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Urbanization predicts flight initiation distance in feral pigeons (*Columba livia*) across New York City

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Variation in behavioural traits is especially important in novel habitats where selection forces determine successful colonizers. Prey species must constantly balance the risk versus reward of remaining in an area with threats while gaining possible fitness benefits. Flight initiation distance, the distance at which an animal flees when approached by a human, is a common metric used to assess habituation to stressors and risk behaviour. Here we examine the flight initiation distance of 519 feral pigeons (*Columba livia*) across New York City, U.S.A. We examined this behavioural response across the metropolitan landscape with respect to multiple urbanization factors related to human activity, the abiotic environment and the ecological community. We used principal component analysis (PCA) to transform landcover characters and then liner models to test various anthropogenic variables including landcover, pedestrian traffic and human population size. We found that flight initiation distance in pigeons decreased with increased human activity (measured by pedestrian traffic and human population size) and more urban landcover (specifically longer road length and greater amounts of impervious surface). We also found that flight initiation distance was shorter in areas with more peregrine falcon, *Falco peregrinus*, sightings, but longer in areas with more red-tailed hawk, *Buteo jamaicensis*, sightings. Overall, this research demonstrates that feral pigeon behaviour varies with urbanization, human activity and ecological attributes. Since behavioural changes are often the most rapid phenotypic response to change, this study demonstrates that pigeons are responding to anthropogenic stressors, which may set the stage for adaptive changes.

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Urbanization is increasing around the world, drastically altering the natural landscape and species interactions (Alberti, 2015). Cities are associated with denser human populations, increased environmental toxins and higher amounts of light and noise pollution, which have negative consequences for most animals. However, some urban animals are able to benefit via indirect interactions (e.g. anthropogenic structures creating artificial perches for birds and lizards) as well as direct interactions (e.g. active feeding of wildlife).

As urban environments expand, animals encounter a novel set of biotic and abiotic conditions that may necessitate altered behavioural responses. Risk assessment behaviours are particularly relevant in urban habitats. Antipredator behaviour and risk avoidance affect behaviour in a multitude of ways from influencing the time of day animals are active (Connolly & Orrock, 2018) to the amount of time prey engage in risky behaviour (Orrock & Fletcher, 2014). For example, urban coyotes, *Canis latrans*, are more active at night to avoid human interactions (Gehrt & McGraw, 2007), Túngara frogs, *Physalaemus* (= *Engystomops*) *pustulosus*, and birds are louder in urban areas where the predation threat is lower (Halfwerk et al., 2019; Slabbekoorn & Peet, 2003), and urban great tits, *Parus major*, engage in riskier behaviour with both a common predator (sparrowhawks, *Accipiter nisus*) and humans (Vincze et al., 2019).

Successful urban species tend to have behavioural modifications that reduce costs of living in human-dominated habitats in terms of stress, signal interference, persecution and balancing risks versus rewards (Lyons, Mastromonaco, Edwards, & Schulte-Hostedde, 2017; Mueller, Partecke, Hatchwell, Gaston, & Evans, 2013). Behaviours that increase fitness may be further shaped by the unique conditions encountered in these habitats, resulting in phenotypically distinct urban-adapted populations. Behavioural variation

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within and between urban populations is common, with some animals expressing extreme wariness while others are more likely to explore (Ducatez, Sol, Sayol, & Lefebvre, 2020). Behavioural variation is, therefore, essential as a substrate for natural selection, resulting in both plastic and genetically based trait shifts in these novel urban habitats (Sol, Lapiedra, & González-Lagos, 2013).

Specific behavioural phenotypes, such as tolerance of human activity, characterize the species likely to colonize and persist in cities (Lowry, Lill, & Wong, 2013). Animals living in urban environments are likely to exhibit behavioural flexibility to deal with variation in human encounters and resource availability (Sol et al., 2013). Escape behaviour in response to humans can have carryover effects on feeding success, reproduction and body condition, and if an animal does not correctly assess a threat it may experience reduced fitness (Whitfield, Ruddock, & Bullman, 2008). The theory of economic escape behaviour predicts that willingness to flee should increase as a perceived threat approaches and should decrease as escape costs increase (Blumstein, 2003; Ydenberg & Dill, 1986). While fleeing has obvious benefits, it also has a high cost since an individual must cease its current activity and expend energy in order to flee. For example, if food density is high, the extra time spent feeding may be worth the increased risk if a potential threat is allowed to approach more closely (Bowers & Breland, 1996; Real & Caraco, 1986).

Escape behaviour is also influenced by ecological community composition, which may covary with degree of urbanization and human presence. Research on predator presence and abundance in urban landscapes have shown that prey in areas with lower numbers of hawks, falcons and buzzards allow closer approach before initiating flight responses (Díaz et al., 2013), suggesting that urban prey populations may have diverged from rural populations in response to changes in predator abundance. Additionally, human presence may influence predators and prey in different ways, leading to a suite of complex interactions among human and nonhuman residents of urban environments (Muhly, Semeniuk, Massolo, Hickman, & Musiani, 2011).

Feral pigeons (*Columba livia*), commonly known as the common pigeon, rock pigeon or rock dove, are a common human commensal (i.e. an organism that lives in close association with and benefits from humans) in cities around the world (Johnston & Janiga, 1995). However, pigeon abundance varies throughout the urban landscape and tends to be highest in areas where people congregate and accidentally or intentionally drop food (Tang, Low, Lim, Gwee, & Rheindt, 2018). Pigeons in these areas appear to be less fearful, with pedestrians often walking within 1 m of them before the pigeons change direction or fly away (Johnston & Janiga, 1995). Urban raptors commonly feed upon pigeons (Johnston & Janiga, 1995; Palleroni, Miller, Hauser, & Marler, 2005), meaning that many raptors reach their highest densities in areas where pigeons co-occur (Sorace, 2002). This has led to a complex eco-evolutionary dynamic in which many cities now support native raptors that derive their primary food source from non-native prey. In areas where pigeons are in high abundance, like New York City, U.S.A., high predator density may influence pigeon behaviour. For example, the ability to detect and avoid predation is linked to flock size, since larger flocks are better able to detect predators and alert conspecifics (Kenward, 1978). Pigeons are a commonly encountered urban wildlife that follow the same behavioural trends as many other urban birds (Burger & Gochfeld, 1991; Mikula, 2014; Morelli et al., 2018); therefore, in-depth studies of pigeon behaviour can help us understand how complex eco-evolutionary interactions shape the success of urban organisms.

Here we examine the variability in flight behaviour of pigeons across the five boroughs of New York City (Brooklyn, Manhattan, Queens, Staten Island and the Bronx) using the common metric of flight initiation distance (FID). This metric is defined as the distance at which an escape response is initiated when encountering a threatening stimulus (typically a human) and is commonly interpreted in light of habituation and risk assessment (Blumstein, 2003, 2006). To this end, we examine how different features of the urban landscape as well as predator presence and pigeon behaviour relate to FID. Within this framework, we make several specific predictions: (1) FID will decrease with increasing human disturbance of the landscape, represented by greater amounts of developed landcover; (2) FID will decrease with increasing human presence, represented by human population size and pedestrian traffic; (3) FID will be influenced by predator prevalence, with greater FID when predators are more prevalent.

METHODS

Study Location

We conducted sampling across the five boroughs of New York City: the Bronx, Brooklyn, Manhattan, Queens and Staten Island. These five boroughs were historically governed independently but were incorporated in 1898 to become the modern-day New York City. The boroughs differ in geographical size, with Queens being the largest borough (151 km^2) and Manhattan being the smallest borough (59 km^2; United States Census Bureau, 2015). The boroughs also differ in population density, with Manhattan being the most densely populated (27 544 people/km^2) and Staten Island being the least densely populated (3150 people/km^2; United States Census Bureau, 2015). Together, the five boroughs make up New York City, the largest city in the United States of America, containing a total of 8.3 million people across 783 km^2. Carlen and Munshi-South (2020) have previously shown that the pigeon population in New York City constitutes a single population; thus, we consider all pigeons sampled during this study as part of a single population.

Field Sampling

We recorded flight initiation distance using a modified version of a method developed by Blumstein (2003). We walked through each study location until we spotted a pigeon on the ground and recorded our transect tracks using the smart phone application MapMyWalk (Under Armour, Inc., Baltimore, MD, U.S.A.) to ensure we did not retrace our steps. For each pigeon tested, we recorded date, time of day, pigeon behaviour before approach (i.e. moving, feeding, stationary) and location recorded as latitude and longitude using the native iPhone compass application (Apple Inc., Cupertino, CA, U.S.A.). We sampled no more than three pigeons at any location and identified pigeons by unique plumage characteristics, since pigeon plumage is a complex character composed of highly variable patterns and colours. This allowed us to uniquely identify individual pigeons during the trial, but not across days, such that we did not sample individuals from the same location with similar colours or patterns to minimize the chance of double sampling the same individual. However, given that pigeon home range size is small (1.64 ha; Sol & Senar, 1995) and reported mean daily movement is short (590 m; Rose, Nagel, & Haag-Wackernagel, 2006), we think it is unlikely that we conducted multiple FID trials on the same individual. Nevertheless, we acknowledge this as a potential limitation of our study and suggest that future studies examine how home range size varies across an urbanization gradient. We also collected information about the size of the flock the pigeon was in; specifically, we counted the number of individuals in each flock of 20 individuals or less and approximated the flock size for flocks over 20 individuals, with a flock defined as a group of pigeons such

that no individual pigeon was further than 3 m from at least one other group member.

One researcher (R.L.) then walked towards the pigeon at a steady pace (approximately 0.5 m/s) while maintaining eye contact with the subject. As in Blumstein (2003), we assumed the focal animal was relaxed before it was approached, but we were unable to determine whether it had detected us before the trial began. We estimated researcher starting distance (distance from researcher to focal animal when first spotted and FID trial initiated) and measured the distance at which the focal animal moved away in a stereotypical escape response to the researcher (flight initiation distance) using a transect tape. We also noted whether the pigeon fled terrestrially (i.e. walked away) or aerially (i.e. flew away) from the researcher. We conducted all FID trials between May 2017 and August 2017 in New York City.

Ethical Note

Animal safety for this protocol was approved by the Institutional Animal Care and Use Committee of Fordham University (IACUC no. EC-17-01). All research adhered to the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching (ASAB/ABS, 2020).

Landscape Metrics

Using QGIS (QGIS Development Team, 2019), we placed a 590 m circular buffer around each sample point. We selected a buffer of 590 m because previous research in Basel, Switzerland found this to be the mean daily distance travelled by an urban pigeon from their home roost (Rose et al., 2006). Although mean daily distance travelled likely varies across cities, Rose et al.'s (2006) finding was the only information available at the time of our study for urban pigeons. From these buffer zones, we extracted data representing landscape features, human presence and predator communities in the urban environment, including impervious surface, landcover, canopy cover, road length, human population size, pedestrian traffic and predator prevalence. All layers were set to a common datum (NAD 83) and projected to UTM zone 18N.

We collected impervious surface (e.g. roads, rooftops, and parking lots), landcover and canopy cover using the 2011 National Land Cover Database (NLCD; Homer et al., 2015; Yang, Huang, Homer, Wylie, & Coan, 2003). The NLCD categorizes land use into many different and specific variables, which we combined to create broader and more inclusive descriptions of landcover: developed low-intensity (NLCD 22), developed medium-intensity (NLCD 23), developed high-intensity (NLCD 24), open space (developed open space, barren land – NLCD 21, 31), water (open water, woody wetlands, emergent herbaceous wetlands – NLCD 11, 90, 95), forest (deciduous forest, evergreen forest, mixed forest – NLCD 41, 42, 43) and herbaceous (shrub/scrub, grassland/herbaceous – NLCD 51, 71). Next, we extracted total length of roads using the NYS Streets database (NYS GIS Program Office, 2019). After importing our file and clipping the roads to our buffer, we then calculated the total length of roads within each buffer in QGIS (QGIS Development Team, 2019). Although ground vegetation could potentially impact detectability and flight initiation distance (Burger & Gochfeld, 1981), we do not think this was a significant issue due to New York City's intense urbanization and general lack of vegetation in areas with pigeons (i.e. we encountered pigeons in open, predominantly paved environments lacking ground vegetation.)

We next extracted the total human population size and pedestrian traffic within the 590 m radius around each observation. We included pedestrian density in addition to human population density because some areas have low household density (i.e. population density) but high tourism, employment or commercial density (e.g. Central Park, Wall Street, Times Square). We obtained human population data from United States Census blocks, the smallest geographical unit in which population data are reported (https://www.census.gov/geographies/reference-maps/2010/geo/2010-census-block-maps.html). Because Census blocks vary in size, we calculated the number of people/km^2 in each Census block. We then intersected our buffer layer with our population data layer and calculated the human population within each buffer based on the percentage of each Census block within the buffer. We obtained human pedestrian traffic data from the New York City Business Atlas (Young, Sangokoya, & Verhulst, 2018), which ranks pedestrian data from low (1) to high (6) across Census-designated neighbourhood tabulation areas (NTAs; Young et al., 2018). We intersected the 590 m buffer around each sample point with the pedestrian data shapefile and calculated the average pedestrian traffic in each buffer based on the proportion of the NTA in the buffer.

Lastly, we calculated the number of observations within each 590 m buffer for three common predators – Cooper's hawk, *Accipiter cooperii*, red-tailed hawk, *Buteo jamaicensis*, and peregrine falcon, *Falco peregrinus* – using data from eBird in 2017 (eBird Basic Dataset, 2019). All three predators are year-round inhabitants in our study range, so we included observations from all months during 2017. This also gave us a better understanding of where the three predators were most abundant. We chose to examine these three predators because they are the only three diurnal avian predators known to nest in New York City (Fowle & Kerlinger, 2001) and eat pigeons (Dunn & Tessaglia, 1994; López-López, Verdejo, & Barba, 2009; Roth & Lima, 2003).

Although other predators (e.g. house cats, *Felis silvestris*, coyotes) may influence FID, we were unable to obtain reliable observation records for these taxa. Based on diet studies of raptors, feral pigeons constitute a large portion of urban raptor diets (Cade, Martell, Redig, Septon, & Tordoff, 1996; Johnston & Janiga, 1995) whereas New York City coyotes and feral cats most frequently prey on anthropogenic food waste (e.g. chicken) and house mice, *Mus musculus*, respectively (Henger, 2020; L. Plimpton, personal communication). Even so, diet may not accurately capture the impact of these species on feral pigeons. Urban predators such as feral cats are known to have significant impacts on other bird species and small mammals (Loss, Will, & Marra, 2013) but may be less effective and have nonlethal negative consequences on urban wildlife (e.g. Tyler, Winchell, & Revell, 2016), which may also contribute to behavioural modifications.

Statistical Analysis

We first examined potential covariates of FID: starting distance, date (as a sequential integer by day, from 1 to 89, starting 17 May and ending 9 August), time of day (as a fractional 24 h number, during 1000–2000 hours) and flock size. Although we first observed focal pigeons at distances up to 55 m, we set a maximum starting distance at 20 m, which was the maximum distance our meter could reliably measure. We fitted a single linear model of FID by all four possible covariates and found starting distance and date to be positively correlated and time of day to be negatively correlated with FID (starting distance: $\beta = 0.131$, $t_{503} = 6.845$, $P < 0.001$; sequential date: $\beta = 0.007$, $t_{503} = 2.042$, $P = 0.042$; fractional time: $\beta = -0.089$, $t_{503} = -2.043$, $P = 0.042$). Consequently, we included all three variables as covariates in all downstream analyses of FID. Flock size was not significantly related to FID ($t_{503} = 1.199$, $P = 0.231$). We tested for multicollinearity among these covariates

using the function 'vif' executed in the 'car' package in R. All four covariates had a variance inflation factor ranging from 1.03 to 1.11.

Spatial analyses

FID measurements such as ours may vary across the landscape for reasons other than variation in habitat features associated with urbanization. Because of socioeconomic variation and the ways in which residents of different boroughs interact with the environment, there may be differences that are not captured by landscape variables. To address this, we first asked whether FID differed across the New York City (NYC) metropolitan area by borough using a one-way ANCOVA of FID by borough with our covariates starting distance, date and time. We evaluated significance of borough with type II ANOVA implemented with the function 'Anova' in the 'car' package. We next asked whether our FID measures were spatially correlated with a Mantel test on the spline correlogram of our spatial data (using functions 'spline.correlog' and 'mantel.test' in the R package 'ncf'; Bjornstad, 2020). Unlike the Mantel correlogram, which bins distance into distance classes, the spline correlogram estimates spatial dependence as a continuous function (Bjørnstad & Falck, 2001). Since some observations were taken nearby, and the GPS application we used rounded location estimates, a small number of our FID measurements ($N = 39$) had identical GPS points; therefore, we adjusted the latitude of these points by 0.00001 decimal degrees (~1 m) so that each FID observation was identified by a unique location. Lastly, we evaluated alternative models for each of the linear models described above, accounting for spatial correlation with five different correlation structures: exponential, Gaussian, linear, spherical and ratio. We compared Akaike information criterion values corrected for small samples (AICc) of these models against those for the model without spatial correlation to determine whether spatial structure should be incorporated into our linear models using the function 'model.sel' in the R package 'MuMIn' (Barton, 2019).

Landscape analysis

To capture the multivariate nature of urban habitat space, we considered all 10 of our landscape variables (impervious surface, canopy cover, developed low-intensity landcover, developed medium-intensity landcover, developed high-intensity landcover, open space landcover, forest landcover, herbaceous landcover, water and road length) to describe the indirect effects of human presence via landscape modification. Although human presence certainly helps define urban habitat space, we chose not to include pedestrian traffic or human population density in this PCA because we wanted to be able to distinguish between direct effects of human presence (i.e. interaction with humans) and indirect effects (i.e. landscape modification) in our downstream analyses. We used principal components analysis to reduce dimensionality of these data for use in our downstream analyses using the function 'prcomp' in the base 'stats' package in R v.1.1.456 (R Core Team, 2018). We retained all principal components with eigenvalues >1 for our subsequent linear model. We then investigated whether the significant principal components varied by borough using MANOVA and incorporated significant principal components into our subsequent linear models.

Linear models

We used linear models to investigate (1) relationships between landscape features and FID – "landscape model", (2) the influence of the predator community and flock size on FID – "predator model", (3) behaviour and escape strategy in relation to FID – "behaviour model" and (4) escape strategy in relation to predator abundance and presence – "escape model". Details regarding model terms and structure are elaborated below. We included our three covariates (starting distance, date, time) in the first three models and performed all statistical analyses in R (R Core Team, 2018) as described below. Specific code can be found on Zenodo, https://doi.org/10.5281/zenodo.3936120.

First, we fitted a linear model of FID by the first four PCs from our principal component analysis of landscape as well as population size, pedestrian traffic and our three covariates (landscape model). For our predator model, we tested for correlations between predator presence and predator abundance using Pearson's correlation test in R. We then fitted a linear model of FID by predator presence and predator abundance for our three common aerial predators: Cooper's hawks, red-tailed hawks and peregrine falcons. We included both presence within the buffer (recorded as present/absent) and total number of sightings to examine the difference between areas where predators may occasionally be detected versus areas where predators occur more frequently. We also included pigeon flock size in the predator model since pigeons in a flock may be better able to spot predators compared to solo pigeons (Johnston & Janiga, 1995; Kenward, 1978) as well as our three covariates. We performed model selection by Akaike's information criterion (AIC) using the 'MuMIn' package for both the landscape and predator models. Specifically, we used the function 'dredge' to create a table of models with all combinations of fixed effects and then the model-averaging function to average these models. To confirm our models, we also used the 'step' function in the R base 'stats' (R Core Team, 2018) with backwards selection.

We next investigated how behaviour prior to approach and flight response varied with two models. For our behaviour model, we fitted a linear model of FID by response (terrestrial or aerial fleeing), distance moved when fleeing and behaviour just prior to approach (feeding, moving, stationary) and our three covariates. We evaluated significance of categorical variables with type II ANOVA, implemented with the function 'Anova' in the 'car' package in R (R Core Team, 2018). We also fitted a logistic generalized linear model of flight response (aerial or terrestrial fleeing) by flock size and both presence and number of sightings for each of the three predators (escape model). We performed stepwise backwards model selection on our escape model using the function 'step' in R base 'stats' package (R Core Team, 2018).

RESULTS

We made a total of 519 FID observations from 17 May 2017 to 13 August 2017. Flight initiation distance across all locations ranged from 0.1 m to 15 m (mean = 3.5 ± 2.4 m). We detected spatial variation in FID across the metropolitan landscape that was correlated with specific ecological and abiotic landscape features.

Spatial Variation in FID Across the Metropolitan Landscape

We found that flight initiation distance varied across the NYC landscape (Fig. 1) and differed by borough (type II ANOVA; $F_{4,500} = 20.284$, $P < 0.001$). Pigeons in Brooklyn and Manhattan had the lowest FID, pigeons in Staten Island had the highest FID, and pigeons in the Bronx and Queens had intermediate FIDs (Appendix, Fig. A1). The spline correlogram across the study range indicated a very weak but statistically significant localized autocorrelation of FIDs at distances < 10.4 m (Mantel test: $r = -0.034$, $P < 0.001$). Although we do not suspect this weak correlation had a substantial impact on our results, we nevertheless tested alternative models incorporating spatial structure into all our models examining FID. In all models, the best supported model was the one that did not incorporate spatial correlation (Appendix, Table A1).

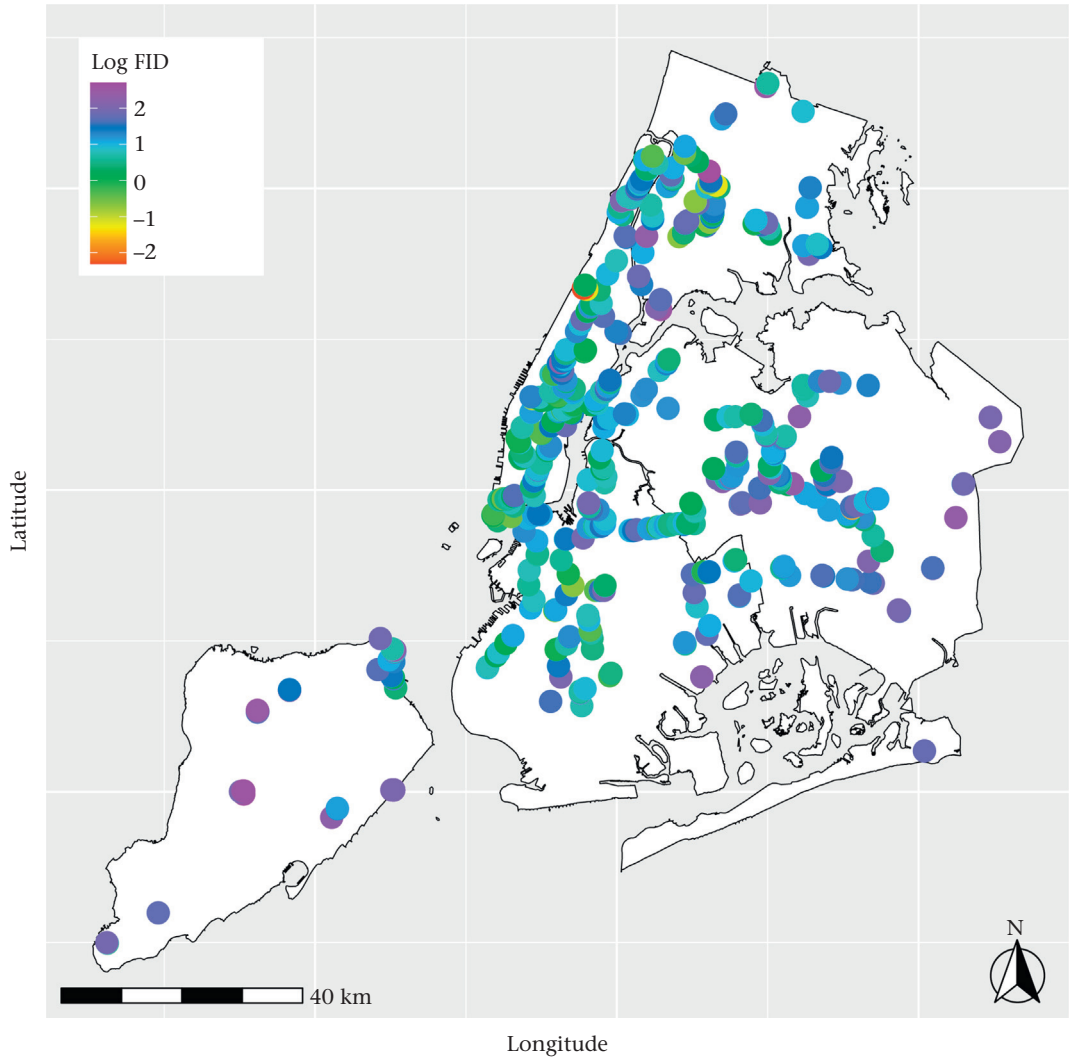

Figure 1. Map of New York City showing locations of flight initiation distance (FID) observations. The colour of each observation is correlated with the ln-transformed FID. Purple observations have longer FIDs, blue and green observations have intermediate FIDs, while red observations have shorter FIDs.

FID and Landscape Features

Our principal component analysis captured 74.1% of the variation in landcover across our study range in the first four components (Fig. 2, Appendix, Figs A2–A4). Higher values of PC1 indicate less low-intensity development and open space and more high-intensity development. Higher values of PC2 indicate less impervious surface and fewer roads and more tree canopy. Higher values of PC3 indicate less forest and open space and more medium-intensity development. Higher values of PC4 indicate less forest and more herbaceous landcover and water. All four principal components differed across our study range by borough (MANOVA; Appendix, Table A2).

Our best-supported landscape model included the following variables: PC2, PC3, PC4, pedestrian traffic and population size (Table 1; see Appendix, Tables A3–A5 for alternative single linear models). Pigeons had shorter FIDs in areas with lower values of PC2, which represents more impervious surface cover and roads and lower tree canopy cover ($\beta = 0.228 \pm 0.076$, $z = 3.005$, $P = 0.003$). Pigeons also had shorter FIDs in areas with more pedestrians ($\beta = -0.325 \pm 0.088$, $z = 3.665$, $P < 0.001$) and more dense human populations ($\beta = -3.244 \times 10^{-5} \pm 1.095 \times 10^{-5}$, $z = 2.956$, $P = 0.003$) (Fig. 3). Pigeon FID was not significantly correlated with any other landscape feature, although PC3 and PC4 were retained in the best-fit model.

FID and Predator Community

We found a weak correlation between presence and number of sightings for Cooper's hawks ($r = 0.290$), red-tailed hawks ($r = 0.363$) and peregrine falcons ($r = 0.413$). Our best-supported predator model included red-tailed hawk sightings and peregrine falcon sightings (Table 1, Fig. 4). Number of sightings, and not simply presence of predators, was correlated with FID. Pigeons had shorter FIDs in areas with fewer sightings of red-tailed hawks ($\beta = 0.063 \pm 0.017$, $z = 3.598$, $P < 0.001$) and more sightings of peregrine falcons ($\beta = -0.100 \pm 0.028$, $z = 3.619$, $P < 0.001$) (Appendix, Fig. A5). Variation in FID was not correlated with number of sightings of Cooper's hawks ($\beta = 5.45 \times 10^{-5} \pm 0.005$, $z = 0.011$, $P = 0.991$).

Behaviour before and after Approach

Pigeon FID was associated with stationary behaviour (i.e. not moving) when approached but not with the other two observed prior behaviour types (moving or feeding) or with response

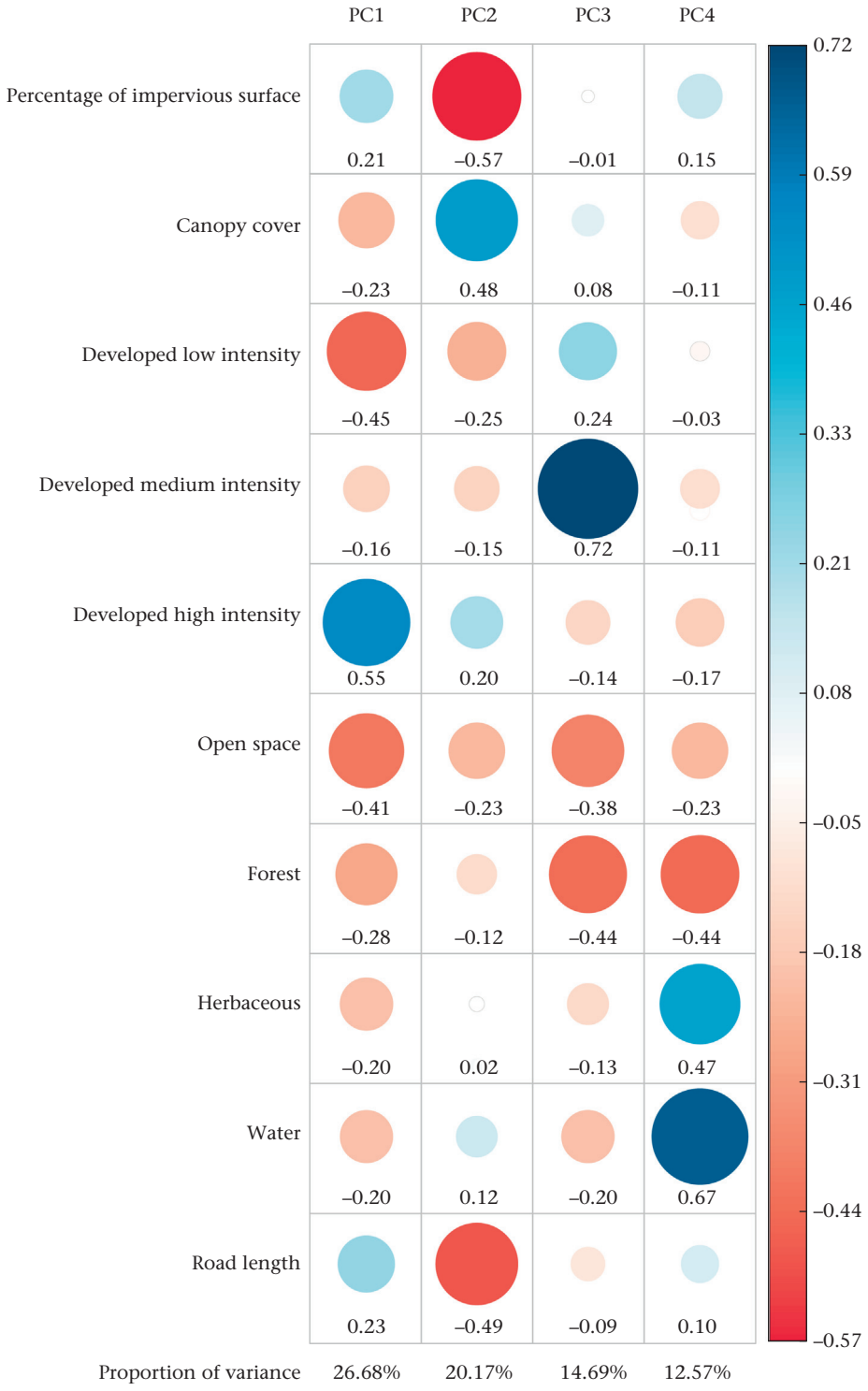

Figure 2. PC loadings for the first four principal components of landscape variables, which represented 74.11% of the variation in landcover across our study range. Blue represents positive correlations while red represents negative correlations. The size of each circle is proportional to the correlation coefficient.

(aerial or terrestrially fleeing) (stationary: $N = 54$; moving: $N = 251$; feeding: $N = 200$; type II ANOVA: behaviour: $F_{2,496} = 3.709$, $P = 0.025$). Birds that were moving prior to approach had shorter FIDs compared to those that were stationary. Escape mode (aerial or terrestrially fleeing) was not correlated with flock size or predator abundance, but only with presence of Cooper's hawks (Table 2). Pigeons were more likely to flee terrestrially than aerially at locations where Cooper's hawks had been observed (presence) ($\beta = 0.536 \pm 0.263$, $z_{504} = 2.035$, $P = 0.042$) and slightly more likely to flee terrestrially (versus aerially) when Cooper's hawks were present (i.e. pigeons fled terrestrially 83.44% of the time when Cooper's hawks were present and only 76.23% of the time when Cooper's hawks were not present).

Table 1
Models for pigeon flight initiation distance (FID) in New York City for our landscape model and our predator model

Model	Full average			
	β	SE	*z*	*P*
Landscape				
Starting distance	0.108	0.018	6.050	**<0.001**
Date	0.001	0.002	0.260	0.795
time	−0.075	0.050	1.511	0.131
PC1	0.004	0.031	0.141	0.887
PC2	0.228	0.076	3.005	**0.003**
PC3	0.055	0.079	0.700	0.484
PC4	0.119	0.105	1.136	0.256
Pedestrian traffic	−0.325	0.088	3.665	**<0.001**
Population size	0.000	0.000	2.956	**0.003**
Predator				
Starting distance	0.117	0.019	6.084	**<0.001**
Date	0.006	0.004	1.411	0.158
Time	−0.078	0.054	1.436	0.151
Flock size	0.006	0.010	0.616	0.538
Cooper's hawk presence	−0.043	0.149	0.290	0.771
Red-tailed hawk presence	−0.009	0.155	0.057	0.955
Peregrine falcon presence	0.029	0.157	0.187	0.851
Cooper's hawk sightings 2017	0.000	0.005	0.011	0.991
Red-tailed hawk sightings 2017	0.063	0.017	3.598	**<0.001**
Peregrine falcon sightings 2017	−0.100	0.028	3.619	**<0.001**

We used the R package 'MuMIn' to automate model selection. The full average of these models is shown. Estimate (β) and standard error (SE) for each term are provided. Values in bold represent significant terms ($P < 0.05$). All terms are rounded to the nearest hundredth.

DISCUSSION

In this study, we examined escape responses of 519 pigeons across New York City in relation to landscape features, human activity and predator community. We specifically examined FID in relation to common urban features (e.g. impervious surface, pedestrian density) and urban predators to shed light on the complex nature of the eco-evolutionary interactions that take place within a city and found that pigeons had shorter FIDs in areas with increased urban landcover (i.e. longer roads and higher impervious surface) and human activity (i.e. pedestrian traffic and human population size). We also found that pigeon FID was associated with predator sightings. Specifically, pigeon FID was longer in areas with more red-tailed hawk sightings but shorter in areas with more peregrine falcon sightings.

Quantifying urbanization and identifying drivers of phenotypic variation remains an outstanding problem in the young field of urban evolutionary ecology. Biotic and abiotic effects of urbanization are inherently multidimensional, yet many urban ecology and evolution studies rely on only a single metric to describe urban habitats. For example, previous FID studies have used one of the following variables to categorize urbanization: road speed (Legagneux & Ducatez, 2013), distance to closest anthropogenic food source (Ducatez, Audet, Rodriguez, Kayello, & Lefebvre, 2016), pedestrian density (Mikula, 2014), human exposure (Engelhardt & Weladji, 2011) and proportion of built-up space (Lin et al., 2012). These studies have clearly demonstrated that FID in a variety of taxa

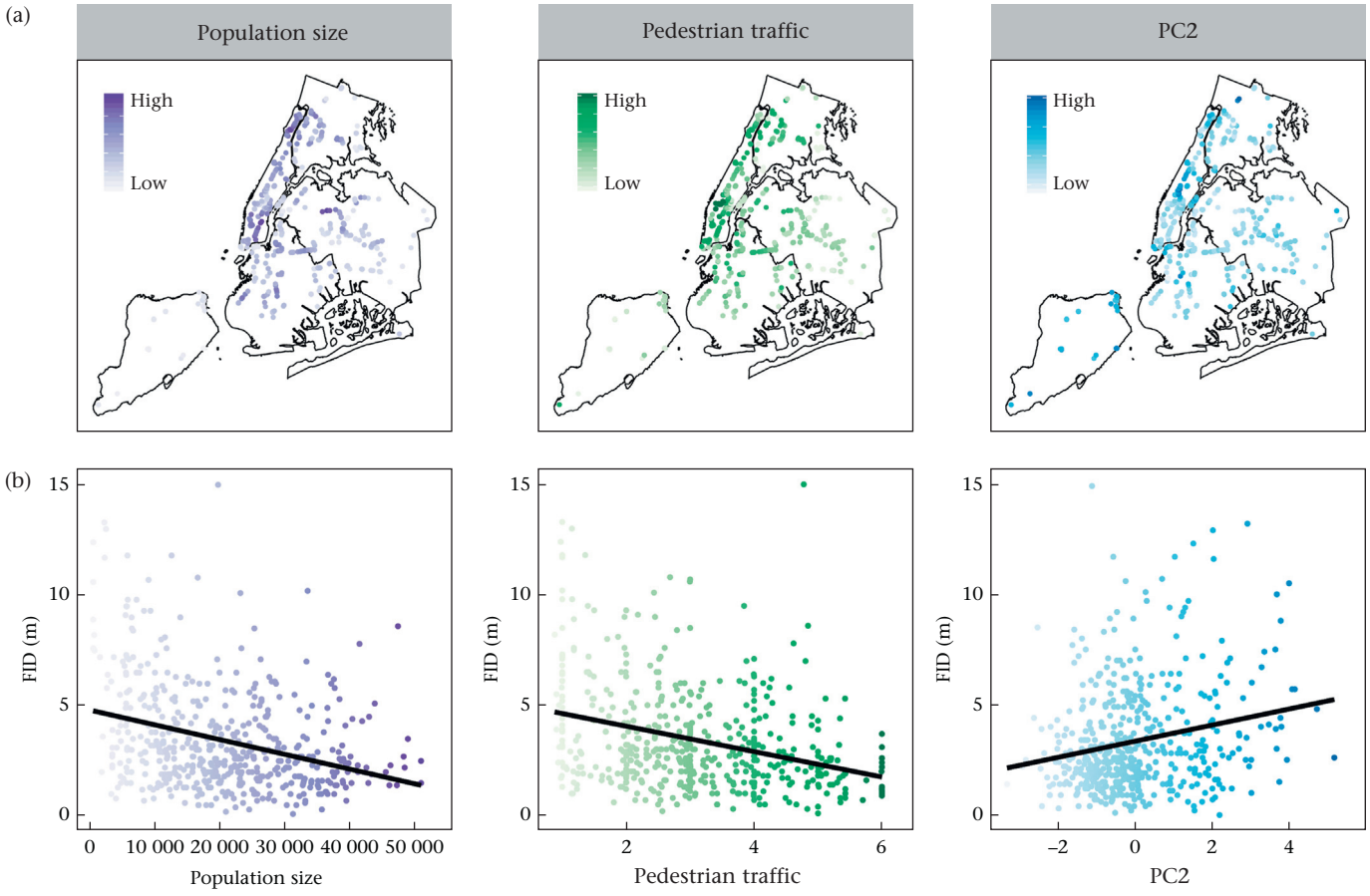

Figure 3. Flight initiation distances (FIDs) across New York City in relation to significantly correlated landscape variables. Each point is coloured by the variable value, where PC2 represents less impervious surface, fewer roads and more tree canopy. Within each plot, darker colours represent higher values and lighter colours represent lower values. (a) Maps showing the location for each FID observation. (b) Scatter plots showing FID as a function of each variable with trend lines shown in black.

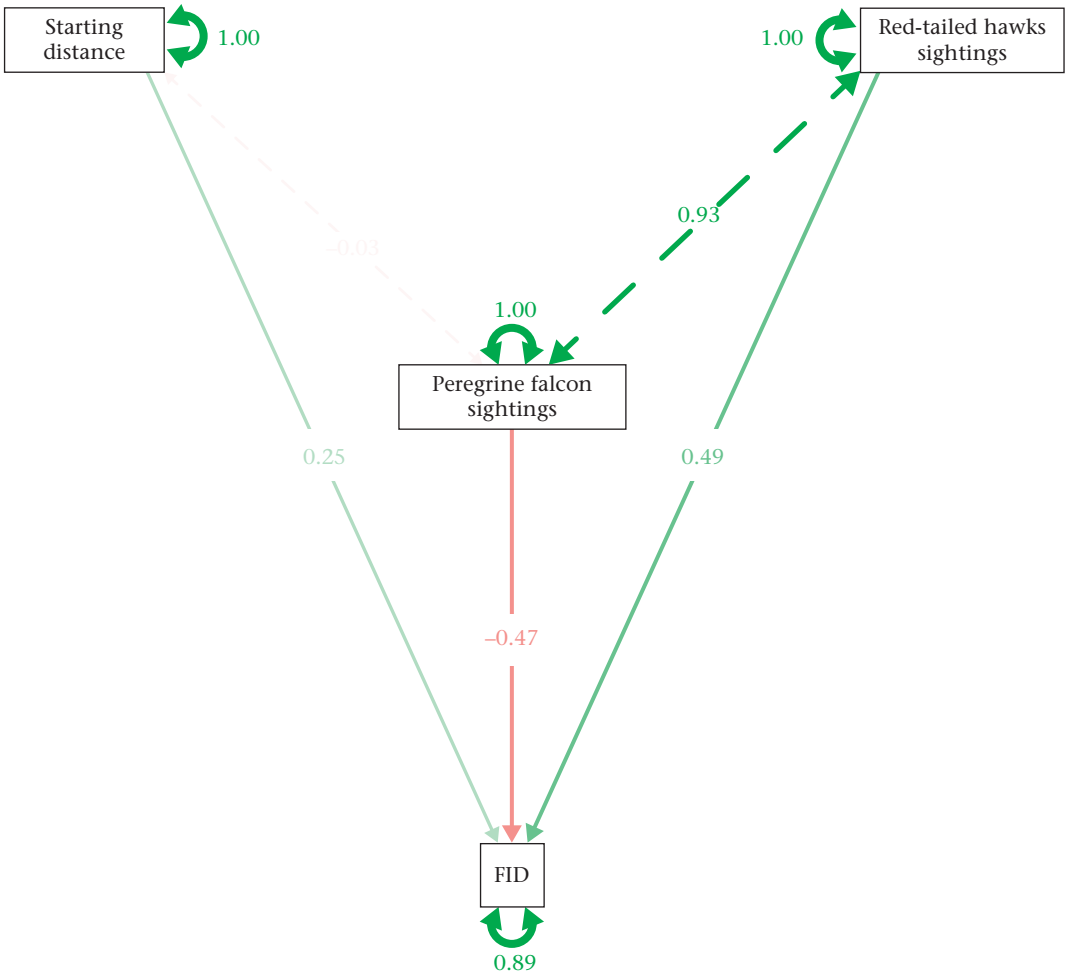

Figure 4. Path analysis showing the interactions between each significant variable in our predator model. Positive correlations are shown in green, and negative correlations are shown in red. Arrows and line weights show the direction and strength of each correlation. The dashed line represents an unanalysed correlation. See Appendix, Fig. A6 for a path analysis of the full predator model plus pedestrian traffic and population size.

tends to decrease with increasing urbanization. Yet, in using a single metric to describe urbanization, these studies may also be missing or misidentifying key habitat features associated with this behavioural change (Szulkin, Garroway, Corsini, Kotarba, & Dominoni, 2020). In our study, we attempted to capture the multidimensionality of urbanization by considering human activity and an array of landscape features in our assessment of behavioural responses in urban habitats. Consistent with our prediction and with other studies, we found that pigeons have shorter FIDs (allow closer approach) in more urbanized areas, characterized by greater human population size, pedestrian traffic, with less impervious surface, roads and tree canopy.

Shorter FIDs in more urban areas are likely linked to increased fitness, since allowing closer approach by humans can provide benefits (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). For example, having a shorter flight distance prevents a pigeon from expending energy to move away unnecessarily and may provide access to new resources (e.g. if food is dropped by a human). We found that pigeons had short FIDs in areas with greater human presence (i.e. human population density and pedestrian density), suggesting that pigeons in these areas may have a plastic response (are habituated to humans) or may have a heritable response linked to higher fitness in areas with more people. However, further study would be needed to directly test whether pigeons

Table 2
Full and reduced models for response model

Response model	Full model (AIC: 836.45)				Reduced model (AIC: 828.48)			
	β	SE	*z*	*P*	β	SE	*t*	*P*
Flock size	0.001	0.011	0.053	0.958				
Cooper's hawk presence	0.627	0.300	2.090	**0.037**	0.536	0.263	2.035	**0.042**
Red-tailed hawk presence	−0.290	0.342	−0.848	0.397				
Peregrine falcon presence	0.112	0.312	0.360	0.719				
Cooper's hawk sightings 2017	−0.016	0.010	−1.609	0.108	−0.018	0.010	−1.903	0.057
Red-tailed hawk sightings 2017	0.043	0.025	1.717	0.086	0.036	0.020	1.783	0.075
Peregrine falcon sightings 2017	−0.017	0.035	−0.473	0.636				

Estimate (β) and standard error (SE) for each term are provided. Values in bold represent significant terms ($P < 0.05$).

with short FIDs have higher fitness in more urban areas. Urbanization is correlated with increased tolerance of humans in several bird species, and species exposed to urbanization for longer periods tend to be more tolerant of humans (Symonds et al., 2016). An increased tolerance of humans over time suggests that selection may act on urban bird populations such that individuals that are more tolerant of humans have a fitness advantage (Carrete & Tella, 2017). Alternatively, pigeons that occupy more urban niche space may do so specifically because of their ability to tolerate humans and urbanization, whereas intolerant individuals may select less urban areas (Holtmann, Santos, Lara, & Nakagawa, 2017; van Dongen, Robinson, Weston, Mulder, & Guay, 2015). Moreover, pigeons may not only be more tolerant of human presence but also learn to interpret and predict human behaviour in ways that influence their flight behaviour (Bateman & Fleming, 2014).

Urbanization can be a reflection of human population density and pedestrian traffic, but urbanization is also reflected in the ways in which people transform the environment. Areas in New York City with more roads are also likely to have more pedestrians since only 45.5% of New York City households own cars compared to a national average of 91.3% (United States Census Bureau, 2017). We found that pigeons in areas with more roads had lower FIDs. This result may reflect the complex nature of vehicular and pedestrian traffic in New York City wherein areas with vehicular traffic (and thus many roads) also have high pedestrian traffic. Lower pigeon FIDs in these areas may confer increased fitness, an intriguing possibility. Another consequence of road development in urban areas is that it also directly decreases natural habitat and increases habitat fragmentation. Greater amounts of natural habitat and greater habitat connectivity are associated with longer FIDs (Engel, Carlen, Losos, & Winchell, 2020; Grolle, Lopez, & Gerson, 2014). We found that pigeons had longer FIDs in areas with greater tree canopy cover. This may be a reflection of selection pressures from red-tailed hawks that nest in or within the immediate vicinity of city parks (Grubel, 2008).

In addition to considering abiotic and human aspects of urban habitats, we also considered how the urban-associated predator community might influence escape behaviour. Consistent with our prediction, we found that pigeons had longer FIDs (fled more readily) in areas with more red-tailed hawk sightings. Contrary to our prediction, pigeons had shorter FIDs (fled less readily) in areas with peregrine falcons. The observed relationship between FID and raptorial predator type could be the result of complex interactions that lead to red-tailed hawks, Cooper's hawks and peregrine falcons exhibiting different tolerances to urbanization and human presence. On average, predators tend to be larger than their prey and larger organisms tend to have longer FIDs (i.e. flee from a further distance) (Blumstein, 2006). Yet, this effect likely varies by predator and depends on the predator's tolerance of urbanization and human presence. For example, some hawk species are generally tolerant of human activities (e.g. Harris's hawks, *Parabuteo unicinctus*, red-tailed hawks) whereas white-tailed hawks, *Geranoaetus albicaudatus*, despite being found in and around cities, will flee their nests if there is human activity within 500 m (Boal & Dykstra, 2018; Stevenson & Meitzen, 1946).

Despite detecting differences in pigeon FID in areas with more red-tailed hawks and more peregrine falcons, we found no difference in the nature of escape response by pigeons (aerially or terrestrially fleeing) in areas with these two predators. Escape behaviour, instead, seemed to be related only to the presence of Cooper's hawks, which are aerial predators (Roth & Lima, 2003). When Cooper's hawks were present, pigeons did not alter their FID response but were more likely to flee terrestrially. Our results suggest that FID and behavioural responses to humans differ depending on the type of raptorial predators that coexist in the habitat with people and pigeons. Although pigeons may be used to aerial predators, and we acknowledge that our terrestrial predator simulation differs from this relationship, the perception of humans as a terrestrial threat (or not) provides insight into the complex nature of human–wildlife interactions in cities. Notably, our analysis did not take into account interactions between predators and only begins to shed light on the complex relationship between prey flight behaviour and predator presence and abundance in cities. Nevertheless, our results imply that similar to other birds, pigeons may modify their escape behaviour depending on the urban predator community and allow humans to approach more closely in areas with predators that are fearful of humans (Møller & Díaz, 2018).

Our results provide insight into pigeon–predator behaviour in three ways: (1) peregrine falcons may respond to urbanization differently than red-tailed hawks, (2) different hunting strategies may lead to different prey responses, or (3) pigeons may use people as protection from peregrine falcons but not red-tailed hawks. Other raptorial predators respond to urbanization differently, with some tolerating urbanization whereas other take advantage of urbanization. For example, Skagen, Knight, and Orians (1991) found that bald eagles, *Haliaeetus leucocephalus*, rarely fed at sites near human disturbance compared to undisturbed sites, whereas glaucous-winged gulls, *Larus glaucescens*, increased their feeding at disturbed sites. In New York City, peregrine falcons may tolerate urbanization whereas red-tailed hawks may take advantage of the increased pigeon population (Dykstra, 2018; Rutz, 2008). Hunting strategies also differ among raptorial predators, including those included in this study. Peregrine falcons tend to hunt in the air, grabbing their prey while in flight, whereas red-tailed hawks are more likely to be ground hunters, flying down and grabbing their prey on the ground (Dykstra, 2018). Adams, Camelio, Orique, and Blumstein (2006) found that some prey can distinguish between different predators; therefore, pigeons may be aware of areas with greater abundance of peregrine falcons or red-tailed hawks and respond to predatory stimuli differently in these areas based on the most likely threat. This, in turn, may also be linked to pigeons using people as protection from predators. Red-tailed hawks generally tolerate humans more than do peregrine falcons (Boal & Dykstra, 2018; Bosakowski & Smith, 1997), meaning peregrine falcons may be less willing to hunt pigeons in areas with more humans.

Overall, our results suggest that FID is variable even within a single metropolitan area and that, in areas with increased urbanization, measured both in terms of landscape features and human population, pigeons allowed closer approach. However, more research is needed to understand the factors driving the behavioural responses of pigeons to predators, and detailed analysis is needed to understand whether pigeons tolerate humans to avoid certain predators. Additionally, the heterogeneity of urbanization across the landscape may contribute to the variable behavioural responses of pigeons living within cities. Future urban FID studies should be careful with how they define urbanization, especially given that a single variable does not always reflect the complex nature of urban landscapes. Moreover, FID studies, especially urban FID studies, should consider how predators, which interact with the urban environment in different ways, may influence their findings.

Data Availability

Sampling data, as well as the R code that was used to analyse the data, are available on Zenodo, https://doi.org/10.5281/zenodo.3936120.

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Appendix

Table A1
We tested for spatial autocorrelation in each of our four models using Mantel tests

	No spatial correlation	Gaussian	Ratio	Linear	Spherical	Exponential
Borough						
Intercept	2.861	2.960	2.962	2.958	2.958	2.958
Date	0.008	0.007	0.007	0.007	0.007	0.007
Time	−0.091	−0.085	−0.086	−0.086	−0.086	−0.086
Starting distance	0.111	0.100	0.100	0.100	0.100	0.100
Borough	+	+	+	+	+	+
df	9	10	10	10	10	10
Loglik	−1100.134	−1103.326	−1103.342	−1103.401	−1103.412	−1103.441
AICc	**2218.600**	2227.100	2227.100	2227.200	2227.300	2227.300
Delta	0	8.46	8.5	8.61	8.64	8.69
Weight	0.936	0.014	0.013	0.013	0.012	0.012
Landscape						
Intercept	4.974	4.913	4.920	4.919	4.920	4.924
Date	0.002	0.002	0.002	0.002	0.002	0.002
Time	−0.093	−0.086	−0.085	−0.085	−0.085	−0.085
Starting distance	0.110	0.099	0.099	0.099	0.099	0.099
PC1	0.018	−0.004	−0.007	−0.006	−0.007	−0.008
PC2	0.227	0.202	0.201	0.201	0.201	0.201
PC3	0.113	0.092	0.094	0.094	0.095	0.095
PC4	0.158	0.149	0.146	0.147	0.146	0.145
Pedestrian traffic	−0.329	−0.306	−0.307	−0.308	−0.308	−0.309
Population size	0.000	0.000	0.000	0.000	0.000	0.000
df		12	12	12	12	12
Loglik	−1099.519	−1119.523	−1119.513	−1119.552	−1119.559	−1119.575
AICc	**2221.600**	2263.700	2263.700	2263.700	2263.700	2263.800
Delta	0.00	42.11	42.09	42.16	42.18	42.21
Weight	1	0	0	0	0	0
Predator						
Intercept	3.174	3.238	3.232	3.225	3.224	3.224
Date	0.008	0.008	0.008	0.008	0.008	0.008
Time	−0.102	−0.092	−0.093	−0.093	−0.094	−0.094
Starting distance	0.118	0.102	0.103	0.103	0.103	0.103
Peregrine falcons	−0.102	−0.103	−0.103	−0.102	−0.102	−0.102
Red-tailed hawks	0.064	0.065	0.065	0.064	0.064	0.064
df	7	8	8	8	8	8
Loglik	−1129.062	−1131.105	−1131.098	−1131.223	−1131.234	−1131.268
AICc	**2272.3**	2278.500	2278.500	2278.700	2278.800	2278.800
Delta	0.00	6.10	6.10	6.30	6.40	6.40
Weight	0.824	0.038	0.038	0.034	0.033	0.032
Behaviour						

(*continued on next page*)

Table A1 (*continued*)

	No spatial correlation	Gaussian	Ratio	Linear	Spherical	Exponential
Intercept	2.837	3.225	3.209	3.197	3.193	2.837
Date	0.008	0.007	0.007	0.007	0.007	0.008
Time	−0.098	−0.090	−0.091	−0.091	−0.091	−0.098
Starting distance	0.126	0.112	0.113	0.113	0.113	0.126
Behaviour	+	+	+	+	+	+
Response	+	+	+	+	+	+
Distance moved	0.010	−0.006	−0.006	−0.006	−0.006	0.010
df	9	10	10	10	10	9
Loglik	−1123.959	−1125.875	−1125.827	−1125.918	−1125.944	−1139.783
AICc	**2266.300**	2272.200	2272.100	2272.300	2272.300	2297.900
Delta	0.000	5.910	5.820	6.000	6.050	31.650
Weight	0.83	0.04	0.05	0.04	0.04	0.00

We found weak support for spatial autocorrelation in FID at distances < 10.4 m (Mantel test: $r = 0.034$, $P < 0.001$). We therefore evaluated each model with different spatial autocorrelation structures and compared models with AIC. Models with the highest weight (lowest AICc) are shown in bold and in each, the model not accounting for spatial autocorrelation was the best supported. The '+' indicates that the variable was included in the model, however the values are not reported because the variable is categorical and not continuous.

Table A2
MANOVA of the four principal components (PCs) by borough

Principal component	*df*	Sum of squares	Mean square	*F* value	*P* value
PC1	4	97.27	24.32	9.74	<0.001
PC2	4	252.81	63.20	41.29	<0.001
PC3	4	18.54	4.64	3.21	<0.05
PC4	4	45.41	11.35	9.65	<0.001

Degrees of freedom (*df*) are shown along with relevant statistics (sum of squares, mean squares, *F* values and *P* values).

Table A3
Linear mixed-effects models as alternative analyses to all linear models presented in the main text

Variable	Linear model			Linear mixed-effects model		
	Estimate ± SE	*F*	*P*	Estimate ± SE	*F*	*P*
Covariate model						
Starting distance	0.131 ± 0.019	46.86	**<0.001**	0.114 ± 0.018	39.5288	**<0.001**
Date	0.007 ± 0.004	4.17	**0.042**	0.008 ± 0.003	4.7215	**0.030**
Time	−0.089 ± 0.043	4.17	**0.042**	−0.089 ± 0.042	4.495	**0.034**
Flock size	0.013 ± 0.011	1.44	0.2309	0.006 ± 0.010	0.395	0.53
Landscape model						
Starting distance	0.110 ± 0.018	37.64	**<0.001**	0.107 ± 0.018	36.91	**<0.001**
Date	0.002 ± 0.003	0.25	0.615	0.004 ± 0.004	1.18	0.274
time	−0.094 ± 0.040	5.41	**0.020**	−0.091 ± 0.042	4.75	**0.029**
PC2	0.228 ± 0.071	10.25	**0.001**	0.226 ± 0.081	7.51	**0.006**
PC3	0.113 ± 0.079	2.04	0.154	0.137 ± 0.078	3.11	0.078
PC4	0.160 ± 0.087	3.37	0.067	0.067 ± 0.089	0.55	0.455
Pedestrian density	−0.328 ± 0.086	14.66	**<0.001**	−0.234 ± 0.09	6.69	**0.010**
Population size	0.00003 ± 0.00001	10.18	***0.002***	0.00002 ± 0.00001	2.58	*0.106*
Predator model						
Peregrine falcon presence	NA	–	–	0.686 ± 0.272	6.32	***0.012***
N red-tailed hawks	0.064 ± 0.015	18.98	**<0.001**	0.057 ± 0.016	12.49	**<0.001**
N peregrine falcon	−0.102 ± 0.024	18.37	**<0.001**	−0.086 ± 0.028	9.10	**0.003**
Starting distance	0.118 ± 0.019	39.20	**<0.001**	0.111 ± 0.018	38.83	**<0.001**
Date	0.008 ± 0.003	5.69	***0.018***	0.007 ± 0.003	3.73	*0.054*
Time	−0.102 ± 0.042	5.78	**0.017**	−0.1 ± 0.041	5.79	**0.016**
Behaviour model						
Flight response		0.14	0.713		0.05	0.831
Approach behaviour		2.43	**0.019**		2.36	**0.022**
Distance moved	0.013 ± 0.017	0.59	0.442	0.006 ± 0.016	0.14	0.711
Starting distance	0.124 ± 0.019	41.84	**<0.001**	0.111 ± 0.018	37.81	**<0.001**
Date	0.008 ± 0.004	4.72	**0.030**	0.007 ± 0.004	4.10	**0.044**
Time	−0.100 ± 0.043	5.44	**0.020**	−0.101 ± 0.042	5.88	**0.016**
Flight response model						
Cooper's hawk presence	0.536 ± 0.263	2.04	**0.042**	0.536 ± 0.263	2.04	**0.042**
N Cooper's hawk	−0.018 ± 0.01	−1.90	0.057	−0.018 ± 0.01	−1.90	0.057
N red-tailed hawk	0.036 ± 0.02	1.78	0.075	0.036 ± 0.02	1.78	0.075

All explanatory variables in the full models are the same as presented in the text for each model with the addition of borough included as a random effect. We present model estimates with standard error, the test statistic (*F* or *z*) and associated *P* value per term for both models reduced with backwards model selection (as described in the main text) here for comparison. All significant results at $P < 0.05$ are shown in bold, with results differing between the two models shown in italics. In all cases the models support the same conclusions and are nearly identical. Variables retained in one model but not the other are indicated with NA in the estimate column.

Table A4
We evaluated a single linear model with all explanatory variables with backwards model selection as an alternative analysis to the three models presented in the main text and in Table A3

Variable	Linear model			Linear mixed-effects model			Separate linear models		
	Estimate ± SE	*F*	*P*	Estimate ± SE	*F*	*P*	Estimate ± SE	*F*	*P*
Covariates									
Starting distance	0.102 ± 0.018	32.94	**<0.001**	0.102 ± 0.017	34.32	**<0.001**			
Date	0.004 ± 0.003	1.41	0.236	0.004 ± 0.003	1.04	0.309			
Time	−0.112 ± 0.04	7.91	**0.005**	−0.102 ± 0.041	6.07	**0.014**			
Landscape									
PC1	NA	–	–	NA	–	–	NA	–	–
PC2	0.312 ± 0.078	16.10	**<0.001**	0.262 ± 0.086	9.02	**0.003**	0.228 ± 0.071	10.25	**0.001**
PC3	NA	–	–	NA	–	–	0.113 ± 0.079	2.04	0.154
PC4	NA	–	–	NA	–	–	0.160 ± 0.087	3.37	0.067
Pedestrian density	−0.267 ± 0.085	9.85	**0.002**	−0.217 ± 0.088	5.95	**0.015**	−0.328 ± 0.086	14.66	**<0.001**
Human population	*0.000 ± 0.000*	*7.28*	***0.007***	*0.000 ± 0.000*	*2.47*	*0.117*	0.000 ± 0.000	10.175	**0.002**
Predator									
N Cooper's hawk	NA	–	–	NA	–	–	NA	–	–
N red-tailed hawk	0.051 ± 0.014	13.86	**<0.001**	0.045 ± 0.014	9.35	**0.002**	0.064 ± 0.015	18.98	**<0.001**
N peregrine falcon	−0.100 ± 0.023	18.77	**<0.001**	−0.082 ± 0.025	10.32	**0.001**	−0.102 ± 0.024	18.37	**<0.001**
Cooper's hawk presence	NA	–	–	NA	–	–	NA	–	–
Red-tailed hawk presence	NA	–	–	NA	–	–	NA	–	–
Peregrine falcon presence	NA	–	–	NA	–	–	NA	–	–
Behaviour									
Approach behaviour		*2.00*	*0.053*		*2.04*	***0.048***		2.43	**0.019**
Flight response	NA	–	–	NA	–	–		0.14	0.713
Flight distance	NA	–	–	NA	–	–	0.013 ± 0.017	0.59	0.442

Both a linear model and a linear mixed effects model with borough as a random effect are presented here (in their reduced form after model selection) with model estimates and standard error, the test statistic (*F* or *z*) and associated *P* value per term for both models. All significant results at $P < 0.05$ are shown in bold, with results differing between the linear mixed-effects (LME) and linear (LM) models shown in italics. The LM and LME models supported the same conclusions and were nearly identical. In the right column we summarize the separate linear models from the main text (and in Table A3). Starting distance, date and time were not included in the comparison because they were included as covariates in all three models. Variables that were not retained in the reduced model but were retained in the reduced separate linear models in the main text are indicated by NA in the estimate column.

Table A5
Full and reduced models for pigeon flight initiation distance (FID) for our landscape model and our predator model

Model	Full Model					Reduced Model				
	β	SE	*t*	*P*	AIC	β	SE	*t*	*P*	AIC
Landscape					777.4					775.5
Starting distance	0.11	0.02	6.11	**<0.001**		0.110	0.018	6.136	**<0.001**	
Date	0.00	0.00	0.54	0.59		0.002	0.003	0.503	0.615	
Time	−0.09	0.04	−2.32	**0.02**		−0.094	0.040	−2.327	**0.020**	
PC1	0.02	0.06	0.31	0.75						
PC2	0.23	0.07	3.18	**<0.01**		0.228	0.071	3.202	**0.001**	
PC3	0.11	0.08	1.43	0.15		0.113	0.079	1.459	0.154	
PC4	0.16	0.09	1.82	0.07		0.160	0.087	1.835	0.067	
Pedestrian traffic	−0.33	0.09	−3.84	**<0.001**		−0.328	0.086	−3.829	**<0.001**	
Population size	0.00	0.00	−3.20	**<0.01**		0.000	0.000	−3.190	**0.002**	
Predator					836.45					828.48
Starting distance	0.121	0.019	6.304	**<0.001**		0.118	0.019	6.261	**<0.001**	
Date	0.008	0.004	2.186	**0.029**		0.008	0.003	2.385	**0.018**	
Time	−0.099	0.043	−2.295	**0.022**		−0.102	0.042	−2.405	**0.017**	
Flock size	0.013	0.011	1.194	0.233						
Cooper's hawk presence	−0.170	0.257	−0.659	0.510						
Red-tailed hawk presence	−0.007	0.311	−0.022	0.983						
Peregrine falcon presence	0.143	0.284	0.503	0.615						
Cooper's hawk sightings 2017	0.000	0.009	−0.001	0.999						
Red-tailed hawk sightings 2017	0.066	0.021	3.201	**0.001**		0.064	0.015	4.357	**<0.001**	
Peregrine falcon sightings 2017	−0.105	0.031	−3.404	**0.001**		−0.102	0.024	−4.286	**<0.001**	

For this analysis. We performed stepwise backwards model selection by Akaike's information criterion (AIC). Estimate (β) and standard error (SE) for each term are provided. Values in bold represent significant terms ($P < 0.05$). All terms are rounded to the nearest hundredth.

Table A6
Full and reduced models for response model

Response model	Full model (AIC: 836.45)				Reduced model (AIC: 828.48)			
	β	SE	*z*	*P*	β	SE	*t*	*P*
Flock size	0.001	0.011	0.053	0.958				
Cooper's hawk presence	0.627	0.300	2.090	**0.037**	0.536	0.263	2.035	**0.042**
Red-tailed hawk presence	−0.290	0.342	−0.848	0.397				
Peregrine falcon presence	0.112	0.312	0.360	0.719				
Cooper's hawk sightings 2017	−0.016	0.010	−1.609	0.108	−0.018	0.010	−1.903	0.057
Red-tailed hawk sightings 2017	0.043	0.025	1.717	0.086	0.036	0.020	1.783	0.075
Peregrine falcon sightings 2017	−0.017	0.035	−0.473	0.636				

Estimate (β) and standard error (SE) for each term are provided. Values in bold represent significant terms ($P < 0.05$).

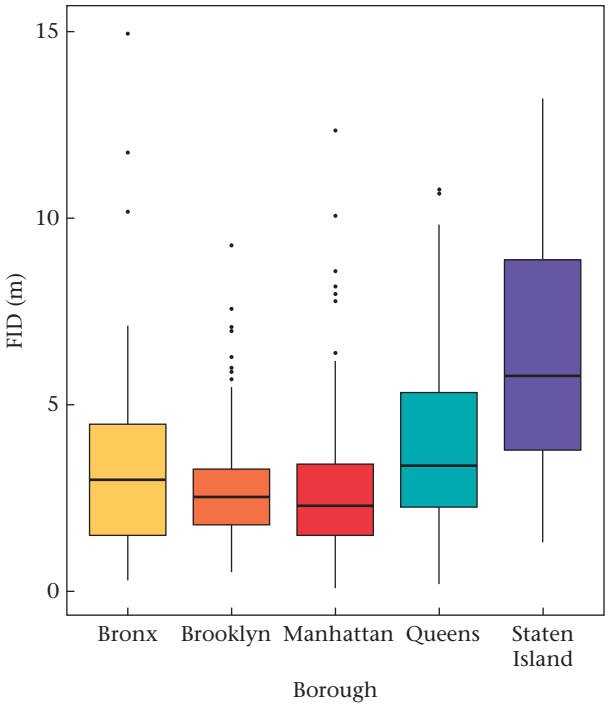

Figure A1. Box plot of flight initiation distance (FID) by borough. Box plots show the mean, first and third quartiles with black dots representing outliers. This effect may represent spatial autocorrelation (which we address in the main text with a Mantel test and in the Appendix, Table A1) or may reflect covariation of influential habitat variables with borough (e.g. see Appendix, Fig. A5).

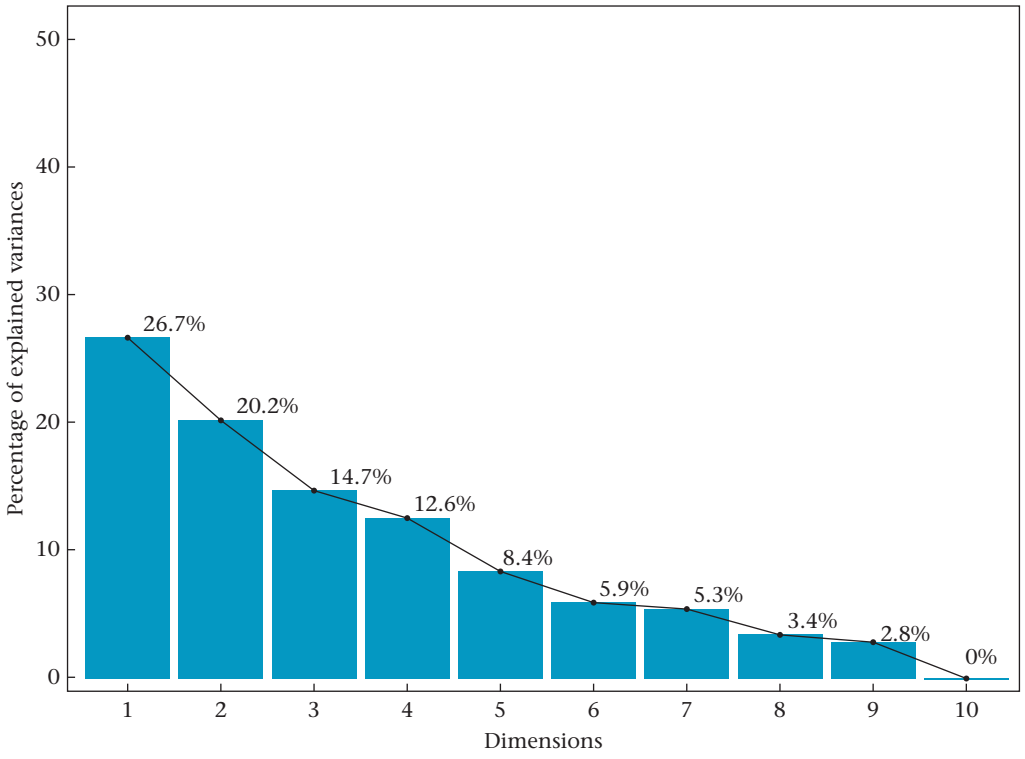

Figure A2. Scree plot of the percentage of explained variances against the number of dimensions for the landscape principal components.

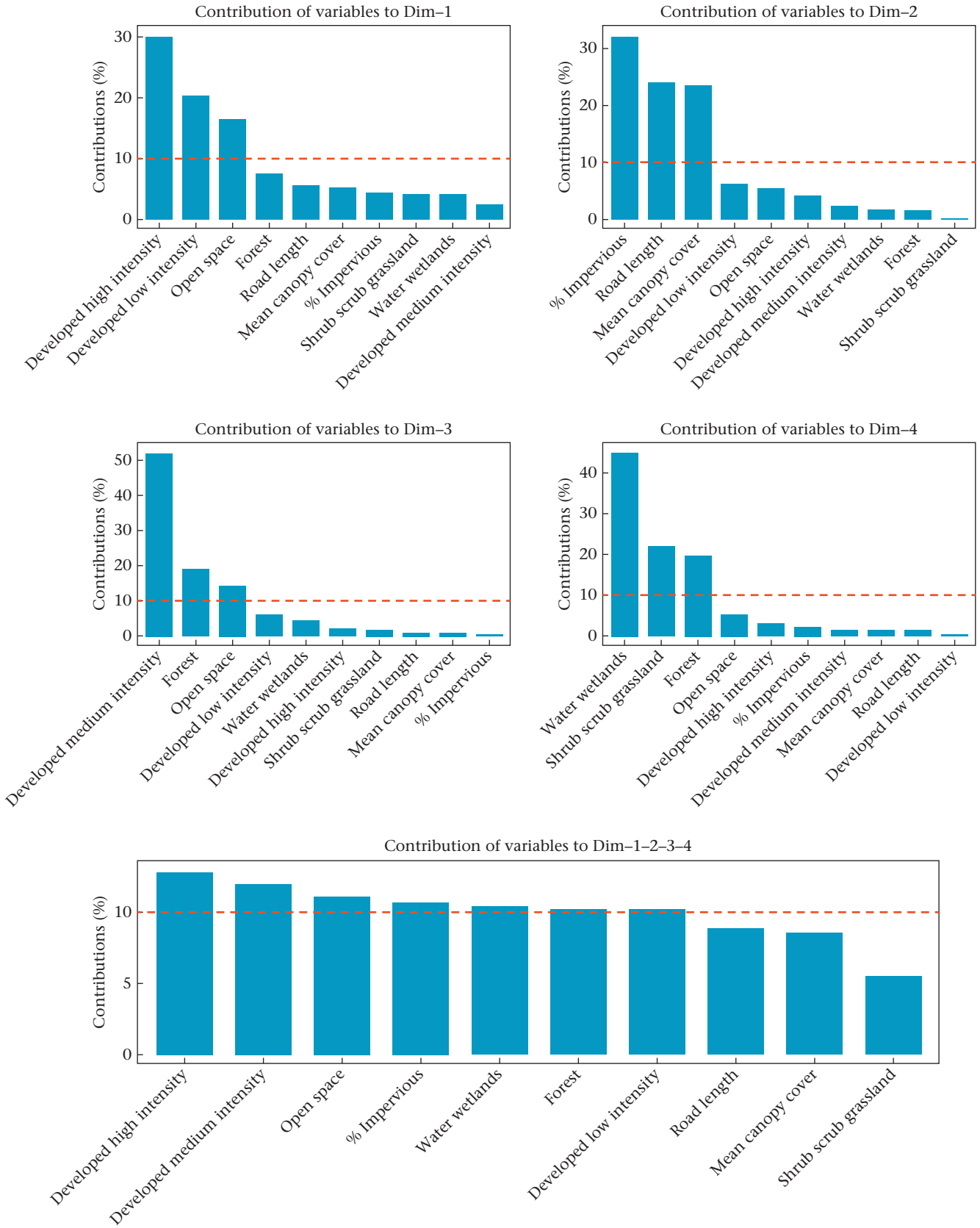

Figure A3. Plot of the percentage contribution of each landscape variable in each dimension (Dim-1, Dim-2, Dim-3, Dim-4) separately and combined.

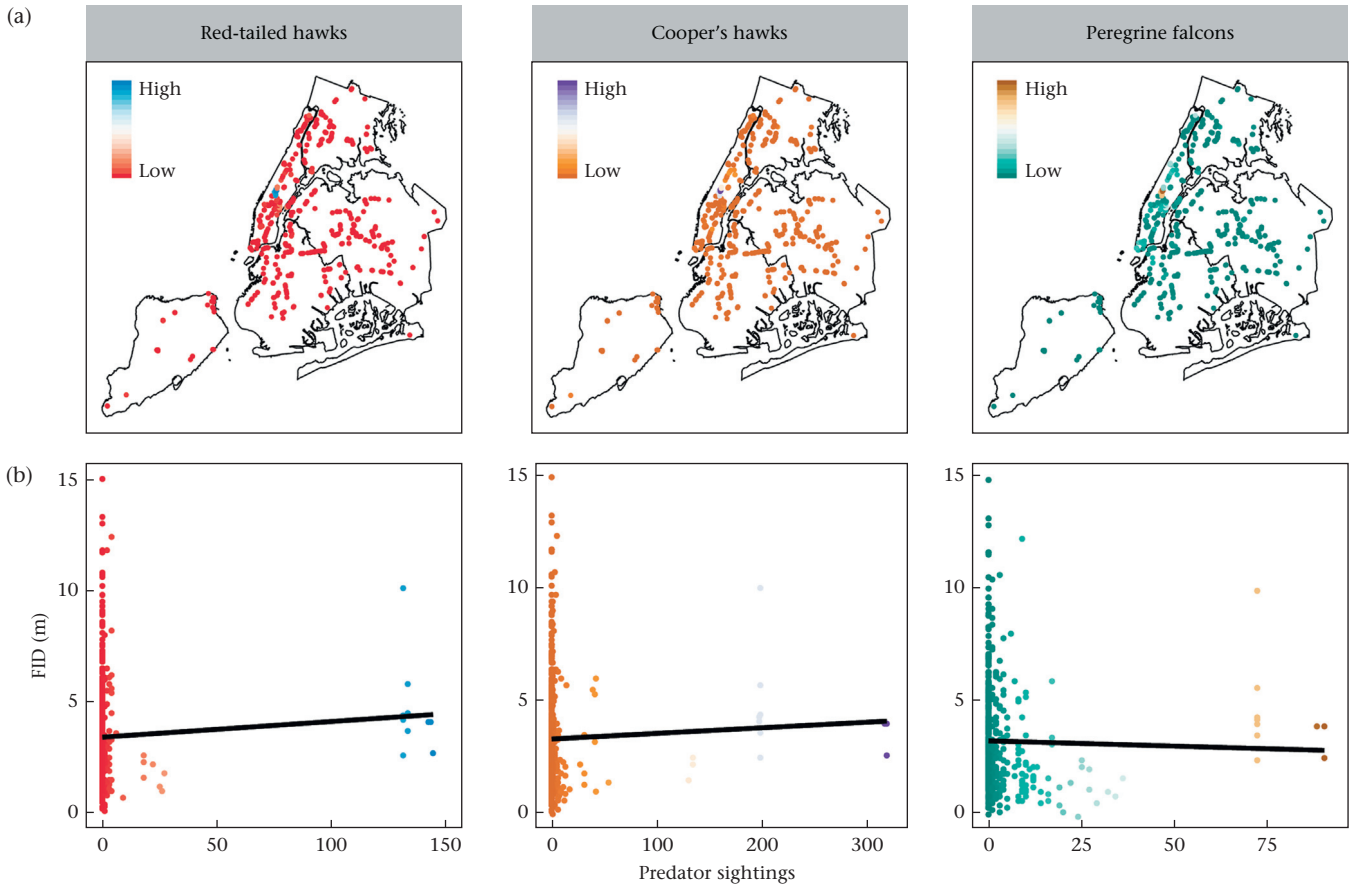

Figure A4. Flight initiation distances (FIDs) across New York City in relation to predator sightings. Each point is coloured by the variable value. (a) Maps showing the location for each FID observation. (b) Scatter plots showing FID as a function of each variable with trend lines shown in black.

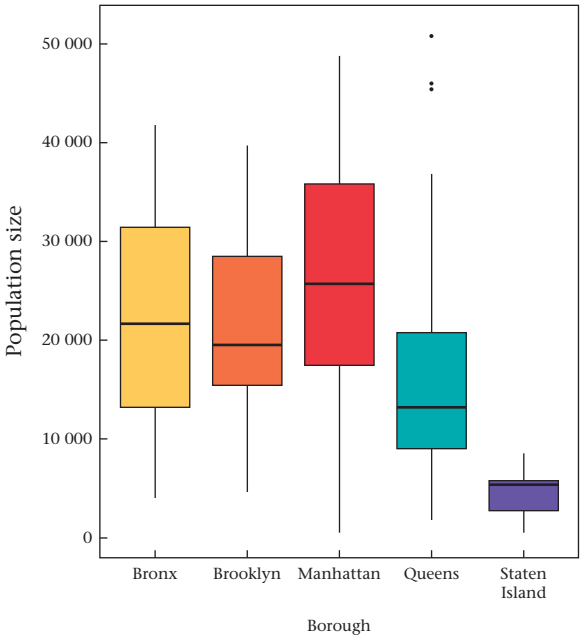

Figure A5. Relation between population size and borough (ANOVA: $F_{4,503} = 44.05$, $P < 0.001$). We included only population size in our linear models as an explanatory variable and did not include borough as a covariate or random effect despite the association of borough with FID (Appendix, Fig. A1).

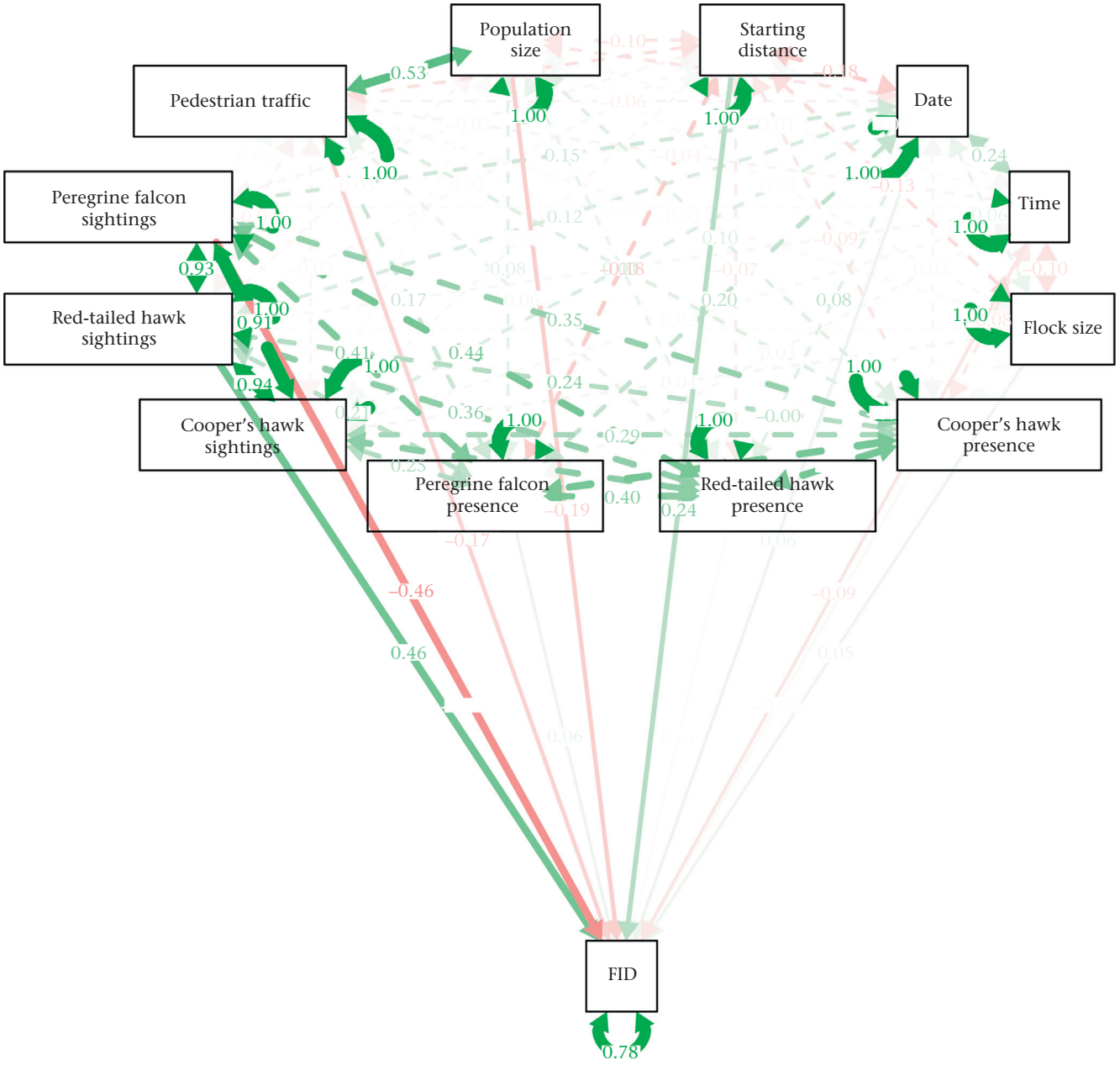

Figure A6. Path analysis showing the interactions between each variable in our full predator model (see Fig. 4), with the addition of pedestrian traffic and population size. Positive correlations are shown in green, and negative correlations are shown in red. Arrows and line weights show the direction and strength of each correlation. The dashed line represents an unanalysed correlation.