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RESEARCH

Domestic cat density is not associated with variation in avian risk assessment in a mega-city

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Abstract

Domestic cats (*Felis catus*) kill an estimated 1.3–4.0 billion birds annually in the United States and are a major source of mortality for urban birds. While their lethal impacts are well documented, fewer studies address sublethal effects such as changes in avian risk assessment. We analyzed a dataset of 1,120 experimental approaches by human observers on 48 bird species across 11 sites in the Los Angeles metropolitan area, which varied in free-roaming cat and human population densities. Using Bayesian mixed models, we examined ecological and intrinsic predictors of avian flight initiation distance (FID). At the community scale, cat and human population densities had no significant effects on FID, suggesting that predator and human presence may already exceed a threshold across the urban landscape beyond which additional variation does not produce detectable changes in avian escape behavior. Species-specific analyses revealed that black phoebe (*Sayornis nigricans*) FID increased with human population density. We found no community-level interaction effect of human density and cat density, but house finches (*Carpodacus mexicanus*) and rock pigeons (*Columba livia*) tolerated closer approaches in areas with both high human and cat density, suggesting that habituation to humans may lower perceived predation risk for some urban species. Heavier species, ground-foraging individuals, and actively foraging birds had shorter FIDs. Birds also flushed at greater distances as the time of day progressed. These results highlight the complex interplay of intrinsic and environmental factors shaping avian escape behavior and underscore how behavioral adaptation in megacities may alter predator–prey dynamics in urban landscapes.

Keywords Urban ecology · Antipredator behavior · Avian risk assessment · Flight initiation distance (FID)

Introduction

Domestic cats (*Felis catus*) are among the most abundant predatory mammals globally, with populations estimated in the hundreds of millions (Kays et al. 2020). Because domestic cats are closely associated with humans and often depend on people for food, water, and shelter, their distribution and density in urban environments are frequently linked to human activity and presence (Ferreira et al. 2011; Beckerman et al. 2007). Free-ranging cats are widely recognized as an important anthropogenic source of bird mortality, with regional and national studies attributing substantial numbers of avian deaths to cat predation across both natural and human-modified landscapes (Beckerman et al. 2007; Winter and Wallace 2006; Woinarski et al. 2017; Kays et al. 2020); in the United States, they are estimated to kill 1.3–4.0 billion birds annually (Loss et al. 2013). In addition to preying on adults, cats have also been shown to affect bird fitness and survival through nest predation, feeding on fledglings,

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and, in some cases, eggs (Woods et al. 2003; Dauphiné and Cooper 2009; Stracey 2011).

Although the direct effects of cat predation on bird mortality are well documented, the indirect effects of cats on avian behavior and fitness remain less understood. Cats may affect birds through sublethal and indirect pathways, including fear-mediated changes in reproduction and parental care. For example, Beckerman et al. (2007) used simulation modelling to show that fear-mediated reductions in fecundity could contribute to significant declines in urban passerine populations even when direct predation was low. Similarly, Bonnington et al. (2013) found that fear of cat predation reduced parental provisioning in urban common blackbirds (*Turdus merula*) in the United Kingdom, with potential consequences for chick growth and post-fledging survival. In addition to fear-mediated effects, cats may indirectly affect birds through resource competition, as predation on small mammals can reduce prey availability for raptors and potentially affect their fitness (Baker et al. 2003; Dauphiné and Cooper 2009).

Flight initiation distance (FID), defined as the distance at which prey begin to flee from an approaching threat, is commonly used as a proxy for risk assessment in birds and other mobile animals (Cooper and Blumstein 2015). Longer FIDs are generally interpreted as indicating greater perceived risk, although escape behavior can also vary with ecological and environmental factors such as climate, group size, predator lethality, foraging opportunities, and refuge availability (Ydenberg and Dill 1986; Cooper and Blumstein 2015; Díaz et al. 2021; Morelli et al. 2019, 2022). Variation in risk assessment can affect investment in fitness-related behaviors, including foraging, courtship, mating, brooding, chick-rearing, and nest defense (Blumstein 2006; Thomson et al. 2006). Thus, although FID does not directly measure demographic impacts, it can help identify species, guilds, life-history groups, or locations that are especially sensitive to cat-related disturbance (Díaz et al. 2022; Nepali et al. 2024). For example, Díaz et al. (2022) found that birds in Madrid perched higher and had longer FIDs at sites with high cat-colony abundance than at paired sites with few or no colonies, suggesting that greater local abundance of free-ranging cats may increase perceived risk during approaches by humans. Such information can inform urban conservation and environmental management by helping prioritize further monitoring, cat-free refuges or buffer zones, protection of migratory stopover habitats, or habitat features that provide safer foraging and escape opportunities (Loss and Marra 2017; Díaz et al. 2022).

The effects of cat-related risk may also vary among species and regions. Díaz et al. (2022) found that species identity explained a substantial portion of variation in FID, suggesting that interspecific differences may shape antipredator responses. Because bird species differ in behavior, morphology, and life history, examining FID across ecologically similar groups may help identify taxa that are more sensitive to sublethal predator effects. In addition, geographic context may also matter: European bird populations have shown longer FIDs in regions with higher predator abundance and human use intensity (Díaz et al. 2015), whereas comparative analyses have revealed different patterns of antipredator behavior in North American bird populations (Møller et al. 2014). These differences suggest that relationships between predator communities and avian escape behavior may be context dependent, particularly in cities where domestic cats are human subsidized.

As urbanization intensifies, wildlife increasingly encounters humans and human infrastructure, often disrupting natural predator-prey interactions (Markovchick-Nicholls et al. 2008). The human shield hypothesis (HSH) postulates that predators tend to avoid humans, allowing prey to exploit areas of human activity as protective buffers (Berger 2007; Atickem et al. 2014; Granados et al. 2023). However, domestic cats complicate this dynamic. As human-subsidized predators, their survival depends on human support, making them more likely to co-occur with human activity. In such cases, proximity to humans may increase rather than reduce predation risk for birds and small mammals (Díaz and Møller 2023). Investigating prey fear responses across gradients of human and cat density can therefore clarify how the predictions of the HSH are modified in urban ecosystems with human-subsidized predators.

Although free-roaming cats are widespread in North American cities (Loss et al. 2013), it remains unclear whether spatial variation in their abundance predicts behavioral adjustments in urban bird communities. Thus, we investigated the association between the density of free-roaming domestic cats and variation in avian flight initiation distance (FID) across study sites in Los Angeles (LA), a mega-city with an estimated population of 3,868,718 (Census Reporter 2024). We hypothesized that if cats represented a significant source of predation risk, birds would exhibit heightened wariness in areas where cats were more abundant. Accordingly, we predicted that mean avian FID would be greater in regions with higher densities of free-roaming cats, even after controlling for other factors that influence escape behavior. Because birds may also mitigate predation risk through vertical positioning and have been observed to perch higher in areas with cat colonies (Díaz et al. 2022), we also predicted that perch height would increase with cat density.

Furthermore, we evaluated whether human density modified the relationship between cat density and avian FID, testing the predictions of the human shielding hypothesis in urban ecosystems with human-subsidized predators. If human presence provides a protective buffer from predation risk, we expected avian FIDs to decrease in areas of high human density relative to areas with similar cat densities but lower human activity. Conversely, if human presence facilitates higher densities of cats, birds in areas with both high human and cat densities should exhibit longer FIDs, indicating elevated perceived predation risk despite proximity to people.

Materials and methods

Data collection

Our data were collected across 11 study sites in the Los Angeles metropolitan area, defined using neighborhood boundaries described by the *Los Angeles Times* (Fig. 1). Sites were selected to capture spatial heterogeneity in domestic cat density (Longcore 2022), allowing us to sample flight initiation distances (FIDs) along a cat-density gradient (Table 1). Observers collecting FID data were blinded to cat density estimates to avoid sampling bias.

Within each site, sampling was conducted across publicly accessible urban microhabitats, including residential streets and sidewalks, commercial areas, public parks, and outdoor recreation spaces. Sampling locations within each neighborhood were varied across randomized visits to distribute observations broadly and minimize spatial clustering. Our goal was to collect approximately 80–100 observations per site. Data collection occurred primarily during periods of high bird activity, typically between 06:30 and 09:30 AM.

Birds selected for approach were initially perched on or above the ground within accessible areas and exhibiting non-vigilant behaviors. Nesting individuals were not approached. During each trial, observers approached the focal bird until it flushed. Focal birds were approached

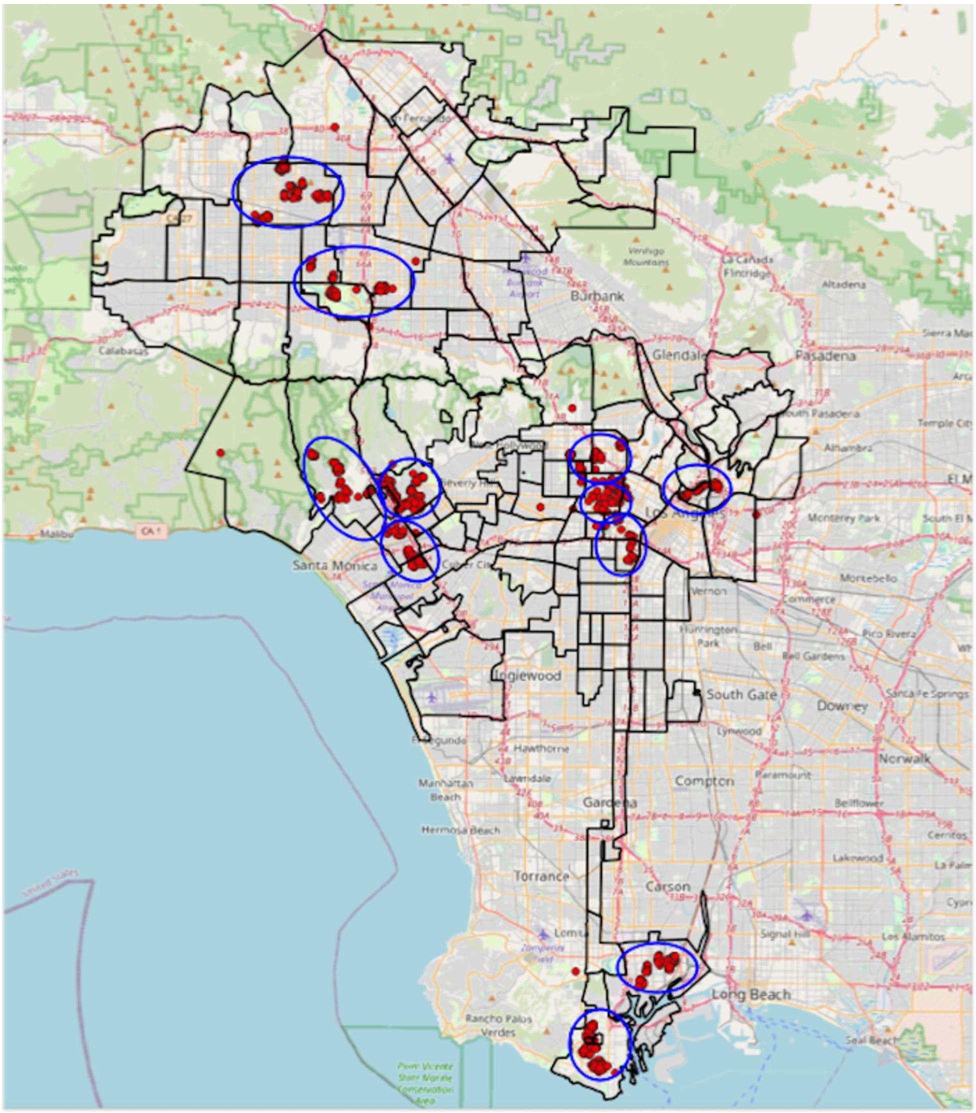

Fig. 1 Map of Los Angeles, California, USA, showing 11 data collection sites (circled in blue), and locations of individual FID observations (red points). Base layer adapted from neighbourhood boundaries by the *LA Times* Data Desk, used under CC BY 4.0

Table 1 Number of complete FID records at each site, with unique species count and summary statistics for log-transformed relative cat density values derived from kernel density estimation of LA animal services call-for-service records and summarized within 1 km² grid cells

Site	Sampling		Cat density (log transformed)				
Site	*N*	*Number of Species*	*Mean*	*SD*	*Median*	*Min*	*Max*
East Hollywood	93	15	3.734	0.311	3.946	2.266	3.983
Pico-Union	81	13	3.498	0.090	3.500	3.318	3.616
Koreatown	73	13	3.463	0.163	3.401	2.986	3.667
Wilmington	95	15	3.063	0.268	2.977	1.538	3.524
San Pedro	81	17	3.006	0.370	3.015	1.907	3.831
Chinatown	101	16	2.934	0.234	2.902	2.619	3.261
Sawtelle	93	15	2.616	0.332	2.619	1.882	3.547
Northridge	123	22	2.193	0.245	2.139	1.720	2.769
Westwood	129	15	2.156	0.514	2.353	0.746	2.939
Lake Balboa/Van Nuys	155	24	1.828	0.655	1.782	1.256	3.361
Brentwood	96	20	0.611	0.241	0.630	0.169	2.005

irrespective of species (species identity was recorded after the flush), and individuals typically remained stationary during the approach before initiating flight. Because observations were collected across a range of microhabitats within each site, potential microhabitat effects were effectively randomized rather than experimentally controlled.

We quantified FID using standardized protocols (Blumstein 2006). The observer, wearing neutrally colored clothing with minimal reflectance, dropped a first marker (weighted flag) at the starting point of the approach and walked toward the focal bird at a standardized pace (0.5–1 m/s). A second marker was dropped when the bird first oriented toward the observer (alert distance, AD), and a third marker was dropped when the bird initiated escape. The observer then continued to the bird's initial position and stopped. Horizontal distances between the bird's initial position and each marker were measured in paces and recorded as starting distance (SD), alert distance (AD), and flight initiation distance (FID), respectively (Fig. 2a). Distance to the nearest vegetation cover/trees or water (when applicable) was also measured in paces.

Before data collection, all observers calibrated their pace length and walking speed by repeatedly walking a 30 m tape measure and recording the number of steps and time required to cover that distance. This process established an observer-specific conversion factor (meters per pace), ensuring a standardized approach speed and distance estimation. Following data transcription, all distances recorded

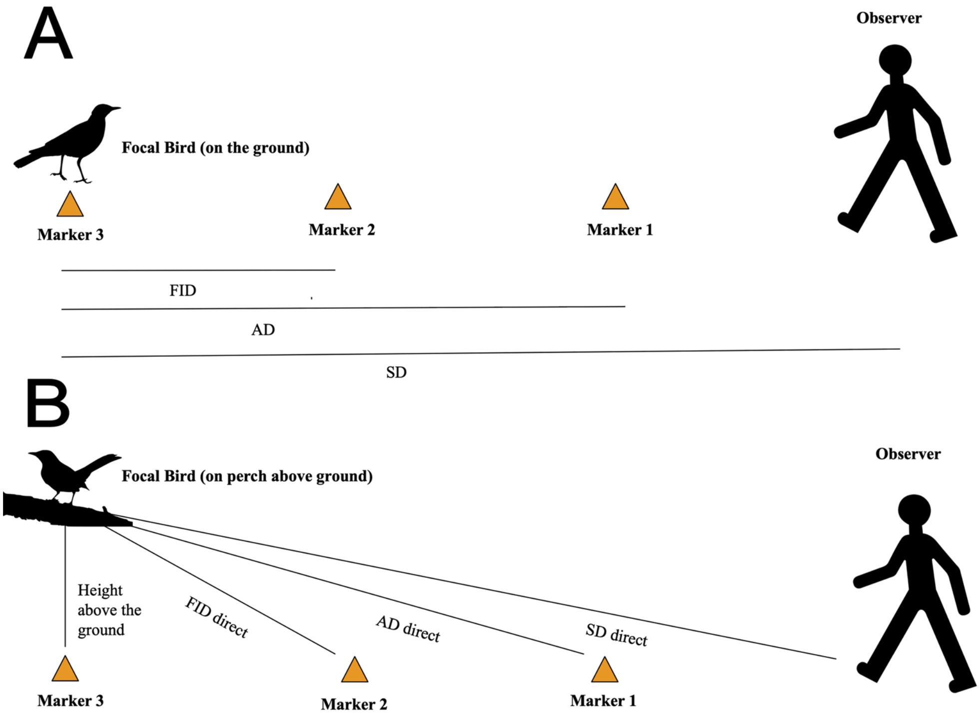

Fig. 2 Illustration of how FID data was collected for A) focal birds on the ground, and B) focal birds perched at a height above the ground

in paces were converted to meters using each observer's calibration factor. When birds were perched above the ground, vertical height (in meters) was estimated using the Arboreal Tree smartphone application (Arboreal AB 2024). Because both horizontal distances and perch height were expressed in meters, direct SD, AD, and FID were calculated as the hypotenuse of the right triangle formed between the observer and the focal bird (Blumstein et al. 2004; Fig. 2b).

In addition to distance measures, observers recorded GPS location (latitude/longitude), date, time, species, age (if known), sex (if known), initial behavior, initial position (ground or elevated), perch height, escape mode (flight or terrestrial), percent cloud cover, wind intensity (Beaufort scale), number of conspecifics and heterospecifics within 10 m, habitat type (reeds, shrubs, grass, or trees), site, and observer identity. Initial behavior was categorized into three groups: "perched," "foraging," and "other," as detailed in the ethogram (Supplementary Table S1). Several of these variables have been shown to influence antipredator responses (Blumstein 2006; Cooper and Blumstein 2015; Sol et al. 2018; Díaz et al. 2021; Morelli et al. 2022). Finally, any free-roaming cats observed during surveys were recorded with GPS coordinates.

Estimating cat and human population density

FID records were first spatially analyzed using QGIS (QGIS Development Team 2024). To define neighborhood boundaries within Los Angeles, we used publicly available GIS data from the LA Times Neighborhood Boundaries dataset on the Los Angeles Vision Zero GeoHub (City of Los Angeles 2025). The dataset provides polygon shapefiles delineating neighborhood boundaries based on LA Times mapping standards. These shapefiles were downloaded and added as a first layer to QGIS. A second layer containing the collected FID records was then overlaid on the neighborhood boundaries using the associated latitude and longitude coordinates. All other data associated with each record were saved as attributes.

We used Los Angeles Animal Services (LAAS) calls-for-service records for cats between 1 September 2020 and 1 July 2023 to estimate the density of free-roaming cats across the Los Angeles metropolitan area. The LAAS dataset contained 3,892 records documenting public requests for assistance or concerns related to stray cats. Each request included a street address and ZIP code, which we geocoded into decimal coordinates (latitude and longitude) using the Google Maps geocoding API in Google Sheets. These coordinates were then imported into QGIS, where we generated a continuous surface of estimated cat density using the Kernel Density Estimation (KDE) Heatmap tool. KDE was implemented using a quartic (biweight) kernel function with a 2,000 m bandwidth (search radius) and a 100 m × 100 m output raster resolution, with all observations equally weighted. The KDE was initially computed in geographic coordinates (WGS84) and subsequently projected into WGS84/UTM Zone 11 N for spatial analysis.

To validate the resulting density surface, we implemented a presence–availability framework. We georeferenced 69 independent field observations of free-roaming cats and extracted predicted density values at these locations ("presence"). We then generated 690 randomly distributed "available" points across the study area and extracted density values at these locations to characterize landscape-wide availability. Modelled cat density at observed cat locations was significantly higher than at random locations (Supplementary Fig.S1; Wilcoxon rank-sum test: $W = 9418$, $p = 6.57 \times 10^{-14}$, rank-biserial correlation = 0.55). A binomial logistic regression further confirmed that modelled density was a strong positive predictor of cat occurrence ($\beta = 0.0618$, $p = 8.07 \times 10^{-12}$; odds ratio = 1.064, 95% CI: 1.045–1.083), indicating that cats were disproportionately observed in areas of higher predicted density. Together, these results support the ecological validity of the KDE-derived cat density surface.

The raster layer was then overlaid with a grid of 1 km² cells, a scale chosen based on typical home-range sizes of free-roaming domestic cats (Castañeda et al. 2019; Kays et al. 2020) and the spatial distribution of service-call records. Finally, using the "Join attributes by location" tool in QGIS, each FID observation was assigned the mean estimated cat density value of the grid cell in which it occurred.

Following this, we derived data for human population density using the most recent U.S. Census Bureau TIGER/Line census tract shapefiles for Los Angeles County, together with American Community Survey (ACS) 5-year population estimates (2019–2023; U.S. Census Bureau n.d.). The tract boundary shapefile and tabular population data were imported into QGIS and joined by GEOID to associate each tract polygon with total population counts (B01003_001E). The tract layer was then reprojected to a common projected coordinate reference system (EPSG:32611 – WGS 84/UTM Zone 11 N) and used to calculate tract-level population density (people/km²) by dividing total population by tract area (area_km2). This density surface was intersected with the project's existing 1 km² spatial grid to compute the mean human population density within each grid cell via area-weighted overlap. Finally, grid-level density values were spatially joined to individual FID sampling locations (uploaded as latitude/longitude point data) using a one-to-one "within" join, producing a dataset in which each FID observation was associated with the corresponding human population density of the grid cell in which it occurred for downstream modelling in R.

Data management and statistical methods

All statistical analyses were conducted in R version 4.3.3 (R Core Team 2024) using RStudio (Posit Team 2022). Before model fitting, several data management steps were carried out to prepare the dataset and ensure that variables were appropriately formatted for analysis.

As part of data preprocessing, we first evaluated whether observer identity influenced measured FID. Exploratory analyses indicated that one observer (MH) recorded significantly higher FIDs relative to the reference observer (PB), who conducted the majority of observations $n=664$). To minimize potential observer bias, we removed these 59 observations from the final dataset prior to further analysis.

Next, data on body mass for each species—shown to be an important predictor of avian FID (Møller 2015)—were obtained from the AVONET database of avian functional traits (Tobias et al. 2022) and merged with the dataset. We then examined the distributions of continuous variables using histograms to identify skewness and deviations from normality. Log transformations were applied where appropriate, including for flight initiation distance (FID), starting distance (SD), cat density, human population density, total flock size (number of conspecifics and heterospecifics within 10 m), distance to vegetation cover, and body mass.

Initial behavior was incorporated into subsequent models as a categorical predictor with three levels ("perched", "foraging", and "other") with "perched" specified as the reference category (see Supplementary Table S1).

Finally, time of day was converted from HH: MM: SS format to radians and decomposed into sine and cosine components to account for its circulate (24-hour) structure and avoid imposing artificial linear boundaries on a cyclical variable. Although observations were conducted primarily between 06:30 and 09:30, preliminary analyses indicated significant temporal variation in FID within this period, justifying the inclusion of time of day as a continuous cyclical predictor.

We explained variation in FID by fitting Bayesian regression models with multiple predictors using the 'brm' function in the *brms* package (v. 2.22.0) (Bürkner 2017). We first constructed two base models: (1) a phylogenetically informed model that incorporated a species-level random intercept structured by a phylogenetic covariance matrix, and (2) a non-phylogenetic model that included species as a random intercept but assumed independence among species (i.e., no phylogenetic covariance structure). Both base models looked at FID (the response variable) as a function of SD, cat density, the interaction between SD and cat density, and human population, with species and site as random intercepts to account for variation across levels. All continuous predictors were centred and scaled (mean = 0, SD = 1) to improve numerical stability and sampling efficiency in our Bayesian models and to place predictors on comparable scales for easier interpretation of effect sizes. We assessed multicollinearity among continuous predictors by constructing a correlation matrix and examining Pearson's correlation coefficients, using a threshold of $|r| \geq 0.7$ to indicate potentially problematic correlations. Additionally, we calculated Variance Inflation Factors (VIF) using the vif() function from the *car* package (Fox and Weisberg 2019), and considered VIF values < 4 to indicate acceptable levels of multicollinearity. Furthermore, all categorical predictors were converted to factors to ensure that the 'brm' function read them as discrete variables with multiple unordered levels.

Models were fitted using a Gaussian error distribution with an identity link function and two MCMC (Markov Chain Monte Carlo) chains, each run for 2000 total iterations, including 1000 warm-up iterations and 1000 post-warm-up sampling iterations. To reduce the likelihood of divergent transitions, we increased the target average proposal acceptance rate to 0.999 and set the maximum tree depth to 15 (Bürkner 2017). In the phylogenetically informed models, we specified weakly informative priors for all fixed-effect coefficients using a Normal (0, 10) distribution (mean = 0, SD = 10), implemented in *brms* as set_prior("normal(0,10)", class = "b"). Because all continuous predictors were standardized before analysis, this prior was intentionally broad relative to the expected parameter scale. For all other parameters—including the intercept, group-level standard deviations for random intercepts, and the residual standard deviation (σ)—as well as for the non-phylogenetic models, we used the default priors implemented in *brms* for Gaussian models. These defaults consist of Student-t priors for intercepts and variance parameters and flat (improper uniform) priors for regression coefficients when not otherwise specified. Convergence was assessed using standard Stan diagnostics, including potential scale reduction factors ($\hat{R}$), effective sample sizes, and visual inspection of trace plots. All parameters had $\hat{R}$ values < 1.05 (generally ≈ 1.00), indicating good mixing between chains, and posterior predictive checks confirmed that the models adequately reproduced the observed data distribution (see Supplementary Information).

The phylogenetically informed Bayesian model was created by constructing a phylogenetic covariance matrix and incorporating it into the model with species as a random factor. To do this, we first put our species list from the dataset into the online Birdtree phylogeny tool (http://birdtree.org) (Jetz et al. 2012) and downloaded 100 randomly generated phylogenies using the "Hackett All Species" source. The 'ape' package (v. 5.8-1.8) (Paradis and Schliep 2019) was used to read the phylogenies into R, after which we generated the Maximum Clade Credibility (MCC) tree with the 'maxCladeCred' function within the 'phangorn' v. 2.12.1 package (Schliep 2011). Finally, we constructed the complete phylogenetic covariance matrix using the MCC tree and the 'inverseA' function from the 'MCMCglmm' v. 2.36 package (Hadfield 2010). Model fit and predictive power were assessed using the leave-one-out cross-validation information criterion (LOOIC) computed with the loo() function from the loo package, conditional and marginal R^2 values obtained using the r2_bayes() function from the brms package, and posterior predictive checks performed with the pp_check() function from the brms package.

Evaluation of model performance revealed that the non-phylogenetically informed model had a lower LOOIC than the phylogenetically informed model and was therefore used as the baseline framework for further analyses. Predictors of interest were then iteratively added to the model, with model fit and predictive performance assessed at each step, and retained only if they significantly improved model performance. Predictor significance was assessed using 95% credible intervals (CI), with effects considered statistically supported when the 95% CI did not overlap zero.

To better understand our results, we conducted several additional analyses. First, we incorporated species-level foraging attributes from the EltonTraits 1.0 database (Wilman et al. 2014), filtering the dataset to include only ground-foraging species—those that spent at least 50% of their foraging time on the ground. After filtering, we re-fitted the final model on this subset, because we assumed that ground-foraging species were more vulnerable to cat predation and may exhibit different effects.

Second, because perch height can represent a vertical component of antipredator behavior in birds, we used the same Bayesian modelling framework to examine height above ground at the start of approach as a response variable. Previous work has shown that birds may perch higher in areas with cat colonies, suggesting that vertical positioning may reflect perceived predation risk from terrestrial predators (Díaz et al. 2022). We therefore first fitted a baseline model with just cat density as a predictor, and then an expanded model incorporating additional covariates, while accounting for species and site as random intercepts.

Third, we performed a species-level analysis by subsetting the dataset by species and applying the final model to each subset, retaining site as the only random intercept. Because these models did not benefit from partial pooling across species, we excluded subsets with fewer than ten observations and fewer than two sites to prevent unstable parameter estimates.

Finally, to evaluate predictions of the human shielding hypothesis, we tested whether human population density modified the relationship between cat density and avian FID. We first incorporated a three-way interaction between starting distance, cat density, and human population density (SD × cat density × human density) into both the baseline and expanded models. Because the human shielding hypothesis predicts that human presence alters predator–prey risk relationships, we also evaluated a more direct formulation by including a two-way interaction between cat density and human population density. These interaction terms were tested both at the community level and in species-specific subset models to determine whether any shielding effects emerged across the community or within individual species.

Results

Final dataset

The final dataset included 1120 complete FID records for 48 different species collected between February and August 2024 across the following 11 sites within the LA area - Westwood, Brentwood, Sawtelle, Lake Balboa/Van Nuys, Wilmington, San Pedro, Northridge, Pico-Union, Koreatown, Chinatown, and East Hollywood (Table 1).

Model results

Our non-phylogenetic base model demonstrated better overall fit, with a substantially lower LOOIC (1505.0) and higher conditional ($R^2 = 0.400$) and marginal ($R^2 = 0.252$) R^2 values than the phylogenetically informed base model (LOOIC = 1524.6; conditional $R^2 = 0.390$; marginal $R^2 = 0.247$). Since the inclusion of phylogenetic structure did not improve model performance, we selected the simpler non-phylogenetic Bayesian regression model for subsequent analyses.

Our final model (see Methods for model selection procedures) had a LOOIC of 1334.3, with a conditional R^2 of 0.440 and a marginal R^2 of 0.306. This expanded model included FID as the response variable and predictors for starting distance, cat density, their interaction (starting distance × cat density), body mass, on-ground status (whether the focal bird was on the ground during approach), initial behavior, and time of day (modelled using sine and cosine components). Site and species were retained as random intercepts to account for hierarchical structure in the dataset. Posterior predictive checks produced a unimodal distribution, with the observed data closely aligning with the predicted distribution (Supplementary Fig. S2). Furthermore, model diagnostics indicated well-mixed trace plots and unimodal density distributions, suggesting stable estimates (Supplementary Figs. S3a-c). No signs of poor mixing or multi-modality were observed. The correlation matrix among continuous predictors showed no evidence of high

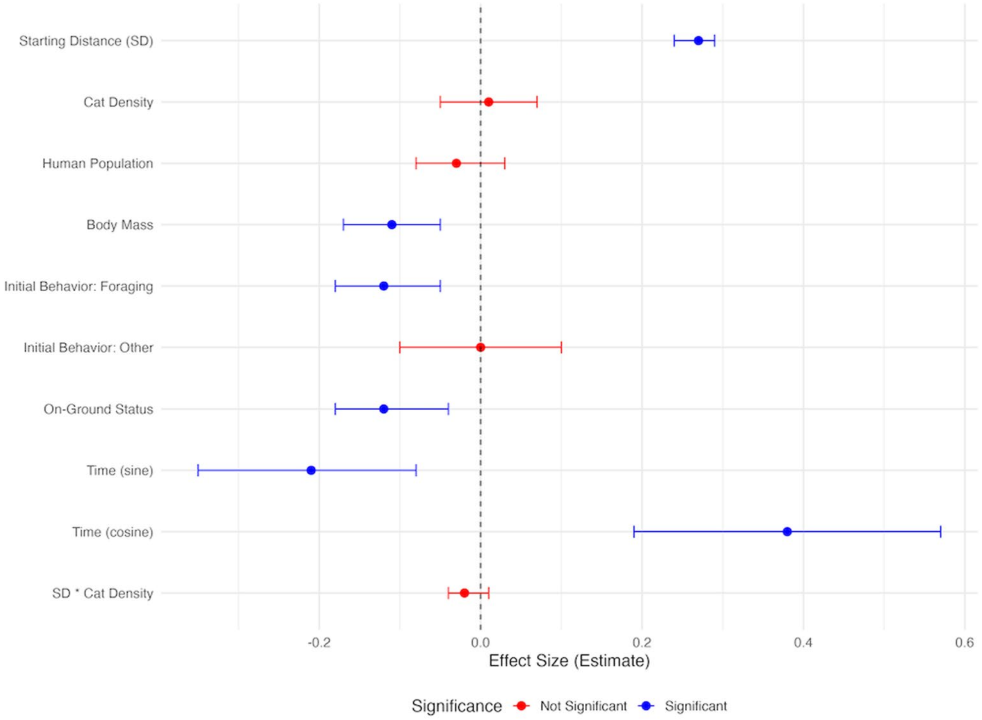

Fig. 3 Effect sizes (±95% credible intervals) of predictors in final model. Significant predictors are shown in blue, while insignificant predictors are shown in red

collinearity (Supplementary Table S3). Consistent with this, variance inflation factor (VIF) values for continuous predictors and interactions were low indicating no multicollinearity issues (Supplementary Table S4). Finally, model residuals were approximately normally distributed (Supplementary Figs. S4, S5).

The final model accounted for hierarchical structure by including random intercept effects for Site (11 levels) and Species (46 levels). The standard deviation of the random intercept for Site was low (0.10, 95% CI: [0.05, 0.18]), indicating minimal variation between sites. However, the standard deviation for Species was higher (0.18, 95% CI: [0.12, 0.25]), suggesting greater variability among species in their responses.

Among the fixed effects included in the model, cat density, human population density, and the interaction between starting distance (SD) and cat density were not significant predictors of flight initiation distance (FID), as indicated by their 95% confidence intervals (CIs) that included zero (Fig. 3). However, several ecological, behavioral, and observer related variables emerged as significant predictors of FID, even after accounting for variation at the species and site levels.

First, starting distance was positively associated with FID (β=0.27, 95% CI: [0.24, 0.29]), indicating that birds escaped at greater distances when approached from further away. Additionally, the time of day had an important influence on FID. More specifically, the cosine component of circular time was positively associated with FID (β=0.38, 95% CI: [0.19, 0.57]), while the sine component of time had a negative effect on FID ((β = −0.21, 95% CI: [−0.35, −0.08]). This suggests that birds allow closer approach at dawn, and flush at greater distances as time progresses toward midday.

Intrinsic and behavioral factors also played a crucial role in explaining FID. Body mass was negatively associated with FID (β = −0.11, 95% CI: [−0.17, −0.05]), meaning that larger-bodied species generally tolerated closer approaches before fleeing. Additionally, birds' behavior at the time of approach influenced their escape response. Specifically, foraging birds had shorter FIDs compared to perched individuals (β = −0.12, 95% CI: [−0.18, −0.05]), and birds that were on the ground flushed at shorter distances than those above ground (β = −0.12, 95% CI: [−0.18, −0.04]).

Further analyses

To further explore patterns in avian escape behavior in our dataset, we conducted several additional analyses examining (1) responses among ground-foraging species, (2) variation in perch height, (3) species-specific responses, and (4) whether human population density modified the relationship between cat density and FID (human shielding hypothesis).

Restricting the dataset to ground-foraging species using EltonTraits 1.0 data did not alter the overall conclusions. Across both filtering thresholds (species that spent ≥ 50% and > 50% of their foraging time on the ground), cat density and human population density remained non-significant predictors of FID. Instead, the same predictors identified in the full dataset remained significant, including starting distance, body mass, initial behavior, on-ground status, and time of day (Supplementary Table S7). Full parameter estimates for these models are reported in Supplementary Table S5.

When modelling height above ground as a response variable across our complete dataset, we again detected no effect of cat density or human population density. Perch height instead varied primarily with behavioral, intrinsic, and temporal factors. Individuals exhibiting "other" behaviors and those observed later in the morning tended to perch higher above the ground, whereas larger-bodied birds and individuals engaged in foraging were more often positioned closer to the ground (Supplementary Table S7). Complete model outputs are provided in Supplementary Table S6.

When we examined each species separately, retaining site as a random intercept and omitting body mass (as it was constant within species), we found no consistent effect of cat density, human population, or the interaction between starting distance (SD) and cat density on FID across species (Supplementary Table S2). Starting distance remained the most consistent predictor of FID, while significant positive effect of human population density was detected only for *Sayornis nigricans* (β = 0.24, 95% CI: [0.01, 0.46]; 69 observations across 11 sites).

Finally, testing the human shielding hypothesis revealed no evidence that human density modified the relationship between cat density and avian FID at the community level. The three-way interaction between starting distance, cat density, and human population density was not supported in either the baseline or expanded models, as the 95% credible intervals overlapped zero. When this same model structure was applied to species-level subsets, the three-way interaction remained unsupported for all species.

We then tested a more direct formulation of the hypothesis by including a two-way interaction between cat density and human population density. This interaction term likewise showed no effect at the community level in either the baseline or expanded models. However, species-specific analyses revealed significant interaction effects for two species: *Carpodacus mexicanus* (β = −0.19, 95% CI: [−0.37, −0.01]; 132 observations across 11 sites) and *Columba livia* (β = −0.60, 95% CI: [−0.87, −0.31]; 71 observations across 10 sites). In both cases, the negative interaction term indicates that birds allowed closer approach (shorter FIDs) in areas where both cat density and human density were high.

Importantly, across all additional analyses, cat density did not emerge as a consistent predictor of avian antipredator behavior, which reinforces the findings of our primary community-level models (see Sect. 3.2).

Discussion

Understanding the factors that shape antipredator responses in urban wildlife is essential for understanding how species persist in human-altered environments (Møller and Díaz 2018). In this study, we found no consistent effect of domestic cat density on avian FID or perch height across the Los Angeles metropolitan area. This pattern was robust across multiple analyses, including community-level models, species-specific subsets, and a dataset restricted to ground-foraging species. Collectively, these results suggest that spatial variation in cat density does not strongly influence antipredator behavior in the urban bird assemblage sampled in this study.

One potential explanation for this pattern is a threshold effect, whereby predator abundance across the study area may already exceed the level at which prey behavior responds detectably to additional increases in predator density. If domestic cats occur at consistently high densities across urban landscapes such as Los Angeles, birds may perceive predation risk as chronically elevated, resulting in limited variation in antipredator behavior across sites. Under such conditions, additional spatial variation in predator density may not produce measurable differences in behavioral responses such as FID. Similar threshold effects have been proposed in predator–prey systems under the risk-allocation hypothesis, which predicts that prey responses plateau as prey experience consistently high-levels of predation risk (Lima and Bednekoff 1999; Ferrari et al. 2009).

Another explanation for the lack of a detectable cat density effect is that birds may adjust antipredator behavior primarily in response to immediate predator encounters rather than background predator abundance across the landscape. In many predator–prey systems, antipredator behavioral decisions are triggered by direct sensory cues indicating the presence of a predator, such as visual detection, olfaction, or sounds (Roth et al. 2008; Amo et al. 2017; Arteaga-Torres et al. 2020; Zuo et al. 2024). Predator recognition may therefore be cue- and context-dependent, such that birds may not consistently recognize domestic cats as relevant predation threats in this system unless cats provide immediate cues of danger, such as being directly visible, moving, hunting, or near nests. Because domestic cats are ambush hunters and are often detected at close range, birds may initiate escape primarily when a cat is directly perceived rather than according to spatial variation in cat density. Thus, high predation rates reported in the literature may not necessarily translate into measurable changes in FID if birds assess cat-related risk mainly at the encounter scale; under this scenario, the landscape-scale cat density metric used in our study may not strongly influence the distance at which birds initiate escape from a human observer.

Methodological considerations may also contribute to this pattern. FID in this study was measured using human approaches rather than simulated predator encounters, creating a potential mismatch between the stimulus used to elicit escape behavior and the predator of interest. Because humans rarely pose direct predation threats to birds, individuals may respond differently to human approaches than they would to an approaching cat. This mismatch could weaken our ability to detect behavioral responses specifically associated with cat density, particularly if birds respond to cats only when predator-specific cues are present. In highly urbanized environments such as Los Angeles, birds frequently encounter humans and may become habituated to their presence, resulting in reduced responsiveness to human approaches and shorter FIDs overall (Møller 2008; Díaz et al. 2013; Samia et al. 2015). If habituation to humans is widespread across the study area, variation in human density may also fail to produce detectable behavioral differences. In this context, the widespread presence of both humans and human-associated predators may obscure behavioral responses that would otherwise occur in less urbanized landscapes.

Finally, we emphasize that the bird assemblage sampled in this study consists largely of highly urban-adapted taxa that may exhibit greater tolerance to the selection pressures of megacity habitats. Consequently, the observed behavioral responses may not be representative of habitat-restricted, disturbance-sensitive species that are underrepresented in, or absent from, such highly urbanized environments.

Although human population density did not influence FID at the community level, we detected a significant positive relationship between human population density and FID in *Sayornis nigricans* (black phoebes). Individuals of this species flushed at greater distances in areas with higher human density, suggesting heightened wariness in more heavily urbanized environments. Black phoebes frequently occupy human-modified habitats, but their behavior may still be influenced by levels of human activity and disturbance, reflecting broad patterns of behavioral adjustments among urban wildlife (Gall et al. 2013; Lowry et al. 2013). However, it is important to note that this result was based on a relatively modest sample size (69 observations across 11 sites), further research with larger datasets is required to confirm whether this pattern reflects a consistent behavioral response in this species.

We also evaluated whether human presence modified the relationship between predator density and perceived risk, as predicted by the human shielding hypothesis (HSH). At the community level, we found no evidence that human density altered the relationship between cat density and FID. However, species-specific analyses revealed significant interaction effects for *Columba livia* (rock pigeons) and *Carpodacus mexicanus* (house finches), indicating that individuals allowed closer approach in areas where both human and cat densities were high.

Rather than supporting the traditional shielding hypothesis (where human presence reduces predation risk by deterring predators) this pattern suggests that human activity may instead reduce perceived risk for some urban prey species, potentially increasing vulnerability to predation. Highly urban-adapted species such as rock pigeons and house finches often exhibit strong habituation to human presence and may therefore tolerate closer approach in densely populated environments. However, because domestic cats are frequently associated with human settlements, areas with high human density may also contain high densities of human-subsidized predators. This pattern is consistent with findings from studies on nature-based tourism, where repeated exposure to humans can increase tolerance to humans in wildlife by increasing boldness and reducing vigilance (Geffroy et al. 2015). Such behavioral changes may elevate predation risk if animals become less responsive to predators in human-dominated landscapes. In urban ecosystems with high abundances of human-associated predators, including domestic cats, this behavioral shift could potentially increase vulnerability for certain prey species despite the presence of humans.

While cat density and human population density did not explain most variation in avian FID, several other predictors were consistently associated with escape behavior. Starting distance had a strong positive association with FID, consistent with the well-established pattern that animals often initiate escape earlier when an approaching threat is detected at greater distances (Blumstein 2003). However, because FID is inherently constrained by starting distance, this association should be interpreted cautiously and may partly reflect mathematical coupling rather than a purely biological response (Dumont et al. 2012). Methods such as quantile regression can help disentangle biological effects from this constraint by evaluating the upper boundary of the starting distance–FID relationship (Chamaillé-Jammes and Blumstein 2012), but this approach was not readily compatible with our phylogenetic modelling framework. We therefore treated starting distance as an important covariate and interpreted its effect primarily as a control for variation in approach conditions rather than as a focal ecological result.

We also detected a negative relationship between body mass and FID, indicating that larger species allowed closer approach before flushing. While previous studies often reported a positive association between body size and escape distance (Blumstein 2006; Weston et al. 2012), larger species may experience lower predation risk from smaller urban predators such as domestic cats, potentially reducing the need for early escape responses (Møller et al. 2010;

Beauchamp 2023), Additionally, larger species may incur higher energetic costs during flight species (Nudds and Bryant 2000; Shestopaloff 2024), making delayed escape advantageous when perceived risk is low.

Behavioral context also influenced escape responses. Birds that were foraging or positioned on the ground had shorter FIDs than perched individuals, likely reflecting a trade-off between vigilance and resource acquisition (Cooper and Blumstein 2015). Similarly, time of day influenced both FID and perch height, with birds generally flushing at greater distances later in the morning. This pattern is consistent with the existing literature (Piratelli et al. 2015; Ferguson et al. 2019) and may reflect shifts in behavioral priorities across the daily activity cycle, where early morning foraging reduces vigilance, whereas later periods allow greater investment in antipredator behavior (Bonter et al. 2013).

Although our findings reveal useful insights into the factors affecting antipredator behavior in megacities, several limitations of our study should be acknowledged. First, estimates of cat density were derived from LAAS calls-for-service data collected between 2020 and 2023. Although these records provided a useful proxy for spatial variation in cat activity, they may not perfectly represent the true distribution of free-roaming cats because they reflect reported sightings rather than systematic surveys. We partially addressed this limitation by validating the density surface using 69 independent field observations of free-roaming cats, which were disproportionately located in areas predicted to have higher cat density (see methods). Nevertheless, direct population surveys of free-roaming cats would provide more precise estimates of predator abundance.

Second, data collection was restricted to publicly accessible urban spaces, such as parks, sidewalks, and residential streets. Urban areas that were inaccessible to observers (such as private properties, industrial zones, or restricted commercial areas) may contain different predator or prey dynamics that were not captured in this study.

Finally, sample sizes varied across species. Although we attempted to collect observations across all study sites, some species were represented by relatively small numbers of observations. Future studies that collect larger numbers of records per species across multiple field seasons would improve statistical power and allow for more detailed investigation of species-specific behavioral responses.

In conclusion, our findings highlight the complex and context-dependent nature of anti-predator behavior in urban settings. Despite the widespread presence of domestic cats in cities, variation in cat density did not appear to influence escape responses in our dataset. Instead, behavioral responses were shaped primarily by environmental factors, intrinsic traits and behavioral context, suggesting that urban wildlife may rely on flexible behavioral strategies rather than spatial variation in predator abundance when assessing risk.

We call for future research that involves comparative studies across a wider range of cities, differing in age, structure, climate, human and predator densities, and socio-ecological histories. Such work will be essential to disentangle the relative contributions of these factors and better understand how urbanization at different scales reshapes ecological interactions and influences the behavioral adaptations of wildlife.

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Author contributions Pranav Bellur: Investigation, Software, Formal analysis, Data curation, Visualization, Writing – original draft, review & editing Mario Díaz: Conceptualization, Methodology, Validation, Writing – review & editing Travis Longcore: Methodology, Investigation, Writing – review & editing. Daniel T. Blumstein: Conceptualization, Methodology, Formal analysis, Validation, Supervision, Writing – review & editing.

Data availability All data and analysis scripts supporting the findings of this study have been uploaded to the Open Science Framework (OSF) repository and are accessible at: [https://osf.io/uvm26/](https://osf.io/uvm26).

Declarations

Ethical statement Animal use protocols were obtained from the University of California Los Angeles (IACUC # 2000−147, renewed annually). By design, the experimental approaches used to quantify flight initiation distance were minimally invasive.

Competing interests The authors declare no competing interests.

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