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; Llacuna 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 "exploiters" (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) *Ile-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)fluoranthene (BbF), benzo(g,h,i)perylene (BghiP), benzo(k)fluoranthene (BkF), Indeno(1,2,3-c,d)pyrene (IP) and dibenzo(a,h)anthracene (dB)), and one monocyclic aromatic hyrocarbon (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 Moeliker 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

Fig. 1 Overview of the relative abundance of House Sparrows (i.e. number of House Sparrows counted per sampled site in Paris) in (**a**) 2003, (**b**) 2008, (**c**) 2012 and (**d**) 2017
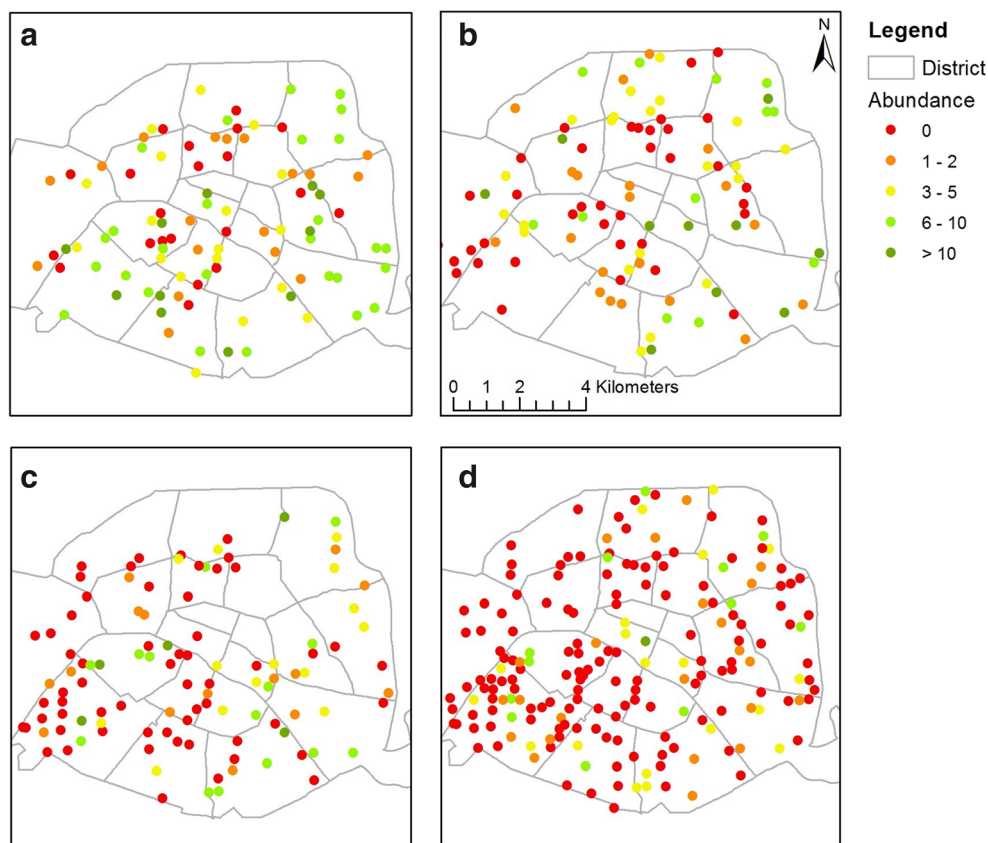
population density because it is a common proxy for the degree of urbanisation.

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; M_2, 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 pollution, breeding Sparrowhawks; with one value per year) to reduce temporal variables to a smaller number of independent correlates. The first principal component (TPC_1) 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). TPC_1 explained 57.12% of the between-year variation for all variables, and decreasing TPC_1 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, PM_{10}, $PM_{2.5}$, and O_3 were significantly correlated with the first principal component (correlations: all r > 0.75, all $p < 0.05$). Weather conditions were not correlated with TPC_1 (correlations: all $p > 0.16$).

We then used GLMMs with House Sparrow counts as the dependent variable and TPC_1 as an explanatory variable. Year was not included as an explanatory variable as it was correlated with TPC_1. 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 (SPC_1) 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 (SPC_2) 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 Dependence of House Sparrow abundance on the linear effect of year (temporal trend). Estimates (E) were obtained with a random-slope-and-intercept GLMM

Model			Random effects				Fixed effects			
			Group	Name	E ± SD	Corr	Name	E ± SE	Z	P
M_1. Year	R^2_m	0.13	Site	(Int)	2.09 ± 1.44		(Intercept)	1.30 ± 0.16	8.12	<0.001
	R^2_c	0.72		Year	0.02 ± 0.13	−0.43	Year	−0.16 ± 0.01	−12.25	<0.001
			Observer	(Int)	0.90 ± 0.95					
M_2. Null model	R^2_m	0.00	Site	(Int)	4.70 ± 2.17		(Intercept)	−0.15 ± 0.17	−0.85	0.397
	R^2_c	0.70		Year	0.03 ± 0.19	−0.78				
			Observer	(Int)	1.04 ± 1.02					

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, M_1, 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 SCP_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.
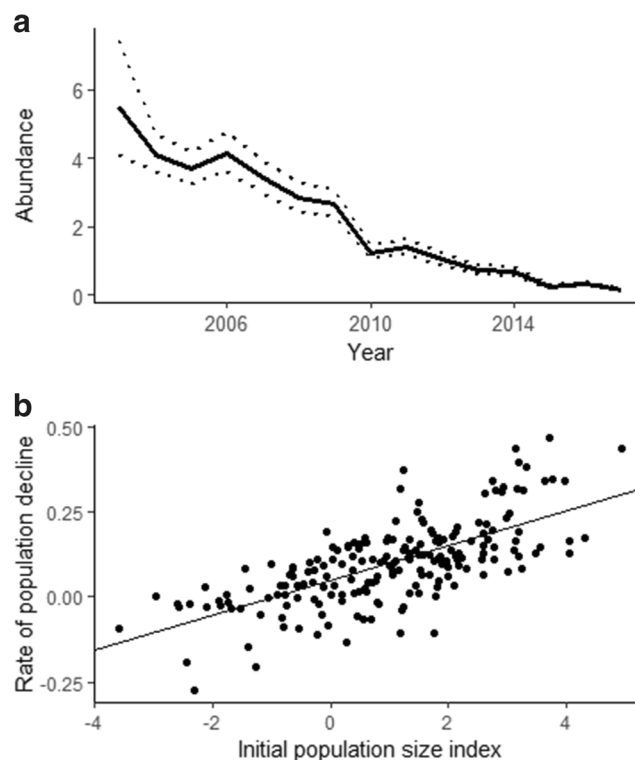

Fig. 2 **a** Estimated House Sparrow abundance (i.e. number of House Sparrows per site) over years in Paris (estimated with GLMM described in "Population trend, weather, pollution, and Sparrowhawks (2003–2016)" section but with Year as a categorical, fixed factor and without the random intercept for years) for all sites (n_{sites} = 196, n = 2005). Dotted lines represent 95% confidence intervals. **b** Dependence of the relative rate of population decline (i.e. random slope for the Year effect per site) to initial population size index (i.e. random intercept for site) for the 196 studied sites (n_{sites} = 196). The relative rate of population decline was calculated after accounting for the average decline across all sites (fixed Year effect)

Table 2 Dependence of House Sparrow abundance on a synthetic covariate of yearly variations in environmental characteristics (decreasing number of breeding Sparrowhawks and increasing air pollution, TPC_1). Estimates (E) were obtained with a random intercept GLMM

Models			Random effects		Fixed effects			
			Group	E ± SD	Name	E ± SE	Z	P
M_1. Null model	AIC	7769.7	Year	0.26 ± 0.51	(Intercept)	0.24 ± 0.20	1.21	0.225
	R^2_m	0.000	Site	1.75 ± 1.32				
	R^2_c	0.668	Observer	1.08 ± 1.04				
M_2. TPC_1	AIC	7751.9	Year	0.06 ± 0.24	(Intercept)	0.24 ± 0.16	1.51	0.131
	R^2_m	0.073	Site	1.75 ± 1.32	TPC_1	0.13 ± 0.02	6.52	<0.001
	R^2_c	0.664	Observer	1.07 ± 1.03				

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) in nearly 200 sites covering the

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

Dependent variable	Year (E ± SE)	t-value	P
Predation pressure			
Breeding Sparrowhawks	0.75 ± 0.08	9.642	<0.001
Pollutants			
Benzene	−0.04 ± 0.01	−4.541	<0.001
NO_2	−0.60 ± 0.11	−5.448	<0.001
SO_2	−0.64 ± 0.05	−13.360	<0.01
Black smoke	−0.73 ± 0.06	−11.880	<0.001
$PM_{2.5}$	−0.12 ± 0.17	−0.690	0.503
PM_{10}	−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
O_3	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

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 Europeans 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 TPC_1 on House Sparrow

Table 4 Dependence of House Sparrow abundance on two synthetic covariates of variations between sites in habitat structure (decreasing level of vegetation and increasing level of built-up areas, SPC_1, increasing surface covered by relatively recent buildings and decreasing level of old buildings, SPC_2). Estimates (E) were obtained with a random-slope-and-intercept GLMM

Model			Random effects				Fixed effects			
			Group	Name	E ± SD	Corr	Name	E ± SE	Z	P
M_1. Year + SPC_1 + SPC_2	R^2_m	0.178	Site	(Int)	1.91 ± 1.38		(Intercept)	1.30 ± 0.16	8.308	<0.001
	R^2_c	0.719		Year	0.02 ± 0.13	−0.47	Year	−0.16 ± 0.01	−12.416	<0.001
			Observer	(Int)	0.91 ± 0.95		SPC_1	−0.27 ± 0.10	−2.674	<0.01
							SPC_2	0.41 ± 0.10	4.086	<0.001

counts; Table 2, Fig. 2b). This result is in agreement with studies from the United-Kingdom suggesting that the increase in Sparrowhawks in urban areas might be involved in the decline of local House Sparrow populations (Bell et al. 2010). The Eurasian Sparrowhawk is indeed a major predator of House Sparrows (Anderson 2006; Bell et al. 2010), especially near urban areas (Tinbergen 1946; Opdam 1979; Frimer 1989; Gotmark and Post 1996; Solonen 1997; Millon et al. 2009; McCabe et al. 2018). By preferentially predating on House Sparrows, Sparrowhawks are likely to have a direct negative effect on House Sparrow populations. However, their effect might also be indirect on this species which has, for long, been released from Sparrowhawk predation pressure (Bell et al. 2010). Because of lower predation risk in cities (Gering and Blair 1999; Shochat 2004), urban House Sparrows might have adopted specific avian predator-free behavioural strategies (e.g. low flushing distance, foraging, and resting in large group sizes and/or in open areas, reduced vigilance, boldness; Blumstein and Daniel 2005). Due to behavioural adjustments subsequent to the arrival of their avian predator, House Sparrows may now aggregate in smaller, more fragmented, and less detectable groups, and they may adopt more cryptic behaviours (Siegfried and Underhill 1975; Barnard 1980; Cresswell 1994; Beauchamp 2004; Blumstein and Daniel 2005). 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 (cf. intercept-slope correlation, Table 1). Altogether, predation and behavioural changes would have reduced the number of detected birds during census sessions. Interestingly, Sparrowhawks 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 1990; Chamberlain et al. 2007; Murgui 2009; Moudrá 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. 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 SPC_1 and SPC_2 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-variate 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 (SPC_2 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 (TPC_1): the highest numbers were counted at the beginning of the period, i.e. when air pollution was maximal. Therefore, air pollution is unlikely to be the cause of the observed decline of House Sparrow populations in Paris.

Climate warming has also been proposed as a cause of the decline of birds (Crick 2004; Robinson et al. 2007; Both et al. 2010; Teyssier et al. 2018). As yearly mean temperature and total rainfall remained stable over the past fifteen years in the French capital city, we conclude that the weather was certainly not responsible for the current observed decline of House Sparrows.

The present study did not assess the potential influence of other urban-specific disturbances that were proposed as proximate causes of the decline of urban House Sparrows. We did not address the potential role of increasing noise (Meillère et al. 2015a, 2015b), light (Dominoni et al. 2013) and/or electromagnetic pollutions (Balmori and Hallberg 2007; Balmori 2009; Singh et al. 2013). We also did not assess the influence of increasing domestic cat abundance (the other major predator of sparrows, which has increased from 9.76 million to 13.48 (+38%) between 1999 and 2015 in France; Churcher and Lawton 1987; Baker et al. 2005), increasing inter-specific competition with other urban exploiters (e.g. the Feral Pigeon *Columba livia*; Summers-Smith 2003, 2005; or the Common Wood Pigeon *Columba palumbus*; Goodwin 1960; Summers-Smith 2003), parasite spill-over from other urban dwellers (again, potentially from urban pigeon species; Bichet et al. 2013) or more generally the ongoing changes in urban bird communities in large cities (Blair 1996; Melles et al. 2003; Francis et al. 2009; Biadun and Zmihorski 2011; Galbraith et al. 2015).

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.

References

Anderson TR (2006) Biology of the ubiquitous house sparrow: from genes to populations. Oxford Univ. Press, Oxford

Angelier F, Brischoux F (2019) Are house sparrow populations limited by the lack of cavities in urbanized landscapes? An experimental test. J Avian Biol 50. https://doi.org/10.1111/jav.02009

Antrop M (2004) Landscape change and the urbanization process in Europe. Landsc Urban Plan 67:9–26. https://doi.org/10.1016/S0169-2046(03)00026-4

Auman HJ, Meathrel CE, Richardson A (2008) Supersize me: does anthropogenic food change the body condition of silver gulls? A comparison between urbanized and remote, non-urbanized areas. Waterbirds 31:122–126

Baker PJ, Bentley AJ, Ansell RJ, Harris S (2005) Impact of predation by domestic cats Felis catus in an urban area. Mammal Rev 35:302–312. https://doi.org/10.1111/j.1365-2907.2005.00071.x

Balmori A (2009) Electromagnetic pollution from phone masts. Effects on wildlife. Pathophysiology 16:191–199. https://doi.org/10.1016/j.pathophys.2009.01.007

Balmori A, Hallberg Ö (2007) The urban decline of the house sparrow (*Passer domesticus*): a possible link with electromagnetic radiation. Electromagnet Biol Med 26:141–151. https://doi.org/10.1080/15368370701410558

Barloy JJ (1966) Recherches sur le moineau domestique, Passer d. domesticus(Linne) 1758: cycle biologique, ecologie, dynamique de population; sa place dans l'avifaune parisienne. Thèse de doctorat. Sciences Naturelles: Universite de Paris, Faculte des Sciences; 1966

Barnard CJ (1980) Flock feeding and time budgets in the house sparrow (Passer domesticus L.). Anim Behav 28:295–309. https://doi.org/10.1016/S0003-3472(80)80032-7

Barton K (2017) MuMIn: Multi-Model Inference. R package version 1.40.0. https://CRAN.R-project.org/package=MuMIn

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67. https://doi.org/10.18637/jss.v067.i01

Bauer HG, Heine G (1992) Die Entwicklung der Brutvogelbestände am Bodensee: Vergleich halbquantitativer Rasterkartierungen 1980/81 und 1990/91. J Ornithol 133:1–22

Beauchamp G (2004) Reduced flocking by birds on islands with relaxed predation. Proc R Soc Lond Ser B Biol Sci 271:1039–1042. https://doi.org/10.1098/rspb.2004.2703

Bell CP (2011) Misapplied ecology: investigations of population decline in the house sparrow. Int Stud Sparrows 35:24–34. https://doi.org/10.1515/isspar-2015-0009

Bell CP, Baker SW, Parkes NG, Brooke ML, Chamberlain DE (2010) The role of the Eurasian Sparrowhawk (*Accipiter nisus*) in the decline of the house sparrow (*Passer domesticus*) in Britain. Auk 127:411–420. https://doi.org/10.1525/auk.2009.09108

Biadun W, Zmihorski M (2011) Factors shaping a breeding bird community along an urbanization gradient: 26-year study in medium size city (Lublin, SE Poland). Pol J Ecol 59:381–389

Bichet C, Scheifler R, Cœurdassier M, Julliard R, Sorci G, Loiseau C (2013) Urbanization, trace metal pollution, and malaria prevalence in the house sparrow. PLoS One 8:e53866. https://doi.org/10.1371/journal.pone.0053866

Blair RB (1996) Land use and avian species diversity along an urban gradient. Ecol Appl 6:506–519. https://doi.org/10.2307/2269387

Blumstein DT, Daniel JC (2005) The loss of anti-predator behaviour following isolation on islands. Proc R Soc B Biol Sci 272:1663–1668. https://doi.org/10.1098/rspb.2005.3147

Bolger D (2001) Urban birds: population, community and landscape approaches. In: Avian Ecology and Conservation in an Urbanising World. Springer Science & Business Media, Berlin, pp 155–178

Both C, Van Turnhout CAM, Bijlsma RG et al (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc R Soc B Biol Sci 277:1259–1266. https://doi.org/10.1098/rspb.2009.1525

Bower S (1999) Fortpflanzungsaktivitat, Habitatnutzung und populationsstruktur eines Schwarms von Haussperlingen (Passer d. domesticus) im Hamburger Stadtgebiet–Hamburger avifaun. Hamburger avifaun Beitr 30:91–128

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69. https://doi.org/10.1016/j.landurbplan.2004.08.007

Chamberlain DE, Toms MP, Cleary-McHarg R, Banks AN (2007) House sparrow (Passer domesticus) habitat use in urbanized landscapes. J Ornithol 148:453–462. https://doi.org/10.1007/s10336-007-0165-x

Churcher PB, Lawton JH (1987) Predation by domestic cats in an English village. J Zool 212:439–455. https://doi.org/10.1111/j.1469-7998.1987.tb02915.x

Clanché F, Rascol O (2011) Le découpage en unités urbaines de 2010: l'espace urbain augmente de 19% en une décennie. INSEE Première 1364 August 2011

Clergeau P, Croci S, Jokimäki J, Kaisanlahti-Jokimäki ML, Dinetti M (2006) Avifauna homogenisation by urbanisation: analysis at different European latitudes. Biol Conserv 127:336–344. https://doi.org/10.1016/j.biocon.2005.06.035

Cohen M, Baudoin R, Palibrk M, Persyn N, Rhein C (2012) Urban biodiversity and social inequalities in built-up cities: new evidences, next questions. The example of Paris, France. Landsc Urban Plan 106:277–287. https://doi.org/10.1016/j.landurbplan.2012.03.007

Cohn JP (2008) Citizen science: can volunteers do real research? BioScience 58:192–197. https://doi.org/10.1641/B580303

Conrad CC, Hilchey KG (2011) A review of citizen science and community-based environmental monitoring: issues and opportunities. Environ Monit Assess 176:273–291. https://doi.org/10.1007/s10661-010-1582-5

Cresswell W (1994) Song as a pursuit-deterrent signal, and its occurrence relative to other anti-predation behaviours of skylark (Alauda arvensis) on attack by merlins (Falco columbarius). Behav Ecol Sociobiol 34:217–223. https://doi.org/10.1007/BF00167747

Crick HQP (2004) The impact of climate change on birds: impact of climate change on birds. Ibis 146:48–56. https://doi.org/10.1111/j.1474-919X.2004.00327.x

Dadam D, Robinson RA, Clements A, Peach WJ, Bennett M, Rowcliffe JM, Cunningham AA (2019) Avian malaria-mediated population decline of a widespread iconic bird species. R Soc Open Sci 6:182197. https://doi.org/10.1098/rsos.182197

De Coster G, De Laet J, Vangestel C et al (2015) Citizen science in action—evidence for long-term, region-wide house sparrow declines in Flanders, Belgium. Landsc Urban Plan 134:139–146. https://doi.org/10.1016/j.landurbplan.2014.10.020

De Laet J, Summers-Smith JD (2007) The status of the urban house sparrow Passer domesticus in North-Western Europe: a review. J Ornithol 148:275–278. https://doi.org/10.1007/s10336-007-0154-0

Dickinson JL, Zuckerberg B, Bonter DN (2010) Citizen science as an ecological research tool: challenges and benefits. Annu Rev Ecol Evol Syst 41:149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

Dingemanse NJ, Dochtermann NA (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. J Anim Ecol 82:39–54. https://doi.org/10.1111/1365-2656.12013

Dominoni DM, Quetting M, Partecke J (2013) Long-term effects of chronic light pollution on seasonal functions of European blackbirds (Turdus merula). PLoS One 8:e85069. https://doi.org/10.1371/journal.pone.0085069

Dott HEM, Brown AW (2000) A major decline of house sparrows in Central Edinburg. Scott Birds 21:61–68

Easterbrook TG (1999) Population trends of wintering birds around Banbury, Oxfordshire, 1975–96. Bird Study 46:16–24. https://doi.org/10.1080/00063659909461111

Eeva T, Lehikoinen E (1995) Egg shell quality, clutch size and hatching success of the great tit (Parus major) and the pied flycatcher (Ficedula hypoleuca) in an air pollution gradient. Oecologia 102:312–323. https://doi.org/10.1007/BF00329798

Eeva T, Lehikoinen E (1996) Growth and mortality of nestling great tits (Parus major) and pied flycatchers (Ficedula hypoleuca) in a heavy metal pollution gradient. Oecologia 108:631–639. https://doi.org/10.1007/BF00329036

Eeva T, Hakkarainen H, Belskii E (2009) Local survival of pied flycatcher males and females in a pollution gradient of a Cu smelter. Environ Pollut 157:1857–1861. https://doi.org/10.1016/j.envpol.2009.01.015

Evans KL, Gaston KJ, Sharp SP, McGowan A, Simeoni M, Hatchwell BJ (2009) Effects of urbanisation on disease prevalence and age structure in blackbird Turdus merula populations. Oikos 118:774–782. https://doi.org/10.1111/j.1600-0706.2008.17226.x

Faeth SH, Warren PS, Shochat E, Marussich WA (2005) Trophic dynamics in urban communities. BioScience 55:399. https://doi.org/10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2

Fischer JD, Schneider SC, Ahlers AA, Miller JR (2015) Categorizing wildlife responses to urbanization and conservation implications of terminology: terminology and urban conservation. Conserv Biol 29:1246–1248. https://doi.org/10.1111/cobi.12451

Follett R, Strezov V (2015) An analysis of citizen science based research: usage and publication patterns. PLoS One 10:e0143687. https://doi.org/10.1371/journal.pone.0143687

Francis CD, Ortega CP, Cruz A (2009) Noise pollution changes avian communities and species interactions. Curr Biol 19:1415–1419. https://doi.org/10.1016/j.cub.2009.06.052

Frimer O (1989) Food and predation in suburban Sparrowhawks Accipiter nisus during the breeding season. Dansk Orn Foren Tidsskr 83:35–44

Frontier S (1976) Étude de la décroissance des valeurs propres dans une analyse en composantes principales: Comparaison avec le modḋle du bâton brisé. J Exp Mar Biol Ecol 25:67–75. https://doi.org/10.1016/0022-0981(76)90076-9

Galbraith JA, Beggs JR, Jones DN, Stanley MC (2015) Supplementary feeding restructures urban bird communities. Proc Natl Acad Sci 112:E2648–E2657. https://doi.org/10.1073/pnas.1501489112

Gering JC, Blair RB (1999) Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography 22:532–541. https://doi.org/10.1111/j.1600-0587.1999.tb01283.x

Gestraud Y, Malher F (2012) L'implantation de l'Epervier d'Europe Accipiter nisus dans Paris intra-muros. Le Passer:12–23

Goodwin D (1960) Comparative ecology of pigeons in inner London. British Birds 53:201–212

Gotmark F, Post P (1996) Prey selection by Sparrowhawks, Accipiter nisus: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. Philosophic Transact Royal Soc B: Biol Sci 351:1559–1577. https://doi.org/10.1098/rstb.1996.0141

Greenwood JJD (2007) Citizens, science and bird conservation. J Ornithol 148:77–124. https://doi.org/10.1007/s10336-007-0239-9

Hartup BK, Dhondt AA, Sydenstricker KV, Hochachka WM, Kollias GV (2001) Host range and dynamics of mycoplasmal conjunctivis among birds in North America. J Wildl Dis 37:72–81. https://doi.org/10.7589/0090-3558-37.1.72

Heij CJ, Moeliker CW (1990) Population dynamics of Dutch house sparrows in urban, suburban, and rural habitats. In: Pinowski J, Summers-Smith JD (eds) Granivorous birds in the agricultural landscape. PWN-Polish Scientific Publishers, Warsaw, pp 59–85

Jones EL, Leather SR (2012) Invertebrates in urban areas: a review. Eur J Entomol 109:463–478. https://doi.org/10.14411/eje.2012.060

Lê S, Josse J, Husson F (2008) FactoMineR: An R Package for Multivariate Analysis. J Stat Softw 25. https://doi.org/10.18637/jss.v025.i01

Liker A, Papp Z, Bókony V, Lendvai ÁZ (2008) Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. J Anim Ecol 77:789–795. https://doi.org/10.1111/j.1365-2656.2008.01402.x

Llacuna S, Gorriz A, Riera M, Nadal J (1996) Effects of air pollution on hematological parameters in passerine birds. Arch Environ Contam Toxicol 31:148–152. https://doi.org/10.1007/BF00203919

Lüdecke D (2018) Sjstats: statistical functions for regression models. R package version 0.14.0. https://doi.org/10.5281/zenodo.1284472

MacLeod R, Barnett P, Clark J, Cresswell W (2006) Mass-dependent predation risk as a mechanism for house sparrow declines? Biol Lett 2:43–46. https://doi.org/10.1098/rsbl.2005.0421

Malher F, Jiguet F, Julliard R et al (2010) Le Moineau domestique Passer domesticus à Paris : Résultats de 5 ans d'enquête. Alauda 78:217–224

Marzluff JM, Bowman R, Donnelly R (2001) Avian ecology and conservation in an urbanizing world. Springer US, Boston

McCabe JD, Yin H, Cruz J et al (2018) Prey abundance and urbanization influence the establishment of avian predators in a metropolitan landscape. Proc R Soc B Biol Sci 285:20182120. https://doi.org/10.1098/rspb.2018.2120

McCaffrey RE (2005) Using citizen science in urban bird studies. Urban Habit 3:70–86

McCarthy M (2000) Where have all the sparrows gone? The Indepenent Newspaper 18, March 2000

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst 11:161–176. https://doi.org/10.1007/s11252-007-0045-4

Meillère A, Brischoux F, Parenteau C, Angelier F (2015a) Influence of urbanization on body size, condition, and physiology in an urban exploiter: a multi-component approach. PLoS One 10:e0135685. https://doi.org/10.1371/journal.pone.0135685

Meillère A, Brischoux F, Ribout C, Angelier F (2015b) Traffic noise exposure affects telomere length in nestling house sparrows. Biol Lett 11:20150559. https://doi.org/10.1098/rsbl.2015.0559

Meillère A, Brischoux F, Henry P-Y, Michaud B, Garcin R, Angelier F (2017) Growing in a city: consequences on body size and plumage quality in an urban dweller, the house sparrow (Passer domesticus). Landsc Urban Plan 160:127–138. https://doi.org/10.1016/j.landurbplan.2016.12.014

Melles S, Glenn SM, Martin K (2003) Urban bird diversity and landscape complexity: species-environment associations along a multiscale habitat gradient. Conserv Ecol 7. https://doi.org/10.5751/ES-00478-070105

Millon A, Nielsen JT, Bretagnolle V, Møller AP (2009) Predator-prey relationships in a changing environment: the case of the sparrowhawk and its avian prey community in a rural area: predator response to changes in prey community. J Anim Ecol 78:1086–1095. https://doi.org/10.1111/j.1365-2656.2009.01575.x

Mitschke A, Geissler HH, Andersen L (1999) Ornithologischer Jahresbericht 1996 und 1997 für das Hamburger Berichtsgebiet. Hamburger Avifaun Beitr 30

Moudrá L, Zasadil P, Moudrý V, Šálek M (2018) What makes new housing development unsuitable for house sparrows (Passer domesticus)? Landsc Urban Plan 169:124–130. https://doi.org/10.1016/j.landurbplan.2017.08.017

Murgui E (2009) Seasonal patterns of habitat selection of the house sparrow Passer domesticus in the urban landscape of Valencia (Spain). J Ornithol 150:85–94. https://doi.org/10.1007/s10336-008-0320-z

Murgui E, Macias A (2010) Changes in the house sparrow Passer domesticus population in Valencia (Spain) from 1998 to 2008. Bird Study 57:281–288. https://doi.org/10.1080/00063651003716762

Nielsen AB, van den Bosch M, Maruthaveeran S, van den Bosch CK (2014) Species richness in urban parks and its drivers: a review of empirical evidence. Urban Ecosyst 17:305–327. https://doi.org/10.1007/s11252-013-0316-1

Opdam P (1979) Feeding ecology of a Sparrowhawk population (Accipiter nisus). Ardea 66:137–155

Peach WJ, Vincent KE, Fowler JA, Grice PV (2008) Reproductive success of house sparrows along an urban gradient. Anim Conserv 11:493–503. https://doi.org/10.1111/j.1469-1795.2008.00209.x

Peach WJ, Sheehan DK, Kirby WB (2014) Supplementary feeding of mealworms enhances reproductive success in garden nesting house sparrows Passer domesticus. Bird Study 61:378–385. https://doi.org/10.1080/00063657.2014.918577

Peach WJ, Mallord JW, Ockendon N, Orsman CJ, Haines WG (2015) Invertebrate prey availability limits reproductive success but not breeding population size in suburban house sparrows Passer domesticus. Ibis 157:601–613. https://doi.org/10.1111/ibi.12264

Prowse A (2002) The urban decline of house sparrow. British Birds 95:143–146

Ringsby TH, Sæther B-E, Tufto J, Jensen H, Solberg EJ (2002) Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment. Ecology 83:561–569. https://doi.org/10.1890/0012-9658(2002)083[0561:ASDOAH]2.0.CO;2

Robinson RA, Siriwardena GM, Crick HQP (2005) Size and trends of the house sparrow Passer domesticus population in Great Britain: house sparrow population size and trends. Ibis 147:552–562. https://doi.org/10.1111/j.1474-919x.2005.00427.x

Robinson RA, Baillie SR, Crick HQP (2007) Weather-dependent survival: implications of climate change for passerine population processes: weather-dependent passerine survival. Ibis 149:357–364. https://doi.org/10.1111/j.1474-919X.2006.00648.x

Saetre G-P, Riyahi S, Aliabadian M et al (2012) Single origin of human commensalism in the house sparrow: human commensalism in the house sparrow. J Evol Biol 25:788–796. https://doi.org/10.1111/j.1420-9101.2012.02470.x

Schwarz N (2010) Urban form revisited—selecting indicators for characterising European cities. Landsc Urban Plan 96:29–47. https://doi.org/10.1016/j.landurbplan.2010.01.007

Seress G, Bókony V, Pipoly I, Szép T, Nagy K, Liker A (2012) Urbanization, nestling growth and reproductive success in a moderately declining house sparrow population. J Avian Biol 43:403–414. https://doi.org/10.1111/j.1600-048X.2012.05527.x

Seto KC, Guneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc Natl Acad Sci 109:16083–16088. https://doi.org/10.1073/pnas.1211658109

Shaw LM, Chamberlain D, Evans M (2008) The house sparrow Passer domesticus in urban areas: reviewing a possible link between post-decline distribution and human socioeconomic status. J Ornithol 149:293–299. https://doi.org/10.1007/s10336-008-0285-y

Sheldon EL, Griffith SC (2017) A high incidence of non-cavity nesting in an introduced population of House Sparrows suggests that the species should not be constrained by cavity-nest site availability. Avian Res 8. https://doi.org/10.1186/s40657-017-0087-0

Shochat E (2004) Credit or debit? Resource input changes population dynamics of city-slicker birds. Oikos 106:622–626. https://doi.org/10.1111/j.0030-1299.2004.13159.x

Shochat E, Warren P, Faeth S et al (2006) From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186–191. https://doi.org/10.1016/j.tree.2005.11.019

Siegfried WR, Underhill LG (1975) Flocking as an anti-predator strategy in doves. Anim Behav 23:504–508. https://doi.org/10.1016/0003-3472(75)90126-8

Singh R, Kour DN, Ahmed F, Sahi DN (2013) The causes of decline of house sparrow (Passer domesticus, Linnaeus 1758) in urban and suburban areas of Jammu region, J and K. Munis J Zool Entomol 8:803–811

Solonen T (1997) Effects of Sparrowhawk Acciper nisus predation on forest birds in southern Finland. Ornis Fennica 74:1–14

Summers-Smith D (1959) The house sparrow Passer domesticus: population problems. Ibis 101:449–455. https://doi.org/10.1111/j.1474-919X.1959.tb02403.x

Summers-Smith JD (2003) The decline of the house sparrow: a review. British Birds 96:439–446

Summers-Smith JD (2005) Changes in the house sparrow population in Britain. Int Stud Sparrows 30:23–37

Summers-Smith D (2010) The sparrows. A&C Black, London

Teyssier A, Rouffaer LO, Saleh Hudin N, Strubbe D, Matthysen E, Lens L, White J (2018) Inside the guts of the city: urban-induced alterations of the gut microbiota in a wild passerine. Sci Total Environ 612:1276–1286. https://doi.org/10.1016/j.scitotenv.2017.09.035

Tinbergen L (1946) The sparrowhawk (Accipiter nisus L.) as a predator of passerine birds. Ardea 34:1–213

Tulloch AIT, Possingham HP, Joseph LN, Szabo J, Martin TG (2013) Realising the full potential of citizen science monitoring programs. Biol Conserv 165:128–138. https://doi.org/10.1016/j.biocon.2013.05.025

UN-Habitat (2015) National Urban Policy: a guiding framework. UN-Habitat, Nairobi

UN-Habitat (2016) Urbanization and development: emerging futures. UN-Habitat, Nairobi

van de Pol M, Wright J (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. Anim Behav 77:753–758. https://doi.org/10.1016/j.anbehav.2008.11.006

van der Poel G (2000) Are House Sparrow numbers increasing or decreasing in Gooi & Vecht region in the Netherlands? http://www.xs4all.nl/~amvdpoel. Accessed 11 Sep 2017

Vangestel C, Braeckman BP, Matheve H, Lens L (2010) Constraints on home range behaviour affect nutritional condition in urban house sparrows (Passer domesticus): ranging behaviour in urban house sparrows. Biol J Linn Soc 101:41–50. https://doi.org/10.1111/j.1095-8312.2010.01493.x

Vincent K (2006) Investigating the Causes of the Decline of the Urban House Sparrow Population in Britain. PhD thesis, De Montfort University

Wilkinson N (2006) Factors influencing the small-scale distribution of house sparrows Passer domesticus in a suburban environment. Bird Study 53:39–46. https://doi.org/10.1080/00063650609461414

Witt K (2000) Situation der Vögel im städtischen Bereich: Beispiel Berlin. Vogelwelt 121:107–128

Woodward ID, Massimino D, Hammond MJ et al (2018) BirdTrends 2018: trends in numbers, breeding success and survival for UK breeding birds. British Trust for Ornithology See www bto org/birdtrends, Thetford

Zuur AF (ed) (2009) Mixed effects models and extensions in ecology with R. Springer, New York