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RESEARCH ARTICLE

Sex matters: European urban birds flee approaching women sooner than approaching men

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Abstract

1. Flight initiation distance (FID) is a metric often used to study an individual's perceptions of risk when facing a predatory threat. Longer FID indicates lower risk-taking, while shorter FID identifies bolder individuals who tolerate greater risk.
2. Until now, no studies have tested the potential effect of the observer's sex on the escape behaviour of wild birds. Given observed differences in how laboratory animals may respond to the sex of humans interacting with them, the lack of reports in the field is surprising.
3. In five European countries, we tested whether urban birds perceived the risk posed by approaching female versus male observers differently, using FID as a response variable. First, we matched the female and male observers according to their height and clothing. Then, we fitted Bayesian regression models, controlling for the phylogenetic relatedness of bird species, to test for the effect of human observer sex after controlling for a variety of other important factors known to explain variation in FID (starting distance, flock size, sex of the target bird, land use characteristics and vegetation cover).
4. We found that male birds were more risk-tolerant than females and – unexpectedly—birds in general escaped sooner when approached by women than by men. The escape difference associated with the observer's sex (~1 m longer when approached by women than by men) was consistent in populations across all five examined European countries. We discussed various hypotheses to explain birds' escape responses related to the observer's sex; however, further research is necessary to fully understand this phenomenon.

KEYWORDS
birds, escape behaviour, human disturbance, observer sex

1 | INTRODUCTION

When an animal faces a potential predatory threat, the most common behaviour across animals is to escape (Lima & Dill, 1990). Evaluating the costs and benefits of escape is an essential factor in managing predation risk (Ydenberg & Dill, 1986). Flight initiation distance (hereafter FID) is often used as a tool to investigate the cost–benefit trade-offs related to the risk of predation (Abou-Zeid et al., 2024; Berryman & Hawkins, 2006; Blumstein, 2019; Díaz et al., 2022; Fernández-Juricic et al., 2006; Morelli et al., 2022; Piratelli et al., 2015). The FID is a metric of fearfulness estimated as the distance between the observer and the target animal when the targeted individual (e.g. a bird) flees (Weston et al., 2012). Even when measured in response to approaching humans without predatory behaviour, FID serves as a reliable proxy for predator-related fear in urban birds (Ye et al., 2024). Longer FIDs can not only reduce the risk of mortality due to predation but also reduce foraging or food-searching efficiency (Ydenberg & Dill, 1986).

Prior FID studies identified several factors that can affect the escape response of birds. These include the type of habitat and environment (Díaz et al., 2013; Mikula et al., 2023; Samia et al., 2017); the level of local human activity (de Resen et al., 2024; Morelli et al., 2018); the urbanization level (Carlen et al., 2021); the abundance and density of predators (e.g. cats, raptors) (Díaz et al., 2013, 2022), as well as the availability and distance to potential refugia (e.g. trees and bushes) (Morelli et al., 2022). Species' traits can also affect the escape behaviour of birds. Longer FIDs are associated with larger birds, perhaps because larger birds require longer times to effectively get airborne and flee, avoiding the predator (Fernández-Juricic et al., 2006; Hemmingsen, 1951; Møller, 2008; Weston et al., 2012). Risk-taking behaviour could also be associated with the level of camouflage and the plumage colouration of birds (McQueen et al., 2017; Møller et al., 2019). The sex of the bird individuals approached could also change their response to potential predators (Kalb et al., 2019). Additionally, the number of individuals approached (i.e. flock size) was also found to be positively correlated with the FID, especially in gregarious urban birds (Morelli et al., 2019), with different responses for other bird species (Shuai et al., 2024). Finally, the characteristics of the observers recording the FID observations may play a role, with birds escaping differently when perceiving observers as potentially more dangerous (e.g. strangers or people carrying popguns) (Blum et al., 2020; Liu et al., 2025; Yuan et al., 2024). Additionally, the number of observers affects the escape behaviour of birds (de Resen et al., 2024; Geist et al., 2001), while the ornithological experience of observers (e.g. previous involvement in FID measurements) has no association with FID (Guay et al., 2013). The colours of the observers' clothing may influence FID (Gould et al., 2004), but this may act in different ways for rural and urban birds (Gould et al., 2004; Zhou & Liang, 2020). On the other hand, the height of approaching observers seemingly does not explain significant variation in avian FID (Van Dongen et al., 2015).

Despite the extensive literature on avian FID (Blumstein, 2019; de Resen et al., 2024; Sol et al., 2018), there are no specific studies about the effect of the observer's sex on the perception of risk in birds. This is an important gap, especially considering that a previous study on primates suggested a higher tolerance of monkeys to human females than males (Mitchell et al., 1991). Also, captive rats around women behave differently than around men because rodents respond to different chemicals produced by men and women, and this modifies their behaviour (Sorge et al., 2014). For shelter dogs, the sex of the human walker can strongly influence dog–human interactions (McGuire et al., 2023). Furthermore, domestic dogs are better able to recognize and match men's than women's voices and faces (Ratcliffe et al., 2014). So we can hypothesize that birds' perception of risk can differ when facing women or men, and this might reflect sexual dimorphism or other sex-linked traits in humans (e.g. size, gait or olfactory signals). We aimed to address this knowledge gap by testing whether the risk perception of urban birds was influenced by the human observer's sex after controlling for a set of other demonstrably important variables.

2 | METHODS

2.1 | Study area, flight initiation distance and refuge type

We collected data on avian escape behaviour (i.e. 'flight initiation distance' or FID) in five European countries (Figure 1), specifically in urban areas (typically parks and green areas in the cities). In four countries (Czech Republic, Poland, Germany and Spain), a single city was used; in France, we sampled FID in three small cities (Table S1). FID of birds was recorded during the spring (breeding season) of 2023 (April–July), mainly in the first 4h after sunrise (6:00AM–10:00AM), usually on weekdays, under dry, calm (Beaufort scale ≤2) conditions. In each city, two observers—one woman and one man—collected data at all sites (in total, four women and four men, all expert ornithologists, were involved in the study). The observer pairs were of similar height and wore similarly coloured clothes during the sampling trials (white, grey or black). We compared sex-specific data on the height and body mass of observers by using the Wilcoxon signed rank test for paired samples. The mean difference in observers' height by sex was 5.5cm, while the mean difference in observers' body mass was 7.3kg; however, neither of which was statistically different between women and men observers (Table S2). Female observers did not collect data while menstruating. Both

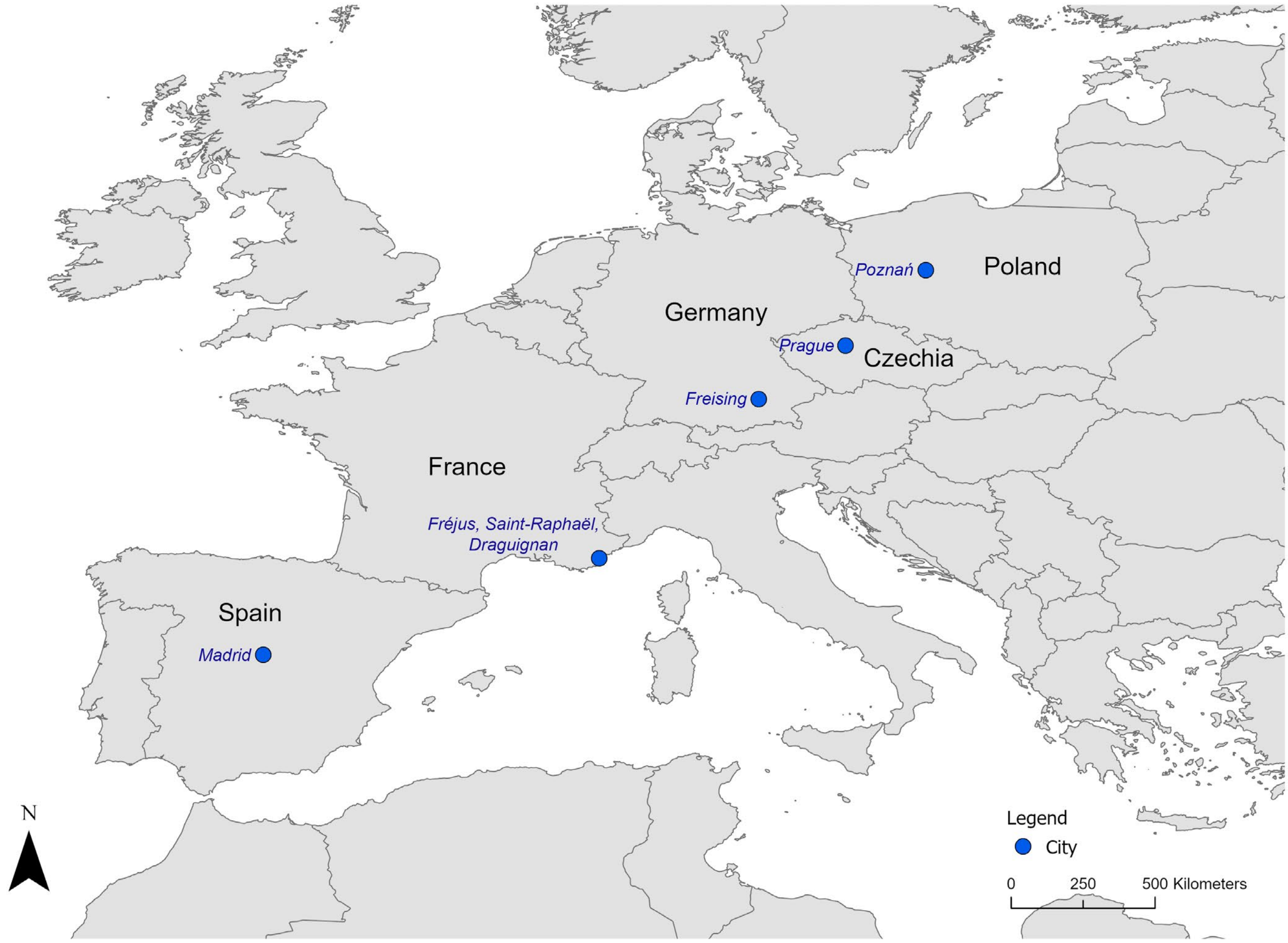

FIGURE 1 A map of the study area where bird Flight initiation distance (FID) data was collected from seven cities in five European countries. Blue dots indicate the geographical position of the centroid of sample site areas.

members of the collector pairs were coordinated at each site before the fieldwork to minimize as many interpersonal discrepancies in the methodology as possible. For example, several estimations of random distances were performed before the main FID collection to ensure that the sampling error was reduced between observers. Observers also tried to control for any potential 'habituation' effect of birds and therefore rotated who started the observations (e.g. if at a given site the man started first, the woman started first at the next site).

The procedure to measure FID is well described in the literature (Blumstein, 2006; Hall et al., 2020; Weston et al., 2012) and can be briefly described as follows: The target bird was approached in a straight line by the single observer walking at a normal and constant speed with head and eyes turned directly to a focal bird. When the observer started the approach, she or he measured the 'starting distance' or SD (i.e. distance to the targeted bird, in metres) (Blumstein, 2013). If the focal bird showed some activity related to the approaching observer (e.g. it looked around, or fixed its eyes on the approaching human), the distance from the observer where this occurred was recorded as 'alert distance' or AD (in metres). Finally, FID was measured as the distance (in metres) between the observer and the point where the bird flew or otherwise moved away from the approaching person. In this study, we recorded the 'flock size' for each approach as the number of bird individuals of the same species staying, moving or feeding together (Morelli et al., 2019). Whenever possible, we also recorded the sex of the bird approached. The same individual was not intentionally sampled more than once, and site re-sampling was avoided. All observers approached only birds foraging or engaged in 'relaxed behaviour' (e.g. roosting or preening). During each sampling trial, we quantified the percentage of land use 50 m around the point where the FID was recorded (built, grass, bare soil and water), and vegetative cover (bush and tree). Ethical approval was not required because the research involved no human subjects and was conducted without the capture or direct manipulation of animals. The full dataset used in this study is published in a figshare repository (https://doi.org/10.6084/m9.figshare.28284848.v1).

2.2 | Statistical analyses

For the main analysis, we used only a subset of data containing only species with ≥10 FID observations, considering that such sampling provides reliable estimates of FID for a given population and species (Sol et al., 2018). Data on *Corvus corone cornix* (35 observations) and *Corvus corone corone* (26 observations) (Table 1 and Table S3) were merged to avoid issues related to the available species-level phylogenies (see also below).

The potential correlation between FID and predictors or covariates was tested using a multi-predictor Bayesian phylogenetically informed regression model, using the brm function in the 'brms' v. 2.6.13 package (Bürkner, 2017). Specifically, we modelled FID (response variable) as a function of starting distance, flock size, bird sex, observer sex, land use composition (built, grass, bare soil, water) and vegetation cover (bush, tree) as predictor variables. Alert distance was not included as a predictor since it was strongly positively correlated with FID (Figure S1) and was available only for a small subset of observations; thus, its inclusion would have significantly decreased sample sizes (Table S3). All continuous predictors were

TABLE 1 List of 37 bird species with at least 10 FID observations, no. of observations, and values of starting distance (mean), alert distance (mean) and flight initiation distance (mean, min and max) recorded from seven cities in five European countries (Czech Republic, France, Germany, Poland and Spain). In the main analyses, *Corvus corone cornix* and *Corvus corone corone* were merged.

Species	No. observations	SD (mean)	AD (mean)	FID (mean)	FID (min)	FID (max)
Turdus merula	362	21.7	9.4	5.9	0.7	57.0
Columba palumbus	318	31.2	17.4	10.2	0.8	59.0
Pica pica	263	33.0	17.4	13.0	1.9	48.0
Parus major	153	17.5	9.0	5.7	1.0	25.0
Passer domesticus	142	20.6	8.5	6.6	0.8	30.8
Columba livia	129	26.0	8.4	3.5	0.3	18.0
Fringilla coelebs	114	19.2	9.8	7.0	1.0	69.0
Sylvia atricapilla	84	19.0	9.8	6.2	1.0	19.0
Parus caeruleus	69	18.7	8.8	6.1	0.8	40.0
Sturnus vulgaris	66	29.9	14.0	11.2	2.0	36.0
Dendrocopos major	64	27.3	14.8	11.1	2.0	42.0
Erithacus rubecula	64	18.3	8.8	6.2	1.0	17.0
Anas platyrhynchos	58	26.3	13.3	5.9	0.0	40.0
Corvus monedula	47	30.9	16.1	9.5	2.0	22.0
Phylloscopus collybita	47	18.3	9.3	6.0	2.0	13.0
Passer montanus	44	27.0	8.8	7.1	2.1	24.5
Sitta europaea	44	19.6	8.8	5.5	1.0	18.6
Sturnus unicolor	42	32.7	14.5	13.4	2.1	35.0
Garrulus glandarius	39	30.6	23.3	10.3	1.0	30.0
Corvus cornix	35	24.4	11.0	6.8	1.0	18.0
Motacilla alba	35	21.2	10.5	8.7	2.0	25.0
Carduelis carduelis	34	22.6	10.4	8.2	3.0	21.0
Certhia brachydactyla	34	20.3	8.6	5.4	1.9	25.4
Turdus philomelos	32	23.7	11.4	9.2	2.0	31.0
Carduelis chloris	30	22.2	11.5	8.5	3.0	20.0
Troglodytes troglodytes	30	17.7	8.1	6.3	2.0	12.0
Phoenicurus phoenicurus	29	26.0	8.8	8.2	0.0	16.0
Corvus corone	26	27.4	17.5	12.3	1.0	40.0
Picus viridis	25	30.5	21.2	16.2	2.1	36.0
Streptopelia decaocto	23	24.1	13.1	10.2	2.0	20.0
Serinus serinus	20	27.8	12.7	9.0	2.4	25.6
Aegithalos caudatus	17	15.5	7.0	3.6	1.0	13.0
Luscinia megarhynchos	14	30.3	12.3	5.8	2.0	12.0
Turdus pilaris	14	22.4	11.0	8.0	3.0	21.0
Myiopsitta monachus	13	27.4	9.0	5.8	0.7	13.0
Phoenicurus ochruros	13	23.6	10.1	9.0	3.0	19.0
Gallinula chloropus	11	21.7	9.0	9.8	2.0	20.0
Parus ater	11	24.1	5.6	5.0	0.8	10.4

scaled before the analysis. The model was fitted using the Gaussian family and a log-link function (Díaz & Møller, 2023). Considering the non-independence of the data due to shared ancestry among bird species (Paradis, 2012), 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 the BirdTree web tool (http://birdtree.org) (Jetz et al., 2012). We then constructed the Maximum Clade Credibility tree (MCC) using these phylogenies, using the function 'maxCladeCred' in the library 'phangorn' v. 2.8.1 package (Schliep, 2011). Subsequently, we created a phylogenetic covariance matrix using the 'inverseA' function in the 'MCMCglmm' v. 2.32 package (Hadfield, 2010). Additionally, to mitigate any confounding effect due to the differences among cities and countries (Table S4), we incorporated 'city' as a random factor in the regression model. We ran two Markov Chain Monte Carlo chains with default priors (i.e. uninformative, flat priors for fixed effects) and used 2000 sampling iterations (1000 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). As a measure of the goodness-of-fit of the 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 the 'r2_bayes' function in the 'performance' v. 0.8.0 package (Lüdecke et al., 2021). We also fitted a simple generalized linear mixed model (GLMM) without the phylogenetic covariance matrix, but we added species as a random factor together with the city and used the same predictor variables. Both models produced congruent results; hence, we report only the result of the phylogenetically informed model in the main text. The GLMM output is presented in the Supporting Information (Table S5). All statistical analyses and data explorations were performed in the R software v. 4.1.1 environment (R Development Core Team, 2023).

3 | RESULTS

We recorded a total of 2701 FID observations on 77 bird species in urban areas in seven cities from five European countries (Table S3). Excluding data from species with <10 FID observations, our final dataset consisted of 2581 FID records on 37 species (Table S3). The total number of bird species sampled ranged from a minimum of 19 species in France to a maximum of 50 species in Poland (Table S1). Overall, the top five bird species most frequently targeted in this study were *Turdus merula*, *Columba palumbus*, *Pica pica*, *Parus major* and *Passer domesticus* (Table S3). The bird species with comparatively the longest FIDs were *Picus viridis*, *Sturnus unicolor*, and *Pica pica*, while those species with comparatively the shortest FIDs were *Columba livia*, *Aegithalos caudatus* and *Parus ater* (Table 1).

The results of the multi-predictor Bayesian phylogenetically informed regression model showed that the escape behaviour of birds was positively associated with the starting distance (Table 2). Male birds were more tolerant of human approach than female ones (i.e. their FID was shorter), and the FID was longer when there was greater tree cover and shorter when there was greater bush cover (Table 2). Finally, birds escaped earlier (i.e. FID was longer) when women approached them than when they were approached by men (Figure 2). This difference associated with the observer's sex was statistically significant (Table 2) and was found in all countries studied (Figure 3).

An analysis that excluded the phylogenetic covariance matrix (i.e. GLMM) produced similar results (Table S5). Further graphical exploration showed that the differences in FID associated with the observer's sex (e.g. birds escaping sooner when approached by women than by men) seem to still be present when separating bird observations by the sex of bird individuals, with the effect seemingly more pronounced in male birds (Figure S2) than in female birds (Figure S3).

TABLE 2 Results of a multi-predictor Bayesian phylogenetically informed regression model evaluating the association between flight initiation distance (response variable) and the following predictors: Starting distance, flock size, sex of the targeted bird (female, male), sex of the observer (female, male), land use composition (built, grass, bare soil, water) and vegetation cover (bush, tree).

Variables	Estimate	SE	Lower 95% CI	Upper 95% CI
Fixed factors				
Intercept	2.20	0.30	1.64	2.79
Starting distance	**0.21**	**0.01**	**0.19**	**0.23**
Bird sex (male)	**−0.13**	**0.05**	**−0.23**	**−0.03**
Flock size	−0.06	0.02	−0.09	−0.03
Observer sex (male)	**−0.14**	**0.02**	**−0.19**	**−0.09**
Built	0.01	0.02	−0.02	0.04
Grass	−0.01	0.02	−0.05	0.03
Bare soil	0.01	0.02	−0.03	0.05
Water	−0.02	0.02	−0.05	0.02
Tree	**0.10**	**0.02**	**0.07**	**0.13**
Bush	**−0.09**	**0.02**	**−0.12**	**−0.05**
Random factors				
City ($N=7$)	0.23	0.12	0.01	0.52
Species ($N=38$)	0.55	0.09	0.41	0.75
Conditional R^2	0.33		0.31	0.35
Marginal R^2	0.17		0.03	0.34

Note: The model incorporated a phylogenetic covariance matrix and species as a random factor (groups = 37) to account for statistical phylogenetic relatedness in the data. Additionally, 'city' was added as a random factor (groups = 7) to account for the potential spatial non-independence in the data. The table reports parameter estimates along with their standard errors (SE) and 95% credible intervals, as well as 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 alone). Significant results (i.e. those where credible intervals do not cross zero) are highlighted in bold. $N=2581$ observations and 37 species.

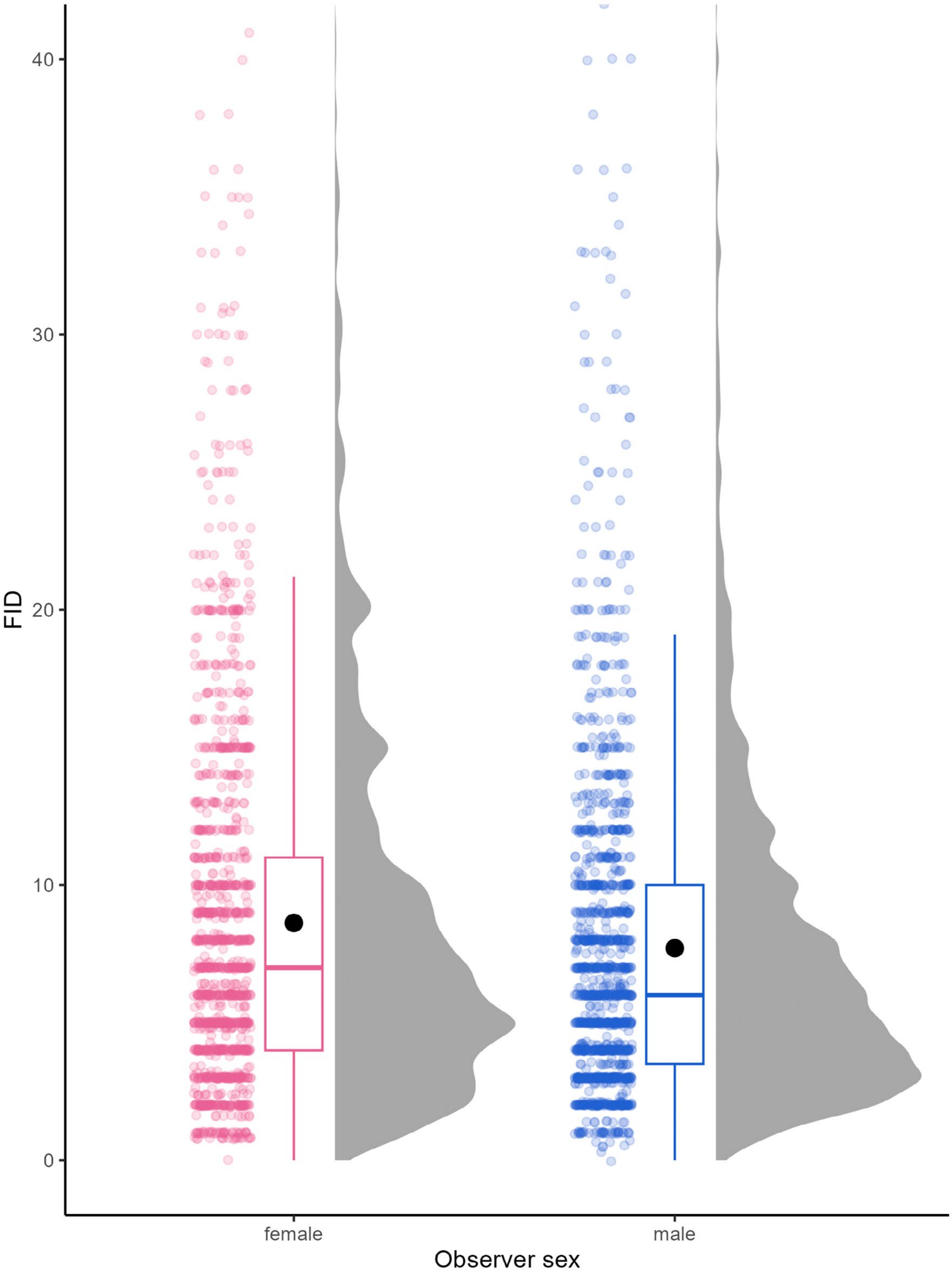

FIGURE 2 Flight initiation distance (FID, m) values and observer sex (pink = women or females, blue = men or males), when merging the values recorded in all countries. Box plots show the median (a bar in the middle of rectangles), upper and lower quartiles (length of rectangles), maximum and minimum values (whiskers) and mean FID values (black dots). Overall, the mean values of FID per observer's sex were 8.5 m (female) and 7.5 m (male), *N* = 2581.

4 | DISCUSSION

Our study revealed that, after accounting for other variables influencing significant variation in FID, birds on average tended to escape from a distance of about 1 m longer when approached by women compared to men. Birds were less tolerant of women than of men, and this result was geographically consistent. These differences were still present when exploring FID versus observer's

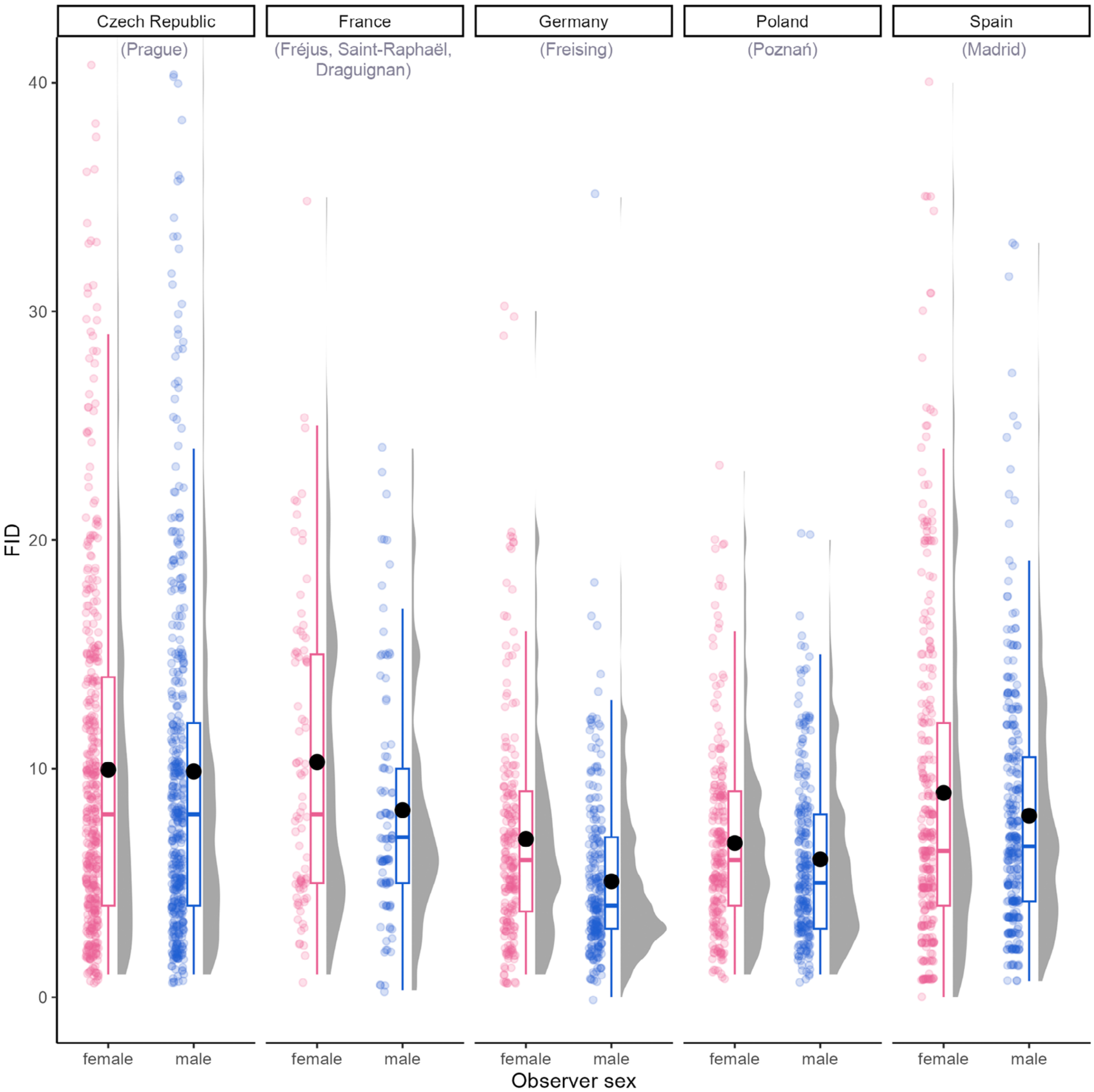

FIGURE 3 Flight initiation distance (FID, m) values recorded from seven cities in five European countries and observer sex (pink = women or females, blue = men or males). Box plots show the median (a bar in the middle of rectangles), upper and lower quartiles (length of rectangles), maximum and minimum values (whiskers) and mean FID values (black dots). *N* = 2581.

sex separately for bird males and females in the cities of each country. On average, birds escaped 1 m (11% of their mean escape distance) earlier when approached by women than by men (Figure 1).

While we found a consistent observer sex-specific pattern, the mechanisms or causes that underlie this pattern are unknown. There are several factors that can potentially explain the observed differences in the birds' reactions to people. Differences in the physical appearance of observers (e.g. hair length, body size, height, etc.), movement patterns (e.g. hip movement, overall walking gait) or different clothing could be candidate factors. But we can reject these because, in our study, they were either controlled or their differences were non-significant. We can reject gross morphology since the woman and man working at a given site were similarly tall and hid their hair if it was longer than their partner's. Additionally, bird FIDs were not related to the height of approaching observers in a recent study (Van Dongen et al., 2015). However, despite our attempts to minimize obvious differences in appearance between male and female observers, birds still may be able to detect subtle external morphological differences in hair length/style, waist-hip ratio or gait, as well as odour, which would necessitate specific field experimental designs.

Considering that men were traditionally considered hunters and women as gatherers in human societies (Kelly, 2013) and, as demonstrated by Carrete et al. (2016), a long exposure to different threats should promote adaptive heritable behaviour in birds, we expected that birds would perceive men as more threatening than women. However, our results challenge the potential long-lasting heritability of escape responses to humans concerning how threatening humans are to birds. We can hypothesize that such a difference (e.g. birds less tolerant of women) could be due to a not-full sex division of labour in hunter-gatherer societies in the past (Anderson et al., 2023). Nevertheless, the prominent involvement of women in hunting is still controversial and mostly contradicted by empirical evidence (Venkataraman et al., 2024). Based on our results, we can speculate that women, if they hunted, could have focused more on smaller prey (e.g. birds), while males hunted mainly larger prey (Marlowe, 2005).

Another potential mechanism behind a bird's response to predators could be associated with olfactory responses. Chemical signals represent one of the most fundamental forms of communication that organisms use to interact with each other and their environments, but birds have historically been considered to rely primarily on visual and auditory stimuli (Caro et al., 2015). However, recent studies have highlighted the important role of olfaction in predator avoidance behaviour in birds (Amo et al., 2011), and their reproductive behaviour (Bonadonna & Mardon, 2010; Whittaker et al., 2011), foraging (Yang et al., 2015) and nesting (Amo et al., 2017; Ekner & Tryjanowski, 2008). For instance, Amo et al. (2011) demonstrated in a field experiment the innate capacity of great tits (*Parus major*) to display predator avoidance behaviour by detecting predator chemical signals. Amo et al. (2011) highlighted also the ability of great and blue (*Cyanistes caeruleus*) tits to detect pheromones emitted by their prey (Amo et al., 2011). In contrast, Dotta et al. (2024) found that birds' avoidance of predator odours may not be ubiquitous across contexts and species, and some species do not respond to predator chemical signals (Stanback & Rollfinke, 2023). For example, only male house sparrows (*Passer domesticus*) exhibit predator avoidance behaviour in response to chemical cues at their nesting sites (Griggio et al., 2016). Research on how birds respond to predator odour cues during foraging is scarce, and the recent findings in this area are inconsistent (Roth et al., 2008; Zidar & Løvlie, 2012). In our study, even if we cannot fully exclude some olfactory mechanism at work in the reaction of birds, as used by mammals, we consider it less probable because we were not handling birds; rather, we approached them from a distance and refrained as much as possible from providing sex-specific chemical information.

Our results also showed that male birds were generally bolder than females because they allowed a closer approach by humans (Kalb et al., 2019). In species with male-biased dichromatism, males may escape later than females (Thiel et al., 2007), and this reaction could be an 'honest signal' indicating their quality to conspecifics (Kalb et al., 2019). We also found the widely reported positive association between the starting distance and the flight initiation distance (Morelli et al., 2023; Tätte et al., 2018). The observed pattern may stem from birds considering longer approaches as a more purposeful, and thus a higher predation risk (Stankowich & Blumstein, 2005). We also found longer FIDs in areas more covered by trees, while shorter FIDs were associated with an increased coverage of shrubs and bushes. This result is opposite to a previous study (Morelli et al., 2022), but could be associated with the balance between available and effectively used refugia. When available, birds prefer using trees over bushes or human-made structures as refuges after escaping (Morelli et al., 2022). In this study, however, we have not measured distances to the nearest potential refuges, so we cannot test this hypothesis properly. Interestingly, flock size did not explain significant variation in FID. This could be due to two main reasons: First, most records (82%) were from solitary birds, so the database had a low variance for this variable (e.g. flock size). Second, this study focused on all types of urban birds, not only on gregarious ones, whose escape behaviour is most influenced by flock size (Morelli et al., 2019). A recent review confirms that FID is not always affected by flock size (Shuai et al., 2024).

To conclude, we found that the sex of human observers consistently influenced bird escape behaviour, showing less tolerance to approaching women than men. Male and female birds reacted similarly in all countries studied (Figure S3). The causal mechanisms remain unclear, but the results underline the sophisticated evaluation by birds of their environment, and that subtle differences in human observers could influence important reactions by the subjects of study.

AUTHOR CONTRIBUTIONS

Federico Morelli, Yanina Benedetti, Eva Vincze, Peter Mikula, Mario Díaz, Daniel T. Blumstein, Piotr Tryjanowski and Gábor L. Lövei designed the study; Federico Morelli, Yanina Benedetti, Peter Mikula, Mario Díaz, Alicia Page, Piotr Tryjanowski and Marta K. Nowak collected data; Federico Morelli performed the statistical analysis; Federico Morelli, Yanina Benedetti, Peter Mikula, Daniel T. Blumstein and Gábor L. Lövei wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

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.

DATA AVAILABILITY STATEMENT

The dataset used in this study was archived and made available on the FigShare repository (https://figshare.com/). Morelli et al. (2025). Urban birds FID and observers' sex. figshare. Dataset. https://doi.org/10.6084/m9.figshare.28284848.v1.

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REFERENCES

Abou-Zeid, F., Benedetti, Y., Siretckaia, A., & Morelli, F. (2024). Urban noise slows down the antipredator reaction of Eurasian Magpies. *Frontiers in Ecology and Evolution*, *12*, 1345971. https://doi.org/10.3389/fevo.2024.1345971

Amo, L., Tomás, G., & López-García, A. (2017). Role of chemical and visual cues of mammalian predators in nest defense in birds. *Behavioral Ecology and Sociobiology*, *71*, 49. https://doi.org/10.1007/s00265-017-2281-9

Amo, L., Visser, M. E., & van Oers, K. (2011). Smelling out predators is innate in birds. *Ardea*, *99*, 177–184. https://doi.org/10.5253/078.099.0207

Anderson, A., Chilczuk, S., Nelson, K., Ruther, R., & Wall-Scheffler, C. (2023). The Myth of Man the Hunter: Women's contribution to the hunt across ethnographic contexts. *PLoS One*, *18*, e0287101. https://doi.org/10.1371/journal.pone.0287101

Berryman, A. A., & Hawkins, B. A. (2006). The refuge as an integrating concept in ecology and evolution. *Oikos*, *115*, 192–196. https://doi.org/10.1111/j.0030-1299.2006.15188.x

Blum, C. R., Fitch, W. T., & Bugnyar, T. (2020). Rapid learning and long-term memory for dangerous humans in ravens (*Corvus corax*). *Frontiers in Psychology*, *11*, 581794. https://doi.org/10.3389/fpsyg.2020.581794

Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: How life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, *71*, 389–399.

Blumstein, D. T. (2013). Flight-initiation distance in birds is dependent on intruder starting distance. *The Journal of Wildlife Management*, *67*, 852–857.

Blumstein, D. T. (2019). What chasing birds can teach us about predation risk effects: Past insights and future directions. *Journal für Ornithologie*, *160*, 587–592. https://doi.org/10.1007/s10336-019-01634-1

Bonadonna, F., & Mardon, J. (2010). One house two families: Petrel squatters get a sniff of low-cost breeding opportunities. *Ethology*, *116*, 176–182. https://doi.org/10.1111/j.1439-0310.2009.01725.x

Bürkner, P. C. (2017). “brms”: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28.

Carlen, E. J., Li, R., & Winchell, K. M. (2021). Urbanization predicts flight initiation distance in feral pigeons (*Columba livia*) across New York City. *Animal Behaviour*, *178*, 229–245. https://doi.org/10.1016/j.anbehav.2021.06.021

Caro, S. P., Balthazart, J., & Bonadonna, F. (2015). The perfume of reproduction in birds: Chemosignaling in avian social life. *Hormones and Behavior*, *68*, 25–42. https://doi.org/10.1016/j.yhbeh.2014.06.001

Carrete, M., Martínez-Padilla, J., Rodríguez-Martínez, S., Rebolo-Ifrán, N., Palma, A., & Tella, J. L. (2016). Heritability of fear of humans in urban and rural populations of a bird species. *Scientific Reports*, *6*, 31060. https://doi.org/10.1038/srep31060

de Resen, N. C., Teixeira, C. P., & de Azevedo, C. S. (2024). Flight Initiation Distance in an urban bird: Influence of the number of people, gaze orientation, and bird behavior. *Birds*, *5*, 255–264. https://doi.org/10.3390/birds5020017

Díaz, M., Fernández, J., & Page, A. (2022). Cat colonies and flight initiation distances of urban birds: Dealing with conflicting sources of citizen wellbeing. *Science of the Total Environment*, *827*, 154401. https://doi.org/10.1016/j.scitotenv.2022.154401

Díaz, M., & Møller, A. P. (2023). Lockdown effects on fear revealed direct and indirect effects of human presence on perceived predation risk. *Science of the Total Environment*, *872*, 162122. https://doi.org/10.1016/j.scitotenv.2023.162122

Díaz, M., Møller, A. P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Markó, G., & Tryjanowski, P. (2013). The geography of fear: A latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS One*, *8*, e64634. https://doi.org/10.1371/journal.pone.0064634

Dotta, A., Yaman, B., & Van Huynh, A. (2024). No evidence of predator odor avoidance in a North American bird community. *Avian Research*, *15*, 100155. https://doi.org/10.1016/j.avrs.2023.100155

Ekner, A., & Tryjanowski, P. (2008). Do small hole nesting passerines detect cues left by a predator? A test on winter roosting sites. *Acta Ornithologica*, *43*, 107–111. https://doi.org/10.3161/000164508X345392

Fernández-Juricic, E., Blumstein, D. T., Abrica, G., Manriquez, L., Adams, L. B., Adams, R., Daneshrad, M., & Rodriguez-Prieto, I. (2006). Relationships of anti-predator escape and post-escape responses with body mass and morphology: A comparative avian study. *Evolutionary Ecology Research*, *8*, 731–752.

Geist, C., Liao, J., Libby, S., & Blumstein, D. T. (2001). Does intruder group size and orientation affect flight initiation distance in birds? *Animal Biodiversity and Conservation*, *28*, 69–73.

Gould, M. L., Green, L., Altenau, B., & Blumstein, D. T. (2004). A study of the species-confidence hypothesis with Spiny-cheeked Honeyeaters (*Acanthagenys rufogularis*). *Emu - Austral Ornithology*, *104*, 267–271. https://doi.org/10.1071/mu03033

Griggio, M., Fracasso, G., Mahr, K., & Hoi, H. (2016). Olfactory assessment of competitors to the nest site: An experiment on a passerine species. *PLoS One*, *11*, e0167905. https://doi.org/10.1371/journal.pone.0167905

Guay, P.-J., McLeod, E. M., Cross, R., Formby, A. J., Maldonado, S. P., Stafford-Bell, R. E., St-James-Turner, Z. N., Robinson, R. W., Mulder, R. A., & Weston, M. A. (2013). Observer effects occur when estimating alert but not flight-initiation distances. *Wildlife Research*, *40*, 289–293. https://doi.org/10.1071/WR13013

Hadfield, J. D. (2010). MCMC methods for multi-response generalised linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*, 1–22.

Hall, M. J., Burns, A. L., Martin, J. M., & Hochuli, D. F. (2020). Flight initiation distance changes across landscapes and habitats in a successful urban coloniser. *Urban Ecosystem*, *23*, 785–791. https://doi.org/10.1007/s11252-020-00969-5

Hemmingsen, A. (1951). The relation of shyness (flushing distance) to body size. *Spolia Zoologica Musei Hauniensis*, *11*, 74–76.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*, 444–448. https://doi.org/10.1038/nature11631

Kalb, N., Anger, F., & Randler, C. (2019). Flight initiation distance and escape behavior in the black redstart (*Phoenicurus ochruros*). *Ethology*, *125*, 430–438. https://doi.org/10.1111/eth.12867

Kelly, R. L. (2013). Men, women, and foraging. In *The lifeways of hunter-gatherers: The foraging spectrum* (pp. 214–240). Cambridge University Press. https://doi.org/10.1017/CBO9781139176132

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640. https://doi.org/10.1139/z90-092

Liu, Y., Liu, Y., & Liang, W. (2025). Breeding barn swallows recognize householders from strangers. *Animal Cognition*, *28*, 33. https://doi.org/10.1007/s10071-025-01956-z

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, *6*, 3139.

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology*, *14*, 54–67. https://doi.org/10.1002/evan.20046

McGuire, B., Kok, P., Garland, M., Guy, B., Jackson, A., & Haber, S. (2023). Influence of walker sex and familiarity on scent-marking behavior of juvenile and mature shelter dogs. *Animals*, *13*, 3649. https://doi.org/10.3390/ani13233649

McQueen, A., Naimo, A. C., Teunissen, N., Magrath, R. D., Delhey, K., & Peters, A. (2017). Bright birds are cautious: Seasonally conspicuous plumage prompts risk avoidance by male superb fairy-wrens. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170446. https://doi.org/10.1098/rspb.2017.0446

Mikula, P., Tomášek, O., Romportl, D., Aikins, T. K., Avendaño, J. E., Braimoh-Azaki, B. D. A., Chaskda, A., Cresswell, W., Cunningham, S. J., Dale, S., Favoretto, G. R., Floyd, K. S., Glover, H., Grim, T., Henry, D. A. W., Holmern, T., Hromada, M., Iwajomo, S. B., Lilleyman, A., … Albrecht, T. (2023). Bird tolerance to humans in open tropical ecosystems. *Nature Communications*, *14*, 2146. https://doi.org/10.1038/s41467-023-37936-5

Mitchell, G., Steiner, S., Dowd, B., Tromborg, C., & Herring, F. (1991). Male and female observers evoke different responses from monkeys. *Bulletin of the Psychonomic Society*, *29*, 358–360. https://doi.org/10.3758/BF03333944

Møller, A. P. (2008). Flight distance of urban birds, predation and selection for urban life. *Behavioral Ecology and Sociobiology*, *63*, 63–75. https://doi.org/10.1007/s00265-008-0636-y

Møller, A. P., Liang, W., & Samia, D. S. M. (2019). Flight initiation distance, color and camouflage. *Current Zoology*, *65*, 535–540. https://doi.org/10.1093/cz/zoz005

Morelli, F., Benedetti, Y., Díaz, M., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Tätte, K., Markó, G., Jiang, Y., Tryjanowski, P., & Møller, A. P. (2019). Contagious fear: Escape behavior increases with flock size in European gregarious birds. *Ecology and Evolution*, *9*, 6096–6104. https://doi.org/10.1002/ece3.5193

Morelli, F., Benedetti, Y., Mikula, P., Díaz, M., Tryjanowski, P. (2025). Urban birds FID and observers sex. Dataset in Figshare repository. https://doi.org/10.6084/m9.figshare.28284848.v1

Morelli, F., Leveau, L. M., Mikula, P., MacGregor-Fors, I., Bocelli, M. L., Quesada-acuña, S. G., González-lagos, C., Gutierrez, P., Franzoi, G., Delgado-v, C. A., Garitano, A., Campos, J., Ortega-álvarez, R., Contreras-rodríguez, A. I., Souza, D., Cecília, M., Toledo, B., Sarquis, A., Giraudo, A., … Benedetti, Y. (2023). Are birds more afraid in urban parks or cemeteries? A Latin American study contrasts with results from Europe. *Science of the Total Environment*, *861*, 160534. https://doi.org/10.1016/j.scitotenv.2022.160534

Morelli, F., Mikula, P., Benedetti, Y., Bussière, R., Jerzak, L., & Tryjanowski, P. (2018). Escape behaviour of birds in urban parks and cemeteries across Europe: Evidence of behavioural adaptation to human activity. *Science of the Total Environment*, *631–632*, 803–810. https://doi.org/10.1016/j.scitotenv.2018.03.118

Morelli, F., Mikula, P., Blumstein, D. T., Díaz, M., Markó, G., Jokimäki, J., Kaisanlahti-jokimäki, M., Floigl, K., Abou-Zeid, F., Siretckaia, A., & Benedetti, Y. (2022). Flight initiation distance and refuge in urban birds. *Science of the Total Environment*, *842*, 156939. https://doi.org/10.1016/j.scitotenv.2022.156939

Paradis, E. (2012). *Analysis of phylogenetics and evolution with R* (2nd ed.). Springer New York. https://doi-org.infozdroje.czu.cz/10.1007/978-1-4614-1743-9

Piratelli, A. J., Favoretto, G. R., & de Almeida Maximiano, M. F. (2015). Factors affecting escape distance in birds. *Zoologia*, *32*, 438–444. https://doi.org/10.1590/S1984-46702015000600002

R Development Core Team. (2023). *R: A language and environment for statistical computing*.

Ratcliffe, V. F., McComb, K., & Reby, D. (2014). Cross-modal discrimination of human gender by domestic dogs. *Animal Behaviour*, *91*, 127–135. https://doi.org/10.1016/j.anbehav.2014.03.009

Roth, T. C., Cox, J. G., & Lima, S. L. (2008). Can foraging birds assess predation risk by scent? *Animal Behaviour*, *76*, 2021–2027. https://doi.org/10.1016/j.anbehav.2008.08.022

Samia, D. S. M., Blumstein, D. T., Diaz, M., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Tätte, K., Marko, G., Tryjanowski, P., & Møller, A. P. (2017). Rural-urban differences in escape behavior of European birds across a latitudinal gradient. *Frontiers in Ecology and Evolution*, *5*, 66. https://doi.org/10.3389/fevo.2017.00066

Schliep, K. P. (2011). phangorn: Phylogenetic analysis in R. *Bioinformatics*, *27*, 592–593.

Shuai, L., Morelli, F., Mikula, P., Benedetti, Y., Weston, M. A., Ncube, E., Tarakini, T., Díaz, M., Kaisanlahti-jokim, M., & Cao, Y. (2024). A meta-analysis of the relationship between flock size and flight initiation distance in birds. *Animal Behaviour*, *210*, 1–9. https://doi.org/10.1016/j.anbehav.2024.01.013

Sol, D., Maspons, J., Gonzalez-Voyer, A., Morales-Castilla, I., Garamszegi, L. Z., & Møller, A. P. (2018). Risk-taking behavior, urbanization and the pace of life in birds. *Behavioral Ecology and Sociobiology*, *72*, 59. https://doi.org/10.1007/s00265-018-2463-0

Sorge, R. E., Martin, L. J., Isbester, K. A., Sotocinal, S. G., Rosen, S., Tuttle, A. H., Wieskopf, J. S., Acland, E. L., Dokova, A., Kadoura, B., Leger, P., Mapplebeck, J. C. S., McPhail, M., Delaney, A., Wigerblad, G., Schumann, A. P., Quinn, T., Frasnelli, J., Svensson, C. I., … Mogil, J. S. (2014). Olfactory exposure to males, including men, causes stress and related analgesia in rodents. *Nature Methods*, *11*, 629–632. https://doi.org/10.1038/nmeth.2935

Stanback, M. T., & Rollfinke, M. F. (2023). Tree Swallows (*Tachycineta bicolor*) do not avoid nest cavities containing the odors of house mice (*Mus musculus*). *The Wilson Journal of Ornithology*, *135*, 79–85. https://doi.org/10.1676/22-00045

Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2627–2634. https://doi.org/10.1098/rspb.2005.3251

Tätte, K., Møller, A. P., & Mänd, R. (2018). Towards an integrated view of escape decisions in birds: Relation between flight initiation distance and distance fled. *Animal Behaviour*, *136*, 75–86. https://doi.org/10.1016/j.anbehav.2017.12.008

Thiel, D., Ménoni, E., Brenot, J.-F., & Jenni, L. (2007). Effects of recreation and hunting on flushing distance of capercaillie. *Journal of Wildlife Management*, *71*, 1784–1792. https://doi.org/10.2193/2006-268

Van Dongen, W. F. D., McLeod, E. M., Mulder, R. A., Weston, M. A., & Guay, P. J. (2015). The height of approaching humans does not affect flight-initiation distance. *Bird Study*, *62*, 285–288. https://doi.org/10.1080/00063657.2015.1026309

Venkataraman, V. V., Hoffman, J., Farquharson, K., Davis, H. E., Hagen, E. H., Hames, R. B., Hewlett, B. S., Glowacki, L., Jang, H., Kelly, R., Kramer, K., Lew-Levy, S., Starkweather, K., Syme, K., & Stibbard-Hawkes, D. N. E. (2024). Female foragers sometimes hunt, yet gendered divisions of labor are real: A comment on Anderson et al. (2023) The Myth of Man the Hunter. *Evolution and Human Behavior*, *45*, 106586. https://doi.org/10.1016/j.evolhumbehav.2024.04.014

Weston, M. A., Mcleod, E. M., Blumstein, D. T., & Guay, P. J. (2012). A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu*, *112*, 269–286. https://doi.org/10.1071/MU12026

Whittaker, D. J., Richmond, K. M., Miller, A. K., Kiley, R., Bergeon Burns, C., Atwell, J. W., & Ketterson, E. D. (2011). Intraspecific preen oil odor preferences in dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology*, *22*, 1256–1263. https://doi.org/10.1093/beheco/arr122

Yang, S. Y., Walther, B. A., & Weng, G. J. (2015). Stop and smell the pollen: The role of olfaction and vision of the oriental honey buzzard in identifying food. *PLoS One*, *10*, e0130191. https://doi.org/10.1371/journal.pone.0130191

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behaviour*, *16*, 229–249. https://doi.org/10.1016/S0065-3454(08)60192-8

Ye, H. Y., Yu, J., Hong, K., Li, Y. L., & Zhao, J. M. (2024). Similar tolerance of urban birds towards both benign human and lethal cat predators. *Journal of Ornithology*, *166*, 157–164. https://doi.org/10.1007/s10336-024-02194-9

Yuan, K., Yang, S., Liu, J., & Liang, W. (2024). Responses of birds to observers holding popguns: Hunting history influences escape behavior of urban birds. *Current Zoology*, *70*, 631–635. https://doi.org/10.1093/cz/zoad049

Zhou, B., & Liang, W. (2020). Avian escape responses to observers wearing clothing of different colors: A comparison of urban and rural populations. *Global Ecology and Conservation*, *22*, e00921. https://doi.org/10.1016/j.gecco.2020.e00921

Zidar, J., & Løvlie, H. (2012). Scent of the enemy: Behavioural responses to predator faecal odour in the fowl. *Animal Behaviour*, *84*, 547–554. https://doi.org/10.1016/j.anbehav.2012.06.006

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Sampled cities, geographical coordinates of the centroid of the surveyed areas, flight initiation distance (FID) observations and number of bird species sampled in urban areas of five European countries. The row 'total' indicates the number of observations and species sampled in the full dataset and the more reliable subset used for modelling purposes, including only species with at least 10 FID observations.

Table S2. Results of the Wilcoxon matched-pairs signed-rank test comparing the height and weight of observers, by sex (female vs male), with the mean difference between variables.

Table S3. A complete list of 77 bird species (taxonomy after Jetz et al., 2012) and FID observations (number; mean, max, min) collected from seven cities in five European countries. The list is ordered by the number of FID observations. For modelling purposes, only species with at least 10 FID observations were included. Data on *Corvus corone cornix* and *Corvus corone corone* were merged in the phylogenetically informed model to avoid issues related to the available species-level phylogenies.

Table S4. Mean land use composition in percentage (built, grass, bare soil, water) and vegetation cover (bush, tree) around points where flight initiation distance observations were recorded at each city in five European countries. The sum of percentages for each category (land use composition and vegetation cover) does not equal 100%, as the table displays the mean values.

Table S5. The result of a generalized linear mixed model (GLMM) modelling flight initiation distance (response variable) as a function of starting distance, flock size, sex of the targeted bird (female, male), sex of the observer (female, male), land use composition (built, grass, bare soil, water) and vegetation cover (bush, tree) as predictor variables, without the phylogenetic covariance matrix, and adding species ($N=37$) and city ($N=7$) as random factors.

Figure S1. Statistically significant and positive correlation between FID and alert distance (AD) of urban birds collected from seven cities in five European countries. $N=1914$. Plotted is the correlation ±95% confidence intervals.

Figure S2. Flight initiation distance (FID, m) values collected in seven cities of five European countries (Czech Republic, France, Germany, Poland and Spain) and observers' sex (pink=female observers, blue=male observers) when using a subset of data with male birds only. Box plots show the median (a bar in the middle of rectangles), upper and lower quartiles (length of rectangles), maximum and minimum values (whiskers) and mean FID values (black dots). $N=718$.

Figure S3. Flight initiation distance (FID, m) values collected in seven cities of five European countries (e.g. Czech Republic, France, Germany, Poland and Spain) and observers' sex (pink=female observers, blue=male observers) when using a subset of data with female birds only. Box plots show the median (a bar in the middle of rectangles), upper and lower quartiles (length of rectangles), maximum and minimum values (whiskers) and mean FID values (black dots). $N=279$.

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