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Flight initiation distance and refuge in urban birds

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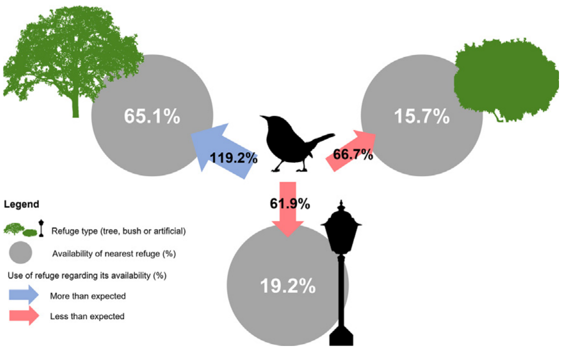
HIGHLIGHTS

- Flight initiation distance (FID) is considered a proxy of antipredator behaviour.
- We investigated changes in FID of birds in relation to refuge type and availability.
- We found that birds preferred tree refuges over artificial and bush refuges.
- Birds escaped earlier if the distance to the nearest available refuge was longer.
- Birds fled longer distances to the refuge when were more afraid (with longer FID).

GRAPHICAL ABSTRACT



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ABSTRACT

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

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

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areas and trees. Our findings provide novel information regarding the importance of refuge proximity and type as factors affecting the escape behaviour of urban birds.

1. Introduction

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

Among the environmental factors affecting FID, many studies have focused on the characteristics of habitat related to a degree of urbanization (Samia et al., 2017), interactions between predators and prey (Møller, 2008b), predator abundance (Díaz et al., 2022, 2013), level of stress of individuals (Tablado et al., 2021), as well as the time of day and season when FID is measured (Mikula et al., 2018; Piratelli et al., 2015). FID could be modulated by food abundance, being shorter in areas with lower food availability (Møller et al., 2015). Variation in the weather also can affect the escape behaviour, with FIDs expected to decrease with increasing temperature and precipitation (Díaz et al., 2021). Additionally, some researchers suggested that birds are able to adapt their escape behaviour strategies to specific characteristics of human-modified habitats, including a road's speed limit (Legagneux and Ducatez, 2013) or the type and intensity of human activities (Morelli et al., 2018).

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

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

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

2. Methods

2.1. Study area, flight initiation distance and refuge type

Data on the flight initiation distance (FID) of birds were collected in urban areas in five cities in four European countries (Table S1) during the breeding seasons of 2020 and 2021. The data were mainly collected during the first 4 h after sunrise (6:00–10:00) on weekdays when it was not raining or excessively windy (Beaufort number ≤ 2). Observers used binoculars to identify birds that were foraging or engaged in "relaxed behaviour" (i.e. roosting or preening). Each individual bird was approached in a straight line by the observer walking at a slow, constant speed. The starting distance was estimated as the distance between the observer and the target when the observer started the approach toward the target (Blumstein, 2013). FID was measured as the distance between the observer and the point where the bird started to escape (fleeing or running). We collected data from as many bird species as possible by systematic searches of the study areas, but avoided sampling the same individual twice by moving to another site immediately after a bird was sampled. Highly vigilant birds (individuals clearly nervous, or altered by the presence of humans before the start of the approach), or birds sitting on their nests were avoided.

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

Each sampled site was classified regarding the level of urbanization into two categories: core (central, densely inhabited and well-urbanized parts of the city) and suburban (areas peripherical to the city centre); the main type of habitat: cemetery, garden, other urban areas (streets, any other urban type of green area) or park. The surrounding area around the FID sampling points was described in terms of land use, considering a fixed radius of 50 m around the observer. We estimated the land use cover in terms of percentage of built-up areas, trees, bushes, and grass. We used the following definition of bush and tree: A bush is a multi-stemmed short woody plant branching at or near the ground, while a tree is a tall perennial plant with a single self-supporting woody stem (Götmark et al., 2016). Additionally, in our study, trees were often taller than bushes (> 4 m).

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

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

2.2. Statistical analyses

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

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

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

To control for statistical non-independence due to shared ancestry among species (Paradis, 2011), we included species as a random factor and a phylogenetic covariance matrix in the models. We randomly downloaded 100 species-level phylogenies (using the "Hackett backbone") from BirdTree web tool (http://birdtree.org) (Jetz et al., 2012). We then constructed the maximum credibility tree (using these 100 trees) using maxCladeCred function in the 'phangorn' v. 2.8.1 package (Schliep, 2011) and created a phylogenetic covariance matrix using inverseA function in the 'MCMCglmm' v. 2.32 package (Hadfield, 2010). We controlled for spatial variation by including country as a random factor in the models. We excluded all observations with missing information on all predictors (for sample sizes in each test, see figures and tables). We also fitted models that used species as a random factor but did not incorporate the phylogenetic covariance matrix; we compared both types of models using the widely applicable information criterion (WAIC) and the leave-one-out information criterion (LOOIC) using the 'loo' package (Vehtari et al., 2017) and found that both model types provided qualitatively almost identical results but phylogenetically informed models were slightly better (although differences in WAIC and LOOIC values were <2 in all cases). Hence, we report only results of the phylogenetically informed models in the main text (for results of non-phylogenetic models, see Table S3-4).

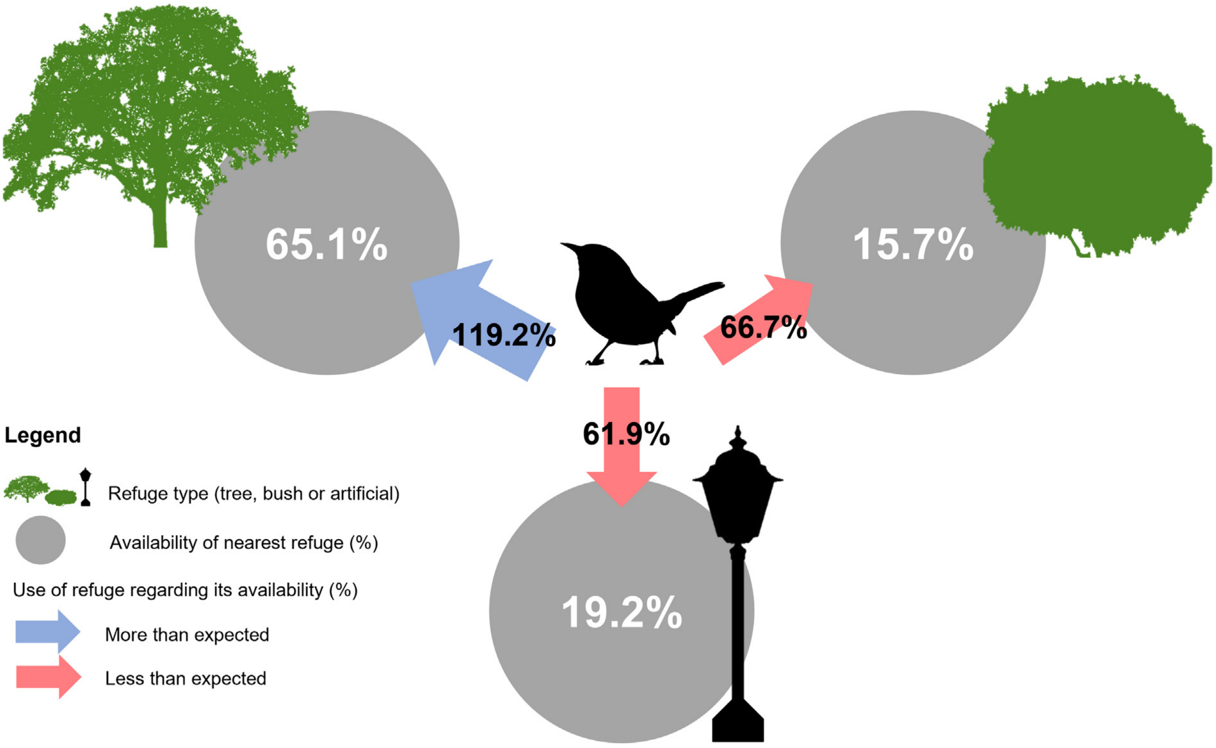

Fig. 1. Schematic representation of the mean availability of the nearest refuge of each type and mean effective use of each type of refuge by birds in urban habitats. Availability and use are showed in percentage. The sum of availability of nearest refuges reaches the 100 %. The percentage of use of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

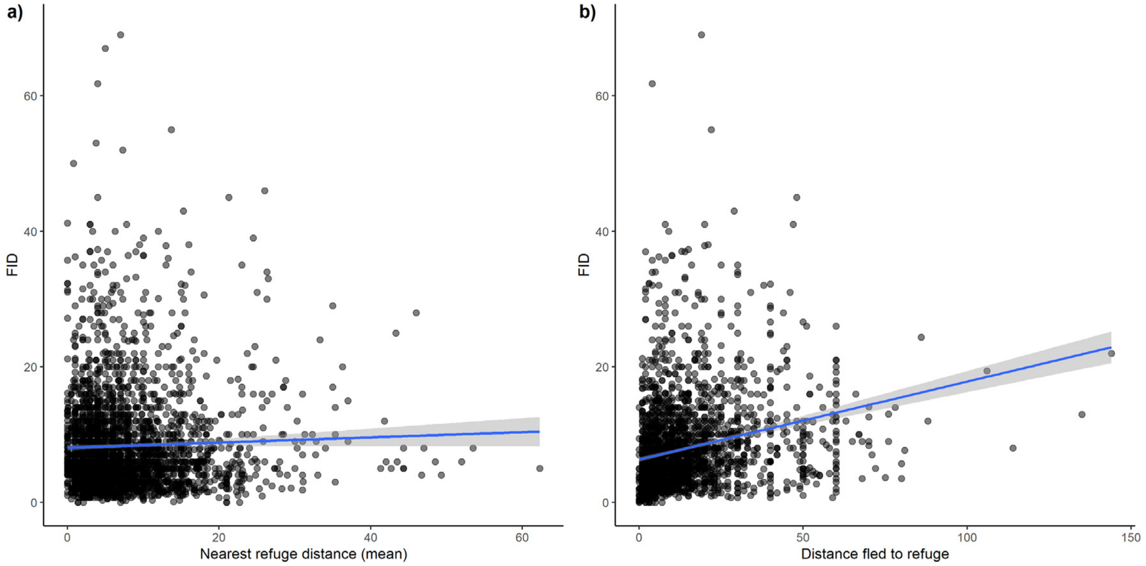

Fig. 2. Association between flight initiation distance (FID, m) and (a) mean nearest available refuge distance (m) and (b) distance fled to the used refuge (m), for birds sampled in this study. Envelopes around linear regression lines are 95 % confidence intervals. $N = 2816$ (mean nearest available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

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

3. Results

A total of 2900 FID observations were collected for 85 bird species recorded in four European countries (Table S1). The most frequently observed bird species were *Columba palumbus*, *Passer domesticus*, *Columba livia*, *Pica pica*, *Turdus merula* and *Parus major*, accounting for >59.2 % of the total observations (Table S2). Overall, bird species with the longest FID were *Sturnus unicolor* and *Picus viridis* (mean FID >17 m, $N = 51$ and 25 observations, respectively). The two species with shortest FID were *Columba livia* and *Corvus corone* (mean FID = 4 and 4.2 m, $N = 312$ and 37 observations, respectively). Considering all species together, the mean values of FID across the five European cities ranged from 4.1 m (standard deviation = 2.7 m) (Budapest, Hungary) to 11.6 m (standard deviation = 8.8 m) (Toledo, Spain) (Table S1).

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

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

The results of the second model identified a marginally significant effect that birds escaped earlier when they were farther from the used refuge (Fig. 2; Table 2). FID differed between birds using different types of refuges: FID was shorter when birds escaped to bushes or landed on the ground compared to escaping to an artificial refuge (Fig. 2; Table 2). Avian FID also increased with starting distance and bush cover and were longer in suburban than core city areas. Conversely, FID decreased with increasing built-up

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

Variables	Estimate	SE	Lower 95 % CI	Upper 95 % CI
Fixed factors				
Intercept	2.06	0.38	1.30	2.83
Distance to nearest refuge	**0.07**	**0.01**	**0.05**	**0.10**
Starting distance	**0.19**	**0.01**	**0.17**	**0.21**
Flock	−0.01	0.01	−0.04	0.01
Built-up cover	**−0.09**	**0.02**	**−0.13**	**−0.06**
Bush cover	**0.06**	**0.02**	**0.02**	**0.09**
Tree cover	**−0.05**	**0.02**	**−0.09**	**−0.01**
Urban level (Suburban)	**0.25**	**0.03**	**0.20**	**0.30**
Habitat (Garden)	−0.15	0.10	−0.35	0.03
Habitat (Other urban)	0.04	0.07	−0.09	0.18
Habitat (Park)	**−0.25**	**0.05**	**−0.35**	**−0.14**
Random factors				
Country	0.60	0.44	0.20	1.79
Species	0.44	0.07	0.33	0.60
Conditional R^2	0.40		0.37	0.42
Marginal R^2	0.12		0.01	0.31

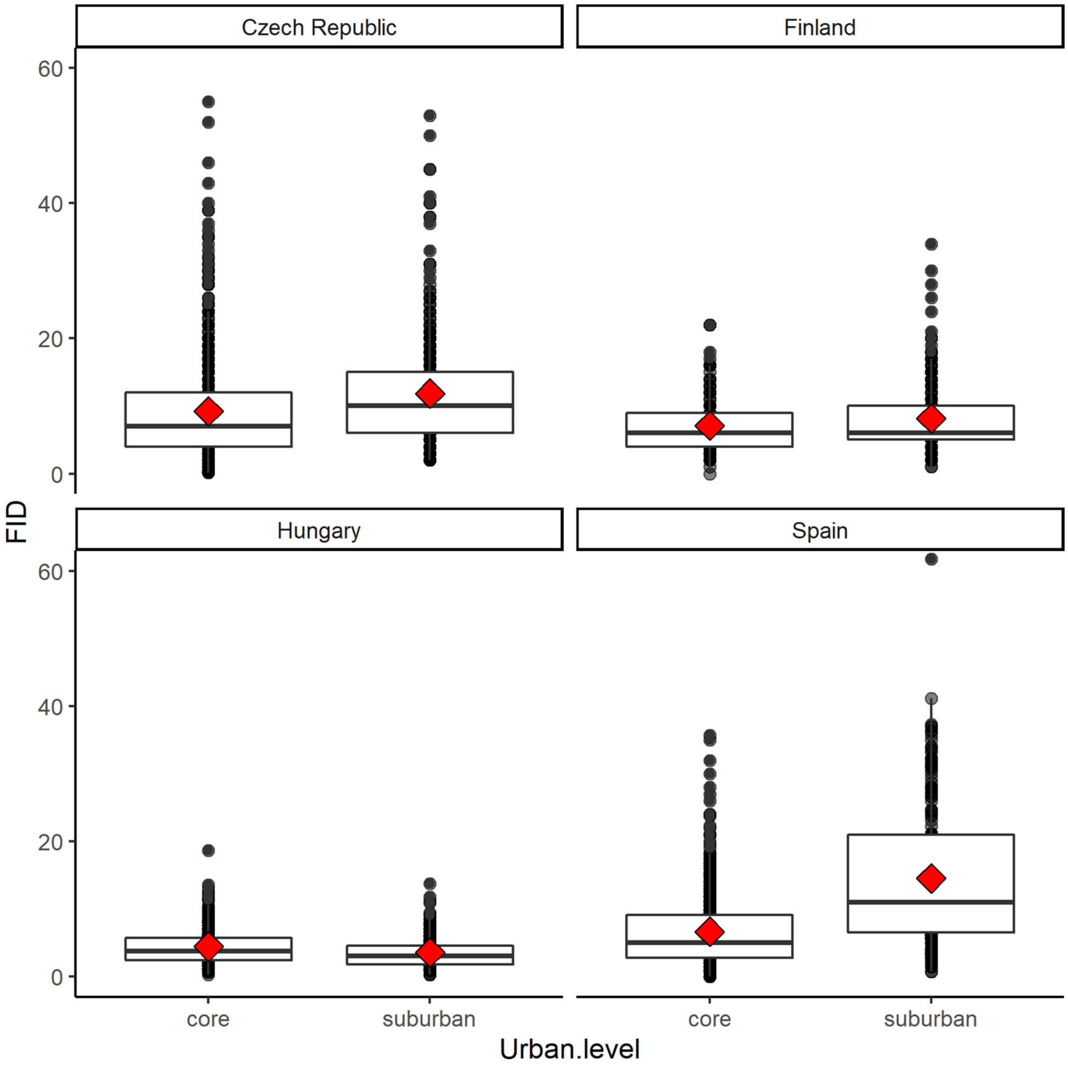

Fig. 3. Association between flight initiation distance (FID, m) of birds and level of urbanization (core or suburban) in the four countries sampled in this study (Czech Republic, Finland, Hungary and Spain). Box plots show the median (the bar in the middle of rectangles), upper and lower quartiles (length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

habitat and tree cover and was shorter in parks than in cemeteries (Table 2). Finally, we found that birds flew longer distances to an artificial or tree refuge than when they aimed for a bush refuge (Games-Howell paired test, $p < 0.001$ for comparison bush vs. artificial, $p < 0.001$ for comparison bush vs. tree, Fig. S1).

4. Discussion

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

The main findings of this study are related to the birds' escape response in relation to the distance to the available and used refuge. We found that birds escaped earlier if: (a) the potential refuge was farther away, and (b) birds had to fly longer distances to the refuge. This final statement was only marginally significant in the modelling procedure, but the positive association was more clear when exploring FID on bird species with larger samples (Fig. S2). Similar findings have been reported for diverse animals, including fishes, reptiles, and mammals. For common wall lizards (*Podarcis muralis*) the distance to the nearest refuge alters escape behaviour (Amo et al., 2005). Similarly to our findings, gray squirrels (*Sciurus carolinensis*) (Dill and Houtman, 1989), woodchucks (*Marmota monax*) (Bonenfant and Kramer, 1996), Cuban curly-tailed lizards (*Leiocephalus carinatus*) (Cooper, 2007), broad-headed skinks (*Eumeces laticeps*) (Cooper, 1997), and African cichlid fishes (*Melanochromis chipokae*) (Dill, 1990) escaped earlier as distance to refuge increased. In contrast to Tätte et al. (2018), we found that FID of birds generally increases with the distance to the nearest available refuge in urban green areas, supporting a prediction of optimal escape theory (Cooper and Frederick, 2007; Ydenberg and Dill, 1986). This implies that birds base their escape decisions also on the relative time required to reach the refuge. Thus, birds could be more afraid of a predatory threat when farther away from a potential refuge.

Table 2

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

Variables	Estimate	SE	lower 95 % CI	upper 95 % CI
Fixed factors				
Intercept	2.11	0.34	1.44	2.77
Distance fled to refuge	0.02	0.01	−0.00	0.04
Refuge type (Bush)	**−0.66**	**0.12**	**−0.91**	**−0.43**
Refuge type (Ground)	**−0.26**	**0.06**	**−0.37**	**−0.15**
Refuge type (Tree)	−0.05	0.05	−0.14	0.04
Starting distance	**0.21**	**0.01**	**0.19**	**0.23**
Flock	−0.02	0.02	−0.06	0.01
Built-up cover	**−0.11**	**0.02**	**−0.16**	**−0.07**
Bush cover	**0.06**	**0.02**	**0.03**	**0.10**
Tree cover	**−0.05**	**0.02**	**−0.08**	**−0.01**
Urban level (Suburban)	**0.22**	**0.03**	**0.16**	**0.28**
Habitat (Garden)	−0.11	0.10	−0.31	0.08
Habitat (Other urban)	0.06	0.07	−0.09	0.20
Habitat (Park)	**−0.18**	**0.06**	**−0.29**	**−0.06**
Random factors				
Country	0.51	0.37	0.17	1.53
Species	0.38	0.07	0.28	0.53
Conditional R^2	0.43		0.40	0.45
Marginal R^2	0.19		0.02	0.39

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

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

Our results also confirmed some findings previously demonstrated in birds. We found a positive and significant association between FID and starting distance which has been widely identified birds, including European urban populations (Blumstein, 2013; Mikula et al., 2021; Tätte et al., 2018). In addition, we found that, overall, FID of birds was longer in suburban areas if compared with core areas of the city, with the only exception of Budapest (Hungary) (see Fig. 3). This result is congruent with numerous previous studies showing a significant effect of the urbanization gradient on avian escape behaviour, with consistently longer avian FID in rural than urban habitats (Møller et al., 2015; Samia et al., 2017, 2015) or FID decreasing with the proximity to the city centre (Battle et al., 2016; Matsyura et al., 2015). Birds from suburban areas could be more sensitive to approaching humans than their conspecifics from the core city areas, because they are less tolerant of anthropogenic disturbances (Bötsch et al., 2018; Samia et al., 2015; Tryjanowski et al., 2020). Interestingly, we found that birds in cemeteries were shier (escaped earlier) than birds in parks. This is in contrast with previous European study which sampled FID of birds during breeding season 2014 in Czech Republic, France, Italy and Poland and found the opposite pattern (Morelli et al., 2018). This may indicate that differences in avian FID between parks and cemeteries may be temporally variable and differ between various countries (Morelli et al., 2018).

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

CRediT authorship contribution statement

FM, PM, MD, GM, JJ, M-L K–J, KF, FAZ, AS, YB collected data; FM and YB suggested hypotheses; FM and PM designed and performed the statistical analysis; FM, PM, DTB and YB wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data availability statement

Data will be made available after the publication, under reasonable request to the authors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156939.

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