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Original Article

Urban habitats and feeders both contribute to flight initiation distance reduction in birds

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Animals respond to approaching predators by taking flight at a distance that optimizes the costs and benefits of such flight. Previous studies have shown that urban populations of birds have shorter flight initiation distances than rural populations of the same species, that this difference is partly explained by differences in the community of predators, and that a longer history of urbanization implies a greater reduction in flight initiation distance in urban populations. The use of birdfeeders may be an additional factor reducing flight initiation distance not only in cities but also elsewhere by among other effects increasing body condition, increasing availability and reliability of food, and hence reducing the relative cost of flight. Here, we tested the prediction that urban habitats and presence of feeders independently accounted for reductions in flight initiation distance using extensive samples from different cities in Poland. We found independent significant effects of urban habitat and presence of feeders on flight initiation distance. These findings suggest that different factors have contributed to the “tameness” of urban birds.

Key words: birds, feeders, flight initiation distance, urbanization.

INTRODUCTION

Predation is a common and widespread cause of mortality having significant impact on behavior, physiology, life history, and population size of prey (Crawley 1992; Caro 2005). Not surprisingly, a high diversity of antipredator behavior that reduces the risk of mortality has evolved (Caro 2005). These range from frontlines of defense in terms of habitat choice and attempts to avoid detection over escape to attempts to avoid death once captured (Endler 1991). Economic escape behavior (Hediger 1934; Ydenberg and Dill 1986; Cooper and Blumstein 2015) accounting for flight initiation distance (FID) has attracted considerable attention because of the link between individual responses to an approaching predator

and the life history of a prey individual (Cooper and Blumstein 2015). FID is the distance at which an individual takes flight when approached by a potential predator such as a human. Thus, individual behavior continuously has to be adjusted to the costs of flight relative to the benefits of staying put. Perhaps not surprisingly, individuals belonging to species exhibiting short FID are particularly susceptible to predation, whereas individuals with long FID suffer from a reduced risk of predation, but at the costs of frequent disturbance during foraging and ordinary maintenance behavior (Møller et al. 2008). Thus, individuals with short FID run a high risk of predation, whereas conspecifics with long FID rarely suffer from predation (Møller 2014b).

Urban birds generally have shorter FID than conspecifics from rural habitats. Møller (2015) showed in a meta-analysis of 207 effect sizes extracted from all studies of FID in birds that

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urbanization had the strongest mean effect out of 13 different categories of effects, accounting for 38% of the variance. Some birds do not occur in urban areas, either because they have long FIDs (Møller 2009, 2012) or because a small brain may prevent exploitation of unusual or novel challenges such as urban habitats (cognitive buffer hypothesis; Allman et al. 1993). Cooke (1980) reported the first such study demonstrating that suburban birds had shorter FID than rural birds of the same species living in more densely built-up habitats. Subsequent analyses revealed that the difference in FID between urban and rural habitats was explained by the timing of urbanization (Møller 2008), variance in FID rather than mean FID was the best predictor of urbanization (Møller 2010; Carrete and Tella 2011a), and differences in predator community accounted for such differences in FID between urban and rural habitats (Díaz et al. 2013). Indeed, Møller and Ibañez-Álamo (2012) showed that nearby populations of birds from urban and rural habitats differed significantly in terms of antipredator behavior, suggesting that populations have diverged significantly in response to recent changes in predator community following urbanization. This effect may arise as a consequence of urban habitats constituting refuges that provide protection against predators (Møller 2012).

At least 3 different mechanisms may account for differences in FID between populations of animals living in urban and rural habitats: habituation, phenotypic sorting, and genetic differentiation. Møller (2015) reviewed the literature on habituation of birds and found no conclusive evidence consistent with this explanation in 8 studies (e.g., Carrete and Tella 2011b; Smith-Castro and Rodewald 2010; Scales et al. 2011; Keyel et al. 2012; Møller and Garamszegi 2012; Selmann et al. 2012). Phenotypic sorting implies that individuals with specific behavior differentially recruit to areas with human habitation simply because individuals showing no or reduced fear responses are able to cope with living close to humans without incurring a negative energy balance (Møller 2014a). There is little evidence for this explanation because of genetic differentiation across urban gradients and within urban areas (review in Møller 2014a). Finally, local adaptation to urban habitats implies that specific genotypes have increased in frequency or become favored among urban individuals. There is evidence for such an effect for the *SERT* gene associated with harm avoidance in urban blackbirds *Turdus merula* (Müller et al. 2013). Furthermore, mean FID among bird species in urban areas is negatively correlated with time since initial urbanization (Møller 2008; Weston et al. 2012), consistent with gradual change in FID as time passes. Food provisioning has been associated with tameness of birds, especially in urban habitats (Robb et al. 2008), raising the possibility that additional factors to urbanization as such may have contributed to the reduction in FID among urban birds.

Although almost all previous studies of FID have occurred during the breeding season (Møller 2015), studies of FID in winter have been very few despite the fact that conditions differ from the breeding season in terms of the constraining effects of reproduction, but more important effects of food shortage during winter than during summer. The objectives of this study were to test whether the change in FID due to urbanization was correlated with the change in FID due to the presence of feeders. More specifically, we tested whether FID could be predicted by presence or absence of urban habitat, presence or absence of feeders, and their interaction. If the presence of these 2 factors caused a disproportionate reduction in FID, we would expect an interaction effect. We tested these predictions using extensive data on FID from 37 species of birds during winter collected in 12 cities and towns across Poland.

MATERIALS AND METHODS

Study sites

Data were collected in December 2013–February 2014 in 12 cities (all larger than 100 000 inhabitants) across Poland and a nearby rural area. The distance between urban and rural paired sites differing in habitats was 2–20 km, mean 10.1 km (SD = 4.1).

Recording FID

Birds were tested during favorable weather conditions (no snow or rain, wind below 4 m s⁻¹) between 8:00 and 14:00. FID was established by using a standard procedure developed by Blumstein (2006). In brief, we walked at ordinary walking speed toward a bird recording the distance from the bird when we started walking, the distance at which the birds initiated escape, and the birds' height in the vegetation. In order to account for the height at which individuals were perched, FID was calculated as the Euclidean distance between the approaching human and the focal bird (which equals the square root of the sum of the squared flight distance and the squared height in the vegetation). An observer moved toward a feeder or another place at normal walking speed while recording the distance at which individual birds left the feeder or the resting/foraging place other than the feeder. Observers wore neutrally colored clothes and behaved as normal pedestrians. Starting distance was kept constant by approaching birds at the feeder or the control sites from a fixed distance. FID was measured by a number of trained observers and therefore data were pooled for analysis.

Birds were categorized as using feeders, when they were observed at typical bird-table feeders with a roof providing different types of food, mainly seeds, and at balls of fat mixed with seeds.

We recorded data for 37 species in total. However, there was only data on FID for 12 species for urban and rural habitats and feeders and nonfeeders. Thus, we made analyses of the global data set of 37 species and the restricted data set of 12 species that were recorded under all 4 different kinds of conditions. All data are reported in [Supplementary Material](#).

Statistical analyses

All analyses were made with JMP (SAS Institute Inc. 2012). We log₁₀-transformed FID to achieve normally distributed data. The difference in FID between urban and rural habitats was quantified as the log₁₀-transformed FID in urban habitats minus the log₁₀-transformed FID in rural habitats. Negative values of this contrast imply shorter FIDs in urban habitats. Likewise, the difference in FID between sites with feeders and other sites was estimated as the log₁₀-transformed FID at feeders minus the log₁₀-transformed FID at other sites. Negative values of this contrast imply shorter FIDs at feeders. We tested if these differences deviated from the expected value to zero using a Wilcoxon matched-pairs signed-rank test. We tested for consistency in effect between urban and rural habitats and between feeders and other sites across species using a Kendall rank order correlation analysis to account for the non-normal distribution of data. We weighted this analysis by sample size to account for differences in sampling effort among species (see differences in sample size in [Figure 3](#) and [Supplementary Material](#); see SAS Institute Inc. 2012 for methods). All statistical tests require that observations have similar sampling effort (Sokal and Rohlf 1995), and if that is not the case, such uneven sampling effort must be accounted for in the analyses. A positive rank order correlation would imply that differences in FID between urban and

rural habitats were correlated differences in FID between presence and absence of feeders. In other words, such a positive correlation would suggest that species responded relatively similarly to urbanization and to feeders.

We developed generalized mixed model with log₁₀-transformed mean FID as the response variable; habitat (urban or rural), feeder (feeder or not), and their 2-way interaction as predictors; and species as a random effect to account for differences in sampling effort among species. We developed an ordinary least squares model with log₁₀-transformed mean FID as the response variable and species, city, habitat, feeder, and the interaction between feeder and habitat as predictors. This model quantified to which extent we could predict FID from a range of the most likely factors.

Observed associations among predictor variables can be influenced by the phylogenetic relationships among the species sampled, as their degree of statistical independence depends on their degree of common ancestry. We used phylogenetic generalized least square regression models implemented in R to control for these effects (see Díaz et al. 2013 for a similar approach). We calculated the phylogenetically corrected effects of habitat, feeder, and its interaction after estimating the phylogenetic scaling parameter lambda (λ). Different populations of the same species were considered as polytomies with a constant small genetic distance of 1 × 10⁻¹⁰ between them. We used the R script and the edited phylogeny supplied as Supplementary Files S1 and S2 in Díaz et al. (2013), but using the function pglm3.3.r instead of the pglm3.1.r in the script and including additional polytomies for rook *Corvus frugilegus* (5), great tit *Parus major* (7), and blackbird *T. merula* (2) populations in the phylogeny.

We estimated the magnitude of associations between predictor and response variables using effect sizes estimated as Pearson's product-moment correlation coefficient based on the standard conversion of *F*-statistics into Pearson's *r* (Rosenthal 1994). We assessed relationships based on effect sizes according to the criteria listed by Cohen (1988) for small (Pearson *r* = 0.10, explaining 1% of the variance), intermediate (9% of the variance), or large effects (25% of the variance).

RESULTS

We recorded 811 FIDs from 37 species of birds during the winter 2013–2014. These showed a significant effect of habitat with longer FID in rural than in urban habitats and longer FID in the absence of feeders than in their presence while the interaction between habitat and feeder was not significant (Table 1 and Figure 1). The lack of significant interaction implied that the 2 effects of habitat and feeder were additive.

Table 1
Relationships between FID and habitat, feeder, and the 2-way interaction between habitat and feeder, after correcting for the effect of the phylogenetic structure of the data set, that was, however, not significant (λ = 0.000, χ² = -0.0103, P = 1.000)

Term	<i>F</i>	df	<i>P</i>	Estimate	SE	Effect size
Intercept	540.14	1	<0.0001	1.059	0.046	
Habitat	13.15	1	<0.0001	0.242	0.067	0.25
Feeder	19.55	1	<0.0001	-0.281	0.064	0.30
Habitat × feeder	0.69	1	0.408	-0.077	0.093	0.06
Error		204				

The model had the statistics *F* = 28.19, df = 4, 204, adjusted *r*² = 0.29, *P* < 0.0001. Effect sizes are Pearson's product-moment correlation coefficients.

Mean FID for different species at feeders was positively correlated with mean FID at other places than feeders (*F* = 9.57, degrees of freedom [df] = 1, 18, *r*² = 0.31, *P* = 0.006, estimate [standard error, SE] = 0.439 [0.142]). Thus, mean FID maintained its relative ranking among species in the presence and the absence of feeders. In contrast, there was no significant correlation between mean FID for different species in urban and rural habitats (*F* = 1.09, df = 1, 21, *r*² = 0.00, *P* = 0.31). In other words, there was no constancy in ranking of mean FID in urban and rural habitats.

The difference in FID between sites with feeders and sites without feeders was -0.028 (SE = 0.020), *N* = 12 species, differing significantly from 0 (Figure 2; Wilcoxon matched-pairs signed-rank

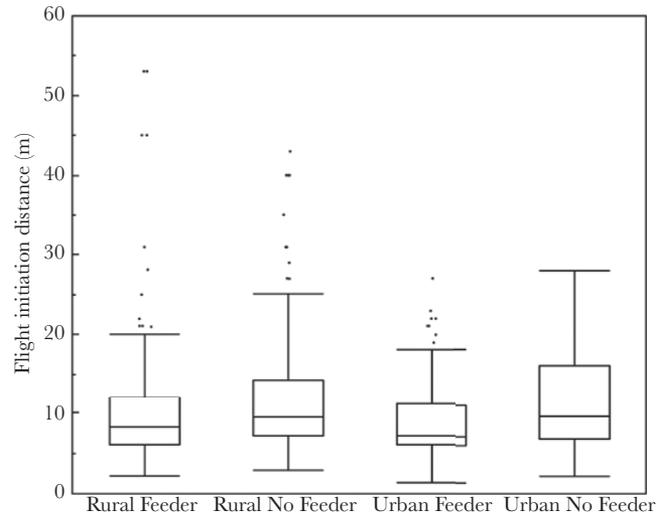


Figure 1
 Box plots of FID (m) in different species of birds in relation to habitat (rural or urban) and presence or absence of feeder. The box plots show medians, quartiles, 5th and 95th percentiles, and extreme values.

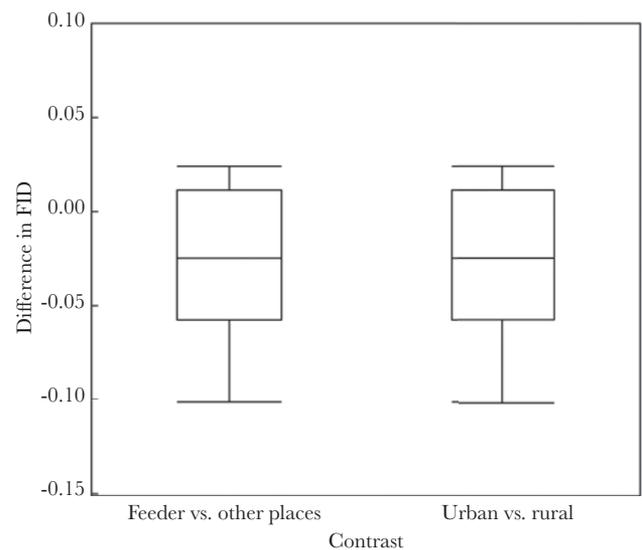


Figure 2
 Box plots of difference in FID between feeders and other places and between urban and rural habitats in 12 species of birds. The box plots show medians, quartiles, 5th and 95th percentiles, and extreme values. The mean negative values imply that FID is shorter at feeders than at other places and in urban than in rural habitats.

test, $U = -33\ 143$, $P < 0.0001$). This implies that there is a general reduction in FID in the presence compared with the absence of feeders. Likewise the difference in FID between urban and rural sites was -0.023 (SE = 0.018), $N = 12$, differing significantly from 0 (Figure 2; Wilcoxon matched-pairs signed-rank test, $U = -54544$, $P < 0.0001$). This implies that there is a general reduction in FID in urban compared with rural habitats. These 2 differences were significantly positively correlated (Kendall $\tau = 0.485$, $P = 0.028$), implying that the same species with a shorter FID in urban areas also had a shorter FID in areas near feeders (Figure 3).

DISCUSSION

The main finding of this study of FID in birds was that urban habitat and the presence of feeders independently and additively reduced FID compared with birds in rural habitats and in sites without feeders. Finally, the magnitude of the urbanization effect on FID was positively correlated with the effect of feeders, showing that species that were strongly affected by urbanization in terms of a reduction in FID were the same species that were strongly, but independently, affected by the presence of feeders.

FID of winter birds in Poland was reduced in urban compared with rural habitats and in birds at feeders compared with other sites. This effect of the presence of feeders on FID independent of the effect of urbanization is novel, and it raises questions about the role of the underlying mechanisms that have caused this divergence in FID among environmental factors. Although previous studies have shown that birds are “tame” when attending feeders (Robb et al. 2008), the present study is the first to quantify this as a general effect across species. We showed across a sample of 12 bird species that the effect of urban habitat on FID was positively correlated with the effect of feeders on FID. This correlation suggests that similar mechanisms may underlie these 2 effects and that species-specific traits make some species more prone to take risks than others. Møller (2009) and Møller and Garamszegi (2012) identified these as being life-history traits like fecundity and adult survival rate. This may arise because of a trade-off between food supply

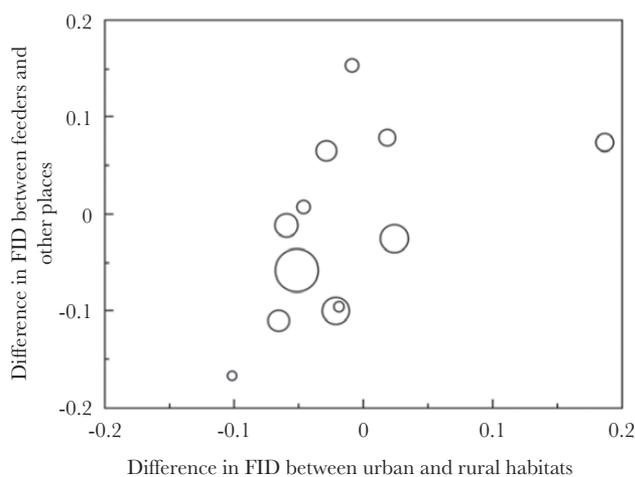


Figure 3

Difference in FID between feeders and locations without feeders in relation to difference in FID between urban and rural habitats in 12 different species of birds. The size of symbols reflects sample size. The positive relationship implies that species that have shortened their FID at feeders compared with other places are the same species that have shortened their FID in urban compared with rural habitats.

and predation risk (Tvardíková and Fuchs 2010). Urbanization constitutes a syndrome affecting a range of phenotypic characters from physiology, morphology, behavior, and life history to inter-specific interactions between predators and prey and between hosts and parasites (Møller 2014a). For example, urbanization in birds and tolerance of human proximity are known to correlate with changes in stress physiology (Deviche and Davies 2014) and changes in antipredator behavior (Møller and Ibañez-Álamo 2012; Cardilini et al. 2013).

Urbanization and feeders were correlated with a change in FID implying that urban habitat and the presence of feeders disproportionate reduced FID compared with rural habitat. The relative difference in FID between presence and absence of feeders in rural areas was 40% and 36% in urban areas. Even urban birds with feeders had a mean FID of 7 m, suggesting that there is scope for further reductions as shown by species that have been urbanized since long such as rock dove *Columba livia*, jackdaw *Corvus monedula*, and house sparrow *Passer domesticus* (Møller 2009). The positive correlation between the partial effect of urbanization and the partial effect of feeders (Figure 3) may suggest that it is similar factors that account for these 2 effects (Møller 2014a). We can exclude the possibility that differences in the quality or the quantity of food between urban and rural habitats accounted for the findings because the same kind of food was provided in feeders in the 2 habitats. Another possibility is that the predator community differed between urban and rural habitats because urban habitats have more cats, whereas rural habitats harbor more raptors, and such a difference in predators have been shown to affect FID and choice of display sites by singing birds (Møller 2011; Díaz et al. 2013).

Although we did not explicitly study possible mechanisms underlying changes in antipredator behavior between feeders and other places and between urban and rural habitats, our findings may merit a brief discussion of such mechanisms. Individuals are highly consistent in their FID among individual tests (e.g., Carrete and Tella 2011b; Møller and Garamszegi 2012; Møller 2014b), suggesting that there is little scope for habituation because habituation would imply a reduction in FID with increasing exposure to humans. Consistent with this interpretation, Møller (2015) reviewed 8 studies of habituation that all showed no significant evidence of habituation for FID. Phenotypic sorting would require directional movement of individuals with specific behavior. Even a single migrant per generation would eliminate any genetic population differentiation. Thus, significant population genetic structure within or across urban boundaries (Fulgione et al. 2000; Rutkowski et al. 2005; Baratti et al. 2009; Evans et al. 2009; Björklund et al. 2010) basically implies that there is little or no migration among such habitats. Finally, we consider our findings consistent with the effects of local adaptation because divergence in FID between urban and rural habitats is correlated with time since urbanization (Møller 2008) and because selective mortality of individuals with long FID during a particularly cold and snowy winter in Central and Northern Europe, but not in Southern Europe. This cold event resulted in a reduction in FID, although only in the parts of Europe experiencing this particularly cold spell, showing that FID indeed responds to intensified selection (Møller et al. 2013). Obviously, we cannot exclude more complex scenarios of multiple mechanisms acting simultaneously or interactively although such complexity would go against the principle of Occam’s razor.

In conclusion, we have shown that FID of birds in winter has diverged in response to urbanization and presence of birdfeeders. Because the magnitude of the 2 effects was positively correlated across species, this suggests that a common underlying cause may constitute the basis for this effect.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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