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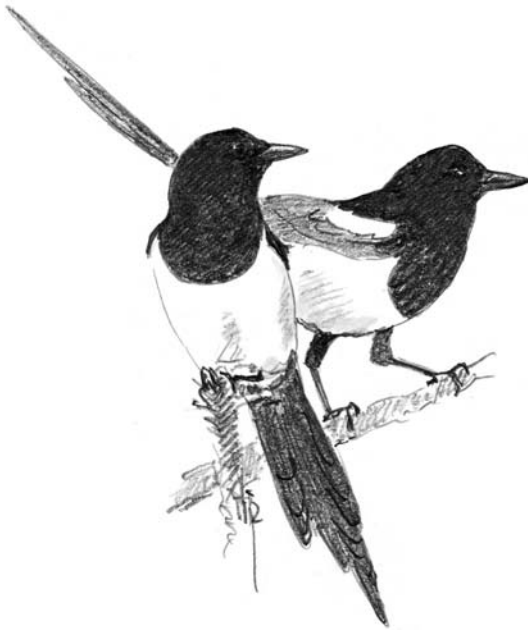
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Pedestrian density influences flight distances of urban birds

Peter Mikula

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Birds inhabiting urban areas have to cope with novel conditions. Unlike natural habitats, birds in urban environments are exposed to an increased human presence which often induces stress. Urban birds with reduced sensitivity to human disturbance can obtain benefits such as longer foraging time or decreased energy costs for escape. Here, I tested the hypothesis that the decrease in flight initiation distance (FID) to a potential predator (an approaching human) reflects adaptation to the level of disturbance expressed as pedestrian density. Moreover, I studied the influence of habitat type and species on observed FIDs. I analysed 2117 flight distances (20 species of European birds) located in ten localities in Prague. I found that species and pedestrian density play a more important role in determining FIDs than the type of habitat. Moreover, urban populations exposed to increased pedestrian density had consistently shorter flight distances. This study provides empirical documentation of changes in anti-predator behaviour, which strongly correlate with the pedestrian density gradient. It could support the idea that the establishment of FID can be highly plastic process depending on local conditions, as it is highly affected by a bird's individuality and its ability to adapt to the local level of disturbance by learning.

Key words: birds, flight distance, habitat, pedestrian density, urban site

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Human activities have a negative impact on natural habitats in many parts of the world (Marzluff *et al.* 2001, McKinney 2002). The growth of human populations is linked to urban development that frequently engulfs habitats of wild animals with a variety of effects on their density, distribution and behaviour (Palmer 2003). Urban sites are occupied by wild species of animals (known as “urban tolerant” species), which are able to cope and adapt to changing conditions (Blair 1996, Partecke *et al.* 2006). Species living in urban conditions have adapted to the proximity of humans and show specific life history characteristics that facilitate colonization of novel habitats: high rates of innovation, a high level of risk-taking and a fast pace of life (Møller 2009). Urban sites are also characterized by higher food availability (Klausnitzer 1989, Stephan 1999). Urban animals could, therefore, live in higher densities than in natural habitats (Batten 1973, Klausnitzer 1989, Stephan 1999), using smaller territories. Urban environments are characterized by higher temperatures and precipitation (Klausnitzer 1989),

offering birds longer nesting periods, which should consequently serve as a selective advantage for multi-cycle species (Batten 1973).

In addition to increased human density, urban environments contain a high number of domestic animals e.g., cats *Felis catus* and dogs *Canis lupus familiaris* (Sorace 2002, Møller & Ibáñez-Álamo 2012), as well as many generalist avian predators (Sorace & Gustin 2009, Díaz *et al.* 2013). In winter, large numbers of avian predators invade cities (e.g. Eurasian Sparrowhawks *Accipiter nisus* and Common Kestrels *Falco tinnunculus* and Common Buzzards *Buteo buteo*). In Prague, Common Kestrels, Common Buzzards and Northern Goshawks *Accipiter gentilis* were recorded as regular breeding birds (Šťastný *et al.* 2006), whereas urban Sparrowhawks nested in higher breeding densities than in the surrounding woodlands, with an average density of 600 ha/pair, but locally even of 150–210 ha/pair (Peške 1987, 1999). Urban areas are also occupied by high numbers of cats (Baker *et al.* 2005) and dogs (more than 86,400 individuals were registered in

Prague in 2010, i.e. an average density of 174 individuals/km²; Blažek 2010). In fact, mammalian predators in urban areas reach higher densities than avian predators. Cat predation is more common in urban than in rural habitats (Baker *et al.* 2008; Sims *et al.* 2008; Stracey 2011), contrary to avian predation (Stracey 2011).

Birds react to potential predators, including man, by adopting escape behaviour (Scheuerlein *et al.* 2001, Møller & Ibáñez-Álamo 2012). Flight initiation distance (FID) can serve as a simple way of testing predation risk under the assumption that stress responses are costly, especially if elicited frequently. Urban conditions could select for a reduction in sensitivity to omnipresent stressors such as humans (Kenney & Knight 1992). Analysis of intra- or interspecific differences in wariness as reflected by flight distances will, therefore, provide important information about the ability of individual/species to adapt to local conditions (Rodgers & Smith 1997, Blumstein *et al.* 2003, Blumstein 2006, Møller 2008).

The objective of this study was to test how FID changed among 20 species of birds in relation to pedestrian activity. I assumed that individuals or species which are exposed to higher levels of human disturbance (expressed as pedestrian density) should have smaller flight distances due to habituation (Webb & Blumstein 2005, Eason *et al.* 2006) or may distribute themselves among breeding sites depending on their individual susceptibility to the local level of human disturbance (Carrete & Tella 2010).

MATERIAL & METHODS

Study area

During April–July from 2011 to 2013 (ca. 100 field days, 400 hours in total), I recorded FIDs in ten urban sites in Prague, capital of the Czech Republic (50°05'N, 14°25'E). Prague is situated in the basin of the Vltava River at 177 to 399 m a.s.l., covering an area of 496.1 km² and is estimated to have a human population of nearly 1.25 million (average density of 2600 inhabitants/km²; Czech Statistical Office 2012). Built-up areas represent 58% of the territory, here defined as continuous houses or multi-storey buildings, interspersed with roads or city parks (Møller 2008). My research was conducted in several districts across the city, such as the historic town centre (1 locality), and compact city (9 localities). Urban habitats in this study encompassed forest, gardens, built-up areas, green areas between prefabs and parks.

Human presence

Similarly to Fernández-Juricic (2000) and Fernández-Juricic *et al.* (2002), I counted the number of individual pedestrians crossing the observed sites, which I subsequently used to estimate human density. In order to estimate pedestrian density, I counted the number of people who walked by in 15-min intervals (human presence index, HPI, or average number of pedestrians per minute; Fernández-Juricic *et al.* 2002). Counts were made at 8:00 h, 13:00 h and 18:00 h and were repeated 5 times throughout the season. HPI was low in four localities (0.1–0.93 pedestrians/min), medium in two sites (1.33–3.6/min), high in three sites (7.3–8.96/min) and extremely high in one site (40.73/min). Similarly to localities, habitats also differed in HPI as follows: forest (0.1/min), gardens (0.73/min), built-up areas (0.93–8.96/min), green areas between prefabs (0.1–1.73/min) and parks (1.33–40.73/min). Sites and habitats significantly varied in pedestrian density (Kruskal-Wallis ANOVA, $F_{9,40} = 45.73$, $P < 0.001$ resp. $F_{9,40} = 25.19$, $P < 0.001$).

Flight distance

Flight distances of individual birds were recorded along chosen transects that do not cross crops, private gardens or houses (Møller 2008). When a bird had been spotted with binoculars, I walked at normal speed towards the individual while recording the number of steps. Walked distance is approximately equal to the number of meters according to comparisons with measured distances (using the method adopted in Møller 2008, I did not find a significant difference between number of steps and number of measured meters; paired *t*-test, $t = -0.18$, $df = 29$, $P = 0.98$). All recordings were made during the breeding season, when most individuals are sedentary, which prevented the same individual from being recorded in different sites. Although measuring FIDs of breeding birds may cause problems when individuals have large home ranges (e.g. kestrels or corvids), several studies pointed out that many urban birds have smaller territories than rural ones and mostly forage within the breeding territory (Batten 1973, Klausnitzer 1989, Gliwicz *et al.* 1994, Stephan 1999). When I was conducting measurements in the same locality more than once, I did not examine birds in previously walked transects to minimize the chance of encountering the same individuals again.

FID is defined as the distance from the observer to the bird when it first takes flight upon a direct approach whilst walking (Blumstein 2006, modified by Díaz *et al.* 2013 and Møller & Liang 2013). When the individual

was positioned in the vegetation, its height above ground was estimated to the nearest meter (ground level zero), using my own length as yardstick (Møller 2008). Taking height above ground into account, FIDs were calculated as the Euclidian distance that equals the square root of the sum of the squared horizontal distance and the squared height above ground level (Blumstein 2006, Møller 2008).

I also measured “starting distance”, being the distance between the bird’s position and the place where I first spotted, and started walking towards, the bird. Earlier studies have shown that starting distance is positively correlated with FID (Blumstein 2003, 2006). To eliminate this problem, I used the method proposed by Díaz *et al.* (2013) and Møller & Liang (2013), who found that the correlation between starting distance and FID (largely) disappeared when chosen individuals were at least 30 m away from the observer. Hence, I excluded observations with starting distance of <30 m. While taking FIDs, I recorded date, time of day and, if possible, sex and age of the individual (if external characteristics or date allowed discriminating between adults and juveniles). Only adult individuals were included to avoid problems caused by juveniles with different flight distances (Stalmaster & Newman 1978, Eason *et al.* 2006). Individuals of unknown age were excluded from analyses (Møller 2008).

Statistical analyses

FID and HPI were \log_{10} transformed to achieve distributions that did not differ from normality. In all analyses, I assumed that estimates based on larger sample sizes are closer to the true population estimate and, therefore, analyses were weighted by sample size to adjust for unequal sampling effort among observed species.

All measured variables such as species, HPI, and habitat type were inserted in a General Linear Model (GLM) to detect their effect on the resulting FID. When GLM results showed that FID is a species-specific trait,

as per Blumstein *et al.* (2003) and Møller (2008), I tested if habitat type or HPI played an important role in the resulting FID, using a paired *t*-test. Although data for 20 species were obtained, the sample size was reduced in some subsequent analyses. Firstly, I compared levels of intraspecific variation between seventeen species distributed to different levels of pedestrian density. Secondly, I compared paired populations of the fourteen species from the different parts of same habitat (park), which distinctly differed in HPI (1.33 and 40.73). Thirdly, I compared paired populations of the thirteen species from different habitats (park and green area between prefabs), which had a very similar HPI (1.33 and 1.73).

Analyses were done using SPSS 20.0 and MS Excel 2007. A Linear model was fitted using the GLM univariate method. I interpret two-sided *P*-values of less than 0.05 as significant. Residuals from GLM were visually checked and did not deviate substantially from normal. Moreover, I reported partial eta-squared value as a measure of effect size (Cohen 1988). I used suggested norms for partial eta-squared effect sizes: small effect (0.01), intermediate effect (0.06) and large effect (0.14; Stevens 2002).

RESULTS

I recorded 2117 flight distances, and present data for 20 species. The overall number of estimates per species ranged from 1 to 389 (median = 31.5). Mean FID ranged from 1 to 38 m (mean \pm SD: 6.70 \pm 6.31). The four species with the shortest relative flight distances were Rock Pigeon *Columba livia*, Common Chaffinch *Fringilla coelebs*, Blue Tit *Cyanistes caeruleus* and Common Wood Pigeon *Columba palumbus*. The four species with the longest relative flight distances were Common Starling *Sturnus vulgaris*, European Green Woodpecker *Picus viridis*, Common Kestrel and Eurasian Sparrowhawk (Appendix 1).

Table 1. Flight initiation distance (FID) in relation to species, pedestrian density (HPI), habitat, and interactions between species, pedestrian density and habitat. Three-way and pedestrian density \times habitat interactions were excluded as they were not significant.

Variable	Sum of squares	df	F	P	Partial eta-squared
Species	37.691	19	79.08	<0.0001	0.421
Pedestrian density	31.358	7	178.57	<0.0001	0.377
Habitat	0.496	1	19.76	<0.0001	0.009
Species \times pedestrian density	0.680	3	9.04	<0.0001	0.013
Species \times habitat	0.006	1	0.22	0.639	<0.001
Error	51.930	2070			

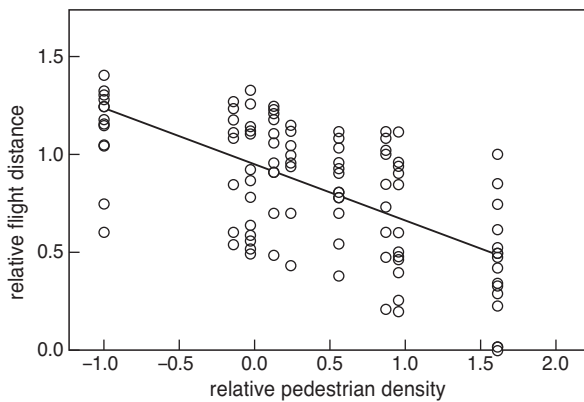


Figure 1. Flight initiation distance (FID) in relation to pedestrian density (HPI) for different populations and species of birds (all data were \log_{10} -transformed). The line shows a linear regression.

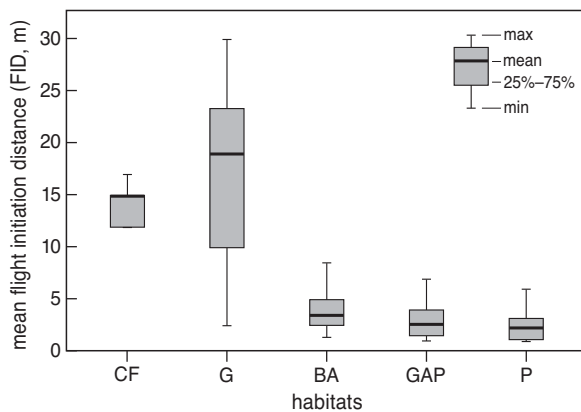


Figure 2. Flight distances across different habitats: city forest (CF), gardens (G), built-up area (BA), green area between prefabs (GAP) and park (P).

\log_{10} -transformed mean FIDs of ten bird populations (combined from all localities) varied among observed species, habitat types and HPI (Table 1). GLM results were highly significant ($F_{46,2070} = 243.3$, $r^2 = 0.84$, $P < 0.0001$, partial eta-squared = 0.844). \log_{10} -transformed mean FID of bird populations strongly correlated with HPI and decreased with increasing pedestrian density (Figure 1). As expected, FID strongly differed between species. I also found considerable variation in FID among individuals within the same species (Fisher's LSD test, $F_{1,16} = 39.4$, $P < 0.0001$). Likewise, FID weakly correlated with habitat type. However, post-hoc analyses indicated that FID did not significantly differ between city forest and gardens (Tukey's test, $P = 0.98$), unlike the other habitat types (Tukey's test, $P < 0.01$; Figure 2).

In order to test the impact of pedestrian density on FID within various species I compared two parts of the same park with a similar species composition but different HPI. The analysis of paired populations showed that fourteen species responded to pedestrian density in different ways (Table 2). Contrarily, thirteen species in different habitats with similar HPIs did not significantly differ in their FIDs (mean \pm SD for gardens: $12.88 \text{ m} \pm 3.53$, built-up area 5.53 ± 2.80 ; paired t -test based on \log_{10} -transformed data: mean: $t = 1.35$, $df = 12$, $P = 0.20$; SD: $t = 0.31$, $df = 12$, $P = 0.76$).

DISCUSSION

In many studies, pedestrian density has been found to correlate negatively with FID (Lord *et al.* 2001, Miller *et al.* 2001, Webb & Blumstein 2005, Møller *et al.* 2013). Similar to my observations, Rodgers & Smith (1997), Rodgers & Schwikert (2002), Webb & Blumstein (2005), Møller (2008), Møller *et al.* (2008, 2013) and Díaz *et al.* (2013) found differences in FID between and within species correlating to various levels of disturbance or human density. Several hypotheses have been proposed to explain this phenomenon by pointing to adaptive or heritable components of such behaviour. The most frequent explanation for changes in FID is that birds habituate to the local level of disturbance and became more tolerant in heavily disturbed areas, as shown in many previous studies (Lord *et al.* 2001, Runyan & Blumstein 2004, Stankowich & Blumstein 2005, Eason *et al.* 2006). An alternative explanation, which does not exclude the first hypothesis, suggests that the distribution of birds is linked, besides to food supply and nesting opportunities, to their tolerance of human disturbance, and thus must have some heritable components (Carrete & Tella 2010). The third hypothesis, suggested by Webb & Blumstein (2005), almost completely lacks empirical evidence and proposes that

Table 2. Mean and SD of FID (m) for pairs of populations of fourteen bird species in city parks with low (1) and high (2) density of pedestrians.

Variable	Park 1	Park 2	t	P
Mean FID	12.15	2.98	2.62	0.021
Range in means	4 – 25	1 – 7		
SD FID	3.08	0.67	3.36	0.005
Range in SD	2.25 – 4.40	0 – 1.04		

birds may remember areas with high disturbance levels and adjust their degree of tolerance depending on where they are at the time.

Many previous studies found a strong species effect on FID (Rodgers & Smith 1997, Rodgers & Schwikert 2002, Blumstein *et al.* 2003, Møller 2008), linked perhaps to species-specific life history traits (Johnston *et al.* 1997, Ghalambor & Martin 2001, Møller & Liang 2013). My finding shows that much variation in FID can be explained by species, which also supports the hypothesis that FID can be considered as a species-specific trait with important implications for management (Blumstein *et al.* 2003). It has been suggested that FID among species may have coevolved with life history traits, showing an increase in FID with decreasing clutch size (Møller & Liang 2013), fewer offspring (Ghalambor & Martin 2001), higher adult survival (Ghalambor & Martin 2001) and with larger body size (Blumstein 2006). Species-specific FIDs may also have coevolved with the size of sense organs, such as brain and eyes, as suggested by Møller & Erritzøe (2014); however, empirical evidence is lacking in this case.

My results indicate that habitat type did not play as important a role as other variables, although this outcome may be biased by the species used in this study (inhabiting a wide variety of habitats offered by urban environment). Large flight distances are to be expected mainly in individuals living in an environment inhabited by stable and dense populations of avian predators, e.g. in city parks or forest. Although habitat type influenced overall FID, a significantly greater proportion of the variation was explained by species or pedestrian density and, importantly, there was no significant interaction between habitat type and other variables. Moreover, additional testing of paired bird populations showed significant differences in FID only between birds which inhabited the same habitat type with different pedestrian densities. However, FID did not differ significantly between different habitat types with similar pedestrian density.

I found a strong correlation between FID and species as well as pedestrian density (both explained approximately a similar proportion of variation), and there was a significant interaction between them which explained an even higher proportion of variation than just habitat type. It has been suggested that some anti-predator behaviour may be heritable (Riechert & Hedrick 1990), but behaviour like FID may be much more phenotypically plastic. Although FID seems to represent species-specific antipredator behaviour (Blumstein *et al.* 2003) and could have heritable components (Murphey *et al.* 1980, Carrete & Tella

2010), it is more likely to be experience-dependent and to vary within species with predator type or density (Møller & Ibáñez-Álamo 2012, Díaz *et al.* 2013), season (Møller *et al.* 2013), food availability (Fernández-Juricic *et al.* 2002), habitat type (Díaz *et al.* 2013, Møller & Liang 2013; but see Blumstein *et al.* 2006) or individual's age (Eason *et al.* 2006). The strong effect of pedestrian density clearly supports the idea that FID may be primarily affected by the bird's individuality and its ability to adapt to local levels of disturbance by learning (Eason *et al.* 2006). Individuals which are not able to adapt to human presence will lose access to resources and incur costs related to flight, increased vigilance (Ward & Low 1997) and reduced foraging (Lord *et al.* 1997). Consequently, the resistance to human-related stress response will determine what bird species are more likely to live in urban environments. Moreover, the large intraspecific variability suggest that some birds are able to change their habits plastically under local conditions in order to reduce costs of escape behaviour with predation risk and/or distribution and abundance of available food resources (Webb & Blumstein 2005, Møller *et al.* 2013). Risk assessment thus appears to be a highly plastic process for predator-savvy prey.

Although urban environments were relatively free of avian predators a few decades ago, nowadays several raptors (mostly hawks *Accipiter* spp., Common Kestrel and Common Buzzard) have colonised cities (reviewed in Chace & Walsh 2006; Peške 1987, 1999, Klausnitzer 1989, Díaz *et al.* 2013, Mikula *et al.* 2013). Variation in food supply and predators' habituation to novel nesting substrates may further influence the spectrum of predators in urban habitats and subsequently change predation risk for urban birds (reviewed in Chace & Walsh 2006). Despite large populations of avian predators inhabiting cities (Peške 1987, 1999), urban birds are threatened more often by mammalian predators such as cats and dogs (Møller & Ibáñez-Álamo 2012) or by disturbance from humans (Fernández-Juricic 2000). Stankowich & Blumstein (2005) found that predator traits that were associated with greater risk such as speed or directness of approach, increased prey escaping distance across animal species. Urban birds are typically exposed to slower and more indirectly moving cats, dogs or humans and, therefore, could have consistently lower FIDs than birds from rural sites (more often threatened by avian predators). Avian communities could be differentially affected when city districts differ in the composition (predominantly mammalian or avian) and density of their predator fauna (Lepczyk *et al.* 2004, Chace & Walsh 2006).

Monitoring predation risk involves cognitive mechanisms allowing birds to distinguish between the dangerous approach of avian predators, the less dangerous approach of mammalian predators, and the marginally dangerous approach of humans. Moreover, similar cognitive mechanisms may allow birds to respond optimally with respect to distribution and accessibility of food resources (Møller *et al.* 2013). In this way, the birds' ability to learn what level of risk is acceptable and what is not could be connected with relative brain size. Large-brained birds seem to be more successful at establishing themselves in novel conditions by adjusting breeding behaviour to the prevailing ecological conditions (Brooker *et al.* 1998), finding novel food resources (Sol *et al.* 2005) or reducing adult mortality (Sol *et al.* 2007). Factors which influence cognitive abilities of species, and subsequently FID, could be used as an important predictor of variability between species. Apparently, species with better cognitive abilities rapidly adjust their response to predation risk and exhibit a larger intraspecific variation depending on local conditions.

Finally, my results confirm that pedestrian density can be used as a predictor of individual risk taking. Moreover, results show that FID differed between and within species; this conclusion supports an idea that FID may have some heritable components but can be changed plastically depending on local conditions. This inter- and intraspecific variation suggests: (1) data for interspecific analyses should be combined from different sites in future studies, (2) intraspecific differences in FID could be used as an important predictor of a species's ability to optimize their escape behaviour and (3) the ability to change antipredator behaviour seems to be plastic and, therefore, further study is needed to distinguish which mechanism allows this phenomenal variety of adaptive traits.

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SAMENVATTING

Vogels staan er om bekend dat ze zich kunnen aanpassen, iets wat ze te stade komt nu de wereld in snel tempo urbaniseert. Soorten of individuen die goed tegen menselijke aanwezigheid kunnen, zouden met verstedelijkte gebieden een nieuw habitat aan hun leefgebied kunnen toevoegen of zich kunnen aanpassen aan een veranderende leefomgeving. Er is veel onderzoek gedaan naar de invloed van mensen op vogels in steden. Een deel van dat onderzoek maakt gebruik van de vluchtafstand, de afstand waarop een vogel vlucht voor een mens. Aan vluchten zijn kosten verbonden, onder meer omdat het een vogel afhoudt van zijn dagelijkse bezigheden. De vluchtafstand is eenvoudig te meten: spot een vogel, loop er op af, en noteer het aantal stappen tot aan de vogel op het moment dat de vogel ervandoor gaat (en ijk je stap aan een meter). In deze studie aan 20 vogels-oorten op 10 locaties in Praag wordt ervan uitgegaan dat vogels met een korte vluchtafstand beter zijn aangepast aan menselijke aanwezigheid dan vogels met een lange vluchtafstand. In het hier gepresenteerde onderzoek bleek dat de vluchtafstand vooral werd bepaald door vogelsoort en voetgangerdichtheid. Het type habitat (bos, tuinen, parken, opgaande bebouwing, groengebieden) was een minder belangrijke factor voor de lengte van de vluchtafstanden. Op verschillende plekken in hetzelfde park,

waar de samenstelling van de vogelbevolking gelijk was maar de voetgangerdichtheid verschilde, varieerde de vluchtafstand voor dezelfde soorten naar gelang de voetgangerdichtheid. Omgekeerd waren de vluchtafstanden van dezelfde soorten in verschillende habitats min of meer gelijk. Soorten met een zeer geringe vluchtafstand waren Stadsduif *Columba livia*, Vink *Fringilla coelebs*, Pimpelmees *Cyanistes caeruleus* en Houtduif *Columba palumbus*, terwijl relatief grote vluchtafstanden werden genoteerd voor Spreeuw *Sturnus vulgaris*, Groene Specht *Picus viridis*, Torenvalk *Falco tinnunculus* en Sperwer *Accipiter nisus* (de laatste drie soorten echter maar met één exemplaar vertegenwoordigd in het onderzoek). Gemiddeld genomen nam de vluchtafstand af met toenemende voetgangerdichtheid. Deze resultaten suggereren dat vogels zich kunnen aanpassen aan menselijke aanwezigheid, maar dat die aanpassing individu- en soortbepaald is. Die eigenschap zal vogels van pas kunnen komen nu steden, toch al een predatorrijke omgeving met al die honden en katten, steeds meer worden bevolkt door roofvogels. En ook nu steeds meer landelijk gebied wordt omgezet in verstedelijkt gebied waar mensen een dominante factor zijn. (RGB)

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Appendix 1. Summary statistics for mean and SD of flight initiation distance (FID, m) for 20 species recorded in Prague, Czech Republic.

Species	Mean FID (m)	SD FID (m)	Sample size for FID
<i>Accipiter nisus</i>	38.00	0.00	1
<i>Anas platyrhynchos</i>	9.08	6.01	272
<i>Columba livia</i>	2.78	1.61	389
<i>Columba palumbus</i>	3.84	2.76	192
<i>Cyanistes caeruleus</i>	3.73	1.70	32
<i>Falco tinnunculus</i>	36.35	0.00	1
<i>Fringilla coelebs</i>	3.00	1.44	24
<i>Gallinula chloropus</i>	12.49	4.55	24
<i>Garrulus glandarius</i>	12.74	3.95	40
<i>Motacilla alba</i>	15.17	3.97	6
<i>Parus major</i>	5.62	3.93	236
<i>Passer domesticus</i>	9.66	9.37	340
<i>Phylloscopus collybita</i>	6.70	2.43	24
<i>Pica pica</i>	8.78	6.79	216
<i>Picus viridis</i>	21.10	0.00	1
<i>Streptopelia decaocto</i>	4.05	1.65	40
<i>Sturnus vulgaris</i>	18.41	2.60	31
<i>Sylvia atricapilla</i>	8.75	3.04	7
<i>Sylvia communis</i>	8.30	4.36	6
<i>Turdus merula</i>	4.92	3.35	235