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Original Article

# Change in flight initiation distance between urban and rural habitats following a cold winter

Anders Pape Møller,[a] Tomas Grim,[b] Juan Diego Ibáñez-Álamo,[c] Gábor Markó,[d,e] and Piotr Tryjanowski[f]

[a]Laboratoire d'Ecologie, Systématique et Evolution, CNRS UMR 8079, Université Paris-Sud, Bâtiment 362, F-91405 Orsay Cedex, France, [b]Department of Zoology and Laboratory of Ornithology, Palacky University, 17. litopadu 50, CZ-77146 Olomouc, Czech Republic, [c]Departamento de Zooogía, Facultad de Ciencias, Campus Universitario de Fuentenueva s/n, Universidad de Granada, E-18071 Granada, Spain, [d]Behavioural Ecology Group, Department of Systematics, Zoology and Ecology, Eötvös Loránd University, 1/C Pázmány Péter sétány, H-1117 Budapest, Hungary, [e]Department of Plant Pathology, Corvinus University of Budapest, 44 Ménesi út, H-1118 Budapest, Hungary, and [f]Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, PL-60-625 Poznan, Poland

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Adaptation to proximity of humans should be particularly advantageous during adverse environmental conditions because the ability to withstand proximity to humans allows for exploitation of abundant food. We carried out flight initiation distance experiments in 207 bird species in 7 pairs of urban–rural areas from northern to southern Europe before and after the extremely cold winter of 2009–2010. Flight initiation distance in different species of birds on average became shorter after the cold winter, but only in resident urban populations (frequently exposed to humans) and not in migratory or rural populations of the same species. There were independent partial effects of human population density with an increase in flight initiation distance from before to after the cold winter of 2009–2010 at low population densities and a decrease at high population densities, and there was an independent effect of latitude with the flight initiation distance increasing from 2009 to 2010 at low latitudes and decreasing from 2009 to 2010 at high latitudes. The difference in flight initiation distance before and after the cold winter increased with severity of the winter across different study areas. Therefore, the difference in flight initiation distance between urban and rural habitats increased after the cold winter, especially in areas with the coldest winter weather. These findings are consistent with the hypothesis that a behavioral component of urbanization is due to reduced flight initiation distance in urban environments and suggest that weather conditions (i.e., cold winters) have played an important role in the process of urbanization.

*Key words*: **antipredator behavior, birds, flight initiation distance, urbanization.**

## INTRODUCTION

Urbanization occurs when wild organisms start to live in close proximity to humans and in that process change their behavior, morphology, physiology, and ecology (Luniak 2004; Dinetti 2009). Urban habitats are characterized by environmental conditions that differ from those of nearby rural habitats (Gaston et al. 2010). Consequently, animals living in cities suffer selective pressures different from those suffered by animals inhabiting rural areas (e.g., Klausnitzer 1989; Jokimäki et al. 1996; Stephan 1999; Evans, Gaston, Frantz, et al. 2009; Ibáñez-Álamo and Soler 2010a; Møller and Ibáñez-Álamo 2012; Tryjanowski et al. 2013). A striking difference is the higher density of humans that increases the frequency of animal–human interactions in urban areas. It is known since long that free-living animals avoid human contact, normally fleeing or at the very least remaining vigilant in their presence (Darwin 1868). However, close proximity of humans is associated with increased food availability during winter (e.g., Schoech and Bowman 2003; Gaston et al. 2005; Chamberlain et al. 2009) and reduced nest predation (e.g., Lindsay et al. 2008; Ibáñez-Álamo and Soler 2010b; Leighton et al. 2010; Ibáñez-Álamo et al. 2012; but see Chamberlain et al. 2009). Exploitation of food in proximity of humans and reduced nest predation may have selected for adaptation to human proximity (Møller 2012). For example,

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Address correspondence to A.P. Møller. E-mail: anders.moller@u-psud.fr.

corticosterone release is significantly reduced in urban populations compared with rural ones (Partecke et al. 2006; Schoech et al. 2007; French et al. 2008). Therefore, urbanization has a number of similarities to domestication that also constitutes a diverse array of adaptations to the close proximity of humans (Møller 2012). These include reduced fear responses, reduced corticosterone release in the presence of humans and other domestic animals such as dogs, reduced aggression, an increased ability to live at high population density, and many other changes (Hoagland 1928; Belyaev 1979; Kohane and Parsons 1987, 1988; Trut et al. 2009; Wirén et al. 2009; Ibáñez-Álamo and Soler 2010a; but see Samaš et al. 2013).

Most animals compromise between foraging and antipredator behavior because these activities are mutually exclusive (Ydenberg and Dill 1986; Caro 2005). In other words, fleeing from an approaching potential predator disrupts foraging, nest building, or any other activity. Furthermore, short flights are particularly energetically costly for birds with flight costs exceeding basal metabolic rate many times (Tatner and Bryant 1986). Flight initiation distance reflects the distance at which individuals take flight when approached by a potential predator (Hediger 1934). Because the density of human populations in urban areas is extremely high compared with nearby rural areas, urban habitats constitute suitable habitat only after adjustment to human proximity. Therefore, short flight initiation distances allow for coexistence with humans without disruption of foraging, low energy expenditure due to rare flights, and no release of stress responses. Thus, it is not surprising that urban birds have much shorter flight initiation distances than rural birds and that the difference in flight initiation distance decreases with time since colonization of urban habitats (Cooke 1980; Møller 2008a, 2009, 2010; Díaz et al. 2013).

Urbanization in birds was initially associated with migratory birds wintering in urban areas without any such wintering birds breeding there (Rosenberg and Viberg 1935; Stephan 1999). After wintering in urban areas for years, such incipiently urban individuals started to breed there and subsequently increased dramatically in abundance (Rosenberg and Viberg 1935; Stephan 1999; Møller et al. 2012). Individuals can overcome cold winters with snow cover either through migration to areas with less severe conditions (Berthold 2001) or through adaptation to proximity of humans (Rosenberg and Viberg 1935; Stephan 1999). If individuals that initially wintered near humans had short flight initiation distances (Møller 2009, 2010), this could select for increasingly sedentary behavior in urban compared with rural populations (Klausnitzer 1989; Gliwicz et al. 1994; Stephan 1999; Partecke and Gwinner 2007). Individuals with short flight initiation distances should do particularly well in urban compared with rural environments during cold winters, causing net growth in urban populations. In contrast, individuals with long flight initiation distances should do better in rural environments where there is less intense selection for ability to sustain proximity of humans and where predators continuously select for vigilance (Møller 2008a; Díaz et al. 2013). This should result in divergent selection on flight initiation distance between urban and rural habitats, eventually leading to genetic differentiation at the level of urban parks and other habitats during recent decades (Rutkowski et al. 2005; Baratti et al. 2009; Evans, Gaston, Sharp, et al. 2009; Björklund et al. 2010) and greater divergence between urban and rural populations at low latitudes where the abundance of predators is high and urbanization started earlier (Díaz et al. 2013). Thus, urbanized populations should reduce flight initiation distance following cold winters, whereas rural populations should not.

Studies of flight initiation distance in urban and rural habitats have shown that birds have considerably shorter flight initiation distances in urban habitats, mainly linked to differences in risk of predation and duration since urbanization (Cooke 1980; Møller 2008a; Díaz et al. 2013). Furthermore, bird species with short and invariable flight initiation distances in their ancestral rural habitat were particularly successful invaders of urban habitats (Møller 2008a, 2009, 2010), followed by an increased variation in flight initiation distance during subsequent establishment and adaptation to urban areas (Møller 2010). Additionally, flight initiation distances also have population consequences because species with long flight initiation distances have negative population trends apparently due to costs associated with frequent disturbance by humans, dogs, and other potential predators (Møller 2008b).

The main objective of this study was to test whether flight initiation distance changed consistently after a cold winter with predicted reductions in flight initiation distance in urban areas but not in rural areas. For this test, we exploited the extremely cold winter of 2009–2010 that had mean temperatures in some areas of Europe that were several degrees below the long-term normal (Cohen et al. 2010). We collected extensive data on flight initiation distance for multiple species of birds during the breeding seasons 2009 and 2010 before and after this cold winter. Our sample of geographical replicates (urban–rural site pairs, see Materials and Methods section) spanned a large latitudinal gradient from southern to northern Europe and thus included sites that varied with respect to local temperature deviation from the long-term normal (see Winter weather of 2009–2010 section). This enabled us to quantitatively test how the temperature deviation affected changes in flight initiation distance. In addition, we explored changes in flight initiation distance between 2009 and 2010 depending on migratory status because migrants are expected to suffer less from a very cold winter in temperate areas than residents. Thus, we predicted that resident populations in urban habitats would benefit from being able to sustain human proximity during a cold winter because such lack of fear would allow exploitation of food sources that could not or only to a lesser extent be exploited in rural habitats, which would not be the case for migratory species. Finally, we investigated whether the change in flight initiation distance was related to human population density, predicting a decrease in flight initiation distance from before to after the cold winter at sites with high human population density.

## MATERIALS AND METHODS

### Study areas

We studied flight initiation distances of birds when approached by a human in 7 cities (each paired with a nearby rural area) across Europe (Figure 1). The distance between urban and rural study sites ranged from 1 to 20 km. The benefits of this approach is that neighboring study sites will share most confounding environmental characteristics including weather, altitude, soil, and many other factors, and individual birds will not be prevented from moving between neighboring urban and rural habitats for distance reasons, although other factors such as philopatry and intraspecific competition may prevent such movement.

The urban study sites all had areas with multistorey buildings, single-family houses, roads, and parks, whereas nearby rural areas consisted of open farmland and woodland but did not contain

**Figure 1**
Geographic location of the 7 pairs of urban and rural study sites in Europe in relation to the major vegetation zones (subtropical, temperate, and continental-subarctic, from darker to lighter shading). For latitudes and city names, see Díaz et al. (2013).

continuous urban areas such as multistorey buildings, single-family houses, roads, and parks. This simple operational definition of urban areas has previously been adopted in other studies (e.g., Klausnitzer 1989; Gliwicz et al. 1994; Stephan 1999), and our definitions of "urban" follow the suggestion of Marzluff et al. (2001).

## Winter weather of 2009–2010

The winter of 2009–2010 was exceedingly cold compared with the normal for 1961–1990 (Cohen et al. 2010). Climate is based on normals derived for 30 years, with the normal for 1961–1990 being the most recent normal. The mean temperature during December–February 2009–2010 was derived from local meteorological information from the 7 study areas and was 0.90° colder than the 1961–1990 normal in Olomouc (Czech Republic), 1.10° colder in Orsay (France), 1.38° colder in Budapest (Hungary), 2.00° colder in Brønderslev (Denmark), 2.27° colder in Oslo (Norway), and 3.32° colder in Poznan (Poland), but 0.73° warmer than the 1961–1990 normal in Granada (Spain).

## Flight initiation distance of rural and urban birds

We collected a total of 9664 flight initiation distances for 295 populations of 207 species of birds during the summer 2009 before the cold winter of 2009–2010 and during the summer 2010 after the cold winter. We recorded flight initiation distances during the breeding seasons 2009 and 2010 using a modified technique of Blumstein (2006). A full description of the procedures and 3 different cross-validations of the data (among observers, among sites, and among years) are reported in Møller (2008a, 2008b, 2008c). In brief, when an individual bird had been located by the observer using a pair of binoculars, the observer moved at a normal walking speed toward the individual bird while recording the number of 1-m steps (Møller et al. 2008). The distance from the observer to the bird when it first took flight was recorded as the "flight initiation distance," whereas the "starting distance" was the distance from where the observer started walking up toward the bird and the location of the bird. If the individual bird was positioned in the vegetation, the height above ground was also recorded to the nearest meter (birds on the ground were assigned a height of 0). While recording these flight initiation distances, we also recorded date and time of day, and sex and age if external characteristics allowed sexing and aging with binoculars. Flight initiation distance and starting distance were estimated 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).

Starting distance is strongly positively correlated with flight initiation distance (e.g., Blumstein 2006), thereby causing a problem of collinearity. We eliminated this problem by searching habitats for birds with a pair of binoculars when choosing an individual for estimating flight initiation distance. In this way, we assured that most individuals were approached from a distance of at least 30 m, thereby keeping starting distances constant across species. Flight initiation distance was weakly negatively related to starting distance in a model that included species, age, habitat, country, and body mass as factors (partial $F_{1,9662} = 34.99$, $P < 0.0001$), explaining less than 0.3% of the variance. Thus, we did not include starting distance in our models.

## Migration status

We classified all populations as residents or migrants (migrating within Europe and North Africa or across the Sahara; Cramp and Perrins 1977–1994).

## Human population density

We extracted information on human population size and the area of cities from www.wikipedia.org. Human population density was estimated as population size divided by area.

## Statistical analyses

We were interested in differences in flight initiation distance before and after the cold winter. Therefore, we used $\log_{10}$-transformed distance in 2009 minus $\log_{10}$-transformed distance in 2010. We included this difference (in $\log_{10}$ units of meters) in flight initiation distance as the response variable in mixed models with normally distributed errors, whereas we included habitat (rural vs. urban), migration (resident vs. migratory), human population density ($\log_{10}$ transformed), and difference in mean winter temperature between 2009 and 2010 and the long-term mean between 1961 and 1990 (mean winter temperature of 1961–1990 minus mean winter temperature of 2009–2010) as fixed effects and species as a random effect (accounting for the variable number of populations per species). We used the difference in flight initiation distance rather than the absolute distances as a response variable. We $\log_{10}$-transformed human population size to normalize the variable. For the species with at least 2 populations, we estimated repeatability of the difference in flight initiation distance as the intraclass correlation coefficient (Becker 1984). We report means (standard error [SE]) throughout. All statistical analyses were made with JMP (SAS Institute Inc. 2012).

# RESULTS

A total of 39 species out of the 207 species had at least 2 estimates of change in flight initiation distance from before to after the cold winter of 2009–2010, allowing for a test of repeatability of change in flight initiation distance estimated as the intraclass correlation. However, there was no significant difference among species in difference in flight initiation distance ($F_{39,51}$ = 1.12, $r^2$ = 0.46, $P$ = 0.34; $R$ = −0.007, SE = 0.059), implying that different populations of the same species did not respond in a species-specific manner. This was probably because differences in flight initiation distance among populations of the same species mainly depended on local climatic conditions rather than on species-specific phenotypic traits. The absence of a species-specific effect also implies that there are no reasons to use phylogenetic comparative approaches to analyze the data because there are no differences among species (Møller and Birkhead 1994).

Overall, flight initiation distances before the cold winter of 2009–2010 were longer than flight initiation distances after the winter (Figure 2; Wilcoxon matched-pairs signed-rank test, $W$ = 208651.5, $n$ = 297 populations, $P$ = 0.0021). Differences in flight initiation distance before and after the cold winter, estimated as log-transformed mean flight initiation distance before minus log-transformed mean flight initiation distance after the winter of 2009–2010, decreased with increasing difference in winter temperature between 2009–2010 and the normal 1961–1990 (Figure 3; $F_{1,291}$ = 11.43, $r^2$ = 0.05, $P$ = 0.0008, slope [SE] = −0.026 [0.008]). This effect of difference in winter temperature ($F_{1,291}$ = 11.77, $r^2$ = 0.05, $P$ = 0.0007, slope [SE] = −0.026 [0.008]) was independent of human population density, which had an additional significant effect on difference in flight initiation distance (Table 1). This implies that in cities with higher human population density, flight initiation distance was longer before than after the cold winter, whereas in smaller cities, the opposite was the case. The distribution of change in flight initiation distance differed between rural and urban habitats (Figure 4A). For rural habitats, the difference was on average −0.024 (SE = 0.012), $n$ = 173 populations, not differing significantly from 0 ($t_{172}$ = −1.96, $P$ = 0.052). In contrast, the difference in flight initiation distance for urban populations was on average 0.040 (0.013), $n$ = 122 populations, differing significantly from 0 ($t_{121}$ = 3.11, $P$ = 0.0023). This implies that flight initiation distance decreased significantly in urban populations, but not in rural populations. None of the interactions were statistically significant (results not shown).

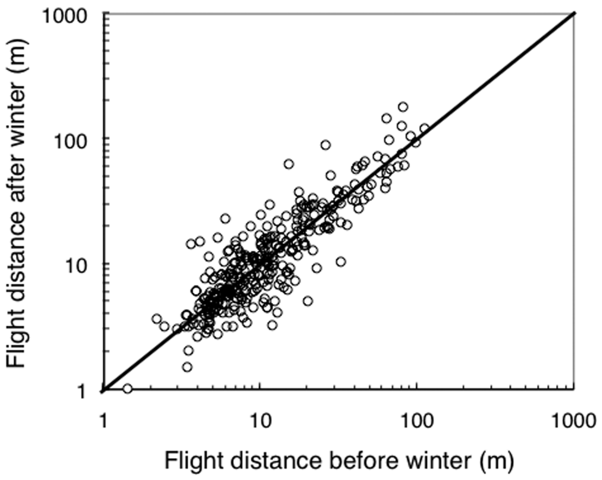

**Figure 2**
Mean flight initiation distance before and after the cold winter of 2009–2010 for populations of different species of birds. The line represents the null hypothesis of no change in flight initiation distance (i.e., $y = x$). There are more observations above than below the line.

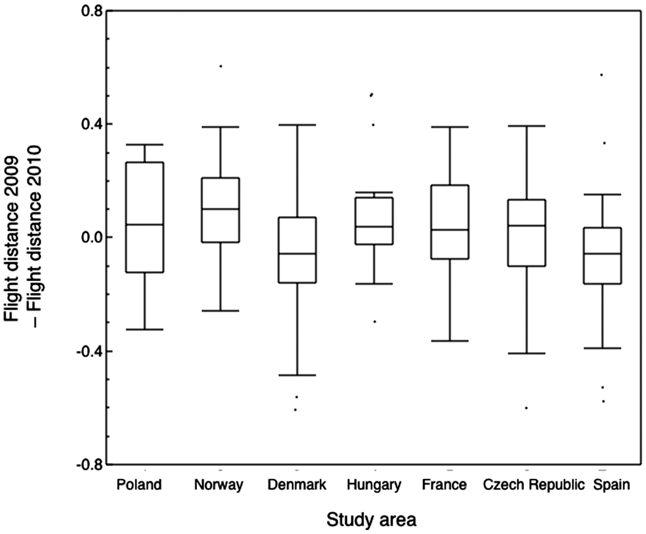

**Figure 3**
Box plots of difference in mean flight initiation distance before and after the cold winter of 2009–2010 for different study areas ranked from coldest (Poland) to warmest relative winter temperatures (Spain).

If we restricted the analysis of change in flight initiation distance before and after the winter of 2009–2010 to migratory species with paired rural and urban populations, the rural difference was on average 0.022 (0.053) and the urban difference was 0.033 (0.053), a difference that was not significant ($t_{24}$ = −0.02, $P$ = 0.99; Figure 4B). In contrast for resident species, the rural difference was on average −0.037 (0.026) and the urban difference was 0.074 (0.026), a difference that was statistically significant ($t_{64}$ = 2.67, $P$ = 0.0095). Thus, changes in flight initiation distance between rural and urban habitats were absent in migrants, whereas residents showed a significant reduction in flight initiation distance for urban populations.

A model of change in flight initiation distance in relation to migratory status, habitat, and human population density explained 7% of the variance (Table 1). Resident species changed their flight initiation distance compared with migrants (Table 1). Indeed, although residents reduced their flight initiation distance compared with the situation before the cold winter, there was no significant change for migrants (Table 1). There was an independent effect of habitat, with urban populations decreasing their flight initiation distance significantly, whereas that was not the case for rural populations (Table 1). In addition, there was an independent effect of latitude, with flight initiation distance increasing from 2009 to 2010 at low latitudes, whereas decreasing from 2009 to 2010 at high latitudes (Table 1). Finally, there was an independent partial effect of human population density with an increase in flight initiation distance from before to after the cold winter of 2009–2010 at low population densities and a decrease at high population densities (Table 1).

## DISCUSSION

Our results support the prediction that urban bird species significantly reduce their flight initiation distances after very cold winter conditions, whereas that is not the case for rural conspecifics. This suggests that the very cold winter of 2009–2010 (Cohen et al. 2010) constituted a significant episode of natural selection on resident bird species, with flight initiation distance in urban populations decreasing significantly, whereas there was no change in nearby

**Table 1**

**Mixed model of the difference in flight initiation distance between 2009 and 2010 in relation to urbanization, migration, and human population density for different populations of birds**

| Predictor | df numerator | df denominator | *F* | *P* | Estimate (SE) | Least square means (SE) |
|---|---|---|---|---|---|---|
| Migration | 1 | 108.6 | 5.21 | 0.024 | 0.027 (0.012) | Migrant: −0.010 (0.013); resident: 0.054 (0.019)* |
| Urbanization | 1 | 283.5 | 4.23 | 0.041 | −0.023 (0.011) | Rural: −0.006 (0.014); urban: 0.030 (0.017)* |
| Human population density | 1 | 292.0 | 16.76 | <0.0001 | 0.086 (0.021) | |
| Latitude | 1 | 291.5 | 10.78 | 0.0012 | 0.006 (0.002) | |

The random effect of species had a variance component of 0.0.00037, 95% confidence interval −0.0029 to 0.0022, accounting for 0.0% of the variance. A model without the random species effect provided qualitatively similar results. Difference was $\log_{10}$-transformed distance in 2009 minus $\log_{10}$-transformed distance in 2010. df, degrees of freedom.
*$P < 0.05$.

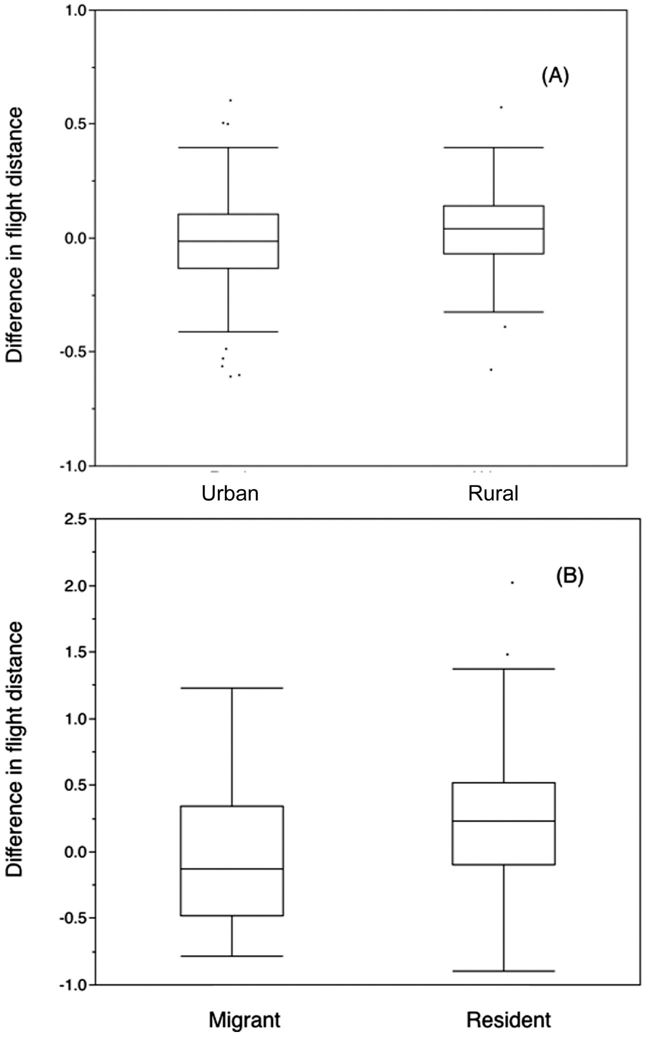

**Figure 4**
Box plots of difference in mean flight initiation distance before and after the cold winter of 2009–2010 ($\log_{10}$-transformed distance in 2009 minus $\log_{10}$-transformed distance in 2010) for (A) urban and rural and (B) migrant and resident populations of birds.

paired rural populations. Furthermore, there was an increase in flight initiation distances from 2009 to 2010 at low latitudes, whereas flight initiation distance decreased from 2009 to 2010 at high latitudes. Finally, within urban areas, there was an increase in flight initiation distance from before to after the cold winter of 2009–2010 at low human population densities and a decrease at high population densities.

Three possible mechanisms may account for these findings: phenotypic plasticity, phenotype sorting, and microevolutionary change. Phenotypic plasticity seems to be responsible for several behavioral changes of urban dwellers (reviewed in Sol et al. 2013). However, this first possibility is unlikely given that individual birds show a high degree of individual consistency of flight initiation distance across environments (Møller and Garamszegi 2012; but see Rodríguez-Prieto et al. 2009). The large changes that we reported here are inconsistent with this explanation. Second, phenotypic sorting would rely on movement of individuals with specific flight initiation distances. Thus, urban birds with long flight initiation distances should have emigrated to rural habitats. This explanation seems unlikely given the significant genetic differentiation of urban birds and their overall short dispersal distances (Rutkowski et al. 2005; Baratti et al. 2009; Evans, Gaston, Sharp, et al. 2009; Björklund et al. 2010). Third, the changes may reflect microevolutionary changes (Hendry et al. 2007) caused by higher mortality among urban individuals with longer flight initiation distances suffering from costs associated with frequent encounters with humans such as reduced food intake, high energy expenditure, and other physiological costs (Tatner and Bryant 1986; Ydenberg and Dill 1986; Sapolsky 2000). We consider the latter explanation to be the most likely.

Our findings are in agreement with those of other studies highlighting the importance of flight initiation distance as an aspect of antipredator behavior for urbanization (Cooke 1980; Stephan 1999; Møller 2008a; Díaz et al. 2013), especially under extreme weather conditions. We can exclude that the changes documented in our study were due to density-dependent effects because population density of birds generally decreases following cold winters (Boyd 1964; Cawthorne and Marchant 1980; reviewed in Newton 2003). Reduced population density following a cold winter should allow individuals to exploit resources further away from human proximity. Our results suggest that ambient temperatures during winter in urban landscapes may impose important costs on birds despite temperatures in urban habitats often being higher than in the surrounding rural areas (Evans 2010).

An alternative explanation for our results could be habituation (Runyan and Blumstein 2004). However, if that was the case, we should expect greater habituation and shorter flight initiation distances in more densely populated cities, especially after a cold winter with many birds approaching humans to find food. There was a decrease in flight initiation distance from before to after the cold winter of 2009–2010 in study areas with high human population densities, whereas there was an increase at low human population densities. Bird species that successfully invaded urban areas had much shorter flight initiation distances already in their ancestral rural habitats (Møller 2009), although the variance in flight initiation distance was reduced following colonization of urban habitats (Møller 2010). This initial loss of phenotypic variation in flight initiation distance was subsequently followed by an increased variation (Møller 2010). The findings reported here cannot easily be reconciled with effects of habituation. Furthermore, previous studies have also found little evidence consistent with habituation (Carrete and Tella 2010; Møller 2010; Møller and Garamszegi 2012).

We did not find a significant species-specific effect on difference in flight initiation distance across the cold winter of 2009–2010. In fact, we should not even expect such an effect because of differences in urbanization history among populations within species (Evans, Gaston, Frantz, et al. 2009), and differences in climate and human population density among cities leading to inconsistent changes in different populations of the same species.

We found a difference in change in flight initiation distance between resident and migrant species as only residents seemed to be affected by the cold winter. Superabundant food, high temperatures, and long growing seasons are advantageous in seasonal environments where an important cause of death is mortality caused by starvation during winter (Lack 1954). Therefore, any adaptation that facilitates the exploitation of such resources in winter, like a reduction in fear responses, could facilitate survival of residents (Klausnitzer 1989). In contrast, migrants do not experience such costs because they spend the winter under generally warmer climatic conditions far away from cold temperate winters (Berthold 2001).

This study also has implications for the study of changes in behavior of animals in response to climate change. Although we might expect changes in behavior because of increasing temperatures, especially at high latitudes, such changes may be reversed during single cold winters that arise as a consequence of changes in major weather patterns (Cohen et al. 2010). That was the case for the effects of the North Atlantic Oscillation on winter conditions in large parts of central and eastern Europe in 2009–2010 (Cohen et al. 2010). A long run of mild winters may allow high survival rates and relaxation of selection on behavior that facilitates the close proximity of humans and birds. When a very cold winter then appears, as was the case during 2009–2010, selection for coping with human proximity may be particularly strong and result in changes in fear responses, as our study has documented.

In conclusion, mean flight initiation distance in urban populations of birds was reduced considerably following a very cold winter, but not in nearby rural populations of the same species. This effect was especially strong in urban areas with the highest human population densities, at high latitudes, in areas with the largest decrease in temperatures compared with long-term normals and in resident species compared with migrants. All these lines of evidence are consistent with the hypothesis that weather conditions (i.e., cold winters) play an important role in the adaptation of birds to urban habitats.

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