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Letter

Are house sparrow populations limited by the lack of cavities in urbanized landscapes? An experimental test

Frédéric Angelier and François Brischoux

F. Angelier (http://orcid.org/0000-0003-2619-167X) (frederic.angelier@cebc.cnrs.fr) and F. Brischoux, Centre d'Etudes Biologiques de Chizé, CEBC, CNRS-ULR, UMR 7372, Villiers en Bois, France.

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Current urban policies are associated with deep changes in urban structures, which may impoverish urban biodiversity. A major concern is the disappearance of nesting sites for wild vertebrate species living in urban areas. New urban structures without any cracks or cavities may especially preclude cavity nesters from breeding in cities and they may cause population declines. In that context, we experimentally investigated this question in an urban exploiter bird species (the house sparrow *Passer domesticus*), which is dramatically declining in most European cities. To test if the lack of cavities is limiting house sparrow populations in urban areas, we equipped 11 sites along an urbanization gradient with nest boxes and we then evaluated the rate of occupancy of these nest-boxes. This urbanization gradient was characterized by very rural places (isolated farms) and moderately urbanized areas (town of medium size, i.e. 60 000 inhabitants). Surprisingly, rural nest boxes were more occupied than urban ones, suggesting that cavity availability is probably more constraining in rural areas relative to urban ones. Therefore, our study suggests that urban house sparrow populations are probably not constrained by a lack of nesting sites in medium size cities with urban designs similar to our city of interest (Niort, western France). This hypothesis definitely needs now to be tested in further urban landscapes (e.g. large cities and urban landscapes with other architecture and management policies).

Keywords: cavities, house sparrow, urbanization

Introduction

Urban sprawl is a worldwide phenomenon, which is associated with multiple abiotic and biotic changes with important consequences on the wild fauna (Grimm et al. 2008). Although urbanization is classically associated with an impoverished biodiversity, some species have managed to benefit from this modified habitat (McKinney 2008). These urban exploiters have colonized cities, co-evolved with human activities and some of them mainly rely on this anthropogenic habitat (Chace and Walsh 2006). However, cities are constantly evolving at a very rapid rate, and current urban changes may prevent these urban exploiters to persist in cities. Current urban policies and landscape planning result in deep changes in urban structures. For example, in

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many cities, old buildings are progressively replaced by new buildings, which are very often built with modern materials. These new structures without any cracks or cavities may preclude cavity nesters from breeding in cities and may cause population declines, especially in cavity-nesting birds (Moudra et al. 2018).

In that context, the house sparrow is particularly relevant to study. Over the last decade, house sparrow populations have dramatically declined in several European cities (Robinson et al. 2005, De Laet and Summers-Smith 2007). Although this decline has first been documented in the UK, it is now a widespread phenomenon in most European countries (i.e. in its native range, Murgui and Macias 2010, De Coster et al. 2015). Surprisingly, the causes of this decline remain poorly understood despite its importance and rapidity (De Laet and Summers-Smith 2007). This sharp decline may be linked to multiple recent modifications of the urban environment, such as 1) an increased predation risk due to the recent rise in the numbers of European sparrowhawks and feral cats in cities, 2) an intensification of multiple sources of pollution (noise, light, electromagnetic, and air pollution), 3) a modification of food availability and food type, or 4) a change in the urban habitat with a reduction of habitat availability for house sparrows (Robinson et al. 2005, Liker et al. 2008, Shaw et al. 2008, Peach et al. 2015, 2018, Herrera-Duenas et al. 2017, Meillère et al. 2017, Moudra et al. 2018).

Interestingly, house sparrows are cavity nesters and they rely on all the small cavities that can be found in old buildings or under old roofs (Anderson 2006). Because new buildings are often characterized by flat roofs, large windows, and flat structures without any cavity, a recent modification of urban architecture could also prevent house sparrows from breeding properly in cities (Shaw et al. 2008). Although several studies have relied, at least partly, on this hypothesis to explain the decline of urban house sparrow populations (reviewed by Shaw et al. 2008), no study has to our knowledge explicitly tested this hypothesis.

In this study, we evaluated the importance of cavity availability by experimentally increasing the number of cavities in several sites along an urbanization gradient (von Post and Smith 2015) ranging from very rural places (isolated farms) to moderately urbanized areas (town of medium size, i.e. 60 000 inhabitants). Specifically, we equipped 11 sites along an urbanization gradient with a dozen of nest boxes each and we then evaluated the rate of occupancy of these nest-boxes. At a given site, nest-box occupancy will depend on the combination of local population size and cavity availability, which both determine inter-individual competition for cavities. Low nest-box occupancy will result from a low competition for available cavities because of a small population and/or a large number of cavities. High nest-box occupancy will on the other hand result from a high competition for available cavities, because of a large population size and/or a limited number of cavities. If the number of cavities is too low relative to house sparrow population sizes in urban areas but not in rural areas, we predicted that urban nest boxes should be occupied to a larger extent than the rural nest boxes.

Material and methods

In 2012, we equipped 7 sites in western France with a dozen of nest boxes. In addition, we respectively equipped one and three additional sites with a dozen of nest boxes in 2013 and 2017 for a total of 11 equipped sites (Table 1). All sites were located in Poitou–Charentes and they were located in the same geographical area (maximal distance between 2 sites: 65 km). Six of these sites were located in the city of Niort while 5 other sites were located in rural sites (Table 1 for a detailed description of each site, Fig. 1 for an example of a rural and an urban site). Niort is a typical middle-sized French city (~60 000 inhabitants), which is mainly characterized by a mix of housing with old tile brick rooftops and red clay tile rooftops and by a few modern buildings with flat roofs. It is also characterized by numerous public green spaces (1.5 km^2 for a total surface of 86 km^2). All the nest boxes were installed during the winter (November–January) on the walls of buildings that did not have any visible cavity. They were installed in specific sites where house sparrows were previously seen feeding or roosting. They were hung at a height of 3 m and all nest boxes were separated by approximately 2 m from each other. These nest-boxes were similar among sites and they are specifically designed for house sparrows with a 34 mm diameter hole and they are regularly used by house sparrows at another site (Angelier et al. 2016 for an example). House sparrow are typical cavity-nesters, although they are quite plastic and can use a wide variety of nesting sites (Anderson 2006). During the spring following the installations of nest boxes, all nest boxes were checked every two weeks for nest building and breeding. At the end of each season, we calculated the occupancy rate (number of nest boxes with nest materials) and the breeding rate (number of nest boxes containing clutches) of each site by house sparrows. In some sites, some nest-boxes were also used by great or blue tits (Table 1). Results remain similar if these nest-boxes were excluded from the calculations of occupancy and breeding rates. In addition, 8 sites were followed during an additional breeding season to test whether low occupancy and breeding rates at some sites could not be explained by a poor detection of these new cavities by the sparrows during the spring following their installation.

To quantify the level of urbanization at each site, we used the method developed by Liker et al. (2008) with slight modifications. Specifically, we used digital aerial photographs (Google Earth) of all sites. For each photograph, we delimited a circled area of 53 000 m^2 (diameter: 260 m) that was subsequently divided into 132 cells. For each site, we calculated 1) the mean building density score, 2) the mean vegetation density score, 3) the mean road density score and we counted the number of cells with 4) high building density, 5) high vegetation density, and 6) high density road

Table 1. Habitat characteristics of the 11 sites.

Site	Year of nest-boxes installation	Number of nest-boxes	Number of nest-boxes used by house sparrows	Number of nest-boxes used by tit species	Urban/rural	Mean building density score	Number of cells with high (> 50%) building density	Mean road density score	Mean vegetation density score	Number of cells with high (> 50%) vegetation density	Urbanization score (PC1)
1	2017	10	10	0	Rural	0.03	0	0.114	1.985	98	−1.360
2	2017	9	9	0	Rural	0.045	2	0.235	1.947	95	−1.247
3	2017	15	15	0	Rural	0.03	0	0.121	1.985	98	−0.992
4	2012	11	7	0	Rural	0.03	0	0.689	1.644	97	−0.471
5	2012	10	3	1	Rural	0.0303	0	0.712	1.5909	68	−0.448
6	2012	15	0	3	Urban	0.53	23	0.583	1.318	73	−0.191
7	2012	15	1	4	Urban	0.712	24	0.954	1.166	41	0.536
8	2012	14	0	3	Urban	0.47	20	1.227	0.886	38	0.634
9	2012	14	0	6	Urban	0.765	19	1.008	1.045	33	0.744
10	2013	15	0	0	Urban	0.939	50	1.129	0.409	21	1.393
11	2012	15	2	6	Urban	0.886	42	1.294	0.553	18	1.403

(Liker et al. 2008). Then, we ran a principal component analysis on these six habitat variables to compute an 'urbanization score' (PC1) for each site (Table 1). Based on eigenvalues, a single factor was retained following the PCA (PC1). The PC1 accounted for 80.12% of the total variance and correlated strongly positively with building surfaces (all $r > 0.980$) and road surfaces (all $r > 0.700$), and negatively with vegetation cover (all $r < -0.950$).

All statistical analyses were run by using SAS software (ver. 9.2). Because our dependent variables were proportions, we ran 2-parameters logistic models to test the influence of the level of urbanization on occupancy and breeding rates the year following nest-boxes settlements (Proc NLIN, SAS). In addition, the repeatability of nest box occupancy and breeding rate between years were calculated from the variance components derived from a one-way ANOVA (Lessels and Boag 1987). Finally, we used Signed-rank Wilcoxon tests for paired data to test whether occupancy and breeding rates increased from the first to the second breeding season following nest boxes installation.

Data deposition

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gh2hh05> (Angelier and Brischoux 2019).

Results

Nest box occupancy rates were significantly higher in rural sites relative to urban sites (logistic model, $F_{2,9} = 687.79$, $p < 0.001$; Fig. 2A). Specifically, all nest boxes were occupied in the most rural sites while almost none were occupied in the most urban sites (Fig. 2A). Similarly, breeding rates were significantly higher in rural sites relative to urban sites (logistic model, $F_{2,9} = 80.28$, $p < 0.001$; Fig. 2B). Specifically, no breeding attempts were recorded in the most urbanized sites while breeding attempts were recorded in more than 75% of the nest boxes in the most rural sites (Fig. 2B). Finally, both occupancy and breeding rates were highly repeatable from one year to another (occupancy rate: $r = 0.996$; breeding rate: $r = 0.977$) and they did not significantly differ between the first and the second breeding season following nest boxes installation (signed-rank Wilcoxon tests, occupancy rate: $p = 0.874$; breeding rate: $p = 0.750$).

Discussion

Contrary to our prediction, we did not find any evidence that urban nest boxes were more occupied than rural ones in our sites of interest. Indeed, we even found the opposite pattern. This suggests that there was a higher competition for cavities in rural areas relative to urban ones in our study. Such low inter-individual competition for cavities in urbanized areas may result from small local population size and/or from a

Figure 1. Picture of one of the rural and one of the urban sites (sites 2 and 10, Table 1). The yellow circles indicate the areas (diameter: 260 m), which were used to quantify the level of urbanization (see the Methods for further details).

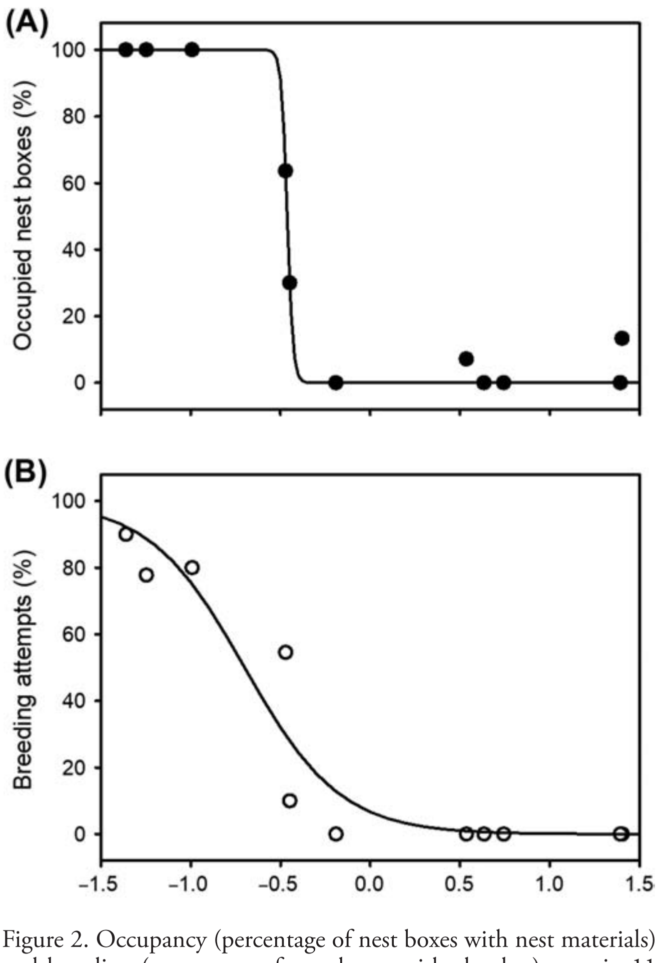

Figure 2. Occupancy (percentage of nest boxes with nest materials) and breeding (percentage of nest boxes with clutches) rates in 11 sites where nest boxes were installed. Black and white symbols respectively indicate occupancy and breeding rates.

large number of available cavities. Overall, our study suggests that urban house sparrow populations are not limited by the number of cavities, at least in a city of moderate size like Niort (~60 000 habitants). Therefore, urban house sparrow populations are probably unlikely to be constrained by a lack of nesting sites in medium size cities with urban designs similar to our city of interest (Niort). However, this hypothesis definitely needs to be tested in further urban landscapes (e.g. large cities and urban landscapes with other architecture and management policies).

Obviously, the rural sites were characterized by a lower density of buildings relative to the urban sites (Fig. 1, Table 1). Actually, there were only a few isolated farms in these rural sites and this lack of building could actually explain why the occupancy and breeding rates of new nest boxes were higher in those sites, especially if there is a high inter-individual competition for cavities in rural places because of large local sparrow population sizes. In Niort, our urban sites were diverse and characterized by different structures and housing densities (Table 1). Despite these differences in housing density, occupancy and breeding rates were very low in all urban sites, suggesting that there is not an important inter-individual competition for cavities in these specific urban landscapes. This low competition probably results from the combination of small local sparrow population sizes and a large availability of cavities (holes in walls, cavities located under roofs, which were seen being used by sparrows in all urban sites). This suggests that nesting cavities is not a limiting factor for house sparrows in this medium size city, even in the areas with very few or no old buildings.

These differences in occupancy and breeding rates could also be explained by the size of the local house sparrow population at each site (von Post and Smith 2015). Occupancy rate of new cavities certainly depends on the number of cavities already available, but also on the number of sparrows that are looking for nesting cavities. Therefore, the low occupancy and breeding rates at urban sites may also result from low population sizes. However, this explanation is unlikely to fully explain our results because we found that almost no nest box was occupied in the urban sites whereas numerous house sparrows were frequently seen in these sites. Such a low occupancy is unlikely to result only from small local population sizes because we equipped each site with a dozen of nest boxes only (i.e. enough cavities for 15 pairs of sparrows maximum) and we were therefore unlikely to 'saturate' the site with nest boxes. Another explanation is that the nest boxes were especially difficult to detect in a fragmented urban landscape for house sparrows, especially because house sparrow's home range seems to decrease as the degree of urbanization increases (Vangestel et al. 2010). However, here again, this is quite unlikely because house sparrows were regularly seen on the urban sites where nest boxes were installed. Furthermore, occupancy and breeding rates were repeatable and did not increase from 2013 to 2014 in 8 sites while house sparrows had more time to detect the nest boxes. Nest-site quality could also partly explain our results. Specifically, nest-boxes could be perceived as good quality breeding sites by rural house sparrows but as poor-quality breeding sites by urban house sparrows. Rural and urban buildings often differ in terms of materials and designs and high quality breeding sites may be scarce in isolated farms relative to a complex and diverse urban landscape. Finally, we also noticed that nest-boxes could be used by other species (blue and great tits) in urban sites (Table 1). Low nest-box occupancy in urban sites might therefore result from inter-specific competition for cavities, especially if tits were dominant over house sparrows. For example, it has recently been reported that great tits could exclude flycatchers from nest-boxes, and could even kill them in order to take over a nest-box (Samplonius and Both 2019). However, this inter-specific competition is also quite unlikely to explain our results because previous studies have suggested that house sparrows are dominant over tits for nest-box occupancy (Charter et al. 2013, Goldshtein et al. 2018). Instead, our results suggest that house sparrows do not have to compete for cavities in urban landscapes similar to Niort.

To conclude, our experiment suggests that the number of cavities is probably not the main limiting factor for urban house sparrow populations, at least in cities of medium sizes characterized by an urban design similar to Niort. House sparrows have co-evolved with humans and they have relied for centuries on human activities for nesting sites and food. Human structures could facilitate the colonization of cities by cavity-nesters (Tomasevic and Marzluff 2017) and therefore explain the preceding success of house sparrows in urbanized environment. Additional experimental studies are now needed to fully test the impact of other urban designs, planning and architectures on nesting site availability for urban house sparrows. Such additional studies are mandatory to test whether our results could be generalized to all urban areas.

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