Investigating temporal and spatial correlates of the sharp decline of an urban exploiter bird in a large European city

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Abstract
Increasing urbanisation and human pressure on lands have huge impacts on biodiversity. Some species, known as “urban exploiters”, manage to expand in urban landscapes, relying on human resources. The House Sparrow (*Passer domesticus*) is the perfect example of a human-commensal species. Surprisingly, this urban exploiter has been declining all over Europe over the past decades. The proximate causes of this decline remain poorly understood. We particularly lack understanding about urban habitat characteristics that are particularly unfavourable for House Sparrows. In the present study, we analysed fine-scale habitat characteristics of House Sparrow population sizes and trends using a fifteen-year House Sparrow census (2003–2017) covering the urban diversity of Paris (nearly 200 census sites), one of the densest European cities. We documented for the first time the dramatic decline (~89%) of the species in Paris over the study period. The temporal decline over the whole city correlates with the concomitant increase in the number of breeding Sparrowhawks. We could not detect statistical influences of annual variations in weather conditions and pollution. The decline of House Sparrows is spatially heterogeneous. Indeed, site-scale analyses revealed sharpest declines at sites that initially hosted the largest numbers of sparrows, which are areas with a relatively high proportion of green spaces and new buildings. Further experimental studies are now needed to disentangle the exact impact of specific characteristics of the urban environment on House Sparrow populations.

Keywords Birds · Landscape ecology · *Passer domesticus* · Long-term population monitoring · Fine-scale habitat study · Urbanisation

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Introduction
With the growth of the world human population and the increase in human pressure on lands, cities are constantly expanding, often leading to a reduction of biodiversity with increasing urbanisation (Marzluff et al. 2001; Chace and Walsh 2006; Clergeau et al. 2006; McKinney 2006, 2008; Clanché and Rascol 2011; Seto et al. 2012). In 2015, 54% of the world population was urban (UN-Habitat 2016) and by 2050, 66% of the world population is expected to live in urban areas (UN-Habitat 2015). The proportion of people living in urban places is higher than 80% in developed countries (Antrop 2004). However, this is a global phenomenon as in developing countries land areas occupied by cities are increasing even more rapidly (UN-Habitat 2016).

Urbanisation can affect wild vertebrates, and especially wild birds, because it leads to habitat fragmentation (Antrop 2004) as well as an increase in disturbances such as air (Eeva and Lehikoinen 1995, 1996; Lacuana et al. 1996; Eeva et al. 2009), noise (Meillère et al. 2015a, b) or light pollution (Dominoni et al. 2013). Urbanisation is also associated with
drastic changes in food sources, predator and competitor pressure (Marzluff et al. 2001; Faeth et al. 2005; MacLeod et al. 2006), disease prevalence (Evans et al. 2009; Dadam et al. 2019), and temperature increases (“urban heat island effect”, Shochat et al. 2006). Interestingly, species differ in their ability to cope with the urban landscape and its distinctive characteristics. Species are commonly classified as urban “avoiders”, “adapters” and “exploitors” (Blair 1996). While “urban avoiders” are negatively affected by urbanisation and are absent from cities, “urban adapters” can adjust to urban landscapes and can be found along the urbanisation gradient (Nielsen et al. 2014). “Urban exploiters” are dependent on human resources and reach their highest abundances in urbanised areas (Blair 1996). Another terminology has also been proposed to take into account responses to the urbanisation gradient and conservation implications in urban adapters and exploiters (Fischer et al. 2015). This updated terminology distinguishes the “urban dwellers”, which are able to persist in urban areas without any immigration from natural areas, from the “urban utilizers”, which either don’t breed in urban landscapes, or highly depend on surrounding natural areas (Fischer et al. 2015).

Cities are known to continuously and rapidly evolve with new urban planning and management policies. This can deeply modify, for example, the structure of specific neighborhood and the intensity and frequency of disturbances that occur in cities. This changing environment may raise new benefits or constraints to wild vertebrate populations, and this can potentially increase or decrease the suitability of the urban environment for species. In that context, the House Sparrow (Passer domesticus) is a relevant model to investigate the conditions that favor (or compromise) urban exploiters, being now strictly commensal of humans (Saetre et al. 2012). Interestingly, this urban dweller has co-evolved with human activities and proved to be sensitive to changes occurring in the urban environment. Historically, the replacement of horse-drawn transport by the automobile (Summers-Smith 2003; Robinson et al. 2005), as well as the improvement of street hygiene, reducing food resources (De Laet and Summers-Smith 2007), led to a first decline of urban House Sparrows during the first half of the twentieth century. Surprisingly, a new drastic decline of urban populations of House Sparrows has been documented in many western European cities over the past decades (Bauer and Heine 1992; Bower 1999; Mitschke et al. 1999; Easterbrook 1999; Dott and Brown 2000; McCarthy 2000; Witt 2000; Prowse 2002; Summers-Smith 2003, 2010; De Laet and Summers-Smith 2007; Murgui and Macias 2010; Biadun and Zmihorski 2011; Seress et al. 2012). This decline suggests that, although urban dwellers are expected to cope better with modifications of urban landscapes than urban utilisers or avoiders, they are still affected by modern modifications of the urban environment, such as new construction trends, reducing the amount of available nesting or sheltering sites (Moudrá et al. 2018), or the improvement of sanitation in cities reducing food resource availability. Studying the causes of the decline of this urban sentinel species might thus help us better understand emerging biological constraints of urban life and their effects on wild vertebrates.

Several hypotheses have been suggested to explain the recent decline of House Sparrows. Among them, increasing inter-specific competition (Summers-Smith 2003, 2005), increasing predation rates (Eurasian Sparrowhawk, Accipiter nisus, Bell et al. 2010; McCabe et al. 2018), or the spread of diseases across species (Hartup et al. 2001) may contribute to the observed decline. Moreover, this decline could also be linked to the emergence or intensification of pollution sources specific to cities: noise pollution (Meillère et al. 2015a, b), light pollution (Dominoni et al. 2013), air pollution (Eeva and Lehikoinen 1995, 1996; Llacuna et al. 1996; Eeva et al. 2009), or even electromagnetic radiations (Balmori and Hallberg 2007; Balmori 2009; Singh et al. 2013). In addition, the decline of House Sparrows could also be the result of habitat modification, and more specifically of the disappearance of feeding, sheltering, or nesting sites (Shaw et al. 2008; Angelier and Brischoux 2019). This decline could also result from a change in food supply (Liker et al. 2008; Bell 2011), notably because of a lack of invertebrate preys, which are crucial for the survival and development of the chicks (Anderson 2006; Vincent 2006; Auman et al. 2008; Peach et al. 2014; Meillère et al. 2017). Such preys are likely to be found in higher densities near green space areas (Jones and Leather 2012) and House Sparrow decline would therefore be expected to vary according to vegetation accessibility. Importantly, the decline of House Sparrows may result from cumulative and interactive effects of these multiple stressors (De Coster et al. 2015).

In this study, we aimed to explore the fine-scale habitat determinants of House Sparrow population trends in Paris, one of the densest cities in Europe (Schwarz 2010), which is also characterized by its diversity of urban habitats (Cohen et al. 2012). To do so, we relied on the data collected by volunteers through a long-term citizen science survey. This monitoring program has been conducted at nearly 200 sites across Paris since 2003 (2005 counts over 15 years at 196 sites, Malher et al. 2010). Citizen science programs are widely and increasingly used by scientists around the world, for example to study bird species or communities, focusing on presence/absence or abundance (McCaffrey 2005; Cohn 2008; Tulloch et al. 2013; Follett and Strezov 2015). Citizen science-based bird counts are particularly successful in urban areas to describe species distribution or abundance, as the potential number of volunteers is often high (Cohn 2008). Despite some limitations (Conrad and Hilchey 2011), such as, for example, the fact that volunteers, by not necessarily being experts, may produce lower quality data, relying on citizens has proven to be a valuable and reliable asset to collect...
data on a large geographic scale during a short period of time (Greenwood 2007; Cohn 2008). Moreover, such citizen science-based monitoring programs are important to raise awareness about long-term ecological changes as well as to increase knowledge and engagement of the public in ecological issues (McCaffrey 2005; Conrad and Hilchey 2011; Tulloch et al. 2013).

In addition to this long-term monitoring of House Sparrows by point counts, we relied on global data to monitor yearly environmental changes of the urban environment that have occurred at the scale of Paris over the study period (temperature, precipitation, 18 air pollutants). Weather fluctuations and air pollution are among the main disturbances in urban habitats, and they are likely to affect the reproduction and the survival of urban birds (Ringsby et al. 2002; Peach et al. 2008). Moreover, the yearly number of known breeding Sparrowhawks in Paris was used to test the hypothesis of predation. Finally, we characterized the fine-scale habitat structure at all census sites by using detailed local planning and management data. By using this unique long-term monitoring design, we want to assess whether specific urban habitats are more suitable than others for urban House Sparrows. Specifically, and according to other studies (Dott and Brown 2000; Witt 2000; Prowse 2002; Murgui and Macias 2010; Biadun and Zmihorski 2011; De Coster et al. 2015), we expect that the number of House Sparrows in Paris has declined over the last 15 years, as in other very large cities (Prediction 1). We also predict that this decline may be explained by temporal changes in specific environmental factors (Prediction 2), such as weather (temperature, precipitations), pollution (air pollutants), or predation pressure (number of breeding European Sparrowhawks). Finally, we predict that the decline in counted House Sparrows varies across sites, depending on local habitat characteristics (Prediction 3).

Materials and methods

Long term House Sparrow census data

From 2003 to 2017, a large House Sparrow census by point counts has been carried out by 127 volunteers and coordinated by the Ligue pour la Protection des Oiseaux (LPO) Île-de-France at 196 sites in the inner Paris (excluding the two surrounding woods). Every year, this census took place in spring, during ten consecutive days (from the last week of March to the first week of April). Specifically, the volunteers stayed at census sites during ten minutes and counted House Sparrows they could see or hear. When a census session was implemented but no House Sparrow was detected, observers reported a null count. For each site and each year, the total number of counted House Sparrows was therefore available, and was used as a measure of relative abundance (called abundance hereafter). Overall, 196 sites have been monitored between 3 and 15 times from 2003 to 2017 (Fig. 1).

Between-year variations in air pollution, weather, and number of breeding Sparrowhawks

For each year from 2003 to 2016, mean temperature and total rainfall data were collected from the E-OBS gridded dataset (0.25 degrees regular grid produced by the European Climate Assessment & Dataset, 16.0 version). Yearly weather conditions were characterised by mean temperature and total rainfall in Paris for the twelve months preceding the counts (i.e. from April of the previous year to March of the current year) as potential covariates of sparrow counts. In addition, we used yearly mean concentrations of 18 air pollutants that have been measured by AirParif in Paris. Air concentrations of pollutants were available for 2.5 μm and 10 μm fine particulate matter (PM_{2.5} and PM_{10}, μg/m^3), ozone (O_3, μg/m^3), carbon monoxide (CO, μg/m^3), nitric oxide (NO, μg/m^3), nitrogen dioxide (NO_2, μg/m^3), sulphur dioxide (SO_2, μg/m^3), black smoke (μg/m^3), two heavy metals (arsenic (As) and cadmium (Cd), ng/m^3), seven polycyclic aromatic hydrocarbons (PAHs, ng/m^3) (benzo(a)pyrene (BaP), benzo(a)anthracene (BaA), benzo(b)fluoranthen (BbF), benzo(g,h,i)perylene (BghiP), benzo(k)fluoranthen (BkF), Benzo(1,2,3-c,d)pyrene (IP) and dibenzo(a,h)anthracene (DB)), and one monocyclic aromatic hydrocarbon (benzene (BEN), μg/m^3). Weather and pollutant data were not yet available for 2017. Regarding Sparrowhawks, we used the yearly number of known breeding pairs in Paris (Yves Gestraud, unpublished data). Indeed, Sparrowhawks have large territories and were only opportunistically monitored by volunteers. To take into account this limitation due to the citizen science nature of the data, we summed numbers of detected breeding pairs to obtain an overall yearly estimate of the Sparrowhawk population at the scale of the whole study area (Paris).

Between-site variation in habitat composition and human population density

Habitat composition was characterised within a 200-m buffer around each census site. The size of this buffer was selected according to available estimates of House Sparrow daily home ranges (Heij and Moellerk 1990; Vangestel et al. 2010). Habitat characteristics were selected according to prediction about their potential influence on House Sparrows. Therefore, we focused specifically on (1) vegetation because of its expected importance in terms of sheltering sites and source of seeds and invertebrate preys, (2) built-up areas because of their expected importance in terms of sheltering and nesting sites, (3) anthropogenic food sources because of their expected importance in terms of food supply, and (4) human
population density because it is a common proxy for the degree of urbanisation.

Regarding vegetation, we calculated, for each census site, the area which was covered by three different layers of vegetation (herbs, shrubs, and trees) in 2000, 2008, 2012 and 2015 (Institut d’Aménagement et d’Urbanisme - IAU, 2017; Mairie de Paris, Direction des Espaces Verts et de l’Environnement, 2015). The total area covered by vegetation was also computed. At site level, vegetation coverage for each layer remained stable throughout the study period (Anova on vegetation covers; all \( p > 0.98 \)). For each census site, the total number of trees in 2017 was also calculated (Mairie de Paris, Direction des Espaces Verts et de l’Environnement, 2017).

Regarding built-up areas, we used three available indices to characterise each census site: (1) age of construction or renovation of buildings (5 classes, corresponding to different structures: 1, before 1914; 2, 1915–1939; 3, 1940–1967; 4, 1968–1989; and 5, 1990-today), (2) roofing type (slate, tile, zinc, concrete or green roof) (Atelier Parisien d’Urbanisme - APUR, 2017), and (3) building height [characterized as high (> 5 floors) or low buildings (≤ 4 floors); IAU, 2012].

To estimate anthropogenic food availability, the area covered by food stands and terraces (Mairie de Paris, Direction de l’Urbanisme, 2017) was calculated for each site within a 200-m buffer.

Human population density was calculated for each district (Paris is divided in 20 districts) using INSEE Census of 2007 (Institut National de la Statistique et des Etudes Economiques - INSEE, 2009).

**Statistical data analyses**

All statistical analyses were conducted with R (RStudio 1.0.153). Firstly, we analysed population trends over the study period (2003–2017; \( n = 2006 \) counts). Secondly, we tested whether population trends could be explained by between-year variations in variables of interest (weather, pollution, breeding Sparrowhawk population size) over the 2003–2016 period (\( n = 1813 \) counts) because these data were not yet available for 2017. Finally, we tested whether local House Sparrow abundance and trend could be explained by habitat composition (vegetation, buildings, food, human population density) at site level over the 2003–2017 period (\( n = 2006 \) counts). As the data to analyse were census counts and models showed no overdispersion (overdispersion checked with ‘overdisp’ function, sjstats package, Lüdecke 2018), we used a Poisson distribution for all the following models. Moreover, in all models, sites and observers were added as random factors to control for the potential bias of such a citizen science monitoring scheme: all sites are not always monitored.
every year and volunteers have a different level in identification and counting skills (Dickinson et al. 2010). Model parameter estimates are reported as mean ± SE, whereas data distributions and random effects are reported as mean ± SD.

**Population trend (2003–2017)**

House Sparrow population trend was studied using generalised linear mixed models (GLMMs, built with the ‘glmer’ function, lme4 package, Bates et al. 2015) with Year as a fixed, linear continuous variable, and random slopes and intercepts to allow the local abundance (intercept for site) and the temporal trend (slope for Year effect per site) to randomly vary between sites (Zuur 2009; van de Pol and Wright 2009; Dingemanse and Dochtermann 2013). We also added the observer as a random effect to control for the potential non-independence of the counts of House Sparrows that were made by a given observer. This random-intercept-and-random-slope model enabled to assess the covariance between abundance and temporal trend at site level (i.e. correlation across sites of intercepts (initial number of sparrows per site) and slopes (linear trend through years per site), Corr). Random intercepts for site effect and random slopes for site-specific linear Year effect were estimated for each site in order to assess the dependence of the rate of population decline to initial population size (Fig. 2b; M2, Table 1; best linear unbiased predictions obtained with the ‘ranef’ function; Bates et al. 2015).

**Population trend, weather, pollution, and Sparrowhawks (2003–2016)**

Because most of the chosen explanatory variables co-varied throughout the study period (see correlation plot, Appendix A, Fig. 1A), we first ran a principal component analysis (PCA built with the ‘PCA’ function, FactoMineR package, all variables included in PCA were centred and scaled, Lê et al. 2008) with all between-year variables (weather conditions, air pollutants, breeding Sparrowhawks; with one value per year) to reduce temporal variables to a smaller number of independent correlates. The first principal component (TPC1) summarizes quantitatively the main temporal changes in environmental conditions. Only this principal component was considered for further analysis according to the broken-stick method (Frontier 1976). TPC1 explained 57.12% of the between-year variation for all variables, and decreasing TPC1 values were associated with an increasing number of breeding Sparrowhawks (correlation: \(r = -0.85\), \(p < 0.01\)), and decreasing levels of most air pollutants. Indeed, all studied air pollutants except dB, PM10, PM2.5, and O3 were significantly correlated with the first principal component (correlations: all \(r > 0.75\), all \(p < 0.05\)). Weather conditions were not correlated with TPC1 (correlations: all \(p > 0.16\)).

We then used GLMMs with House Sparrow counts as the dependent variable and TPC1 as an explanatory variable. Year was not included as an explanatory variable as it was correlated with TPC1. Year, Site, and Observer were added as random factors to take into account the potential non-independence of House Sparrow counts between years, sites, and observers.

**Site-specific abundance and declining trend (2003–2017)**

To analyse the influence of urban habitat structure on local abundance and on local trend in abundance of House Sparrows, a second PCA was used to characterize each count site. The two first principal components were kept for further analyses. They respectively explained 22.64% and 18.15% of the between-site variation in habitat structure. Increasing values of the first site-specific principal component (SPC1) were associated with a decreasing level of vegetation (correlation: all \(r < -0.45\), all \(p < 0.01\)) as well as an increasing level of built-up areas. More precisely, these built-up areas were mainly covered by high and old buildings (1st period: built before 1914), with slate or zinc roofing (correlation: all \(r > 0.67\), all \(p < 0.01\)). Increasing values of the second principal component (SPC2) were associated with an increasing level of area covered by relatively recent buildings (mainly dating from the 4th and 5th periods: 1968-today), concrete and green roofs, as well as

**Table 1**

| Model        | Random effects | Fixed effects |
|--------------|----------------|---------------|
|              | Group Name     | Name E ± SD   | Corr Name E ± SE Z P         |
| M1, Year     | Site (Int)     | 2.09 ± 1.44   | (Intercept) 1.30 ± 0.16 8.12 <0.001 |
|              | Observer (Int) | 0.90 ± 0.95   | Year -0.16 ± 0.01 -12.25 <0.001 |
| M2, Null model | Site (Int)   | 4.70 ± 2.17   | (Intercept) -0.15 ± 0.17 -0.85 0.397 |
|              | Observer (Int) | 1.04 ± 1.02   | Year 0.03 ± 0.19 -0.78 |
high human population density (correlation: all $r > 0.51$, all $p < 0.01$), and with a decreasing level of area covered by old buildings (correlation: all $r < -0.37$, all $p < 0.01$).

Firstly, we used GLMMs with House Sparrow counts as the dependent variable and Year, SPC$_1$, SPC$_2$, and the interactions between Year and SPC$_1$ or SPC$_2$ as explanatory variables. These interactions were designed to test for a difference in temporal trend, depending on the global environmental characteristics of the site. Site and Observer were added as random factors and Year was selected as a fixed, linear continuous variable, and random slopes and intercepts to allow the local abundance (intercept for site) and the temporal trend (slope for Year effect per site) to randomly vary between sites.

GLMMs were performed using ‘glmer’ function (lme4 package, Bates et al. 2015). For each model, marginal $R^2$ ($R^2_m$, representing the variance explained by fixed factors) and conditional $R^2$ ($R^2_c$, representing the variance explained by both fixed and random factors) were calculated with ‘r.squaredGLMM’ function (MuMIn package, Barton 2017). For the study of the spatial correlates of House Sparrow decline, model selection was implemented using MuMIn package (Barton 2017). All possible combinations of the aforementioned covariates (variables and interactions between them) were generated by the ‘dredge’ function. The ‘best’ model (i.e., model with the lowest QAICc value; Barton 2017) was selected.

Results
Decline of the House Sparrow in Paris

The number of House Sparrows at each site significantly decreased through years (linear Year effect, Table 1, Fig. 2a). On average, the number of counted House Sparrows per site decreased by 89.4% between 2003 and 2017 (Fig. 2a). The strong correlation between random intercept for site effects and random slopes for site-specific linear Year effect ($r = -0.43$, M1, Table 1) reveals that the sharpest declines occurred at sites with the highest numbers of House Sparrows at the beginning of the study period, whereas the numbers of House Sparrows were relatively stable at sites with low local abundance (Fig. 2b).

Temporal correlates of the decline

The number of House Sparrows was significantly correlated with the first principal component (TPC$_1$ estimate, Table 2), i.e. the temporal increase in the number of breeding Sparrowhawks and the decrease in air pollution. When testing separately the evolution of each variable over the study period, we found that only the number of breeding Sparrowhawks significantly increased ($t = 9.642$, $p < 0.001$, Table 3) while weather parameters did not vary significantly over time (all $p > 0.19$, Table 3) and air pollution either decreased or did not vary significantly (Table 3).

Spatial correlates of House Sparrow decline

Both spatial principal components significantly affected the number of House Sparrows at site level (SPC$_1$ and SPC$_2$ estimates, Table 4). House Sparrows were more numerous at census sites with mainly green spaces and reduced built-up areas (significant effect of SPC$_1$, Table 4). They were also more numerous at census sites with mainly relatively new buildings than at sites with old buildings (significant effect of SPC$_2$, Table 4). However, the interactions between the effects of Year and SPC$_1$ or SPC$_2$ were not significant in the best model (Table 4 and Appendix A, Table 1A). This suggests that local temporal trends in abundance did not depend on studied habitat characteristics.
Discussion

To our knowledge, House Sparrow populations in Paris had not yet been precisely monitored (Barloy 1966). In this study, we relied on a volunteer-based survey by point counts to assess the recent decline of this urban dweller in the city of Paris. Thanks to citizen science, we obtained an extensive long-term dataset on House Sparrow abundance (over 2000 counts over 15 years; Malher et al. 2010) covering nearly 200 sites over the whole French capital city. Furthermore, we investigated the proximate causes of the decline of House Sparrows.

**House Sparrow trends from 2003 to 2017**

In this study, we evaluated for the first time the current drastic decline (~89%) of House Sparrows in Paris over a fifteen-year period (2003–2017). This alarming decline of urban House Sparrows in Paris concurs with observations at other major European cities over the last decades. The decline of House Sparrow populations appears as a global and widespread phenomenon throughout its native range in Europe (Dott and Brown 2000; Witt 2000; Prowse 2002; De Laet and Summers-Smith 2007; Murgui and Macias 2010; Biadun and Zmihorski 2011; De Coster et al. 2015). The strength of the decline seems to depend on locations, as urban House Sparrow populations would have ceased to decrease in the United-Kingdom where they are now stabilising at very low population size (Woodward et al. 2018) while they are still declining in Southern European countries like France (present study, Malher et al. 2010), Belgium (De Coster et al. 2015), Germany (Witt 2000) or Spain (Murgui and Macias 2010).

Importantly, our results showed that House Sparrow numbers have been declining more rapidly at census sites with the highest House Sparrow abundances at the beginning of the study. This result suggests that specific environmental changes have occurred in Paris during the last 15 years and that the current conditions are not suitable for the maintenance of dense local populations of House Sparrows.

**Possible causes of the decline**

**Increasing predation by Sparrowhawks**

Interestingly, the number of breeding Sparrowhawks in Paris has been increasing over the study period. This colonisation, or recolonization, of urban landscapes by Sparrowhawks is a global and widespread phenomenon (Bell et al. 2010; Biadun and Zmihorski 2011). We found that the increase in Sparrowhawks in Paris correlates with the decline of House Sparrows (significant effect of TPC1 on House Sparrow abundance).

### Table 3 Variation of each temporal correlate of House Sparrow decline studied separately (breeding Sparrowhawks, air pollutants and weather parameters) over time. Estimates (E) and standard errors (SE) of the Year fixed effect were obtained using linear models

| Predation variable        | Year (E ± SE) | t-value | P      |
|---------------------------|---------------|---------|--------|
| Breeding Sparrowhawks     | 0.75 ± 0.08   | 9.642   | <0.001 |
| Pollutants                |               |         |        |
| Benzene                   | −0.04 ± 0.01  | −4.541  | <0.001 |
| NO2                       | −0.60 ± 0.11  | −5.448  | <0.001 |
| SO2                       | −0.64 ± 0.05  | −13.360 | <0.01  |
| Black smoke               | −0.73 ± 0.06  | −11.880 | <0.001 |
| PM2.5                     | −0.12 ± 0.17  | −0.690  | 0.503  |
| PM10                      | −0.07 ± 0.20  | −0.328  | 0.749  |
| BaA                       | −12.54 ± 2.48 | −5.052  | <0.001 |
| BaP                       | −7.80 ± 2.61  | −2.986  | 0.011  |
| BbF                       | −15.19 ± 3.08 | −4.938  | <0.001 |
| BghiP                     | −23.39 ± 3.31 | −7.062  | <0.001 |
| BKF                       | −4.15 ± 1.35  | −3.071  | <0.01  |
| IP                        | −13.36 ± 2.18 | −6.136  | <0.001 |
| dB                        | −0.53 ± 0.48  | −1.105  | 0.291  |
| As                        | −0.03 ± 0.01  | −5.142  | <0.001 |
| Cd                        | −0.02 ± 0.00  | −8.015  | <0.001 |
| NO                        | −0.34 ± 0.09  | −3.647  | <0.01  |
| CO                        | −14.84 ± 4.38 | −3.391  | <0.01  |
| O3                        | 0.12 ± 0.12   | 0.938   | 0.367  |
| Weather                   |               |         |        |
| Temperature               | 0.02 ± 0.04   | 0.388   | 0.705  |
| Precipitations            | 6.13 ± 4.46   | 1.374   | 0.194  |
This hypothesis is also congruent with the fact that, in our study, slopes of the decline were stronger at sites with higher initial numbers of counted House Sparrows (Liker et al. 2008; Meillère et al. 2017), and/or sheltering sites. Actually, several recent studies have emphasized the likely role of decaying food quality and/or quantity in the decline of urban House Sparrows (Liker et al. 2008; Meillère et al. 2015a), and/or sheltering sites. Interestingly, sparrows first bred in Paris in 2008 (Gestraud and Malher 2012), when House Sparrows were already declining (see Fig. 2a). Thus, Sparrowhawks alone cannot explain the entire decline of the species. Moreover, given the correlative nature of the study (correlation between Year and the number of breeding Sparrowhawks: r = 0.94, p < 0.01), and the potential imprecision of a city-scale index measured from opportunistic monitoring by volunteers, we must remain cautious. Further studies are thus needed to assess the possible fine-scale effect of urban Sparrowhawks on House Sparrows. Such studies could rely on a fine-scale Sparrowhawk monitoring scheme covering the whole city of Paris, hence allowing to assess with a higher reliability local numbers of breeding Sparrowhawks and their spatial distribution.

**Fine-scale habitat characteristics**

As the quality and quantity of resources (food, sheltering, or nesting sites) for birds may vary along with urban habitat characteristics, we related House Sparrow numbers with fine-scale habitat structure. We found that House Sparrow numbers were higher at census sites with abundant green spaces and relatively new buildings, in opposition to census sites with no green spaces and dominated by old buildings. These results, in agreement with what have been demonstrated by other studies (Summers-Smith 1959; Heij and Moeliker 1989; Opdam 1997; Frimer 1989; Gotmark and Post 1996; Solonen 1997; Millon et al. 2009; McCabe et al. 2018), suggest that green spaces offer resources for House Sparrows that are otherwise scarce in the urban environment, and that green spaces are necessary to support locally high population sizes. These scarce resources are likely to be food (invertebrate preys, anthropogenic food, and gardening by-products; Anderson 2006; Vincent 2006; Wilkinson 2006; Auman et al. 2008; Peach et al. 2015; Fischer et al. 2015; Meillère et al. 2017), and/or sheltering sites. Actually, several recent studies have emphasized the likely role of decaying food quality and/or quantity in the decline of urban House Sparrows (Liker et al. 2008; Meillère et al. 2017; Moudrá et al. 2018). Because invertebrate preys are crucial for the growth and the development of nestlings (Bolger 2001; Vincent 2006; Seress et al. 2012; Meillère et al. 2012, 2015a), and probably for survival over their first year of life (Bell 2011), a lack of invertebrate preys during the reproductive period has also been suggested as a proximate cause of the decline of urban House Sparrows (Vincent 2006; Bell 2011). Yet, despite our fine-scale study of census site characteristics, we were not able to explain the trend over time of House Sparrows using habitat characteristics. House Sparrows were declining at all sites, whatever the coverage of green space areas (cf. non-significant interaction between linear Year effect and SPC1 and SPC2 in the ‘best’ model, Appendix A, Table 1A). This robust result can be interpreted in two ways.
First, it suggests that even areas with extended green spaces do not provide a habitat of sufficiently good quality to secure the maintenance of large, local populations of House Sparrows. Second, as in many correlative studies using proxies for multi-scalar, multi-variante ecological processes, the environmental variables (and their combination using PCA) that were available to us may not have been sufficiently good indicators of the actual environmental and ecological pressures that drive House Sparrow decline. The use of more refined variables is still needed to identify the subtle processes that drive this decline.

As found in other studies (van der Poel 2000), the number of House Sparrows was higher in census sites covered with newer buildings. Specifically, House Sparrow numbers were positively affected by an increasing level of relatively recent buildings and a decreasing level of old buildings (SPC2 estimate, Appendix A, Table 1A). Contrary to our expectation and to the results of other studies (Heij and Moeliker 1990; Singh et al. 2013; Moudrá et al. 2018), the number of House Sparrows was therefore not higher at census sites covered mainly with old buildings, which are commonly associated with nesting and resting sites. This could mean that House Sparrows do not actually lack nesting sites in urban areas, as suggested by recent studies (Sheldon and Griffith 2017; Angelier and Brischoux 2019).

Other possible causes of the decline

As air pollution is suspected to affect the health of all urban organisms (Eeva and Lehikoinen 1995, 1996; Llacuna et al. 1996; Eeva et al. 2009), we studied the evolution of 18 air pollutants in Paris over our study period and related it to House Sparrow abundances. However, we found that air quality did not deteriorate during our fifteen-year study. Moreover, the number of counted House Sparrows was positively related to our synthetic index including the between-year variation in air pollutant levels (TPC1): the highest numbers were counted to our synthetic index including the between-year variation in the number of counted House Sparrows was positively related. It did not deteriorate during our fifteen-year study. Moreover, House Sparrow abundances. However, we found that air quality did not deteriorate during our fifteen-year study. Nevertheless, House Sparrow numbers were positively affected by an increasing level of relatively recent buildings and a decreasing level of old buildings (SPC2 estimate, Appendix A, Table 1A). Contrary to our expectation and to the results of other studies (Heij and Moeliker 1990; Singh et al. 2013; Moudrá et al. 2018), the number of House Sparrows was therefore not higher at census sites covered mainly with old buildings, which are commonly associated with nesting and resting sites. This could mean that House Sparrows do not actually lack nesting sites in urban areas, as suggested by recent studies (Sheldon and Griffith 2017; Angelier and Brischoux 2019).

Because of the correlative nature of this study and because the decline of House Sparrows may result from several interactive and cumulative effects (De Coster et al. 2015), further complementary and experimental studies are now needed to reveal the proximate, functional impacts of specific characteristics of the urban environment on House Sparrow individuals and populations (e.g. light and noise pollution, diseases and parasites). Moreover, future studies should examine not only House Sparrow abundance, but also the structure of the population (number of young individuals) to better understand whether a poor survival after fledgling, and over the first winter (Bell 2011), could be the dominating functional process responsible for the decline of House Sparrows in urbanised landscapes.

Conclusion

By using a long-term citizen science scheme, we documented the drastic ongoing decline of House Sparrows in Paris, one of the densest European cities. In 15 years, House Sparrow abundance decreased by 89% in our study area. We investigated the possible causes of the decline of this urban dweller using both city-scale and fine-scale covariates. At the scale of the city, we found that air pollution and weather fluctuations were unlikely to be responsible for the decline of urban House Sparrows, while this decline was correlated with the progressive settlement of breeding Sparrowhawks in the city. By studying fine-scale habitat characteristics, we highlighted that although House Sparrows were more numerous in sites characterised by large green space areas and relatively new buildings, they declined at all sites independently of habitat characteristics. This observed decline was even sharpest at sites with the highest numbers of House Sparrows at the beginning of the study period. Thus, we did not find any local habitat characteristic that would favour the maintenance of locally high abundances of this urban sentinel species.
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