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Niche segregation, competition, and urbanization

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Abstract

Urbanization of species is an ongoing process where successful urban colonizers usually obtain large fitness benefits. Mechanisms proposed to explain associations between urbanization and life-history traits are based on behavioral flexibility in food and habitat use and reduced fear responses. We test the novel hypothesis that interspecific competition for proximity to humans is driving urbanization. We recorded the distance during the breeding season to human habitation for 50 pairs of closely related bird species, where one was closely associated with humans while the other species was not. The degree of urbanization was larger as was range size and abundance in the species more closely associated to humans. Flight initiation distance was shorter, and species closely associated with humans were more abundant in ancestral rural habitats. Likewise, species more closely associated with humans reproduced earlier and during longer periods. These results are consistent with the hypothesis that urbanization is promoted by interspecific competition. Resulting isolation by urban habitat may further facilitate contemporary adaptation to urban environments.

Key words: birds, distance to human habitation, isolation by habitat, isolation by time, mechanisms.

Urbanization is the biological process by which living organisms colonize, adapt to, and eventually increase in abundance and distribution in urban compared with ancestral rural counterparts (Marzluff et al. 2001; Gaston 2010; Gil and Brumm 2014). With more than half of all humans currently living in urban areas and even larger populations being projected for the future (United Nations 2015), urbanization has become an increasingly important factor determining changes in abundance and diversity of species. Urban environments may act as ecological filters that decrease local diversity (Sol et al. 2014), but urbanization may also cause directional selection underlying contemporary evolutionary change (Gil and Brumm 2014; Carrete et al. 2016). Indeed, species closely associated with humans such as feral pigeons *Columba livia* and house sparrows *Passer domesticus* may have evolved under the influence of their association with humans (e.g., Sætre et al. 2012). Species that have succeeded in the transition from rural to urban habitats have often vastly expanded their abundance and distribution. Some species

have even become cosmopolitan as a consequence of this association with humans (Gaston 2010; Gil and Brumm 2014), and the number of species that have become urbanized has increased exponentially in recent decades (Møller et al. 2012). Furthermore, urbanized species are more likely to become successful invaders when introduced in other novel environments (Møller et al. 2015).

Intensive research during recent years has shown that several behavioral and life-history traits are consistently associated with successful urbanization, such as tolerance to humans, predators, and noise; mobility and migratory habits; habitat and food requirements, including degree of specialization; breeding traits, including timing, effort, and success; and body and brain size (Carrete and Tella 2011; Møller 2013; Sol et al. 2013; Concepción et al. 2015). Traits favoring urbanization are usually phylogenetically conserved, causing a non-random distribution of urbanized species across phylogenies or, in other words, a strong phylogenetic signal in analyses of urbanization success (Møller 2013). However, the mechanisms

underlying these associations, and hence successful colonization of urban areas, largely remain to be determined (Sol et al. 2013; Díaz et al. 2015; Samia et al. 2017). Proposals to date include behavioral adjustments in habitat selection or foraging, singing, and risk-scanning routines by means of generalist or plastic responses (Sol et al. 2013) as well as reduced fear, that allows for more efficient exploitation of urban habitats (Díaz et al. 2013, 2015; Møller 2015).

If urbanization has such large ecological benefits in terms of increased distribution and abundance for successful city dwellers as developed above, why are most species not yet urbanized? Here, we suggest that mechanisms of interspecific competition may play an important role in urbanization. Interspecific competition between closely related species that only differ little in morphology or behavior may facilitate urbanization for individuals of the competitively dominant species while this factor may preclude urbanization for its sister species. Exploitation and interference competition may result from superior access to limited resources such as food and shelter (Brown and Wilson 1956). Such competition may result in divergence among closely related taxa caused by differences in morphology, behavior, habitat use, or timing of reproduction (e.g., Hendry and Day 2005). Divergence may be due to ecological sorting of specific kinds of individuals among habitats of already different taxa at local scales, phenotypic plasticity within individuals, or to microevolutionary change favoring extreme phenotypes of competing species (character displacement; Brown and Wilson 1956; Stuart and Losos 2013).

Several mechanisms may reduce the level of competition, and they may be associated with urbanization or proximity to humans and their domesticated animals. However, direct tests of these mechanisms, and even the mere demonstration of the existence of interspecific competition, will require manipulative experiments of addition and removal of the supposedly interacting species at proper spatial and temporal scales, an approach that it is usually logistically unfeasible at least for free-ranging animal communities (Schoener 1983). Alternatively, multiple comparisons of traits related to explicit mechanisms for competitive release among closely related species may provide indirect, but robust tests of the competition hypotheses (Godoy et al. 2014). These indirect tests would be especially strong when trait similarity rather than divergence is the expectation due to the phylogenetic conservatism quoted above.

Concerning mechanism reducing competition, isolation by time of reproduction occurs when individuals of a single species differentially reproduce with individuals that breed at the same time resulting in reduced inter-breeding as a consequence of reduced gene flow among populations (Théron and Combes 1995; Hendry and Day 2005). Isolation by time may also interact with isolation along other ecologically important axes such as habitat (Théron and Combes 1995; Møller et al. 2011). Thus, if urban individuals differentially reproduce with urban conspecifics, for example, because they all prefer a slightly early emerging food source, this may reduce gene flow. In fact, it has been shown that urban populations often have reduced dispersal distances as established using measures of gene flow compared with rural conspecifics (Evans et al. 2009; Björklund et al. 2010).

Isolation between urban and rural species and populations may also occur as a consequence of susceptibility or exposure to predation (Díaz et al. 2013; Samia et al. 2017). Some individuals, populations, and species of birds are ancestrally less fearful of humans thereby facilitating colonization of urban environments (Carrete and Tella 2010; Møller 2010; Samia et al. 2015; Carrete et al. 2016). Higher population density and less fearfulness when encountering

humans imply a competitive advantage for urban compared with rural individuals when competing for access to limiting resources in urban areas. Furthermore, lack of fear of humans may prevent or reduce risk of predation and nest parasitism because predators such as raptors (Møller 2012) and brood parasites such as cuckoos keep much longer distances from humans (Møller et al. 2016). In this situation, human habitation may constitute virtual refuges for urbanized populations (Møller et al. 2016).

Urbanization mediated by interspecific competition would imply that individuals of species that are less disturbed by human proximity gain more benefits from the proximity of humans in terms of protection from predators and access to food, and such species will be favored numerically compared with their ancestral congeners or closely related species that do not cope with the proximity of humans. This line of arguments rests on the assumption that there are direct benefits of urban life. For example, a higher density of individuals in cities imply more eyes looking for predators. Likewise, urban environments contain more food per capita as revealed by excess food being present at feeders and elsewhere in cities. Here, we directly measure the distribution of individuals with respect to proximity to human habitation, rather than classifying species or populations as urbanized or not, or estimate the degree of urbanization from differences in abundance among rural and urban populations (Møller et al. 2012; Sol et al. 2014). Species with individuals that are distributed closer to humans should obviously be locally more urbanized (higher abundance in urban compared with nearby rural habitats), but individuals of such species should also produce more surviving progeny and therefore enjoy a competitive advantage by further increasing their abundance in both urban habitats and elsewhere. Thus, we predicted that (1) species distributed closer to human habitation have consistently higher population density in both the ancestral rural habitat and the urban habitat nearby than species that are less associated with humans, and (2) they should also gain a greater benefit in terms of increase in population size in urban compared with the ancestral rural habitats. For example, higher density may imply better defence against predators because more eyes look out for predators. We also predict that (3) species more closely associated with humans have larger ranges, population sizes, and densities than species that are less associated with humans. Species distributed closer to humans are expected to be (4) smaller in body size because small species may differentially find refuge near human habitation (Møller 2012). These species were also predicted to have (5) shorter migration and dispersal distances, the latter indicated by a larger number of subspecies per unit area (the number of subspecies is an index of genetic differentiation, at least in birds; Belliure et al. 2000), as usually found for urbanized when compared with non-urbanized bird species (Carrete and Tella 2011; Møller 2013; Sol et al. 2013; Concepción et al. 2015). Furthermore, we predicted that (6) species distributed closer to humans have weaker fear responses when approached by humans because closer proximity of humans selects for weaker fear responses. Finally, we predicted that (7) they reproduce earlier and have a longer reproductive season than closely related species less strongly associated with humans because phenology in urban areas generally is advanced compared with that in nearby rural habitats. We tested these predictions in 50 pairs of closely related species of birds from Europe, where one species lives close to human habitation while the other does not. Based on historical records dating back 500 years we can state that the 50 species that are not currently associated with humans were not so either during the latest centuries. Significant differences in comparisons among pairs of closely related species that were distributed

differentially according to human presence may be explained by different hypotheses. These alternative hypotheses may include phenotypic plasticity, chance effects, ecological sorting, or shifts in resource use and shifts in microhabitat use (Stuart and Losos 2013). Paired comparisons of a large number of species scattered across phylogenies preclude consistent effects of most of these, with the exception of ecological sorting of species according to environmental variation. We tested this alternative hypothesis by comparing habitat use range across the Palearctic region among paired species. Significant differences were expected if habitat sorting was associated with differential distribution of paired species.

Materials and Methods

Study areas

The study was conducted in Toledo (Spain), Orsay (France), and Brønderslev (Denmark), all inland medium-sized cities in Western Europe. Details on city size and location can be found in Díaz et al. (2013). The study areas were mainly composed of urban habitats (60%) with 20% covered by forest and 20% by farmland in Toledo and Orsay, and 5% by forest and 35% by farmland in Brønderslev. Classification of urban and rural habitats follows Marzluff et al. (2001): urban habitats have >50% built-up area and >10 buildings/ha, whereas rural habitats 5–20% and <2.5/ha, respectively. Forest areas have isolated buildings, if any.

Distance to human habitation

Six transects of 5 km each were located in 50-km^2 areas centered in each city, 3 crossing urban habitats and 3 rural habitats. Transect design aimed at sampling as thoroughly as possible habitat variation within study areas, while ensuring sampling enough individuals of the species inhabiting exclusively rural areas. All transects were made during the peak breeding season in April–May 2015 (Toledo), April–May 2012 (Orsay), and May–June 2012 (Brønderslev). Each transect was surveyed during 3 h around sunrise 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.

All birds seen or heard were located and the distance to the nearest inhabited house was recorded to the nearest meter. Distances were measured directly from the point where the individual was first seen using a Nikon Forestry 550 hypsometer if close to the transect line, and by triangulation of measured distances to the individual and to the nearer house if far from it. Locations exceeding the 500-m distance measurable with the hypsometer (67 out of 9732, 0.7%) were recorded on a fine scale map. Species-specific log$_{10}$-transformed distances were highly repeatable (repeatability R (SE) = 0.87 (0.00), $F_{60, 6267} = 48.30$; $R = 0.37$ (0.02), $F_{68, 1634} = 15.08$; $R = 0.44$ (0.00), $F_{61, 1638} = 21.16$, $P < 0.0001$ for Spain, France, and Denmark, respectively). Mean (SE) distance to the nearest human habitation was estimated for all species detected in the 3 study areas. We selected, from the full list of species detected in the transects, all pairs of closely related species (within the same genus or, occasionally, family) occurring in each study site, and we classified them as either distributed close to or further away from human habitation according to mean distances obtained previously (see above). We assume that comparisons among pairs of closely related species will minimize biases due to confounding factors, because closely related species are by definition similar in most respects (Møller and Birkhead 1992).

Flight initiation distance and local population abundance

The analyses reported here are based on extensive data on FIDs and abundance of each species in urban and rural habitat. These estimates were collected during the breeding seasons 2009–2010 in the 3 study areas (Díaz et al. 2013; Møller et al. 2012), before measuring distances to human habitation. Hence, we assume that FIDs and abundances will have changed little, or similarly for all species, between 2010 and 2012–2015. In brief, when an individual bird had been located with a pair of binoculars, the observer moved at a normal walking speed toward the individual, while recording the number of steps. The distance at which the individual took flight was recorded as the FID after multiplying the number of steps by step length. 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. Abundances were estimated by means of standard point count censuses of breeding birds with unlimited recording distance, twice during the breeding season with an interval of 3–4 weeks between the 2 series of point counts, during spring 2010 in both urban and rural habitats in the 3 study areas (50 points by habitat and study area, thus resulting in a total of 300 points).

Species-specific 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. We used data reported in Cramp and Perrins (1977–1994) that are widely used in comparative analyses. Estimates of these traits are reported in Supplementary Material.

Migration distance was estimated as the difference in latitude between the mean values of the northernmost and the southernmost breeding distribution and the mean values of the northernmost and the southernmost winter distribution, relying on information in Cramp and Perrins (1977–1994) and del Hoyo et al. (1992–2008). Migration distance was subsequently estimated as the mean latitude during breeding minus the mean latitude during winter.

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.

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 5 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. This estimate is strongly positively related to population density obtained from territory

mapping according to Cramp and Perrins (1977–1994): $F = 40.41$, df $= 1, 79$, $r^2 = 0.34$, $P < 0.0001$, estimate (SE) $= 1.091$ (0.172).

We used the schematic presentations of the annual cycle for all species in the Western Palearctic provided by Cramp and Perrins (1977–1994) to estimate the start of the breeding season and the duration of the breeding season in units of 10 days. We excluded units when breeding had been recorded, but only rarely.

The number of different habitats in which each species has been known to breed was recorded from the habitat preferences listed by Cramp and Perrins (1977–1994) for each species, restricting the lists to the habitats that appeared in glossary to increase precision (Belliure et al. 2000). Examples of such habitats include copse, garigue, glade, park, and scree.

Statistical analyses

We used a paired design for our tests relying on the fact that closely related species share almost their entire evolutionary past, with their recent divergence after their split being the only exception (Møller and Birkhead 1992). We made the choice of pairs of species differing in degree of association with human habitation as follows. If there were 2 congeners, the one with closer distance to human habitation was chosen as such while the remaining was allocated to the other category of species. If there were 3 congeners, we chose the one most closely associated with human habitation and we then chose among the remaining 2 species by picking one randomly. If there were 2 or 3 species in the same sub-family, we adopted the same approach as described above for congeners. Thus, this approach controls for known confounding variables that have evolved after divergence between pairs of closely related species, but also for unknown confounding variables simply because pairs of closely related species by definition are similar in most respects. This pairwise comparison is particularly powerful when analyzing large datasets, because it relies on the assumption that interspecific competition should be the strongest between closely related species due to the largest share of phenotypic traits determining their ecological niches (Godoy et al. 2014). We further considered the strength of interspecific competition by weighting paired data by the inverse of the phylogenetic distance among species within pairs. The duration of divergence was estimated from the consensus tree based on date in Jetz et al. (2012) (Figure 1, Supplementary Material). This procedure gave more weight to comparisons whose phylogenetic distance between species was small. Paired *t*-tests were made on either untransformed or log-transformed data according to homoscedasticity requirements. Lack of effects of country where the study was made on comparisons between pairs of species differing in their distance to the nearest human habitation was tested by means of mixed repeated-measures ANOVA models with country as a random factor. Tests were carried out with STATISTICA 7.0. The number of subspecies was weighted by size of the distribution area before analyses.

We evaluated 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). Cohen (1988) proposed explicit criteria for judging whether effects are small (Pearson $r = 0.10$, explaining 1% of the variance), intermediate ($r = 0.30$, 9% explaining of the variance), or large ($r = 0.50$, explaining 25% of the variance), and we adopt these criteria here.

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 ($n = 6,328$). Only 30% of all birds were expected to be located less than 100 m from human habitation if birds were distributed randomly across the $50 \, km^2$ study areas. Mean distances for 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). Likewise, mean distance to the nearest house for different species in France in 2012 was strongly positively correlated with mean distance in France in 2013 ($F = 2787.45$, df $= 1, 65$, adjusted $r^2 = 0.96$, $P < 0.0001$, estimate (SE) $= 1.03$ (0.02)).

Data on mean distance and its ecological and life-history correlates were compiled for 50 pairs of species, whose phylogenetic distance varied between 3.47 and 31.05 million years (half-patristic distance, i.e., estimated time elapsed since divergence between species: mean $= 11.47$ million years, SD $= 5.11$; Figure 1; Supplementary Material). Mean distance to human habitation of species associated with humans was half the distance for their closest relatives less associated with humans, with a large effect size (Table 1).

Local abundance was larger in species found closer to human habitation than in their closest relatives in both rural and paired urban habitats (Table 1 and Figure 2), although the difference in population abundance among urban and rural habitats was not significantly different (Table 1 and Figure 2). The mean number of habitats in urban species was 7.34 (SE $= 0.47$), while it was 7.80 (0.34) in rural species, a non-significant difference ($t = -0.98$, df $= 49$, $P = 0.33$). This analysis does not support the hypothesis that differences between pairs of urban and rural species were due to habitat sorting (Stuart and Losos 2013).

Breeding range, population size, and population density in the Palearctic region were larger in species found close to houses compared with closely related species distributed further away (Table 1). Species found near human habitation were smaller than closely related species located further away (Table 1). Migration distance differed significantly between pairs of closely related species with the distance being longer in species not associated with human habitation (Table 1). Species associated with human habitation had 4 times more subspecies per unit distribution compared with closely related species breeding further away, although this difference was only marginally significant (Table 1).

Flight initiation distance differed between pairs of species, with FID in species located further away from human habitation on average being 118 m, while the mean FID for species close to human habitation being only 56 m, although this difference was significant only in urban habitats (Table 1 and Figure 3).

Bird species distributed close to human habitation started to breed earlier than closely related species located further away, and the duration of the breeding season was on average longer (Table 1 and Figure 4). Effect sizes for significant paired comparisons were moderate to large; thus, implying consistent associations.

Discussion

Pairs of closely related species of birds from 3 Western European countries were consistently found either close to or far away from human habitation during the breeding season, providing evidence for consistent associations with humans in some species but not in others. Bird species that were closely associated with humans were more abundant in ancestral rural habitats, and they showed weaker fear responses measured in terms of flight initiation distance than
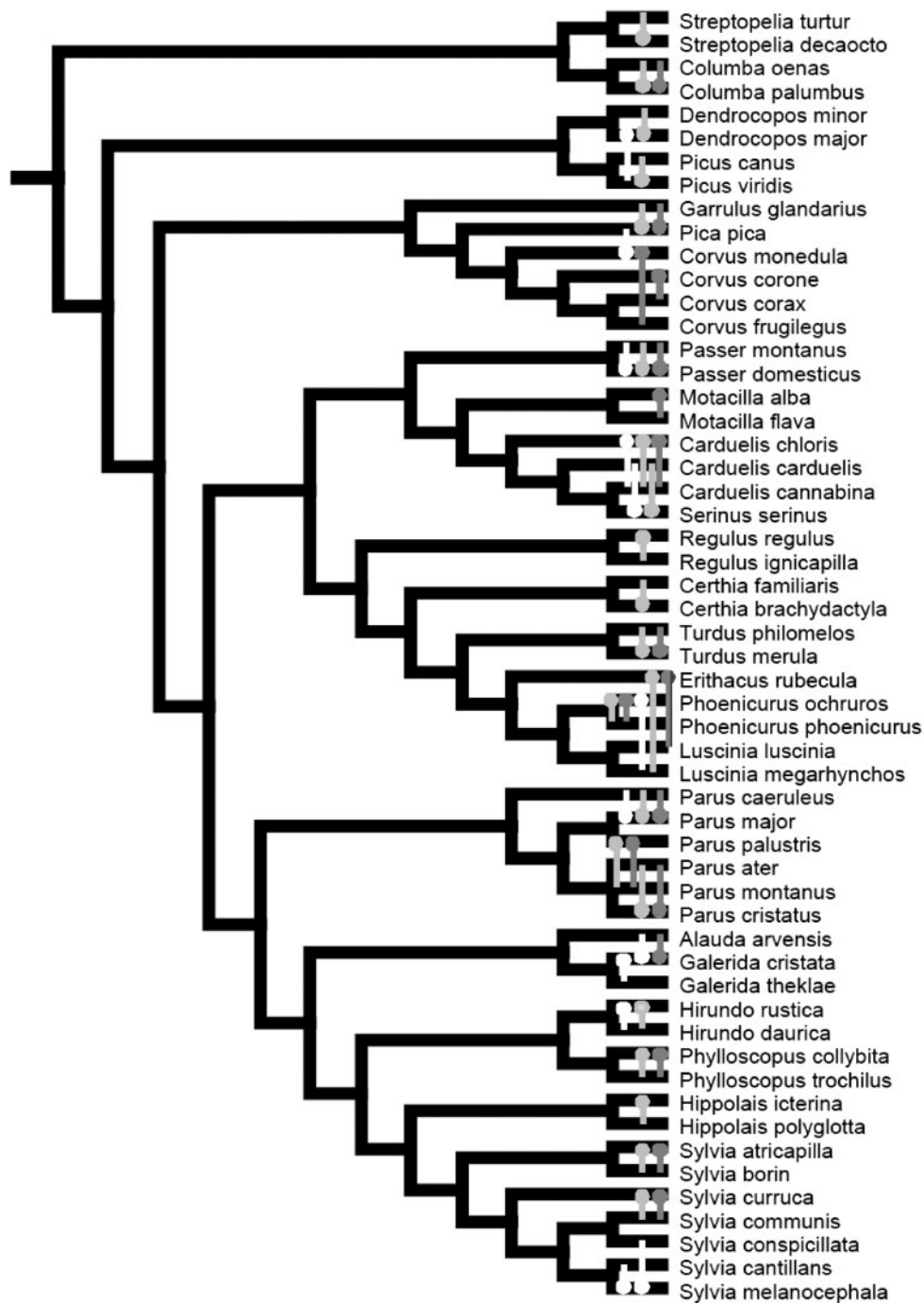
Figure 1. Closely related species pairs mapped on the consensus phylogeny of the study species (after Maddison and Maddison 2011; Jetz et al. 2012). Circles indicate the species in each pair that bred near human habitation. White: Spain; light gray: France; dark gray: Denmark.

species that distributed further away from humans. These former species had larger breeding ranges and larger population densities if breeding close to rather than away from humans. Finally, species associated with humans started to reproduce earlier in spring, and they tended to have longer breeding seasons than closely related species breeding further away from humans. These findings are consistent with urbanization in birds being associated with competition for access to habitats near humans. We are unaware of any other studies linking competition and urbanization in any other taxa, and hence these conclusions can be considered novel and innovative. Thus, one

or more mechanisms related to isolation by habitat, timing of reproduction, or fear responses should facilitate such competitive character displacement. Under the alternative hypothesis of absence of interspecific competition, a high degree of similarity (e.g., lack of significant differences) in the traits analyzed among closely related species pairs would have been expected.

Urban environments can act as ecological filters that decrease local diversity (Sol et al. 2014), or urbanization may cause directional selection underlying adaptation to human proximity (e.g., Gil and Brumm 2014; Carrete et al. 2016). These scenarios are not

Table 1. Mean (SE) and sample size for ecological variables of pairs of closely related bird species where one species is breeding close to human habitation and the other is not, and results of paired *t*-tests for the corresponding comparisons (based on log-transformed data except for migration distance and start and duration of breeding)

Breeding site of species

Variable	Near inhabited houses		Away from inhabited houses					
	Mean	SE	Mean	SE	df	t	P	r
Distance to house (m)	55.6	0.2	118.3	0.2	49	−6.83	**0.000**	0.70
Local population density, rural (number of birds/count)	1.2	0.2	1.1	0.2	49	2.67	**0.010**	0.36
Local population density, urban (number of birds/count)	1.3	0.2	1.1	0.2	49	3.15	**0.003**	0.41
Urban–rural difference in population density	1.1	0.2	1.0	0.1	49	1.46	0.151	0.20
Palearctic range size (km^2 × 10^6)	16.2	0.0	14.2	0.0	49	2.40	**0.020**	0.32
Palearctic population size (pairs × 10^3)	13,267.5	0.0	319.6	0.0	49	7.56	**0.000**	0.73
Palearctic population density (pairs/10 ha)	8.2	0.2	0.2	0.4	49	7.21	**0.000**	0.72
Body mass (g)	31.7	0.2	27.9	0.2	49	2.63	**0.011**	0.35
Migration distance (°)	0.7	0.0	0.9	0.0	49	−3.05	**0.004**	0.40
Richness of subspecies (number)	41.1	0.5	15.0	0.3	49	1.81	0.076	0.25
FID, rural (m)	10.7	0.2	10.8	0.2	48	−0.24	0.808	0.03
FID, urban (m)	7.2	0.2	8.5	0.2	28	−3.52	**0.001**	0.55
Start of breeding (Julian months)	4.1	0.0	4.4	0.0	47	−2.71	**0.009**	0.37
Duration of breeding season (days)	113.5	2.0	96.0	1.8	47	3.42	**0.001**	0.45

Notes: Both mean values and tests were weighted by the inverse of the half-patristic distance between species in each pair. *P*-values in bold are statistically significant at the 5% level. Results (*P*-values) were identical up to the second-third decimal place when including country as a random factor in a repeated-measures ANOVA design to account for (lack of) country effects on paired comparisons. *r* is the effect size estimated as Pearson's product–moment correlation coefficient.
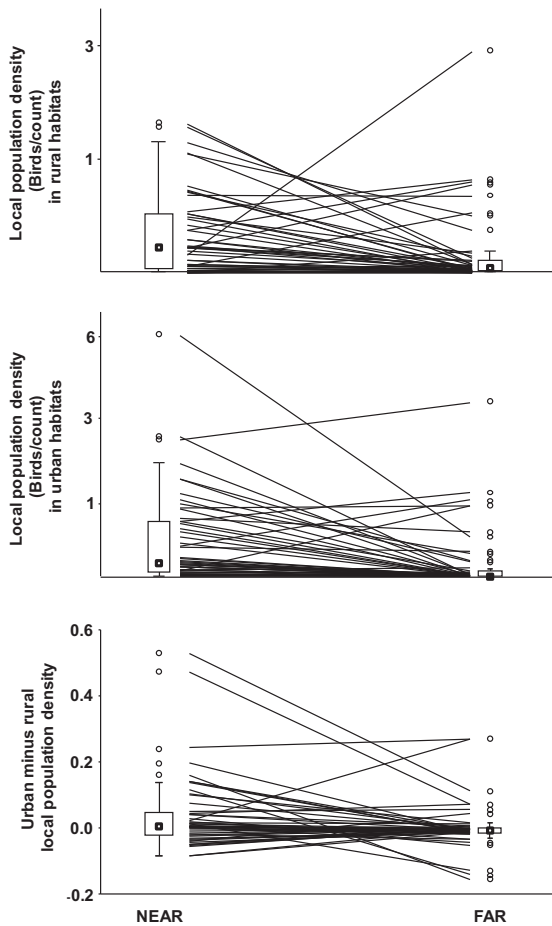

Figure 2. Local abundance in both ancestral rural and nearby urban habitats (and its log-difference, a measure of degree of urbanization; Møller et al. 2012) of species distributed close to human habitation (NEAR) when compared with closely related species less associated with humans (FAR). Box plots show medians, quartiles, 5- and 95-percentiles and extreme values, and lines connect values for pairs of closely related bird species.
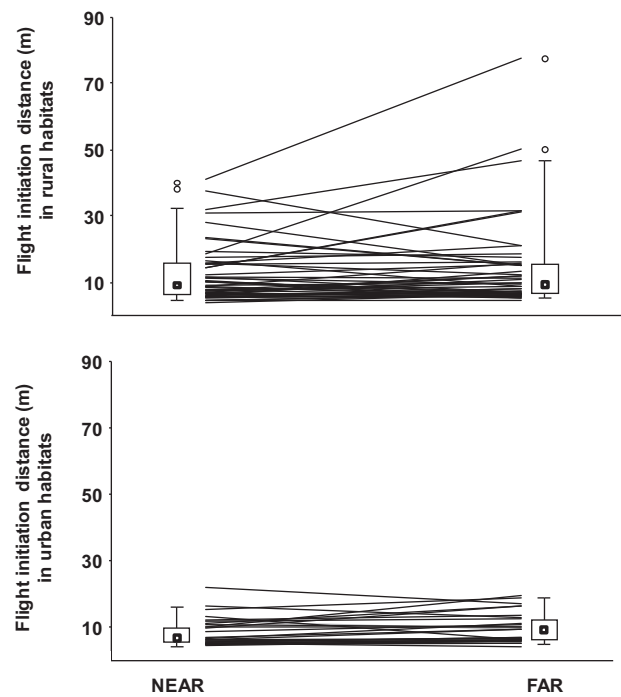

Figure 3. Flight initiation distance of species distributed close to human habitation (NEAR) when compared with closely related species less associated to humans (FAR), both in ancestral rural and urban habitats nearby. Box plots show medians, quartiles, 5- and 95-percentiles and extreme values, and lines connect values for pairs of closely related bird species.

mutually exclusive. If a selective filter allows for regional coexistence of closely related pairs of species (where one is able to tolerate humans and the other not), we should expect little evidence of change in phenotype being related to time since urbanization. In fact, several studies have documented such directional change with
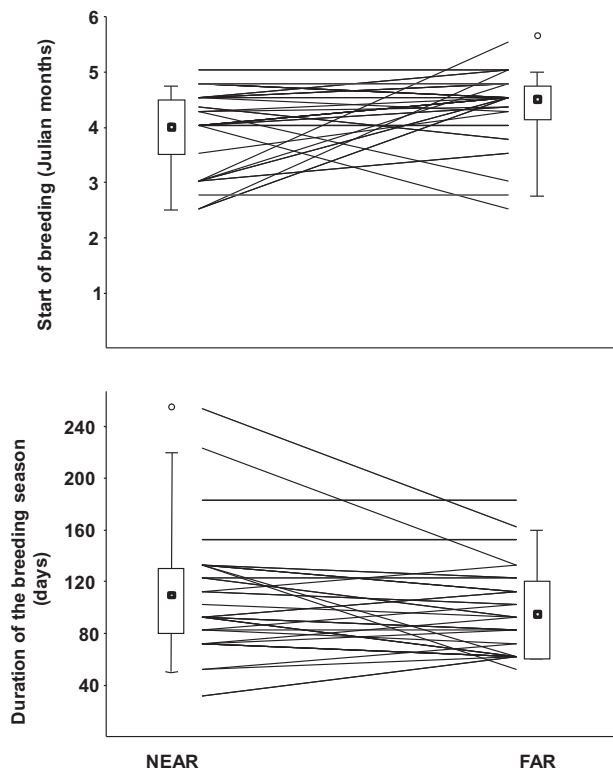
Figure 4. Mean start and duration of the breeding season of species distributed close to human habitation (NEAR) when compared with closely related species less associated to humans (FAR). Box plots show medians, quartiles, 5- and 95-percentiles and extreme values, and lines connect values for pairs of closely related bird species.

time since urbanization as well as genetic signatures of urbanization in several organisms (Alberti 2015). If urbanization is a selective force causing adaptation to the proximity of humans, we should expect gradual changes as stated above. Such a change is also consistent with differences in body mass, migration distance, and subspecies richness between pairs of species differing in their proximity to human habitation.

Bird species that have become urbanized, and hence have population densities in urban areas that are larger than those in nearby rural areas (Møller et al. 2012; Sol et al. 2014), resemble bird species that have become associated with human habitation. The ancestral breeding population density in local rural areas was higher in such species when compared with their closest relatives living further away from human habitation, indicating a competitive numerical advantage over close relatives. Furthermore, Western Palearctic range size, population size, and population density were consistently higher in bird species that eventually became urbanized (Møller 2013), but these species were also more closely associated with human habitation as shown here.

Fear response in ancestral rural habitats in both Europe and South America shows consistent patterns with species successfully becoming urbanized having shorter flight distances in their ancestral rural than closely related species that never managed to cross this ecological barrier (Carrete and Tella 2011; Samia et al. 2015). These findings suggest that fear responses play a crucial role in urbanization. Indeed, a central observation in the domestication literature linking close proximity between wild animals and humans is the loss of or reduction in fear responses in domesticated species (Møller 2013).

We documented extensive evidence consistent with isolation by urbanization, defined as the adaptation that cause divergence between neighboring populations or species due to one or more mechanisms underlying evolutionary divergence. This concept of isolation by urbanization may have consequences for contemporary evolution, as there is extensive evidence that human-induced changes in urban areas is one of its drivers (Alberti 2015). We suggest that the differences between pairs of closely related urban and rural species may constitute such cases of rapid evolutionary divergence.

Gene flow and dispersal are supposedly the 2 main factors affecting isolation between rural and urban populations (Alberti 2015). There is consistently reduced gene flow among populations of birds in urban areas and also between rural and urban populations of the same species (Evans et al. 2009; Björklund et al. 2010). Longer migration distance and fewer subspecies in species breeding away from human habitation compared with closely related species breeding in human proximity are consistent with reduced migration and dispersal and hence gene flow for species more closely associated with human habitation than their closest relatives, a fact that may promote further adaptation to urban environments. Is the increase in population divergence predicted by difference in isolation by timing of reproduction, isolation by habitat, or isolation by fear responses? We did find evidence consistent with isolation by timing and isolation by fear responses.

In conclusion, we have documented widespread evidence of divergence between pairs of closely related species of birds that either have become closely associated with humans and human habitation, or have not achieved this transition. Detailed analyses of data on distribution, population size, fear responses, body size, and timing of breeding were consistent with such character displacement. Future monitoring of change in phenotypic traits in species undergoing urbanization, and lack of change in non-urbanized close relatives, will constitute a further test of our conclusion. So would more extensive pairwise comparisons including data from areas of allopatry where urbanization was reversed among members of species pairs.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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