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Article

Avian preference for close proximity to human habitation and its ecological consequences

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Abstract

Human proximity often have negative consequences for wildlife. However, animals may also benefit from human proximity in terms of availability of resources and protection against predators and parasites. We recorded the distance between all birds detected during the breeding season along 18 5-km transects and the nearest inhabited house in three areas of 50 km² in Spain, France, and Denmark. More than three quarters of birds were located closer than 100 m to the nearest house, while the null expectation was less than a third. Mean distance for species was correlated with degree of bird urbanization and with flight initiation distance. Habitat specialist species with small breeding territories tended to live closer to houses. Birds from species having more broods per year, larger annual fecundity and lower nest predation rate lived closer to human habitation. Breeding range size, population density, and continental breeding population sizes were larger for species living closer to human habitation. Most relationships between distance to houses and bird traits had a strong phylogenetic signal, but most additive trait effects remained after phylogenetic correction. Proximity to human habitation was a main driver of the distribution of birds, with most individuals and species tightly linked to inhabited houses. Living close to human habitation was associated with success in the colonization of urban habitats and with consistent changes in distribution, abundance, behavior, and life history. Replicated measurements of the spatial and temporal variation in these distributions may be useful for monitoring and analyzing the ongoing process of organisms' urbanization.

Key words: birds, distance to nearest house, flight initiation distance, humans, refuge, urbanization.

More than half of all humans live in urban areas, and even larger proportions are projected to live there in the near future (United Nations 2015). Land is increasingly needed for fulfilling growing human habitation demands. As a result, urban areas are expanding at an unprecedented rate, and large fractions of the Earth's surface are being covered by buildings as a result (e.g., Seto et al. 2012; Hennig et al. 2015). Nearby human presence is often shown to have negative consequences for wildlife. In fact, many studies have documented these negative effects by comparing wildlife abundance and diversity along rural–urban gradients (McDonnell and Hahs 2008; Gagné and Fahrig 2011),

or according to regional human density (Gagné et al. 2016) or distance to urban areas, roads or other developments (Martínez et al. 2003; Palomino and Carrascal 2007; Benítez-López et al. 2010; Clarke et al. 2013). Nevertheless, these studies have also found species-specific neutral or even positive effects of nearby human developments.

Animals may gain significant benefits from human proximity in terms of availability of food and water and protection against predators and parasites (e.g., Møller 2012; Díaz et al. 2013, 2015; Møller et al. 2016; Møller and Díaz 2018, and references therein). Species able to live close to humans in urban habitats have often vastly

expanded their abundance and distribution to the extent of having become cosmopolitan (Gaston 2010; Gil and Brumm 2014), because such species are more successful invaders when released outside their original distribution range (Møller et al. 2015a; Sol et al. 2016).

Urbanization is the biological process by which living organisms colonize, adapt to the urban environment and eventually expand there (Gil and Brumm 2014). Mechanisms underlying successful urbanization largely remain to be determined (Sol et al. 2013; Díaz et al. 2015; Samia et al. 2017), although several behavioural and life-history traits are consistently associated with urbanization (Møller 2009; Carrete and Tella 2011; Sol et al. 2013; Concepción et al. 2015; Møller and Díaz 2018). Tolerance to human disturbance has been proposed to be a key factor involved in successful coexistence with humans (Díaz et al. 2013, 2015; Møller 2015; Samia et al. 2015). This is usually estimated as Flight Initiation Distances (FID), the distance at which individuals take flight when approached by a human under standardized conditions (Blumstein 2006). Individuals that tolerate human proximity would be better able to exploit resources close to human habitation, but also save time and energy not allocated to flushing due to approaching humans (Carrete et al. 2016; Samia et al. 2017; Møller and Díaz 2018). Benefits from this association would then translate into higher abundance, both within and outside cities as far as inhabited buildings are present, and wider distribution.

Here, we quantified the association between the distribution of bird species during breeding and inhabited houses to assess the importance of human proximity as a factor determining their local distribution and abundance. Rather than classifying species or populations as urbanized or not, or to estimate the degree of urbanization from differences in abundance among rural and urban populations, we directly measured the distribution of individuals with respect to proximity to occupied houses during the breeding season. This procedure allowed us to obtain large samples sizes of a large number of species to analyze the likely causes and consequences of wildlife proximity to human influence. We predicted that (1) species with individuals that are distributed closer to humans should be classified as more urbanized by the estimates of urbanization developed so far (yes/no classifications, time since first breeding inside cities, use of feeders, and difference in abundance between paired urban and rural populations; Sol et al. 2014; Møller et al. 2012, 2015c). Then, we identified the benefits of habitat choice in terms of availability of superabundant food, reduced risk of predation and parasitism and reduced risk-taking behavior, while considering the costs in terms of risk of mortality, and develop explicit predictions on variation in traits linked to these benefits and costs. We also predicted that (2) FID and mean distance of birds to human habitation should be positively correlated, and that birds with closer proximity to humans would show increased tolerance of human presence due to lower risk of predation (Samia et al. 2015, 2017); (3) bird species distributed closer to human habitation during breeding should enjoy longer breeding seasons, increased reproductive success and reduced rates of nest predation due to the effects of buildings on microclimate (Møller et al. 2016) and reduced predator abundance (Møller, 2012); and (4) breeding range, population size and population density of such species should increase with mean proximity to human habitation, due to positive effects of distance to buildings on breeding performance and predation rate. We tested these predictions in a large data set on breeding birds in the Western Palearctic.

Materials and Methods

Study areas

The study was conducted in three small inland European cities with low industrial development: Toledo, Spain; Orsay, France; and Brønderslev, Denmark. The study areas are dominated not only by urban habitats (60%), but also include forest and farmland (20% each in Toledo and Orsay, and 5% forest and 35% farmland in Brønderslev). Urban habitats have >50% built-up area and >10 buildings/ha, whereas farmland has 5–20% and <2.5/ha, respectively (Marzluff et al. 2001). Forested areas are not cultivated and have isolated buildings. Study areas were chosen to measure distribution of individuals according to human habitation both inside cities and in surrounding nearby rural areas.

Distance to human habitation

Six transects of 5 km each were located in 50-km² areas centred in each city (39° 51' N, 4° 2' W, 48° 69' N, 2° 18' W, 57° 25' N, 10° 00' W for Toledo, Orsay, and Brønderslev, respectively). Three transects crossed urban habitats and three rural habitats, and they were set to sample as thoroughly as possible habitat variation (forest cover, house densities, urban parks, open farmland, etc.) within study areas. Transects were surveyed in April–May 2015 (Toledo), April–May 2012 (Orsay), and May–June 2012 (Brønderslev), during the main breeding season at a time when all migratory birds including the latest migrants had arrived to the breeding grounds. Each transect was surveyed once, from sunrise to 3 h later. Rural and urban transects were run on alternate days with no cloud cover and little or no wind, with an equal amount of time allocated to either rural or urban habitats.

Distance to the nearest inhabited house, i.e., with evident signs of being currently occupied, was recorded for all individual bird detected along transects, generally within bands 50 m wide. Occasional sightings of birds outside these bands were also included if their exact position could be established accurately. We considered that inhabited houses were direct sources of continuous human influence, whereas other developments such as roads, power lines or marketplaces have more variable and discontinuous effects (e.g., Díaz et al. 2011). Distances were measured from the point where the individual was first observed. We used a Nikon Forestry 550 hypsometer to measure directly distances if close to the transect line (i.e., if the observer could reach easily the exact point), and by triangulation of measured distances to the individual and to the nearer house if far away. Locations exceeding 500 m (67 out of 9732, 0.7%) were recorded on a fine scale map and measured with Google Earth. Log₁₀-transformed distances were highly repeatable among species ($r = 0.87 \pm 0.00$ SE, $F_{60, 6267} = 48.30$; $r = 0.37 \pm 0.02$, $F_{68, 1634} = 15.08$; $r = 0.44 \pm 0.00$, $F_{61, 1638} = 21.16$, $P < 0.0001$ for Spain, France, and Denmark, respectively; Becker, 1984; Lessells and Boag, 1987). Mean (SE) distance to the nearest human habitation was estimated for all species in the three study areas.

The expected distance to the nearest inhabited house was estimated by random allocation of 100 data points on maps of the three study areas. This resulted in an expected distance of 136 m (SE = 1.5) in Toledo, 133 m (SE = 5) in Orsay, and 140 m (SE = 6) in Brønderslev. Consequently, 30.4% (SE = 4.1) of random points were located closer to 100 m from the nearest inhabited house. As transects were established haphazardly within study areas, we assumed that mean distances of transects to houses were the same as mean distances measured from random points. We tested this expectation in the

Toledo study area by measuring distance to houses from 102 points randomly selected along the six transects (17 points/transect) within a band of 50 m at either side. As expected, mean distances from random points and from points along transects did not differ (t -test on \log_{10} -transformed distances; $t_{202} = -1.12$, $P = 0.262$; 136.1 ± 14.6 m vs. 162.3 ± 18.8 m, respectively).

Urbanization estimates

Four variables measuring the relative urbanization success of each species were considered: (1) whether a species was considered urbanized or not (after Møller, 2009), (2) whether a species used bird feeders located within urban habitats or not (after Møller et al. 2015c), (3) the estimated year of urbanization for each species in each study area (after Møller et al. 2012), and (4) the difference in population density between paired urban and rural habitats (after Møller et al. 2012). Densities were measured by means of standard point count censuses of breeding birds with unlimited recording distance (e.g., Voříšek et al. 2010), twice during the breeding season with an interval of 3–4 weeks between the two series of point counts, during spring 2010 in both urban and rural habitats in the three study areas (50 points by habitat and study area, thus resulting in a total of 300 points).

Flight initiation distance

The flight initiation distance (FID) of an animal when approached by a human is a widely used estimate of the level of risk taking (Samia et al. 2017). FIDs were recorded during the breeding seasons 2009–2010 in the three study areas (Díaz et al. 2013). Observers (APM in Orsay and Brønderslev and MD in Toledo) moved at a normal walking speed towards individual birds located with a pair of binoculars while recording the number of steps. If the individual was positioned in the vegetation, the height above ground was recorded to the nearest meter. FID was 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). Mean and SD of FIDs for each species were computed from data gathered in both rural and paired urban sites in each study area.

Population and life history traits

We extracted the mean species-specific values for the western Palearctic of several relevant population and life-history traits from the literature, as it was logistically impossible to obtain local data for most species.

Body mass was recorded as the mean mass of males and females from the breeding season, as reported by Cramp and Perrins (1977–1994). If more than one estimate was reported by that source, we used that with the largest sample size. Maximum number of breeding attempts per year and mean clutch size were also estimated from the same source. Information on habitat specialization (estimated as the number of breeding habitats exploited by each species) was obtained from Julliard et al. (2006), while information on breeding coloniality and the size of breeding territories were obtained from Cramp and Perrins (1977–1994).

We estimated susceptibility to collision with windows by relying on a database collected by the taxidermist Johannes Erritzøe. Taxidermists in Denmark are by law required to record information on the cause of death of all specimens that they receive. We estimated the observed frequency of casualties from collision with windows from the data collected by Johannes Erritzøe in Southern

Jutland, Denmark. We obtained expected frequencies from extensive point counts of breeding birds in the same general study area (Møller et al. 2011). An index of susceptibility to collision with windows was estimated as the \log_{10} -transformed observed frequency minus the \log_{10} -transformed expected frequency, adding one to the observed and the expected frequencies before transformation. Møller et al. (2011) report further details about these estimates of susceptibility. Information on nest predation rate was obtained from Cramp and Perrins (1977–1994).

We estimated breeding distributions of the species in the Western Palearctic from the electronic version of Cramp and Perrins (1977–1994) by importing these maps into Adobe Photoshop, separating summer, resident and winter distributions. Next, we imported files containing single distribution patches into the program Image from NIH, and estimated the number of pixels occupied by summer and resident distributions reflecting breeding ranges. Finally, we converted the number of pixels to km^2 by estimating the area of five islands and peninsulas of known size: British Isles, Iceland, Svalbard, Novaya Zemlya, and the Iberian Peninsula, using the same map as a reference.

Population sizes reported by Burfield and van Bommel (2004) were the total number of breeding pairs in the Western Palearctic west of the Ural Mountains, obtained in a consistent way from national bird census programs in all countries. We used the mean of the reported minimum and maximum estimates.

Population density was estimated as population size in the Western Palearctic divided by breeding range size in the Western Palearctic. Local population density was estimated from the point counts made in 2009–2010 (see above and Møller et al. 2012).

Statistical analyses

Relationships between mean distance to the nearest occupied house in each study area and its potential ecological and life history correlates were tested by means of linear regressions on data transformed to meet normality and homoscedasticity requirements following Zar (1999). Mean distances, number of habitats, territory and range sizes, and population sizes and densities were \log_{10} -transformed, and nest predation and window collision rates were square-root arcsine transformed. The wide among-species variation in sample sizes available for distance to the nearest occupied house (between 1 and 1960 observations; Supplementary Material) was accounted for by weighting data by \log_{10} -transformed sample sizes (Garamszegi and Møller 2010). Tests were carried out with the STATISTICA 7.0 software.

Shared phylogenetic descent may bias results because different observations are not statistically independent since taxa have a shared phylogenetic history that varies among species. To control for the effect of phylogenetic relationships, we used phylogenetic generalized least square regression (PGLS) models as implemented in the R statistical environment, using the libraries *ape*, *MASS* and *mutnorm* and the function *pglm3.3.r*, testing whether the phylogenetic scaling parameter λ , which measures statistical dependence due to phylogenetic relationships, differed from 0 (Freckleton et al. 2002). When common descent effects were significant, we combined variance factors due to phylogenetic (λ) and weighting (W) effects of sampling effort following Garamszegi and Møller (2007), also using *pglm3.3.r*. Different populations of the same species were treated as polytomies with a constant small genetic distance of $1 \cdot 10^{-10}$ between conspecific populations (see Díaz et al. 2013 for a similar approach). We obtained the consensus tree for the bird species with available data using the Mesquite

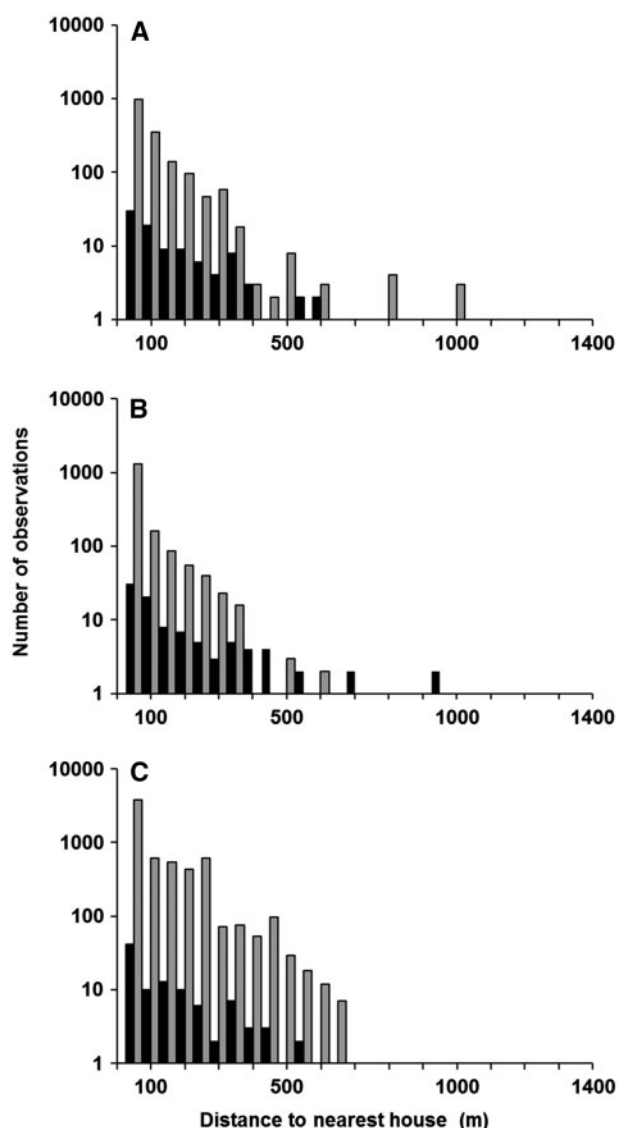


Figure 1. Frequency distribution of distance of birds during breeding (grey bars) and random points (black bars) to the nearest house (m) in (A) Orsay, France, (B) Brønderslev, Denmark and (C) Toledo, Spain. Sample sizes are 1703, 1700 and 6328, respectively, for birds, and 100 each for random points. Note logarithmic scale of the y-axis.

software (Maddison and Maddison 2011) on 100 trees extracted from the phylogeny published by Jetz et al. (2012). The phylogenetic hypothesis can be found in [Supplementary Appendix](#).

Results

A total of 86.5% of all birds were located within a distance of 100 m from the nearest house in Denmark ($n=1,700$), while 77.3% of all birds were within a distance of 100 m from the nearest house in France ($n=1,703$) and 69.0% in Spain ($n=6,328$; [Figure 1](#)). There was a significant difference in distance to the nearest house among species (ANOVA; $F=38.33$, $df=1, 9617$, $P<0.0001$). Mean distance for the 114 species ranged from 1 to 775 m, mean (SE) = 137.3 m (10.6). Distance to the nearest house differed among countries ($F=3.63$, $df=76, 9539$, $P<0.0001$; species \times country interaction in a two-way ANOVA on

log-transformed distances), although mean distances for shared species were strongly positively correlated among countries ($r_{30}=0.53$, $P=0.002$, $r_{25}=0.66$, $P<0.0001$ and $r_{42}=0.67$, $P<0.0001$ for Spain–France, Spain–Denmark, and France–Denmark comparisons, respectively).

Bird species that were classified as urbanized had shorter distances to the nearest house than species that were classified as rural [[Table 1](#), least square means (SE), back-transformed, rural = 159.12 m (1.12), urban = 57.91 m (1.07)]. Mean distance to the nearest house was positively correlated with the estimated year of urbanization ([Table 1](#), [Figure 2A](#)). The mean distance to the nearest house was negatively correlated with the difference in population density in urban minus density in rural habitats ([Table 1](#), [Figure 2B](#)). Therefore, species that lived closer to human habitation had much higher population density in urban than in rural habitats. Bird species that used feeders had shorter distances to the nearest house than bird species that did not use feeders [[Table 1](#), least square mean (SE) feeder users = 54.79 m (1.12); not feeder users = 88.65 m (1.08)].

Flight initiation distance and mean distance of breeding birds to human habitation were positively correlated ([Table 1](#), [Figure 3](#)). Habitat generalism (Julliard et al. 2006) was associated with distance to the nearest house with species breeding next to houses being habitat specialists ([Table 1](#), [Figure 4A](#)). Distance to the nearest house was shorter in colonial than in solitary species [[Table 1](#), mean (SE) colonial = 42.65 m (1.15), solitary 76.18 m (1.08)]. Distance to the nearest house increased with breeding territory size ([Table 1](#), [Figure 4B](#)). Thus, species breeding close to houses were habitat specialists with small territories that lived colonially.

The annual number of broods decreased with increasing distance to the nearest house ([Table 1](#), [Figure 5A](#)). Likewise, annual fecundity tended to decrease with increasing distance to the nearest house ([Table 1](#)), although the effect was only marginally significant. Nest predation rate increased with distance to the nearest house ([Table 1](#), [Figure 5B](#)), implying that species breeding near houses had absolutely and relatively large reproductive success. Susceptibility to collision with windows decreased with distance to the nearest house ([Table 1](#)). Thus, bird species breeding closer to human habitation were more likely to die due to collision with windows.

Breeding range size did not vary consistently with increasing distance from the nearest house ([Table 1](#)), but both local mean population density and mean density across the Palearctic range decreased with increasing distance to the nearest house ([Table 1](#)). Breeding population size in the Western Palearctic decreased with increasing distance to the nearest house ([Table 1](#), [Figure 6](#)). Finally, body mass was not related to distance to the nearest occupied house ([Table 1](#)), implying that body mass was not a confounding variable in these analyses.

Most relationships between distance to houses and population and life history traits had a strong phylogenetic signal ($\lambda=0.40 \pm 0.05$ SE; $n=17$ tests; [Table 1](#)). However, significant trait effects remained after phylogenetic correction in most significant comparisons (12 out of 14). The only ones that became statistically non-significant were the negative relationships between distance to the nearest house and coloniality and susceptibility to collision with windows. Overall, effect sizes (as estimated by adjusted r^2 values of regression models) when correcting for effects due to similarity caused by common phylogenetic descent were 6% lower on average than effect sizes for uncorrected tests (SE = 0.01; $n=17$; [Table 1](#)).

Table 1. Effects of selected ecological and life-history traits on mean distance to occupied houses (m; log-transformed)

| Variable | Uncorrected data | | | | | | Phylogenetically corrected data | | | | | | | | | |
|---|------------------|------|-------|--------|--------|------------|---------------------------------|------------|--------|-------|---------|------|-------|--------|--------|------------|
| | β | SE | F | df | P | Adj. r^2 | λ | χ^2_1 | P | W | β | SE | F | df | P | Adj. r^2 |
| Flight Initiation Distance (FID) (m) | 0.26 | 0.09 | 7.85 | 1, 163 | 0.0060 | 0.04 | 0.60 | 6.69 | 0.0097 | 13.00 | 0.39 | 0.13 | 8.73 | 1, 145 | 0.0037 | 0.05 |
| Year of urbanization | 0.01 | 0.00 | 59.98 | 1, 129 | 0.0000 | 0.31 | 0.00 | 0.00 | 1.0000 | | | | | | | 0.31 |
| Difference in population density between urban and rural habitats | -0.14 | 0.03 | 20.37 | 1, 162 | 0.0000 | 0.11 | 0.00 | 0.00 | 1.0000 | | | | | | | 0.11 |
| Urbanized (1: yes; 0: no) | -0.49 | 0.06 | 61.74 | 1, 195 | 0.0000 | 0.24 | 0.32 | 2.81 | 0.0937 | 13.00 | -0.35 | 0.06 | 33.91 | 1, 191 | 0.0000 | 0.15 |
| Feeder use (1: yes; 0: no) | -0.25 | 0.07 | 12.51 | 1, 195 | 0.0000 | 0.05 | 0.49 | 7.67 | 0.0056 | 3.00 | -0.23 | 0.09 | 7.03 | 1, 191 | 0.0087 | 0.03 |
| Habitat generalism (No. habitats used) | 0.60 | 0.14 | 18.13 | 1, 193 | 0.0000 | 0.08 | 0.48 | 13.25 | 0.0003 | 4.00 | 0.65 | 0.17 | 15.32 | 1, 189 | 0.0001 | 0.07 |
| Coloniality (1: colonial; 0: solitary) | -0.20 | 0.07 | 13.27 | 1, 162 | 0.0004 | 0.07 | 0.48 | 8.42 | 0.0037 | 3.00 | -0.17 | 0.10 | 3.02 | 1, 191 | 0.0841 | 0.01 |
| Breeding territory size (ha) | 0.39 | 0.08 | 26.34 | 1, 144 | 0.0000 | 0.15 | 0.00 | 0.01 | 1.0000 | | | | | | | 0.15 |
| Susceptibility to collision with windows (%) | -0.10 | 0.04 | 5.04 | 1, 150 | 0.0260 | 0.03 | 0.49 | 12.18 | 0.0005 | 2.00 | -0.07 | 0.06 | 1.52 | 1, 134 | 0.2196 | 0.00 |
| Broods/year (No.) | -0.11 | 0.02 | 21.25 | 1, 195 | 0.0000 | 0.09 | 0.51 | 5.95 | 0.0147 | 10.00 | -0.12 | 0.04 | 10.83 | 1, 191 | 0.0012 | 0.05 |
| Annual fecundity (No. of broods \times mean clutch size) | -0.01 | 0.01 | 3.44 | 1, 195 | 0.0650 | 0.01 | 0.53 | 10.57 | 0.0012 | 2.00 | -0.01 | 0.01 | 2.24 | 1, 191 | 0.1358 | 0.01 |
| Nest predation rate (%) | 0.47 | 0.15 | 9.92 | 1, 161 | 0.0020 | 0.05 | 0.49 | 4.59 | 0.0322 | 9.00 | 0.48 | 0.19 | 6.25 | 1, 143 | 0.0136 | 0.04 |
| Breeding range (km ²) | -0.05 | 0.07 | 0.46 | 1, 195 | 0.5001 | 0.00 | 0.51 | 11.12 | 0.0009 | 2.00 | -0.09 | 0.11 | 0.77 | 1, 191 | 0.3810 | 0.00 |
| Local mean population density (No. of birds/count) | -0.05 | 0.01 | 12.71 | 1, 197 | 0.0001 | 0.06 | 0.48 | 7.97 | 0.0048 | 3.00 | -0.03 | 0.02 | 4.25 | 1, 191 | 0.0405 | 0.02 |
| Palaearctic population density (No. of pairs/10 ha) | -0.20 | 0.04 | 24.47 | 1, 195 | 0.0000 | 0.12 | 0.47 | 5.82 | 0.0159 | 4.00 | -0.13 | 0.06 | 5.23 | 1, 191 | 0.0233 | 0.02 |
| Palaearctic population size (No. of pairs) | -0.20 | 0.04 | 28.76 | 1, 195 | 0.0000 | 0.12 | 0.47 | 5.32 | 0.0211 | 4.00 | -0.14 | 0.05 | 7.34 | 1, 191 | 0.0074 | 0.03 |
| Body mass (g) | 0.11 | 0.07 | 2.54 | 1, 195 | 0.1126 | 0.01 | 0.51 | 10.32 | 0.0013 | 2.00 | 0.06 | 0.09 | 0.40 | 1, 191 | 0.5294 | 0.00 |

Results for linear regression models weighted by log-transformed sample sizes are given, both uncorrected and corrected for phylogenetic relatedness among bird species. λ : phylogenetic correction factor, with associated χ^2 and P -values testing the H_0 : $\lambda = 0$; W : weighting factor for sample sizes in the phylogenetic analyses. Boldface indicates significant results. See text for data transformations.

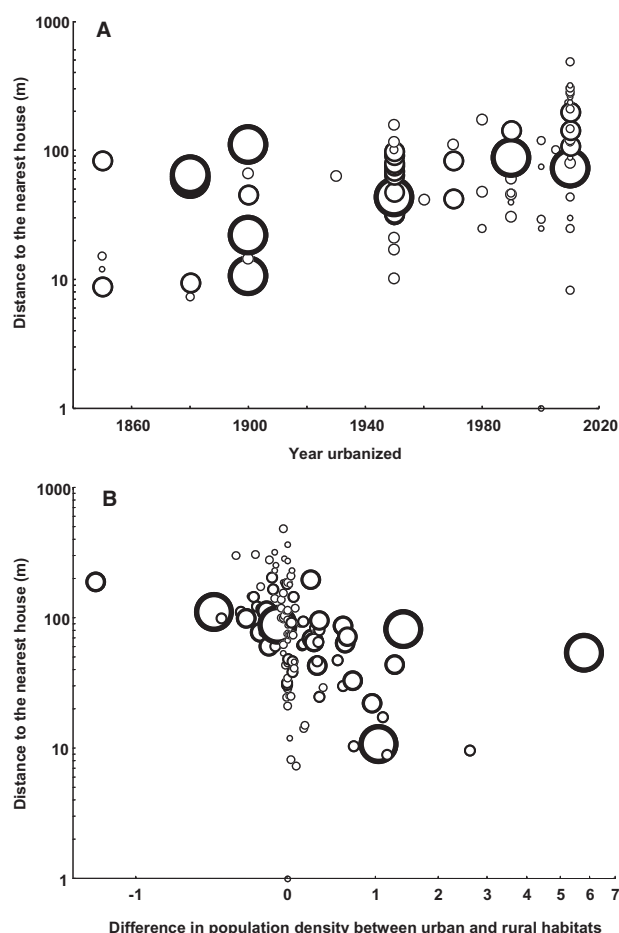


Figure 2. Mean distance to the nearest house (m) in different species of birds in relation to (A) estimated year when the species became urbanized, and (B) the difference in breeding population density between urban and rural habitats. Circles of different size reflect differences in sample size.

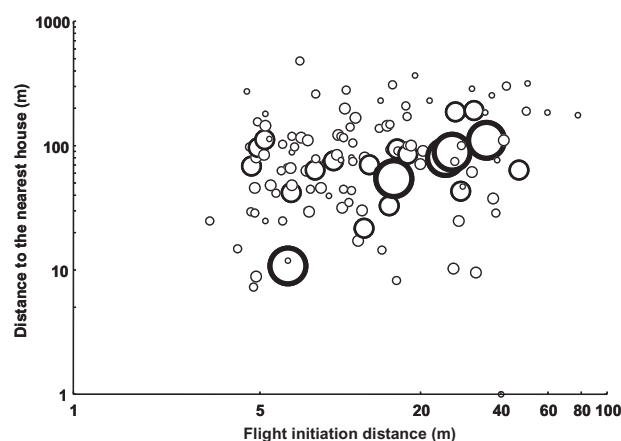


Figure 3. Mean flight initiation distance (m) in different species of birds in relation to mean distance to the nearest house (m). Circles of different size reflect differences in sample size.

Discussion

We have documented tight associations between the spatial distribution of breeding birds and the proximity of human habitation across three study plots in three European cities. These findings suggest that the proximity to inhabited houses is a main driver of the distribution and the abundance of birds in rural and urban landscapes around human settlements. We have also proposed possible underlying mechanisms, by showing how this association between human habitation and abundance and distribution of birds was linked to large-scale differences in density and total population size across the Western Palearctic.

Here we have shown that the association between breeding birds and human habitation was consistent not only within and among study plots, but also among countries. While many studies have documented elevated densities of birds in urban habitats

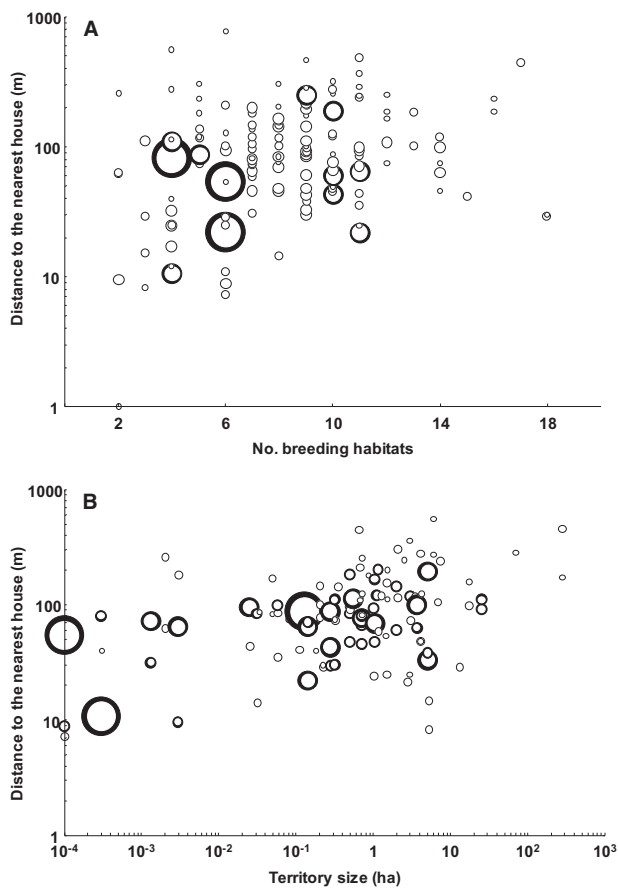


Figure 4. (A) Number of breeding habitats in different species of birds in relation to mean distance to the nearest house (m), and (B) breeding territory size (ha) in relation to mean distance to the nearest house (m). Circles of different size reflect differences in sample size.

(e.g. Tomialojc 1970; Gliwicz et al. 1994; Evans et al. 2011; Møller et al. 2012), the present study is the first to quantify the tight association between distribution and abundance of birds and human habitation. Several studies have suggested that urban birds constitute a small fraction of generalists resulting in *de facto* homogenization of urban communities (Devictor et al. 2007; Møller 2009; Evans et al. 2011; Sol et al. 2014). In our case, however, most individuals were closer to human habitation than expected, and mean distances to human habitation were smaller than mean local random distances in 126 out of 191 comparisons (66%; [Supplementary Material](#)). Hence, bird assemblages tended to be more abundant and more species-rich close to human habitation than far away, as most species were distributed this way.

Associations between humans and wild animals arise from the fitness advantages that accrue to individuals that gain resources including protection against predators and parasites from humans. For example, birds that breed inside buildings have significantly higher reproductive success than nearby conspecifics breeding outdoors (Yeh et al. 2007; Møller 2010). This effect pertains not only to urbanization but also to human habitation in rural habitats. These findings relate to the annual number of broods, annual fecundity, and risk of nest predation. Because breeding birds in urbanized habitats have earlier breeding phenology than conspecifics in rural habitats (Møller et al. 2015b), birds breeding in human proximity have more broods and more offspring, further

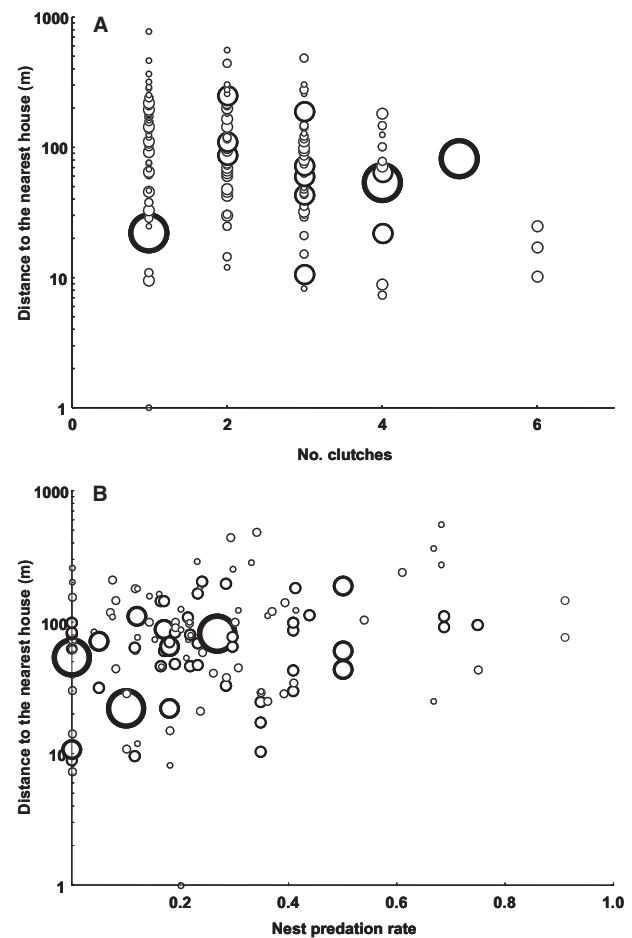


Figure 5. (A) Maximum number of clutches per year in different species of birds in relation to mean distance to the nearest house (m), and (B) nest predation rate in relation to mean distance to the nearest house (m). Circles of different size reflect differences in sample size.

promoting the tight association between distribution and abundance of birds and human habitation. According to our results, these effects of urbanization seem to be related to effects of proximity to human habitation, as they are extended to rural habitat around cities.

Local and global population density are usually positively related (Brown 1995). Here we have shown that high abundance of birds in the proximity of human habitation was associated with larger local population densities, but also larger population densities and larger population sizes at continental scales. There are two interpretations. Either larger global population sizes and densities give rise to large local population sizes and densities, or large local populations of birds close to human habitation give rise to large continental populations. We consider the latter scenario to be most likely. An example is the blackbird *Turdus merula* that used to be a relatively rare forest bird until 200 years ago, while it is now a common urban bird with population densities exceeding 200 pairs/km² in parts of Europe (Evans et al. 2010; Møller et al. 2014). Positive relationships between urbanization and population abundance seem to be general as shown by analyses of population density and timing of urbanization across breeding birds in Europe (Møller et al. 2012).

The findings reported here have a number of important perspectives. First, the underlying mechanisms behind the patterns of

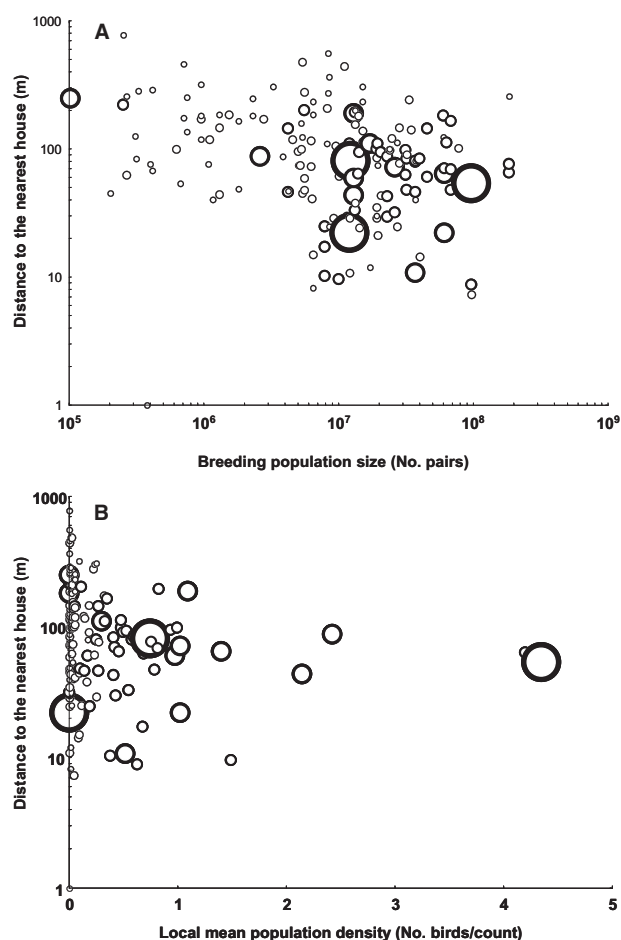


Figure 6. (A) Breeding population size for different bird species in the Western Palearctic in relation to mean distance to the nearest house (m), and (B) mean local population density in relation to mean distance to the nearest house (m). Circles of different size reflect differences in sample size.

distribution and abundance of each species need to be identified amongst the alternatives of changing predation, parasitism, competition, and/or disturbance levels according to proximity to human habitation (Møller 2012; Díaz et al. 2013; 2015; Møller et al. 2016; Samia et al. 2015, 2017; Møller and Díaz 2018). Second, the causal relationships need to be analyzed (e.g., whether local-scale associations with humans are the causes, or the consequences, of large-scale patterns of abundance and distribution). Third, the conservation consequences of the patterns reported here must be taken into account when evaluating the general effects of urban expansion on wildlife, by acknowledging that urban development may indeed have positive rather than negative effects (Torres et al. 2016). We found that most individuals and species lived close to human habitation, and such proximity was in turn tightly associated with success in the colonization of urban habitats, as well as to its ecological and evolutionary consequences in terms of consistent changes in distribution, abundance, behavior, and life history. Probably, this pattern was partly due to a long history of contact between birds and humans in Europe, which seems to have allowed for habituation and adaptation to urban habitats (Gil and Brumm, 2014). Probably, the more sensitive individuals and species have been extirpated long ago from the proximity of human settlements. Adaptation to human proximity is however an ongoing process that surely differs in speed and stage both geographically and temporally (e.g. Díaz et al. 2015).

The method presented here provides large datasets for most bird species with relatively low sampling effort, although its use would be more difficult in remote areas far from human settlements for documenting the patterns described there. Replicated measurements of human–animal associations may thus be useful for monitoring and analyzing the ongoing process of urbanization of organisms, but also for identification of species with conservation requirements that are particularly susceptible to human proximity.

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Supplementary material <https://academic.oup.com/cz>

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