104 birds. This is important, since behavioural responses of animals to human disturbance can  
105 have important implications for conservation and management (Weston et al., 2012). In  
106 the wildlife tourism sector as well as in urban areas, wildlife managers can use FID in  
107 sensitivity and tolerance analyses, which permit them to identify areas beyond which  
108 animals are less disturbed by humans (Fernández-Juricic et al., 2005; Livezey et al., 2016;  
109 Samia et al., 2015).

110 We expect that birds approached by predators and/or humans select among available  
111 refuges based on the characteristics of the surrounding environment, and the distance and  
112 type of available refuge. Thus, we hypothesized that birds escape earlier when the

113 available refuge is far (i.e. FID will be positively associated with potential refuge distance),  
114 since a short distance to a potential refuge should decrease the real or perceived risk of  
115 predation (Dill and Houtman, 1989; Stankowich and Blumstein, 2005). This is because we  
116 expect that when birds are farther away from a potential refuge, the time to reach that  
117 refuge is longer, therefore their risk of being captured is higher. Additionally, considering  
118 that FID is a measure of fearfulness, we can also expect that birds escaping early (longer  
119 FID) will fly longer distances to the used refuge (Tätte et al., 2018). A previous study  
120 showed a positive association between FID and distance fled after the escape, mainly for  
121 larger birds, suggesting that the distance fled is also an informative measure of  
122 antipredator behaviour in birds (Tätte et al., 2018). Escape distances of birds may also be  
123 affected by vegetation structure and decrease with increasing cover of trees and bushes  
124 which are often used as refuges by birds (Fernández-Juricic et al., 2002). Some refuge  
125 types may be perceived as safer than other types of refuges (Lima, 1993) and are related  
126 to predator avoidance strategies.

127 The aim of this study is to compare the escape distances (measured as FID) of birds in  
128 relation to distance to the potential refuge, distance fled to the refuge, refuge type and its  
129 availability in urban areas in four European countries. First, we explored how the  
130 availability of different types of refuges affect frequency of their use by birds and whether  
131 the distance fled to the refuge differed between the different types of refuges. We then  
132 employed multi-predictor Bayesian phylogenetically informed regression models  
133 controlling for the effects of several potentially important factors such as starting distance,  
134 flock size, levels of urbanization or habitat type.

135



## 136 **METHODS**

### 137 **Study area, flight initiation distance and refuge type**

138 Data on the flight initiation distance (FID) of birds were collected in urban areas in five  
139 cities in four European countries (Table S1) during the breeding seasons of 2020 and  
140 2021. The data were mainly collected during the first four hours after sunrise (6:00–10:00)  
141 on weekdays when it was not raining or excessively windy (Beaufort number  $\leq 2$ ).  
142 Observers used binoculars to identify birds that were foraging or engaged in “relaxed  
143 behaviour” (i.e. roosting or preening). Each individual bird was approached in a straight  
144 line by the observer walking at a slow, constant speed. The starting distance was  
145 estimated as the distance between the observer and the target when the observer started  
146 the approach toward the target (Blumstein, 2013). FID was measured as the distance  
147 between the observer and the point where the bird started to escape (fleeing or running).  
148 We collected data from as many bird species as possible by systematic searches of the  
149 study areas, but avoided sampling the same individual twice by moving to another site  
150 immediately after a bird was sampled. Highly vigilant birds (individuals clearly nervous, or  
151 altered by the presence of humans before the start of the approach), or birds sitting on  
152 their nests were avoided.

153 Flock size was defined as the number of conspecifics moving or foraging together;  
154 individuals in the flock were close to each other and were visually separated from  
155 individuals that were not occurring in the same flock. No mixed-species flocks were  
156 approached in this study.

157 Each sampled site was classified regarding the level of urbanisation into two categories:  
158 core (central, densely inhabited and well-urbanized parts of the city) and suburban (areas  
159 peripheral to the city centre); the main type of habitat: cemetery, garden, other urban

160 areas (streets, any other urban type of green area) or park. The surrounding area around  
161 the FID sampling points was described in terms of land use, considering a fixed radius of  
162 50 m around the observer. We estimated the land use cover in terms of percentage of  
163 built-up areas, trees, bushes, and grass. We used the following definition of bush and tree:  
164 A bush is a multi-stemmed short woody plant branching at or near the ground, while a tree  
165 is a tall perennial plant with a single self-supporting woody stem (Götmark et al., 2016).  
166 Additionally, in our study, trees were often taller than bushes (> 4m).

167 From the point where the target bird was observed, we estimated the distance to the  
168 nearest available refuge, considering the following types: artificial (e.g. electric wire, fence,  
169 statue, monument, signal pole, etc.), bush, or tree or patch of trees. We also calculated the  
170 mean distance to the nearest available refuge of each type.

171 After flushing the bird and measuring FID, we recorded the type of refuge used by the bird  
172 (artificial, bush, or tree) and the distance fled to such refuge from the point of escape. If the  
173 bird flew away without using a refuge (e.g. it landed on the ground) or was impossible to  
174 identify it, the fields "type of refuge" and "distance to refuge" were not filled.

## 175 **Statistical analyses**

176 First, a preliminary exploration of the data was performed by using all of the data, without  
177 considering any phylogenetic relationships between bird species. A Pearson's chi-square  
178 test of independence was performed to examine the relationship between availability of the  
179 nearest and the selected refuge, among all types of refuges (i.e. artificial, bush, or tree).  
180 For this test, if the bird flew and then landed on the ground, this was not considered as a  
181 refuge (approx. 30% of total observations). The distance fled to the used refuge was  
182 compared among the different types of refuges using a Games-Howell paired test (Triola,  
183 2012).

184 Second, we considered the non-independence in data values regarding the bird species.  
185 We used only species with  $\geq 10$  observations, because such sampling provides reliable  
186 estimates of FID (Sol et al., 2018). During the data selection procedure, we excluded all  
187 observations for mallards (*Anas platyrhynchos*) and other waterbirds as we wanted to  
188 focus on terrestrial birds. We tested associations between FID (response variable) and a  
189 set of predictors and covariates by multi-predictor Bayesian phylogenetically informed  
190 regression models, using the 'brms' v. 2.6.13 package (Bürkner, 2017). In the first model,  
191 we modelled FID as a function of mean distance of the nearest available refuge of each  
192 type, starting distance, flock size, land use composition (built-up cover, bush cover, grass  
193 cover, tree cover), level of urbanization (core, suburban) and habitat type (cemetery,  
194 garden, other urban areas, park). The category grass cover was excluded from the  
195 modelling procedure to avoid multicollinearity issues, since it was strongly negatively  
196 correlated with built-up cover ( $r = -0.64$ ,  $p < 0.05$ ).

197 In the second model, we modelled FID as a function of the distance fled to the refuge, type  
198 of used refuge (artificial, bush, tree; birds which landed on ground were also included in  
199 the analyses to control for their effect), starting distance, flock size, land use composition,  
200 level of urbanization, and habitat type.

201 To control for statistical non-independence due to shared ancestry among species  
202 (Paradis, 2011), we included species as a random factor and a phylogenetic covariance  
203 matrix in the models. We randomly downloaded 100 species-level phylogenies (using the  
204 "Hackett backbone") from BirdTree web tool (<http://birdtree.org>) (Jetz et al., 2012). We  
205 then constructed the maximum credibility tree (using these 100 trees) using  
206 maxCladeCred function in the 'phangorn' v. 2.8.1 package (Schliep, 2011) and created a  
207 phylogenetic covariance matrix using inverseA function in the 'MCMCglmm' v. 2.32  
208 package (Hadfield, 2010). We controlled for spatial variation by including country as a

209 random factor in the models. We excluded all observations with missing information on all  
210 predictors (for sample sizes in each test, see figures and tables). We also fitted models  
211 that used species as a random factor but did not incorporate the phylogenetic covariance  
212 matrix; we compared both types of models using the widely applicable information criterion  
213 (WAIC) and the leave-one-out information criterion (LOOIC) using the 'loo' package  
214 (Vehtari et al., 2017) and found that both model types provided qualitatively almost  
215 identical results but phylogenetically informed models were slightly better (although  
216 differences in WAIC and LOOIC values were  $<2$  in all cases). Hence, we report only  
217 results of the phylogenetically informed models in the main text (for results of non-  
218 phylogenetic models, see Table S3-4).

219 Models were fitted using a Gaussian family and a log-link function. For each model, we ran  
220 four Markov Chain Monte Carlo chains with default priors (i.e. uninformative, flat priors for  
221 fixed effects) and used 4000 sampling iterations (2000 iterations as a warm-up period). To  
222 minimize the occurrence of divergent transitions, we increased the target average proposal  
223 acceptance probability to 0.999 and the maximum tree depth to 15 (Bürkner, 2017). Model  
224 diagnostics indicated a good model convergence with an  $\hat{R}$  of 1 or close to 1 and sufficient  
225 effective sample size in the bulk and in the tails of the distribution (Vehtari et al., 2021). All  
226 continuous predictors were centred and scaled. For each model, we calculated the  
227 conditional  $R^2$  (the proportion of variance explained by fixed and random effects) and  
228 marginal  $R^2$  (the proportion of variance explained by the fixed effects only) using `r2_bayes`  
229 function in the 'performance' v. 0.8.0 package (Lüdtke et al., 2021). All statistical  
230 analyses and data explorations were performed with R software v. 4.1.2 (R Development  
231 Core Team, 2021).

232

## 233 RESULTS

234 A total of 2,900 FID observations were collected for 85 bird species recorded in four  
235 European countries (Table S1). The most frequently observed bird species were *Columba*  
236 *palumbus*, *Passer domesticus*, *Columba livia*, *Pica pica*, *Turdus merula* and *Parus major*,  
237 accounting for more than 59.2% of the total observations (Table S2). Overall, bird species  
238 with the longest FID were *Sturnus unicolor* and *Picus viridis* (mean FID > 17 m, N = 51 and  
239 25 observations, respectively). The two species with shortest FID were *Columba livia* and  
240 *Corvus corone* (mean FID = 4 and 4.2 m, N = 312 and 37 observations, respectively).  
241 Considering all species together, the mean values of FID across the five European cities  
242 ranged from 4.1 m (standard deviation = 2.7 m) (Budapest, Hungary) to 11.6 m (standard  
243 deviation = 8.8 m) (Toledo, Spain) (Table S1).

244 The most common nearest type of refuge available in all sampling sites was tree and tree  
245 patches (981 cases), followed by artificial structures (289 cases) and bush (237 cases)  
246 (Fig. 1). The mean distances to the nearest refuge available varied from 4.9 m ( $\pm$  4.4 m  
247 standard deviation) (Toledo, Spain) to 13.5 m ( $\pm$  10.7 m) (Rovaniemi, Finland) (Table S1).  
248 Considering the relative availability of each type of refuge, trees were overused as refuge  
249 while bush and artificial structures were underused ( $X^2 = 58.09$ ,  $df = 2$ ,  $p < 0.001$ ; Fig. 1).

250 Birds escaped earlier (i.e. had a longer FID) when the mean distance to nearest refuge of  
251 each type and starting distance were longer (Fig. 2; Table 1). Birds escaped earlier in  
252 suburban than in core areas of the cities, in areas with higher bush cover and lower built-  
253 up and tree cover, and in cemeteries than in parks (Fig. 3; Table 1).

254 The results of the second model identified a marginally significant effect that birds escaped  
255 earlier when they were farther from the used refuge (Fig. 2; Table 2). FID differed between  
256 birds using different types of refuges: FID was shorter when birds escaped to bushes or

257 landed on the ground compared to escaping to an artificial refuge (Fig. 2; Table 2). Avian  
258 FID also increased with starting distance and bush cover and were longer in suburban  
259 than core city areas. Conversely, FID decreased with increasing built-up habitat and tree  
260 cover and was shorter in parks than in cemeteries (Table 2). Finally, we found that birds  
261 flew longer distances to an artificial or tree refuge than when they aimed for a bush refuge  
262 (Games-Howell paired test,  $p < 0.001$  for comparison bush vs. artificial,  $p < 0.001$  for  
263 comparison bush vs. tree, Fig. S1).

264

## 265 **DISCUSSION**

266 We found that risk perception in birds and their escape decisions were affected by  
267 distance to the refuge and type of refuge used, as well as by the built up area and  
268 vegetation cover. We found that birds escaped earlier when the potential or used refugia  
269 were farther (illustrating how distance to safety influenced risk assessment), and in areas  
270 with high bush cover but low built-up and tree cover (illustrating that for the species  
271 studied, this type of cover was obstructive rather than protective). Birds also fled farther  
272 when they used artificial and trees as refuges, rather than bushes, or when they landed on  
273 the ground. Finally, we also found that FID of birds included in this study was related to  
274 some of well-studied factors such as starting distance and the level of urbanization.  
275 Hence, our results suggest that several environmental factors related to the availability and  
276 characteristics of refuges affect avian antipredator behaviour and their decision when and  
277 where to escape.

278 The main findings of this study are related to the birds' escape response in relation to the  
279 distance to the available and used refuge. We found that birds escaped earlier if: (a) the  
280 potential refuge was farther away, and (b) birds had to fly longer distances to the refuge.  
281 This final statement was only marginally significant in the modelling procedure, but the  
282 positive association was more clear when exploring FID on bird species with larger  
283 samples (Fig. S2). Similar findings have been reported for diverse animals, including  
284 fishes, reptiles, and mammals. For common wall lizards (*Podarcis muralis*) the distance to  
285 the nearest refuge alters escape behaviour (Amo et al., 2005). Similarly to our findings,  
286 gray squirrels (*Sciurus carolinensis*) (Dill and Houtman, 1989), woodchucks (*Marmota*  
287 *monax*) (Bonenfant and Kramer, 1996), Cuban curly-tailed lizards (*Leiocephalus carinatus*)  
288 (Cooper, 2007), broad-headed skinks (*Eumeces laticeps*) (Cooper, 1997), and African  
289 cichlid fishes (*Melanochromis chipokae*) (Dill, 1990) escaped earlier as distance to refuge

290 increased. In contrast to Tatte et al. (2018), we found that FID of birds generally increases  
291 with the distance to the nearest available refuge in urban green areas, supporting a  
292 prediction of optimal escape theory (Cooper and Frederick, 2007; Ydenberg and Dill,  
293 1986). This implies that birds base their escape decisions also on the relative time  
294 required to reach the refuge. Thus, birds could be more afraid of a predatory threat when  
295 farther away from a potential refuge.

296 Additionally, we found that longer FIDs were associated with longer distances fled to the  
297 refuge, independently of the type of refuge selected. A relationship between FID and  
298 distance fled to the refuge is relatively poorly understood, and has been mostly studied in  
299 lizards (Cooper, 2007; Cooper and Wilson, 2007). A previous study in birds already found  
300 a positive association between FID and fleeing distance, but only in heavier species (Tatte  
301 et al., 2018). Our study covering tens of bird species, found a similar pattern suggesting  
302 pre- and post-disturbance symmetry in their fear; birds with longer FIDs are also birds that  
303 escaped farther. This result supports the hypothesis that individual level of fearfulness is a  
304 personality trait and, hence, is consistent among different phases of a predatory encounter  
305 (Cooper and Wilson, 2007; Stankowich and Coss, 2007); shyer individuals have longer  
306 FIDs and fled longer distances than bolder individuals. Yet, studies of yellow-bellied  
307 marmots (*Marmota flaviventer*) suggest that boldness may be age-specific (Petelle et al.,  
308 2013). Future avian studies would benefit from testing identified individuals (Blumstein,  
309 2019) and it would be interesting to identify animal groups which adopt different escape  
310 strategies.

311 We also found that FID and distances fled were influenced by the availability of various  
312 types of refugia, with earlier escapes and longer distances fled when using artificial  
313 structures and trees as refugia than bush or landing on the ground. The earlier escape and  
314 longer distance fled to trees (despite their prevalence) may be explained by preferences



315 (Fig. 1). The generally low distance fled to bush refuge may indicate that birds often feed  
316 in the proximity of this type of refuge. Some previous studies found no relationship  
317 between escape distances of birds and vegetation structure and type of area cover  
318 (Rodríguez-Prieto et al., 2009), but we provide evidence that vegetation and built-up cover  
319 may affect escape decision (Fernández-Juricic et al., 2002; Morelli et al., 2018). These  
320 findings may further support the observation that birds in our sample tended to prefer trees  
321 as refuges and were willing to flee longer distances to trees. Artificial structures (e.g. street  
322 lamps or buildings), although not used as frequently as trees, may be perceived by birds  
323 as safer refuges because they are typically higher than bushes and, hence, birds might  
324 respond to approaching humans by decreasing their escape distances in built-up areas  
325 with prevalent artificial structures and be willing to flee farther when using an artificial  
326 refuge. In the visited urban parks and cemeteries, the cover of green areas identified as a  
327 potential refuge (bush and trees) was not particularly higher in suburban areas than in core  
328 city areas (Fig. S3). More work on how birds perceive the built environment is necessary to  
329 develop wildlife-friendly cities (Uchida et al., 2021).

330 Our results also confirmed some findings previously demonstrated in birds. We found a  
331 positive and significant association between FID and starting distance which has been  
332 widely identified birds, including European urban populations (Blumstein, 2013; Mikula et  
333 al., 2021; Tätte et al., 2018). In addition, we found that, overall, FID of birds was longer in  
334 suburban areas if compared with core areas of the city, with the only exception of  
335 Budapest (Hungary) (see Fig. 3). This result is congruent with numerous previous studies  
336 showing a significant effect of the urbanisation gradient on avian escape behaviour, with  
337 consistently longer avian FID in rural than urban habitats (Møller et al., 2015; Samia et al.,  
338 2017, 2015) or FID decreasing with the proximity to the city centre (Battle et al., 2016;  
339 Matsyura et al., 2015). Birds from suburban areas could be more sensitive to approaching  
340 humans than their conspecifics from the core city areas, because they are less tolerant of

341 anthropogenic disturbances (Bötsch et al., 2018; Samia et al., 2015; Tryjanowski et al.,  
342 2020). Interestingly, we found that birds in cemeteries were shier (escaped earlier) than  
343 birds in parks. This is in contrast with previous European study which sampled FID of birds  
344 during breeding season 2014 in Czech Republic, France, Italy and Poland and found the  
345 opposite pattern (Morelli et al., 2018). This may indicate that differences in avian FID  
346 between parks and cemeteries may be temporally variable and differ between various  
347 countries (Morelli et al., 2018).

348 In conclusion, the present study found that escape decision of birds and their willingness  
349 to take a risk is affected by their distance to the potential refuge, the availability of different  
350 refuge types as well as vegetation and built-up cover. Environmental characteristics  
351 related to the potential refuge distribution and availability have been neglected in studies  
352 on escape behaviour of animals, and birds in particular. This study indicates that avian  
353 escape behaviour takes into account refuge proximity and type as well as the general  
354 structure of the surrounding environment. Future studies could explore how the availability  
355 of refuges and their types interact with spatial and temporal heterogeneity in humans and  
356 predator activity and affect avian antipredator behaviour.

357

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546

547 **Tables**

548 **Table 1.** Results of a multi-predictor Bayesian phylogenetically informed regression model  
 549 exploring the associations between flight initiation distance (response variable) and a set  
 550 of predictors: mean distance to the nearest refuge of each type, starting distance, flock  
 551 size, land use composition (built-up cover, bush cover, tree cover), level of urbanization  
 552 (core, suburban) and habitat type (cemetery, garden, other urban areas, park). The model  
 553 incorporated a species (and a phylogenetic covariance matrix) and country as random  
 554 factors to control for statistical phylogenetic and spatial non-independence in data values.  
 555 We report parameter estimates with their standard errors (SE) and 95% credible intervals,  
 556 conditional  $R^2$  (the proportion of variance explained by fixed and random effects) and  
 557 marginal  $R^2$  (the proportion of variance explained by the fixed effects only). Significant  
 558 results (i.e., those where credible intervals do not cross zero) are highlighted in bold. N =  
 559 2309 observations and 34 species.

<b>Variables</b>	<b>Estimate</b>	<b>SE</b>	<b>lower 95% CI</b>	<b>upper 95% CI</b>
<i>Fixed factors</i>				
Intercept	2.06	0.38	1.30	2.83
<b>Distance to nearest refuge</b>	<b>0.07</b>	<b>0.01</b>	<b>0.05</b>	<b>0.10</b>
<b>Starting distance</b>	<b>0.19</b>	<b>0.01</b>	<b>0.17</b>	<b>0.21</b>
Flock	-0.01	0.01	-0.04	0.01
<b>Built-up cover</b>	<b>-0.09</b>	<b>0.02</b>	<b>-0.13</b>	<b>-0.06</b>
<b>Bush cover</b>	<b>0.06</b>	<b>0.02</b>	<b>0.02</b>	<b>0.09</b>
<b>Tree cover</b>	<b>-0.05</b>	<b>0.02</b>	<b>-0.09</b>	<b>-0.01</b>
<b>Urban level (Suburban)</b>	<b>0.25</b>	<b>0.03</b>	<b>0.20</b>	<b>0.30</b>
Habitat (Garden)	-0.15	0.10	-0.35	0.03
Habitat (Other urban)	0.04	0.07	-0.09	0.18
<b>Habitat (Park)</b>	<b>-0.25</b>	<b>0.05</b>	<b>-0.35</b>	<b>-0.14</b>

*Random factors*

Country	0.60	0.44	0.20	1.79
Species	0.44	0.07	0.33	0.60
Conditional R <sup>2</sup>	0.40		0.37	0.42
Marginal R <sup>2</sup>	0.12		0.01	0.31

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560

561

562 **Table 2.** Results of a multi-predictor Bayesian phylogenetically informed regression model  
563 exploring the associations between flight initiation distance (response variable) and a set  
564 of predictors: distance fled to refuge, type of used refuge (artificial, bush, tree; ground  
565 category – even if was not classified as a type of refuge – was also included), starting  
566 distance, flock size, land use composition (built-up cover, bush cover, tree cover), level of  
567 urbanization (core, suburban) and habitat type (cemetery, garden, other urban areas,  
568 park). The model incorporated species (and a phylogenetic covariance matrix) and country  
569 as random factors to control for statistical phylogenetic and spatial non-independence in  
570 data values. We report parameter estimates with their standard errors (SE) and 95%  
571 credible intervals, conditional  $R^2$  (the proportion of variance explained by fixed and random  
572 effects) and marginal  $R^2$  (the proportion of variance explained by the fixed effects only).  
573 Significant and marginally significant results (i.e., those where credible intervals do not  
574 cross zero or slightly cross zero, respectively) are highlighted in bold and italics,  
575 respectively. N = 1953 observations and 33 species.

Variables	Estimate	SE	lower 95% CI	upper 95% CI
<i>Fixed factors</i>				
Intercept	2.11	0.34	1.44	2.77
Distance fled to refuge	0.02	0.01	-0.00	0.04
<b>Refuge type (Bush)</b>	<b>-0.66</b>	<b>0.12</b>	<b>-0.91</b>	<b>-0.43</b>
<b>Refuge type (Ground)</b>	<b>-0.26</b>	<b>0.06</b>	<b>-0.37</b>	<b>-0.15</b>
Refuge type (Tree)	-0.05	0.05	-0.14	0.04
<b>Starting distance</b>	<b>0.21</b>	<b>0.01</b>	<b>0.19</b>	<b>0.23</b>
Flock	-0.02	0.02	-0.06	0.01
<b>Built-up cover</b>	<b>-0.11</b>	<b>0.02</b>	<b>-0.16</b>	<b>-0.07</b>
<b>Bush cover</b>	<b>0.06</b>	<b>0.02</b>	<b>0.03</b>	<b>0.10</b>
<b>Tree cover</b>	<b>-0.05</b>	<b>0.02</b>	<b>-0.08</b>	<b>-0.01</b>

<b>Urban level (Suburban)</b>	<b>0.22</b>	<b>0.03</b>	<b>0.16</b>	<b>0.28</b>
Habitat (Garden)	-0.11	0.10	-0.31	0.08
Habitat (Other urban)	0.06	0.07	-0.09	0.20
<b>Habitat (Park)</b>	<b>-0.18</b>	<b>0.06</b>	<b>-0.29</b>	<b>-0.06</b>
<i>Random factors</i>				
Country	0.51	0.37	0.17	1.53
Species	0.38	0.07	0.28	0.53
Conditional R <sup>2</sup>	0.43		0.40	0.45
Marginal R <sup>2</sup>	0.19		0.02	0.39

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577

578 **Figure legends**

579 **Figure 1.** Schematic representation of the mean availability of the nearest refuge of each  
580 type and mean effective use of each type of refuge by birds in urban habitats. Availability  
581 and use are showed in percentage. The sum of availability of nearest refuges reaches the  
582 100%. The percentage of use of each type of refuge is calculated as the rate between  
583 effective use regarding the total availability of such type of nearest refuge, so values are  
584 unlinked among different types of refuge. The colour and thin of arrows indicate if the type  
585 of refuge is used more (light blue) or less (light red) than expected regarding its availability.  
586 N = 1506.

587

588 **Figure 2.** Association between flight initiation distance (FID, m) and (a) mean nearest  
589 available refuge distance (m) and (b) distance fled to the used refuge (m), for birds  
590 sampled in this study. Envelopes around linear regression lines are 95% confidence  
591 intervals. N = 2816 (mean nearest available refuge distance) and N = 2458 (distance fled  
592 to the used refuge).

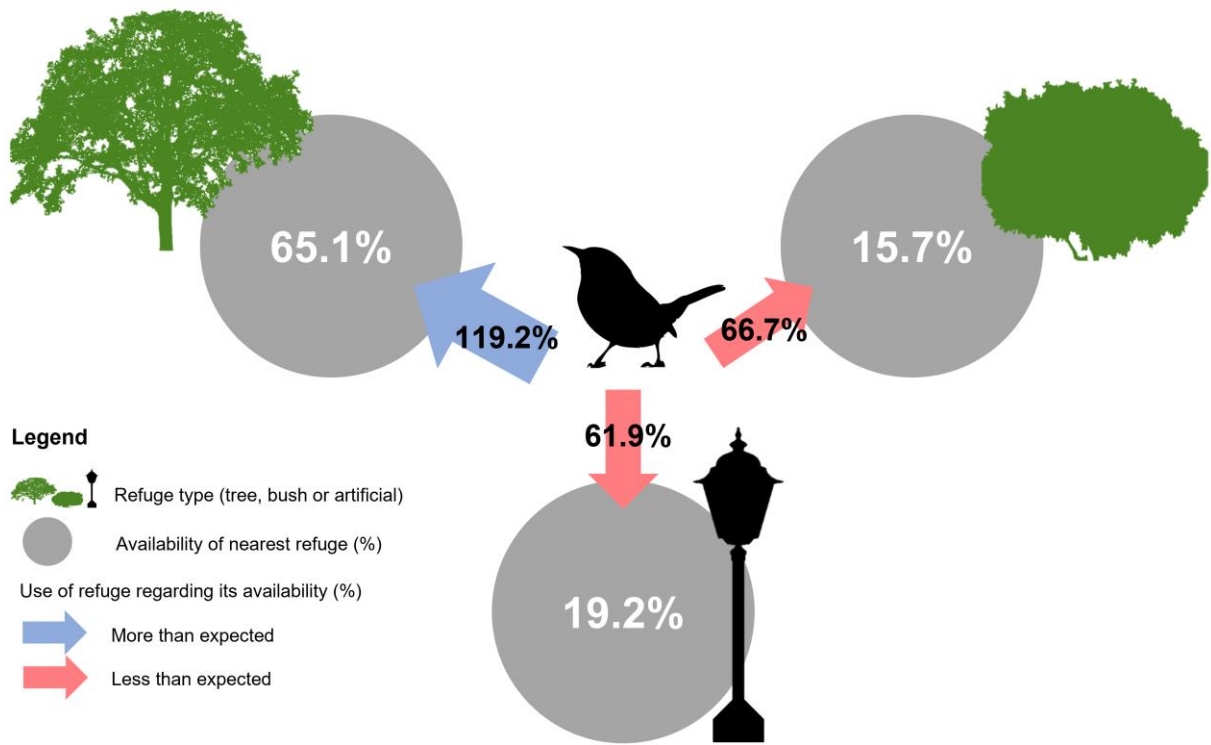
593

594 **Figure 3.** Association between flight initiation distance (FID, m) of birds and level of  
595 urbanization (core or suburban) in the four countries sampled in this study (Czech  
596 Republic, Finland, Hungary and Spain). Box plots show the median (the bar in the middle  
597 of rectangles), upper and lower quartiles (length of rectangles), maximum and minimum  
598 values (whiskers), mean values (red rhombus), and raw FID values (small grey dots). N  
599 total = 2878 (Czech Republic, core = 701, suburban = 354; Finland, core = 158, suburban  
600 = 208; Hungary, core = 207, suburban = 175; Spain, core = 688, suburban = 387).

601

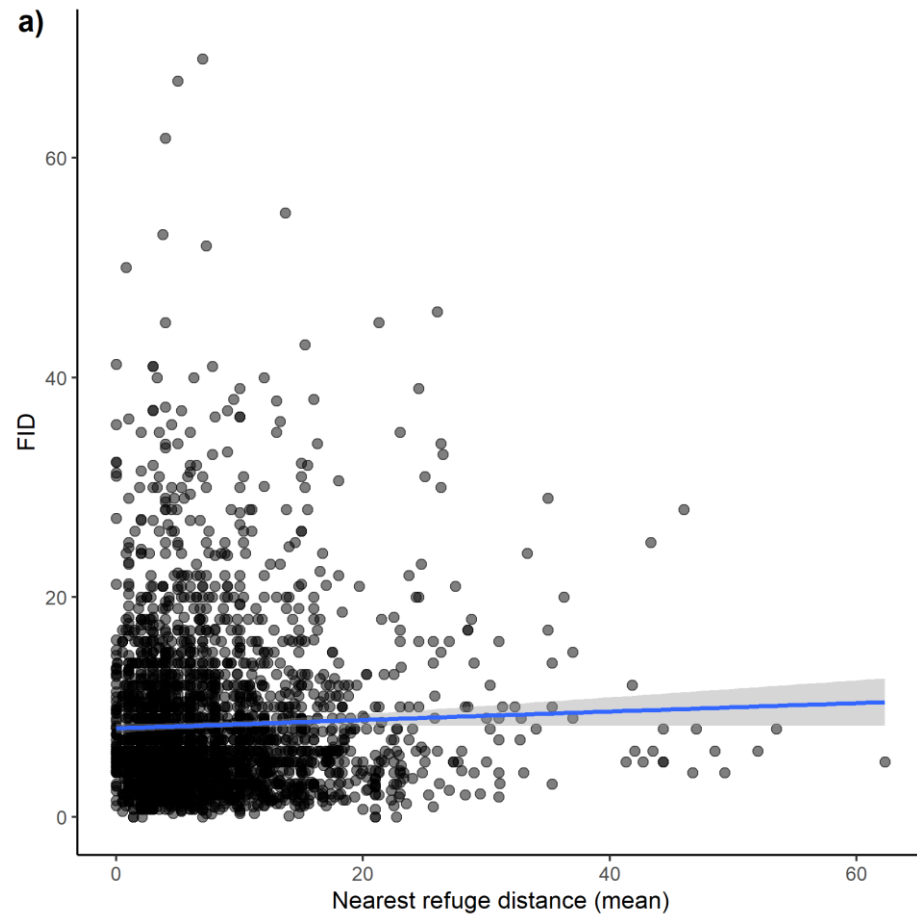


602 Fig. 1



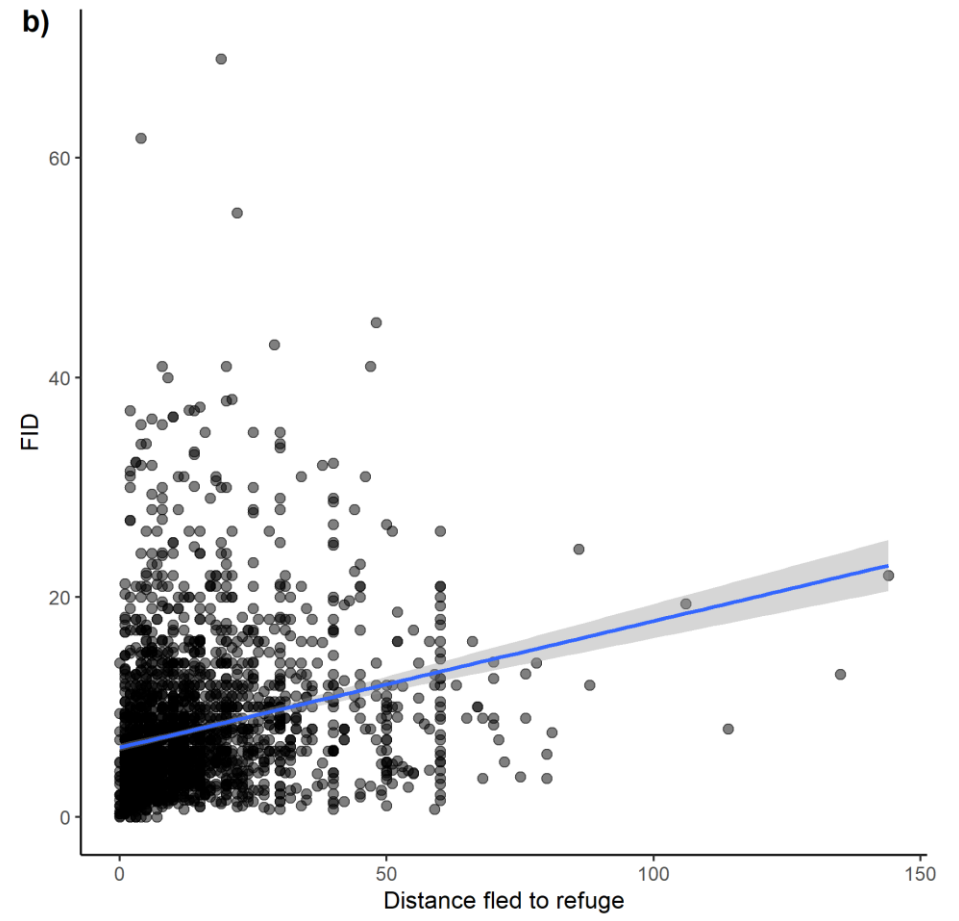
603

604 Fig. 2

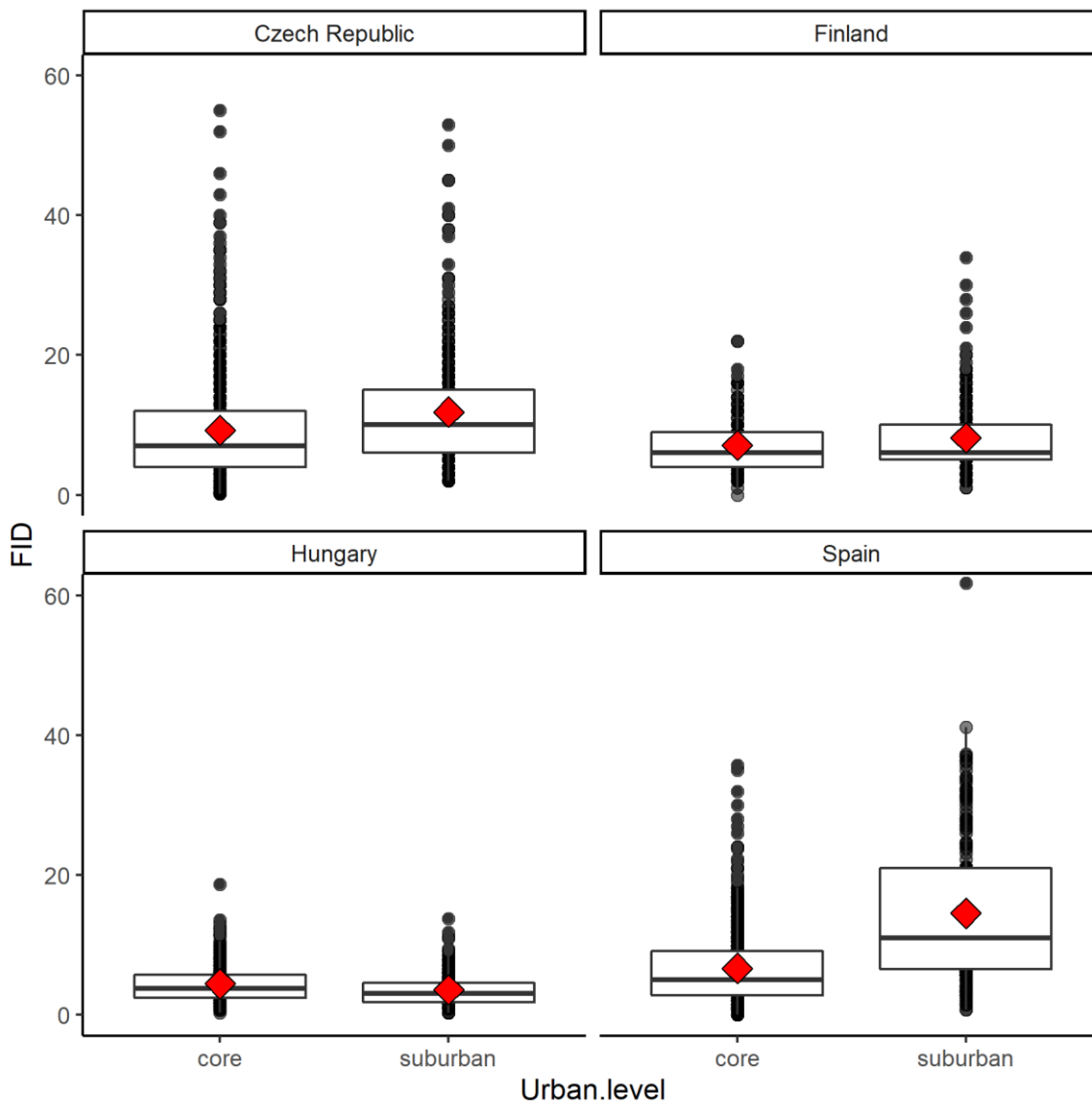


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607 Fig. 3



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