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Developing an integrative understanding of escape mode decisions

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Optimal escape theory predicts that individuals should escape when the costs of staying (risk of being injured or killed) exceed the costs of leaving (energetic costs of escape, lost foraging opportunities and costs incurred for monitoring the approaching predator). We extend these theoretical principles to analyse preferences for alternative escape modes in a model animal group, birds, which can escape by either flight (costlier but safer) or using cheaper but riskier alternatives (jump, walk, or swim). We used a large, published database that included 21 222 records on 179 species taken in 15 European localities during the breeding seasons of 2009–2019, with data on escape mode, latitude, habitat (urban or rural), precipitation and temperature. Most individuals escaped by taking flight (15 940 records; 79%). Variation in escape mode decisions was mostly driven by species-specific traits (body size, diet), whereas external environmental variables (climate, geography, habitat) showed small effects. Flight initiation distances were longer when birds escaped by taking flight than when they chose lower-cost alternatives. Overall, escape mode preferences showed spatial and temporal variation compatible with expectations from risk–energy trade-off optimization. Escape mode decisions seemed more related to predation avoidance and flight initiation distance decisions to energy-saving goals. Thus, escape mode preferences interacted with fleeing–staying decisions, suggesting a behavioural integration of different aspects of escape strategies under a general optimization model.

The trade-off between finding enough food and avoiding disturbance and predation is key to an individual's survival and reproduction (Houston et al., 1993). Many organisms adjust their behaviour in response to changing food, predation and disturbance levels (Blumstein et al., 2016; Cooper & Blumstein, 2015). Understanding an organism's decision rules are especially relevant under rapid human-driven global change (Díaz et al., 2021; Díaz, 2023; Díaz & Møller, 2023). Optimal escape theory predicts that individuals should escape from approaching sources of potential danger when the costs of staying (risk of being injured or killed) exceed the costs of leaving (energetic costs of escape, lost foraging opportunities and costs incurred for monitoring the

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approaching predator; Blumstein et al., 2016; W. E. Cooper & Frederick, 2007; Samia et al., 2013, 2017; Ydenberg & Dill, 1986).

Long after the pioneering observations by Hediger (1934) on how mobile organisms react to the risk of being killed by a predator, recent work has shown how bird flight initiation distances (FIDs), the distances at which individuals escape when approached by a human observer under standardized conditions (Blumstein, 2006), change along geographical, temporal and disturbance gradients (Diamant et al., 2023; Díaz et al., 2013, 2021, Díaz & Møller, 2023; Mikula et al., 2018; Samia et al., 2015). Results suggest that FIDs estimate how individual birds integrate direct and indirect effects of food needs, predation risk and human disturbance into their fearfulness (Díaz et al., 2021). FIDs are generally shorter in urban areas than in nearby rural areas, apparently due to relaxed predation risk and increased human activity that is harmless to birds (Díaz et al., 2013; Díaz & Møller, 2023; Møller, 2012; Morelli et al., 2018). FIDs also tend to be shorter in areas with lower predation risk (St. Clair et al., 2010; Zamora-Camacho & Aragón, 2022), lower food availability (Møller, 2012; Møller et al., 2015) and higher energy needs (Díaz et al., 2021; Møller, 2015a; Møller et al., 2013).

Despite the usual name ('flight initiation distance'), a variety of escape response modes in addition to flying away can be established, such as jumping, running or swimming away (Cooper & Blumstein, 2015). However, despite the numerous studies investigating escape behaviour, comparatively little work has been done on how animals would trade-off the costs and benefits of alternative escape modes (Ekanayake et al., 2022; Grim et al., 2024; Kalb et al., 2019; Novčić & Parača, 2021; Rodríguez-Prieto et al., 2008). Furthermore, the escape mode may also modulate the costs and benefits of staying versus escaping, influencing FIDs. Alternative non-flight escape strategies incur lower-energy costs than flying but can also increase the risk of being caught by a predator (Rodríguez-Prieto et al., 2008).

Here, using birds as a model group because they have a variety of alternative escape modes, we investigated whether the selection of alternative modes follows similar patterns to those already found for FIDs. We also investigated the potential influence of escape mode on FID, under the general hypothesis that escape behaviour reflects an optimal adjustment to changing food, predation and disturbance levels. We used a large database compiled during the breeding seasons of 2006–2019 in 24 European localities spanning a 5000-km latitudinal gradient (Díaz et al., 2021). Data on escape modes started to be gathered regularly from 2009 onwards. Restriction to the breeding season eliminated potential bias due to seasonal changes in perceived risks and food needs (Mikula et al., 2018), and standardization of data collection methods controlled for potential effects of different approaching modes on risk perception (Cooper & Blumstein, 2015). We made several predictions.

First, we expected a stronger prevalence of flying away compared to lower-cost alternatives (i.e. running or jumping away) outside cities and southwards, where predation risk is higher, and the opposite patterns if energy-saving strategies were driving escape mode. Milder climatic conditions (higher temperatures and rainfall) should decrease the use of lower-cost escape modes, although this effect could depend on the bird's body mass and diet. Larger birds should prefer less demanding but riskier escape modes if energy conservation is at stake because the energy costs of flight tend to increase with a bird's body mass (Hedenström & Alerstam, 1992; Møller et al., 2012); hence, body mass effects should be weaker under milder climatic conditions. Potential prey species (i.e. foliage-gleaning insectivores, herbivores and omnivores) should select riskier but more energy-saving modes of escape than active predators (i.e. predators, fish eaters and aerial insectivores), thereby predicting weaker or opposite effects of climatic conditions for predators than for herbivores (Díaz et al., 2021). Preference for flight would be higher for birds perched above ground because the costs of flying from high perches would be lower than flying from the ground (Møller, 2010), although this effect should be lower under lower levels of predation risk (i.e. in urban habitats and northwards).

Second, the optimal FID should be modulated by escape mode (Rodríguez-Prieto et al., 2008). If this is the case, positive effects of starting distance (SD) and/or alert distance (AD, which estimate vigilance costs during approach under the FEAR 'Flush Early and Avoid the Rush' model; Blumstein et al., 2016; Samia et al., 2013, 2017) on FID should be stronger when birds escape by flight than when they use lower-cost alternatives (Blumstein, 2010; Samia et al., 2013). Differences among escape modes in these relationships should be modulated by predation risk and/or food conditions. Riskier conditions and harsher food conditions (i.e. southwards and outside cities for risk, and in colder climatic conditions for food) would decrease the importance of vigilance costs if predation risk effects predominate, leading to decreasing differences among escape modes in the effects of SD and/or AD on FID. By contrast, we should see increasing or no differences among escape modes along food and/or risk gradients if energy-saving effects predominate. Responses to spatial and temporal gradients should be modulated by species-specific body mass and diet in the same way as they would influence escape mode decisions, as these traits influence flight costs and predation risk (see above).

Overall, we expect spatial and temporal patterns in the preference of the escape mode used to react to an approaching human and modulating effects of escape mode on FID if individual birds trade-off delayed escape with their associated costs (Rodríguez-Prieto et al., 2008). Identifying the patterns will help us understand how individuals integrate escape mode and fleeing–staying decisions in response to approaching threats, thus expanding our knowledge of the drivers of escape decisions.

METHODS

Data were extracted from a published database on bird escape distances in European localities, pairing urban and nearby rural sites to consider urbanization effects on fear responses (details in Díaz et al., 2013, 2021; Samia et al., 2017). Urban study sites included areas with multi-storey buildings and roads and parks, while nearby rural areas had open farmland and woodland, single-family houses and did not contain continuous urban elements (e.g. buildings, roads or parks). Behavioural data were recorded in the Spanish localities by M.D., A.P.M. and J.D.I.A.; in France, U.K., Denmark and Norway by A.P.M.; in the Czech Republic by T.G., F.M. and Y.B.; in Hungary by G.M.; in Poland by P.T.; in Estonia by K.T.; and in Finland by J.J., M.-L.K.-J. and A.P.M. (see Díaz et al., 2021 for details).

We recorded FIDs using the standard procedure developed by Blumstein (2006). Observers wore neutrally coloured clothes and behaved as normal pedestrians, moving at ordinary walking speed towards every individual bird previously detected and identified by species, using sight or sound, along random walks across the study areas carried out during the local breeding season under fair weather conditions (no rain, no strong wind; Díaz et al., 2013, 2021). Observers recorded the distance to the focal bird at the start of approach (SD), the distance when the bird showed behavioural signs of detection of the approaching observer and started monitoring the researcher (AD), the distance when birds initiated escape (FID) and the bird's perch height if it was located above ground at the start of the approach (Samia et al., 2013). Horizontal distances were measured by pacing, rangefinders or measuring tapes and heights by rangefinders or by eye to the nearest metre, consistently by different observers in different cities. Distances were calculated as Euclidean distances, which equals the square-root of the sum of the squared horizontal distance and the squared height above ground (e.g. Díaz et al., 2022; Møller, 2010). Juvenile birds and adults engaged in reproductive activities (incubating, food provisioning) were not approached. Sex and age were determined by plumage when possible, and double records were avoided by not approaching birds of the same species, sex and age as previously sampled at the same site.

Escape modes were classified as either taking flight or moving away from the approaching observer by walking/running on the ground, jumping (either on the ground or to nearby perches) or swimming away (for birds located on water that did not fly away when approached). Mean temperature and total precipitation for the breeding season of each study year and site were obtained by either averaging or summing up data from the three months covering the main breeding season for birds in each European city and their surroundings (March–May for Western Europe, April–June for Central Europe, May–July for Southern Scandinavia and Estonia and June–August for Northern Finland). Climate data were downloaded for the corresponding months, years and grid cells from the Essential Climate Variables database of the Copernicus project (following Díaz et al., 2021). Species-specific bird traits (diet and body mass) were taken from Díaz et al. (2021).

Effects of climatic, geographical, habitat and bird trait variables on escape mode selection were tested using generalized linear mixed models (GLMMs) with escape mode as the dependent variable, logit link and binomial distribution of errors. Non-flying modes (walking, jumping and swimming away) were grouped into a single non-flying escape mode due to extremely unbalanced sample sizes (see below). Potential effects of flock size were not considered as recent work has demonstrated them to be small and strongly species-specific (Morelli et al., 2019; Shuai et al., 2024). Species nested within year nested within city were included as the random factor to account for site (including observer's and measurement methods, as each city was usually sampled by a different observer using consistent measurement methods) and year effects other than climate and latitude. We tested whether patterns of phylogenetic relatedness would have biased results by analysing the taxonomic structure (as a surrogate for phylogeny) of the model's residuals using a mixed linear model with Order as the fixed factor and species nested in Genus nested in Family nested in Order as the random factor (Bell, 1989; Díaz et al., 2021). Taxonomy corresponded with that from the Birds of the World database (birdsoftheworld.org/bow/home, accessed 15 February 2024). We used a taxonomic control of potential phylogenetic effects for consistency with previous studies using the same database (Díaz et al., 2021), but we also included results from alternative Bayesian phylogenetic methods to check robustness of the results (see below). We also tested fixed effects of latitude, temperature, precipitation, habitat (rural or urban) and perch height, as well as their interactive effects with body mass and diet.

Modulating effects of escape mode on FID were tested by fitting GLMMs with the same random structure previously described; FID was the dependent variable in this case, and we used a model with a logarithmic link and Gaussian error (Díaz et al., 2021). Independent variables were escape mode, SD or AD, latitude, temperature, precipitation, habitat (rural or urban) and perch height and three-way interactions of escape mode with SD/AD and the other independent variables. These three-way interactions estimated the two-way interactions of escape mode and each environmental factor after accounting for the expected effects of SD and/or AD on FID, which estimate vigilance costs under the FEAR model (Blumstein et al., 2016; Samia et al., 2013, 2017). AD is a more direct surrogate for vigilance costs than SD, but it is less frequently measured and reported because it is harder to estimate accurately; however, SD is also used as this surrogate because of strong correlations with AD and larger sample sizes (Blumstein et al., 2016; Samia et al., 2013, 2017). Second-order interactions were also included to properly estimate the effects of three-way interactions (Underwood, 1996), but the results were not interpreted because we had no predictions for them. Main and interactive effects of body mass and diet were not included because the complexity of the resulting models precluded convergence.

We used type III (orthogonal) sums of squares and the Satterthwaite method to compute approximate degrees of freedom, and independent variables were standardized to mean = 0 and standard deviation = 1 before analyses to improve the interpretability of main and interactive terms (Díaz et al., 2021; Schielzeth, 2010). Statistical analyses were performed with SPSS 29.0. Effect sizes were computed as Pearson's product-moment correlation coefficients from F values ($t > \sqrt{F}$; Wilson, 2023) and interpreted as small ($r < 0.10$), intermediate ($r = 0.11$–0.49) or large ($r > 0.50$), following Cohen (1988).

To check for consistency, we also analysed the effects of climatic, geographical, habitat and bird trait variables on escape mode selection and FID using Bayesian phylogenetic GLMMs via the MCMCglmm v.2.36 package (Hadfield, 2010; Hadfield & Nakagawa, 2010). We incorporated a phylogenetic covariance structure (computed using the inverseA function) estimated from a single maximum credibility phylogenetic tree as a random effect in our models to control for phylogenetic structure. The tree was obtained by generating 1000 phylogenies using the Hackett backbone on BirdTree.org online tool (Jetz et al., 2012), from which the maximum credibility tree was reconstructed using maxCladeCred function in the phangorn v.2.11.1 package (Schliep, 2011). All continuous predictors were centred and scaled before analysis (mean = 0, SD = 1; Schielzeth, 2010). We implemented Bayesian hierarchical models to analyse the influence of predictors on escape mode selection and FID, incorporating year nested in locality as a random effect. We did not incorporate species within the nested design structure for random effects to avoid overparameterization, as species effects were also included in the phylogenetic covariance structure. We specified uninformative inverse-gamma priors for random effects and an uninformative prior for residual variance. For escape mode selection, we used a threshold model with a binomial response, while for FID, we used a Gaussian response model with identity link on log-transformed FIDs (Díaz et al., 2021). We then fitted models using the same predictors and interactions between them as specified in taxonomic models. Models were run for 130 000 iterations with a burn-in of 30 000 and a thinning interval of 100 to reduce autocorrelation. Convergence of model parameters was assessed using the Gelman–Rubin statistic (Gelman & Rubin, 1992), ensuring that within-chain and between-chain variances were comparable, which is most suitable when multiple parameters are estimated (Du et al., 2022). We examined posterior fixed effect distributions using 95% highest posterior density intervals to determine statistical significance, also giving effective sample sizes for each parameter estimate.

Ethical Note

Disturbance to birds while measuring FIDs does not imply additional stress than those derived from normal human activities at the sampling sites. Furthermore, we avoided disturbing adults engaged in reproductive activities. Finally, no permits were needed because the data came from a published database.

RESULTS

The database of Díaz et al. (2021) includes 21 222 records on 179 species with information on escape mode. They were collected at 15 localities during the breeding seasons of 2009–2019. Most individuals escaped by taking flight (15 940 records; 79%), 26% (5265 records) escaped by jumping or walking, and only 17 (0.002%) by swimming away, which were not discarded for consistency with our multi-species, multi-site approach aimed at testing general hypotheses. Further, results obtained after excluding these 17 records were almost identical (not shown). The same was true when excluding species with <5 records (98 records from 49 species). Missing data for SD, AD or perch height reduced sample sizes accordingly in the corresponding models (Tables 1 and 2).

Factors Modulating Escape Mode Decisions

Climatic and geographical factors had small, not significant, pure effects on escape mode decisions, whereas bird traits (body mass and diet) had significant intermediate effects (Table 1). Potential phylogenetic effects were controlled for by the GLMM, as the residual variance accounted for by the random taxonomic structure did not differ from zero (variance = 0.00, $Z = 0.50$, $P = 0.618$). Bayesian models produced the same overall results (Table S2), although they were more powerful at detecting

Table 1
Results of the GLMM testing for the effects of climatic, geographical and bird trait variables, as well as perch height when approach started, on escape mode decisions

Effect	*F*	*df*	*P*	B ± SE	Effect size (*r*)
Precipitation	0.00	1, 20 284	0.999	−3.11 ± 144.76	0.000
Temperature	0.00	1, 20 284	0.982	−0.43 ± 248.55	0.000
Latitude	0.00	1, 20 284	0.986	5.64 ± 251.10	0.000
Habitat	0.01	1, 20 284	0.937	U=R	0.000
Body mass	6.56	1, 1343	0.011*	0.57 ± 0.10	0.176 (I)
Diet	5.16	5, 2089	<0.001*	(Fig. 1)	0.112 (I)
Perch height	0.00	1, 20 284	0.992	3.83 ± 55.06	0.000
Latitude × body mass	8.26	1, 1314	0.004*	−0.27 ± 0.09	0.222 (I)
Latitude × diet	6.13	5, 1832	<0.001*	(Fig. 2)	0.142 (I)
Precipitation × body mass	0.01	1, 1187	0.934	0.01 ± 0.07	0.000
Precipitation × diet	3.05	5, 1756	0.010*	(Fig. 2)	0.073 (S)
Temperature × body mass	2.07	1, 1739	0.150	−0.09 ± 0.06	0.050
Temperature × diet	2.41	5, 1984	0.034*	(Fig. 2)	0.054 (S)
Habitat (R) × body mass	56.18	1, 11 020	<0.001*	−0.71 ± 0.09	0.472 (I)
Habitat (R) × diet	1.87	5, 20 284	0.095		0.013
Perch height × body mass	29.30	1, 20 284	<0.001*	−0.35 ± 0.06	0.202 (I)
Perch height × diet	3.96	5, 20 284	0.001*	(Fig. 2)	0.028 (S)

Binomial error and logit link. Escape mode decisions are scored as 1 for flight and 0 for lower-cost alternatives. Positive coefficients (B) thus indicate higher likelihood of escape by flight, or enforcement of pure effects in the case of interactions, and negative coefficients indicate lower likelihood of flight and attenuation of pure effects. Model statistics: $F_{41,\ 2622} = 18.83$, $P < 0.001$, marginal pseudo-$R^2 = 0.328$, conditional pseudo-$R^2 = 0.522$, AICc = 105190.54. Effect sizes (*r*) were computed from *t* values ($t = \text{B/SE(B)}$) following Wilson (2023) and judged small (S), intermediate (I) or large (L) following Cohen (1988). R: rural habitat.
*$P < 0.05$.

Table 2
Results of the GLMMs testing for the effects of escape mode decisions on relationships between alert distance (AD) on FID, and how climatic and geographical variables influenced such effects

Effect	*F*	*df*	*P*	B ± SE	Effect size (*r*)
Escape mode	389.90	1, 13 320	<0.001*	−0.27±0.02	0.118 (I)
AD	3266.27	1, 13 372	<0.001*	0.47±0.01	0.364 (I)
Precipitation	0.71	1, 1100	0.398	0.00±0.01	0.009
Temperature	20.23	1, 1192	<0.001*	0.04±0.01	0.080 (S)
Latitude	2.24	1, 1184	0.135	0.02±0.01	0.043
Habitat (rural)	1051.92	1, 13 279	<0.001*	0.43±0.01	0.328 (I)
Perch height	410.62	1, 13 372	<0.001*	0.05±0.00	0.108 (I)
Escape mode × AD	82.10	1, 13 351	<0.001*	0.11±0.03	0.038 (S)
Escape mode × precipitation	1.21	1, 13 371	0.271	0.02±0.01	0.010
Escape mode × temperature	15.14	1, 13 291	<0.001*	0.06±0.01	0.034 (S)
Escape mode × latitude	0.05	1, 13 347	0.824	0.00±0.02	0.002
Escape mode × habitat (rural)	2.71	1, 13 160	0.100	−0.04±0.02	0.014
Escape mode × perch height	72.74	1, 13 315	<0.001*	0.07±0.01	0.074 (S)
Mode × AD × precipitation	1.36	1, 13 367	0.244	−0.02±0.01	0.010
Mode × AD × temperature	72.39	1, 13 350	<0.001*	−0.12±0.01	0.073 (S)
Mode × AD × latitude	39.51	1, 13 365	<0.001*	0.08±0.01	0.054 (S)
Mode × AD × habitat (rural)	3.10	1, 13 366	0.078	0.05±0.03	0.015
Mode × AD × perch height	3.69	1, 13 326	0.055	−0.01±0.01	0.017

Gaussian error and log link. Models included all two-way interactions between fixed factors (Table S1), but results are shown only for interactions relevant for the hypotheses tested. Model statistics: $F_{24,\ 6410} = 1346.21$, $P < 0.001$, marginal pseudo-$R^2 = 0.486$, conditional pseudo-$R^2 = 0.671$, AICc = 22 546.95. Effect sizes (*r*) were computed from *t* values ($t = \text{B/SE(B)}$) following Wilson (2023) and judged small (S), intermediate (I) or large (L) following Cohen (1988). AICc: corrected Akaike information criterion; FID: flight initiation distance; GLMM: generalized linear mixed model.
*Indicates $P < 0.05$.

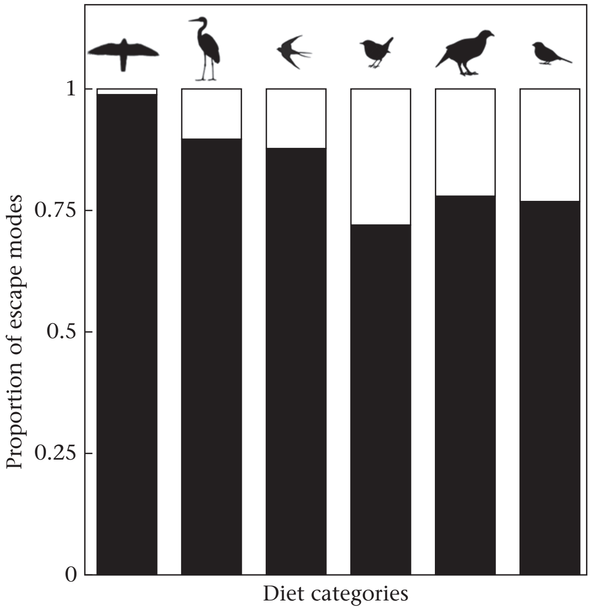

Figure 1. Diet-related differences in escape mode decisions. Filled bars: escape by flight; open bars: lower-energy alternatives (jump, walk or swim away). From left to right: predators ($N = 74$), fish eaters ($N = 38$), aerial insectivores ($N = 397$), foliage-gleaning insectivores ($N = 8552$), herbivores ($N = 2101$) and omnivores ($N = 10\ 060$).

significant effects of climatic and geographical factors: preference for the flight escape mode was larger in rural than in urban habitats, increased with latitude, and decreased with temperature and rainfall.

Larger birds were more prone to escape using low-energy modes than smaller birds, and active predators (raptors, fish eaters and aerial insectivores) took flight to escape more frequently than foliage-gleaning insectivores, herbivores and omnivores (Fig. 1, Table 1). Body mass effects varied with latitude, habitat and perch height and had intermediate effect sizes, whereas diet effects varied with climate, latitude and perch height and had comparatively small effect sizes (Table 1). Latitude, rural habitat and perch height interacted negatively (i.e. reduced) with the positive effects of body mass on preference for lower-cost escape modes, with no significant interactive effects of climate variables (Table 1).

Diet differences in escape mode preference did not vary among habitats, whereas latitude, climate and perch height modulated them (Table 1, Fig. 2). Predator preferences for flight escape were not modulated by these variables (coefficients for the variable × escape mode interaction did not differ from zero; Fig. 2). Preferences for flight escape by fish eaters and aerial insectivores increased with latitude and decreased with precipitation, temperature and perch height (Fig. 2). Foliage-gleaning insectivores showed the same pattern except for perch height, which increased preferences. Omnivore and herbivore

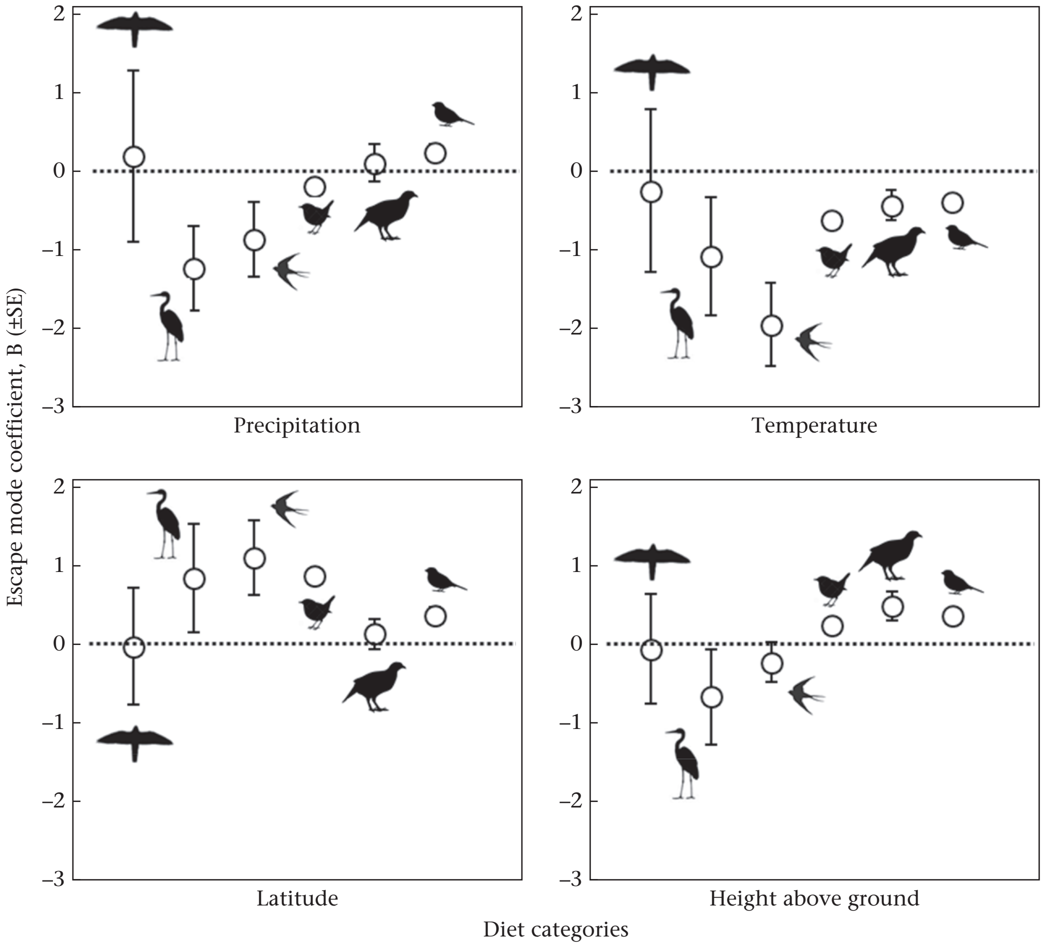

Figure 2. Diet-related differences of changing escape mode preferences along environmental gradients, estimated as the B values for escape mode—environmental variable relationships in generalized linear mixed models correcting for phylogeny carried out separately with data for each diet category. Circles indicate B values and whiskers standard errors. Labels below graphs specify the environmental variable modulating escape mode decisions. Positive B values indicate increased preference for escape by flight along each environmental gradient, and negative values increased preference for lower-cost alternatives. Order of diet categories from left to right, silhouettes and sample sizes as in Fig. 1.

preferences decreased with temperature and increased with precipitation, latitude and perch height, although results were not significant for herbivores along latitude and precipitation gradients (Fig. 2).

Modulating Effects of Escape Mode on Escape Distances

Potential taxonomic effects (as surrogates for phylogenetic effects) were controlled for in the AD GLMM model (residual variance accounted for by the random taxonomic structure = 0.002, $Z = 1.51$, $P = 0.132$) but not in the SD model (variance = 0.002, $Z = 2.26$, $P = 0.024$). Corrected Akaike information criterion (AICc) values were smaller for the AD than for the SD model (22 546.95 vs 41 604.65) despite lower sample sizes ($N = 13\ 397$ vs $N = 18\ 297$) due to more missing data for AD than for SD. Lack of control for taxonomic effects, higher AICc and lower theoretical connection between SD effects and vigilance costs supported not considering the SD model further; besides, the results of both models were very similar (not shown). FIDs were longer when birds escaped by taking flight than when they chose lower-cost alternatives (Fig. 3) after accounting for significant well-known effects of AD, temperature, latitude, habitat and perch height (Table 2). Effect sizes of escape mode on FID were intermediate (Table 2). Bayesian models produced the same overall results, with varying differences at detecting significant effects (Table S3). Results of these models did not change after including potential effects of body mass and were almost the same when testing for SD or AD effects (Table S4).

FID differences between escape modes increased with temperature and perch height, with small effect sizes, and were larger in rural than in urban habitats (Table 2). AD effects on FID were larger when birds escaped by flight than when they used other alternatives (Fig. 4, Table 2). However, the effect sizes were small. Finally, temperature and latitude modulated escape mode differences in AD–FID relationships, with small effect sizes (Table 2). Differences decreased with increasing temperature and latitude (Fig. 5).

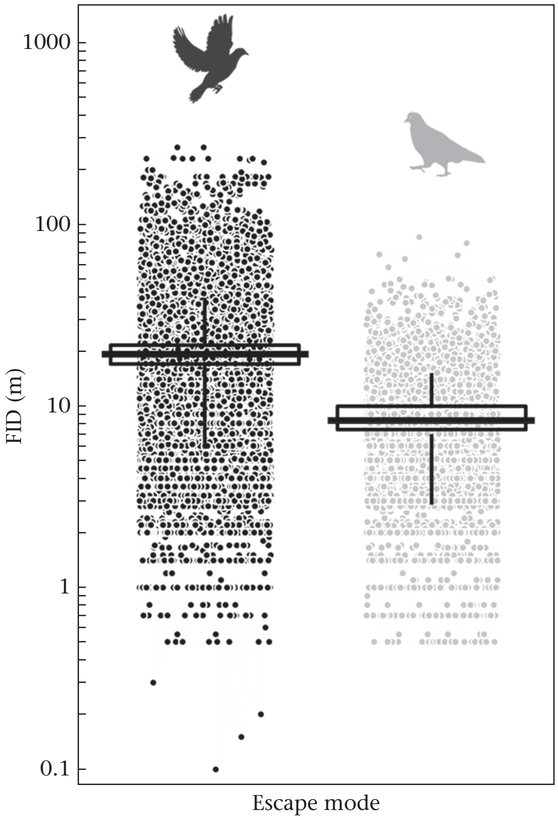

Figure 3. 'Flight' initiation distances (FID, in metres) of birds escaping by taking flight (left side, black dots) or by using lower-energy cost alternatives (right side, grey dots). Thick horizontal lines indicate means, boxes standard deviations and whiskers interquartile ranges. Note log scale of the *Y*-axis. Sample sizes are 15 940 for flight escapes and 5282 for alternative escape modes.

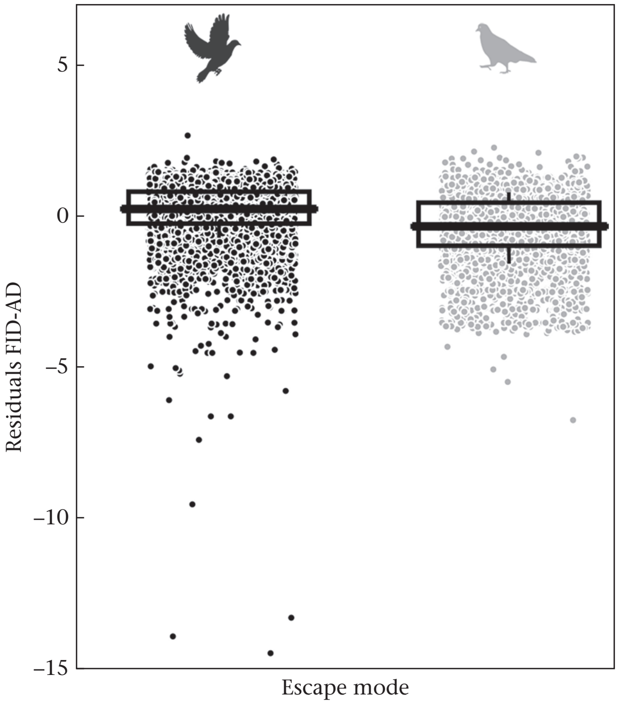

Figure 4. Differences in the effect of alert distance (AD) on flight initiation distance (FID), measured as the residuals for the generalized linear mixed model with log link and Gaussian error, FID as dependent variable, standardized AD as the fixed dependent, and species nested in year nested in locality as the random factor, for birds escaping by taking flight (left side, black lines, symbols and silhouettes) or by using lower-energy cost alternatives (right side, grey lines, symbols and silhouettes). Thick horizontal lines indicate means, boxes standard deviations and whiskers interquartile ranges. Sample sizes are 10 138 for flight escapes and 4174 for alternative escape modes.

DISCUSSION

Escape decisions by animals often include two main steps: (1) when to escape when approached by a potential predator (Blumstein et al., 2016; W. E. Cooper & Frederick, 2007; Morelli et al., 2022; Samia et al., 2013, 2017; Ydenberg & Dill, 1986), and (2) the escape mode for those species that have alternative modes, which may differ in costs and benefits (Grim et al., 2024; Kalb et al., 2019; Novčić & Parača, 2021; Rodríguez-Prieto et al., 2008). Using birds as a model group and a large dataset, we expanded the study of optimal escape behaviour to integrate decisions on escape modes with the decision on when to escape an approaching threat.

Preferences for alternative escape modes varied spatially and temporally in a way consistent with the expectations from risk–energy trade-off optimization. Comparisons with patterns of FID variation along environmental gradients and life history traits allowed us to analyse whether escape mode decisions were complementary or compensatory to escape distance decisions and whether decisions were more associated with risk avoidance or energy-saving strategies. Escape mode preferences interacted

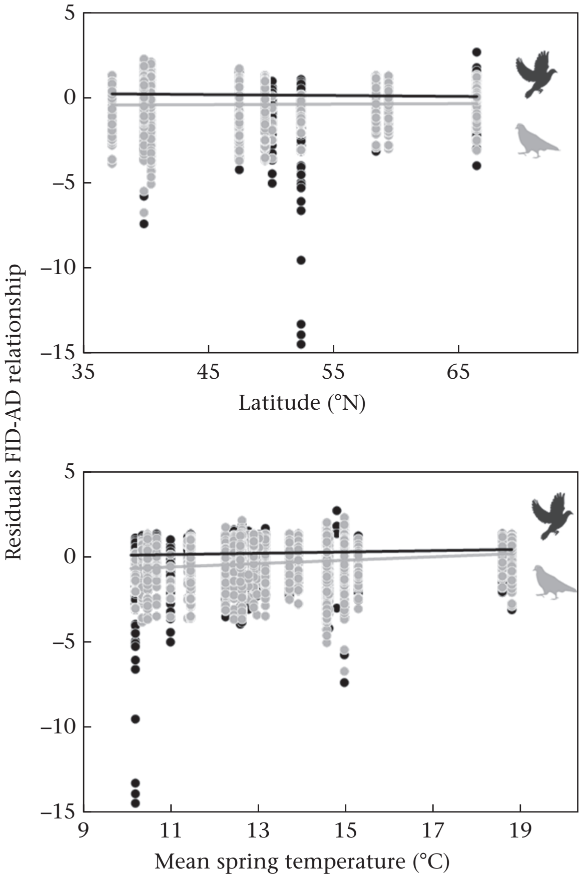

Figure 5. Differences in the effect of alert distance (AD) on flight initiation distance (FID), estimated as the residuals for the GLMM with log link and Gaussian error, FID as dependent variable, standardized AD as the fixed dependent, and species nested in year nested in locality as the random factor, for birds escaping by flight (black lines, symbols and silhouettes) or by using lower-energy cost alternatives (grey lines, symbols and silhouettes), along latitudinal (top) and temperature (bottom) gradients.

with fleeing—staying decisions, suggesting a behavioural integration of different aspects of escape strategies under a general optimization model.

Overall, we found that birds preferred to escape by flight over alternative modes. This may suggest that avoiding risks was relatively more important than energy conservation when birds decided how to move away from an approaching threat. However, this result may also arise from other advantages of flying, such as moving away from potentially depleted patches to explore new ones (e.g. Pulido & Díaz, 2000 and references therein) or moving to exposed places to monitor ambush predators better (Kalb et al., 2019). Escape mode variation along geographical and climate gradients helped test whether escape decisions result from variable effects of energetic and risk avoidance needs, as already done for FID variation (Díaz et al., 2021; Díaz & Møller, 2023).

Surprisingly, environmental variables known to affect FIDs (precipitation and temperature, as surrogates for food availability and needs, and latitude, habitat and perch height, as surrogates for predation risk; Díaz et al., 2021; Díaz & Møller, 2023) had relatively small effects on escape mode decisions, while species-specific traits known to modulate escape distances, namely body mass (Møller, 2015b) and diet (Díaz et al., 2021), had large effects. Increased preference for less demanding but riskier escape modes by larger birds indicated that avoiding predation risk was relatively less important than energy conservation for escape mode decisions because the energy costs of flight tend to increase with a bird's body mass (Hedenström & Alerstam, 1992). However, the probability of attack by a predator decreases for the largest birds (Møller et al., 2012). The modulating effects of latitude and perch height were consistent with this interpretation because body mass effects tended to be weaker at increasing latitudes and perch heights, and in rural compared with urban habitats. Abundance and/or exposure to predators decreases along these environmental gradients and among habitats (Díaz et al., 2013; Møller, 2010) so weaker effects of predation risk on escape mode decisions were expected compared to energy saving.

Results on diet effects suggest that potential prey species (i.e. foliage-gleaning insectivores, herbivores and omnivores) selected riskier but more energy-saving modes of escape than active predators (i.e. predators, fish eaters and aerial insectivores), also indicating stronger importance of energy saving than risk avoidance. Active predators are usually good flyers (Hedenström & Rosén, 2001) so escaping by flight would be less costly for them. There were mixed patterns when we examined diet-related variations in preferences along environmental gradients. Bird and mammal-eating raptor preferences were not sensitive to environmental variation. However, fish- and insect-eating predators escaped by flight less often when food conditions were better or were perched above ground but with decreasing predation risk, a pattern partially consistent with both energy saving and risk aversion strategies. Potential prey (herbivores and omnivores) had comparatively weaker responses to temperature and latitude variation and sometimes had the opposite response: There were increased preferences for the safer but costlier modes with increasing rainfall and height above ground, a pattern not expected under a risk aversion scenario. However, interactive effects of diet on environmental influences on escape mode preferences had small effect sizes, so these mixed results should be taken with caution.

Overall, geographical, climatic and bird trait effects on escape mode selection point to a baseline risk avoidance function of escape mode, secondarily modulated by energy-saving requirements in certain contexts. We emphasize that this interpretation somewhat contradicts current views on the underlying causes of FID decisions. Our results suggest that birds delay escape to avoid energy and lost opportunity costs, but this decision is further influenced by overall levels of predation risk, disturbance or energy needs (Cooper & Blumstein, 2015; Díaz & Møller, 2023).

Escape mode decisions should be integrated in future studies of FID in birds and other animals. Simple models would predict a higher likelihood of flight escapes for shorter FIDs, to compensate for higher risk incurred when allowing a closer approach to decrease energy and lost opportunity costs (Rodríguez-Prieto et al., 2008). Nevertheless, this prediction would change when considering the costs and risks of monitoring a predator (or its human surrogate) during the approach. In this case, longer approaches imply higher costs, so lower-cost escape modes would be selected (Grim et al., 2024; Novčić & Parača, 2021).

Longer FIDs for flight escapes did not support a compensatory integration between escape and fleeing—staying decisions. We further tested this potential integration by analysing how escape mode and environmental conditions influenced the effects of AD on FID under the FEAR model (Blumstein et al., 2016; Samia et al., 2013, 2017). This model predicts positive effects of AD on FIDs because AD estimates the costs of monitoring an approaching predator. Effects of AD on FID were stronger when escape was by flight, whereas stronger effects would have been predicted for less costly escape modes if escape mode selection compensated for monitoring costs. Differences in the effects of AD on FID decreased along temperature and latitudinal gradients, as expected if risk avoidance rather than energy-saving strategies predominate, pointing again towards a risk-managing function of escape mode preferences.

Our study had some limitations. We conducted our research during the breeding season. Therefore, our results are not directly applicable for other seasons, when optimal cost—benefit trade-offs can change due to both changing needs associated with courtship or nest defence (Mikula et al., 2018) or to changing environmental conditions (e.g. lower abundance or accessibility of food sources, or restrictions of alternative escape modes by e.g. snow cover). We did not measure vegetation cover or distance to the refuge, which may influence FIDs (e.g. Morelli et al., 2022), which could also affect escape mode decisions. Small sample sizes for predators and for birds escaping by swimming away also precluded more detailed analyses. These additional aspects should be investigated in future studies.

To conclude, integrating escape mode and escape distance analyses suggest complementary rather than compensatory responses regarding behavioural decisions under the predator risk—food needs trade-off. While FID decisions seem mostly driven by energy and opportunity gain, escape mode seemed more related to reducing predation risk. Future work on escape behaviour should expand the integration of escape mode decisions with FIDs and post-escape behaviour (Kalb et al., 2019; Morelli et al., 2022), using environmental gradients or experiments to test alternative underlying causal explanations (Díaz et al., 2022; Díaz & Møller, 2023).

Author Contributions

Mario Díaz: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Anders P. Møller:** Writing – review & editing, Investigation, Conceptualization. **Yanina Benedetti:** Writing – review & editing, Methodology, Investigation. **Daniel T. Blumstein:** Writing – review & editing, Investigation. **Gábor Markó:** Writing – review & editing, Methodology, Investigation. **Federico Morelli:** Writing – review & editing, Methodology, Investigation. **Juan D. Ibáñez-Alamo:** Writing – review & editing, Methodology, Investigation. **Jukka Jokimäki:** Writing – review & editing, Methodology, Investigation. **Marja-Liisa Kaisanlahti-Jokimäki:** Writing – review & editing, Methodology, Investigation. **Peter Mikula:** Writing – review & editing, Methodology, Investigation, Formal anaysis. **Kunter Tätte:** Writing – review & editing, Methodology, Investigation. **Piotr Tryjanowski:** Writing – review & editing, Methodology, Investigation. **Tomas Grim:** Writing – review & editing, Methodology, Investigation, Conceptualization.

Data Availability

Data used for this study can be freely accessed at https://doi.org/10.20350/digitalCSIC/16728.

Declaration of Interest

We declare no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123338.

References

Bell, G. A. (1989). A comparative method. *American Naturalist, 133*(4), 553–571. https://doi.org/10.1086/284935

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*(2), 389–399. https://doi.org/10.1016/j.anbehav.2005.05.010

Blumstein, D. T. (2010). Flush early and avoid the rush: A general rule of antipredator behavior? *Behavioral Ecology, 21*(3), 440–442. https://doi.org/10.1093/beheco/arq030

Blumstein, D. T., Samia, D. S. M., & Cooper, W. E., Jr. (2016). Escape behavior: Dynamic decisions and a growing consensus. *Current Opinion in Behavioral Sciences, 12*, 24–29. https://doi.org/10.1016/j.cobeha.2016.08.006

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Routledge. https://doi.org/10.4324/9780203771587

Cooper, W. E., & Blumstein, D. T. (Eds.). (2015). *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press. https://doi.org/10.1017/CBO9781107447189.

Cooper, W. E., Jr., & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology, 244*(1), 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011

Díaz, M. (2023). Dealing with global threats to biodiversity: A pressing but realistic challenge. *Frontiers in Conservation Science, 4*, Article 1147470. https://doi.org/10.3389/fcosc.2023.1147470

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

Díaz, M., Grim, T., Markó, G., Morelli, F., Ibáñez-Alamo, J. D., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Tätte, K., Tryjanowski, P., & Møller, A. P. (2021). Effects of climate variation on bird escape distances modulate community responses to global change. *Scientific Reports, 11*(1), Article 12826.

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*, Article 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*(5), Article e64634. https://doi.org/10.1371/journal.pone.0064634

Díaz, M., Ramos, A., & Concepción, E. D. (2022b). Changing urban bird diversity: How to manage adaptively our closest relation with wildlife. *Ecosystems, 31*(1), 2354. https://doi.org/10.7818/ECOS.2354

Diamant, E. S., MacGregor-Fors, I., Blumstein, D. T., & Yeh, P. J. (2023). Urban birds become less fearful following COVID-19 reopenings. *Proceedings Biological Sciences, 290*(2005), Article 20231338. https://doi.org/10.1098/rspb.2023.1338

Du, H., Ke, Z., Jiang, G., & Huang, S. (2022). The performances of Gelman-Rubin and Geweke's convergence diagnostics of Monte Carlo Markov chains in Bayesian analysis. *Journal of Behavioral Data Science, 2*(2), 47–72. https://doi.org/10.35566/jbds/v2n2/p3

Ekanayake, K. B., Gnanapragasam, J. J., Ranawana, K., Vidanapathirana, D. R., Abeyawardhana, U. T., Fernando, C., McQueen, A., Weston, M. A., & Symonds, M. R. E. (2022). Ecological and environmental predictors of escape among birds on a large tropical island. *Behavioral Ecology and Sociobiology, 76*, 31. https://doi.org/10.1007/s00265-022-03138-0

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science, 7*(4), 457–472. https://doi.org/10.1214/ss/1177011136

Grim, T., Dor, R., & Hauber, M. E. (2024). Adaptive patterns of anti-predator escape behavior in a globally introduced bird species. *NeoBiota, 93*, 143–156. https://doi.org/10.3897/neobiota.93.121380

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software, 33*(2), 1–22. https://doi.org/10.18637/jss.v033.i02

Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology, 23*(3), 494–508. https://doi.org/10.1111/j.1420-9101.2009.01915.x

Hedenström, A., & Alerstam, T. (1992). Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *Journal of Experimental Biology, 164*(1), 19–38. https://doi.org/10.1242/jeb.164.1.19

Hedenström, A., & Rosén, M. (2001). Predator versus prey: On aerial hunting and escape strategies in birds. *Behavioral Ecology, 12*(2), 150–156. https://doi.org/10.1093/beheco/12.2.150

Hediger, H. (1934). Zur Biologie und Psychologie der Flucht bei Tieren [On the biology and psychology of flight in animals]. *Biologisches Zentralblatt, 54*, 21–40.

Houston, A. I., McNamara, J. M., & Hutchinson, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London - B, 341*(1298), 375–397. https://doi.org/10.1098/rstb.1993.0123

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*(7424), 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*(7), 430–438. https://doi.org/10.1111/eth.12867

Møller, A. P. (2010). Up, up, and away: Relative importance of horizontal and vertical escape from predators for survival and senescence. *Journal of Evolutionary Biology, 23*(8), 1689–1698. https://doi.org/10.1111/j.1420-9101.2010.02034.x

Møller, A. P. (2012). Urban areas as refuges from predators and flight distance of prey. *Behavioral Ecology, 23*(5), 1030–1035. https://doi.org/10.1093/beheco/ars067

Møller, A. P. (2015a). The value of a mouthful: Flight initiation distance as an opportunity cost. *European Journal of Ecology, 1*(1), 43–51. https://doi.org/10.1515/eje-2015-0006

Møller, A. P. (2015b). Birds. In W. E. Cooper, & D. T. Blumstein (Eds.), *Escaping from predators: an integrative view of escape decisions* (pp. 88–112). Cambridge University Press.

Møller, A. P., Grim, T., Ibáñez-Álamo, J. D., Markó, G., & Tryjanowski, P. (2013). Change in flight initiation distance between urban and rural habitats following a cold winter. *Behavioral Ecology, 24*(5), 1211–1217. https://doi.org/10.1093/beheco/art054

Møller, A. P., Solonen, T., Byholm, P., Huhta, E., Nielsen, J. T., & Tornberg, R. (2012). Spatial consistency in susceptibility of prey species to predation by two *Accipiter* hawks. *Journal of Avian Biology, 43*(5), 390–396. https://doi.org/10.1111/j.1600-048X.2012.05723.x

Møller, A. P., Tryjanowski, P., Díaz, M., Kwieciński, Z., Indykiewicz, P., Mitrus, C., Goławski, A., & Polakowski, M. (2015). Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behavioral Ecology, 26*(3), 861–865. https://doi.org/10.1093/beheco/arv024

Mikula, P., Díaz, M., Albrecht, T., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., Kroitero, G., Møller, A. P., Tryjanowski, P., Yosef, R., & Hromada, M. (2018). Adjusting risk-taking to the annual cycle of long-distance migratory birds. *Scientific Reports, 8*(1), Article 13989. https://doi.org/10.1038/s41598-018-32252-1

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 behaviour increases with flock size in gregarious birds. *Ecology and Evolution, 9*(10), 6096–6104. https://doi.org/10.1002/ece3.5193

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. L., Floigl, K., Zeid, F. A., Siretckaia, A., & Benedetti, Y. (2022). Flight initiation distance and refuge in urban birds. *Science of the Total Environment, 842*, Article 156939. https://doi.org/10.1016/j.scitotenv.2022.156939

Novčić, I., & Parača, V. (2021). Seasonal differences in escape behaviour in the urban hooded crow, *Corvus cornix*. *Journal of Vertebrate Biology, 71*, Article 21066. https://doi.org/10.25225/jvb.21066

Pulido, F. J., & Díaz, M. (2000). Foraging behaviour of Blue Tits *Parus caeruleus* in a patchy environment under contrasting levels of natural food supply. *Journal of Avian Biology, 31*(1), 81–86. https://doi.org/10.1034/j.1600-048X.2000.310111.x

Rodriguez-Prieto, I., Fernández-Juricic, E., & Martín, J. (2008). To run or to fly: Low cost versus low risk escape strategies in blackbirds. *Behaviour, 145*(8), 1125–1138.

Samia, D. S. M., Blumstein, D. T., Díaz, M., Grim, T., Ibáñez-Álamo, J. D., Jokimäki, J., Tätte, K., Markó, 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

Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications, 6*, 8877. https://doi.org/10.1038/ncomms9877

Samia, D. S. M., Nomura, F., & Blumstein, D. T. (2013). Do animals generally flush early and avoid the rush? A meta-analysis. *Biology Letters, 9*(2), Article 20130016. https://doi.org/10.1098/rsbl.2013.0016

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schliep, K. P. (2011). phangorn: Phylogenetic analysis in R. *Bioinformatics, 27*(4), 592–593. https://doi.org/10.1093/bioinformatics/btq706

Shuai, L. Y., Morelli, F., Mikula, P., Benedetti, Y., Weston, M. A., Ncube, E., Tarakini, T., Díaz, M., Markó, G., Jokimäki, J., Kaisanlahti-Jokimäki, M. L., & Cao, Y. 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

St. Clair, J. J. H., García-Peña, G. E., Woods, R. W., & Székely, T. (2010). Presence of mammalian predators decreases tolerance to human disturbance in a breeding shorebird. *Behavioral Ecology, 21*(6), 1285–1292. https://doi.org/10.1093/beheco/arq144

Underwood, A. J. (1996). *Experiments in ecology*. Cambridge University Press. https://doi.org/10.1017/CBO9780511806407

Wilson, D. B. (2023). *Practical meta-analysis effect size calculator* Version 2023.11.27. https://www.campbellcollaboration.org/calculator/.

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

Zamora-Camacho, F. J., & Aragón, P. (2022). Antipredator responses of the morphs of an amphibian species match their differential predation pressures. *Behavioral Ecology and Sociobiology, 76*, 26. https://doi.org/10.1007/s00265-022-03140-6