



# Reproductive differences between urban and forest birds across the years: importance of environmental and weather parameters

Agnès Saulnier<sup>1</sup> · Josefa Bleu<sup>1,2</sup> · Anne Boos<sup>1,2</sup> · Maurice Millet<sup>2,3</sup> · Sandrine Zahn<sup>1,2</sup> · Pascale Ronot<sup>1,2</sup> · Islah El Masoudi<sup>1</sup> · Emilio R. Rojas<sup>1,4</sup> · Pierre Uhlrich<sup>1,2</sup> · Mirella Del Nero<sup>1,2</sup> · Sylvie Massemin<sup>1,2</sup>

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## Abstract

Urban environments pose many challenges to wildlife, not least for insectivorous passerines. Numerous studies have reported on the negative effects of urbanization on reproduction in these species. However, depending on the taxa and cities studied, no particular or positive effects have been reported. This may be related to the different levels of urban environmental stressors. As unfavorable weather can have deleterious effects on birds (e.g. lower prey availability and higher costs of pollutants), annual variations in the differences observed between sites could be related to synergetic effects between the urban environment and weather conditions. In this context, we studied the reproduction of great tit (*Parus major*) at two sites (urban and forest) over four years. First, we quantified pollution, prey availability, and vegetal cover at each site to characterize each environment. Second, we measured the effects of site and weather conditions on tit reproductive success to determine if the influence of weather is higher in the city. Except for the fledging rate, reproductive parameters were lower in the city than in the forest whatever the year probably because of poorer food availability and a predominance of non-vegetated areas in cities. The fledging rate and the nestling number in the urban environment were positively correlated to temperatures during rearing whereas there was no significant correlations in the forest. These results support the hypothesis of additive effects of urban constraints and weather that limit bird productivity in cities.

**Keywords** Urbanization · Weather effect · Metal pollution · Reproductive success

## Introduction

A growing human population has resulted in growing levels of urban development, significantly modifying natural landscapes. Urbanization is associated with a deep restructuring of abiotic parameters, such as temperature or light/noise/chemical pollution, as well as the modification of biotic parameters, such as low vegetation cover or changes in fauna/flora, species interactions, or human density (Gil and Brumm 2013).

These rapid environmental changes have direct consequences on the demography of many species, particularly birds, due to the impact of the environment on the reproductive success of individuals (Chamberlain et al. 2009; Shochat et al. 2015). Numerous factors can influence the reproductive success of urban birds. Urban habitats are considered to be of lower quality compared to rural habitats (Bailly et al. 2016; Kempnaers et al. 2010; Meillère et al. 2015; Schroeder et al. 2012). Modifications of photoperiod and local increase of temperatures due to anthropogenic structures often lead to advance the phenology of urban birds which can result to mismatch between prey phenology and young rearing (Chamberlain et al. 2009). Moreover, urban habitat also offer a lower prey availability due to the poorer invertebrate density associated with a reduced vegetal cover (Fenoglio et al. 2020). Some studies have pointed out that urban food is also of lower nutritional quality, such as lower antioxidant contents (Isaksson and Andersson 2007), which can lead to nutritional deficiencies (Bailly et al. 2017). A lower quality and quantity of prey leads to a reduction of clutch size (Wawrzyniak et al. 2015a) but also to a poorer physical

✉ Agnès Saulnier  
agnes.saulnier@iphc.cnrs.fr

<sup>1</sup> UMR 7178, Université de Strasbourg, CNRS, IPHC, 67000 Strasbourg, France

<sup>2</sup> ZAEU, Maison Interuniversitaire Des Sciences de L'Homme - Alsace (MISHA), 5, Allée du Général Rouvillois, 50008, 67083 Strasbourg Cedex, CS, France

<sup>3</sup> UMR 7515, Université de Strasbourg, CNRS, ICPEES, 67087 Strasbourg Cedex 3, France

<sup>4</sup> Wildstat, 43 Rue de La Hoube, 67280 Urmatt, France

condition of nestlings (Bailly et al. 2017; Meillère et al. 2015) and lower fledging rates. Poor reproductive success and low rates of nestling survival are also correlated with increasing chemical component exposure as a result of increasingly intense anthropogenic activities. Numerous studies have found that pollutants, such as polycyclic aromatic hydrocarbons (PAHs, whose emissions are associated with road traffic) or polychlorinated biphenyl (PCB), can affect egg production and egg quality, leading to higher rates of hatching failure (higher embryonic mortality and development abnormalities, Albers 2006; Fernie et al. 2000; Vos 1972). Similarly, some metals, such as cadmium (Cd) and lead (Pb), whose emissions may be linked to industrial activities, can interfere with calcium metabolism, leading to thinner eggshells (Eeva and Lehikoinen 1995; Scheuhammer 1996) but also to osteogenesis abnormalities (Eeva and Lehikoinen 1996; Goyer 1997) or oxidative stress responses during the growth of nestlings which can jeopardize fledging success (Berglund et al. 2007; Chatelain et al. 2021b).

In this context, the majority of recent studies have reported decreased reproductive success in various bird species in cities, notably insectivorous birds (review by Chamberlain et al. 2009; see also Biard et al. 2017; Halfwerk et al. 2011; Peach et al. 2008; Vaugoyeau et al. 2016). However, not all studies have reported lower reproductive success in cities; in fact, some studies have found no differences or even positive effects of urbanization on reproductive success (see Sepp et al. 2017 for a review). In these studies, it is possible that the constraints of the studied environment were minimal, or alternatively, that the specific urban environment had an advantage over the rural environment, such as lower parasites and a lower prevalence of predation (Sepp et al. 2017). However, for some long-term population studies, a large variance has been reported in terms of the differences in reproductive success between urban and forest populations over the years, which does not always allow for the establishment of a recurrent pattern (Wawrzyniak et al. 2020, 2015a). Therefore, it is very difficult to draw conclusions regarding the impact of city life on individuals based solely on the results of a single-year study. To understand the underlying mechanisms influencing reproductive success in an urban context, it is necessary to take into account the inter-annual variability of reproductive parameters across sites.

One hypothesis for this inter-annual variability is the variation in weather parameters. In fact, the reproductive success of birds is dependent on weather conditions and, nestling survival and fledging rate in passerine birds are often negatively correlated with rainfall and cold temperatures (Cox et al. 2019; Öberg et al. 2015). Low temperatures impose thermal challenge for nestlings which must allocate more energy in thermoregulation at the expense of growth and self-maintenance leading to physiological cost as growth delay (Yahav 2002; Krijgsveld et al. 2003; Dawson et al. 2005) or altered immune functions (Ardia et al. 2010). Harsh condition also increase

reproductive cost for parents notably to maintain the brood to optimal temperature reducing the time for self-maintenance and foraging (Amininasab et al. 2016). Moreover, low temperatures lead to a decline in invertebrates due to emergence delay (Buse et al. 1999), while rain spells increase the difficulty of catching them (Avery and Krebs 2008; Dawson and Bortolotti 2000) and increase the foraging energy expenditure under harsh weather conditions (Cox et al. 2019; Dawson et al. 2005). Similarly high temperatures can also have detrimental effect on nestling growth and survival (Cunningham et al. 2013; Salaberria et al. 2014). Moreover, the presence of mineral surfaces as concrete or asphalt lead to an increase of local temperatures in cities also called urban heat island, which could represent a thermal challenge for urban birds compared to forest birds, especially during heat waves (but see Pipoly et al. 2022). Weather conditions can also amplify or limit the exposure to chemical pollutants. For example, a lack of wind can lead to the stagnation of aerial chemical pollutants (Liu et al. 2015), while heavy precipitation can lead to pollutants being washed off inert urban surfaces (e.g. roads and roofs) and being more easily mobilized in ecosystems (review by Gosset et al. 2016; Shinya et al. 2003). Similarly, weather conditions can also enhance the negative effects of chemical compounds. For example, in tree swallows, unusually high seasonal temperatures have been found to lead to lower reproductive success at mercury-polluted nesting sites, while the number of nestlings at the control sites increased with increasing seasonal temperatures (Hallinger and Cristol 2011). Similarly, a reduction in the surface tension of feathers due to contamination with organic pollutants can increase the permeability of feathers to water while decreasing their insulating properties, which induces additional physiological requirements for thermoregulation during cold weather events (Stephenson 1997). Since invertebrate communities and food availability are already poor in cities (Fenioglio et al. 2020), in addition to having higher levels of pollutant, unfavorable weather conditions could potentially increase urban stress, leading to a more deleterious effect on the reproductive success in cities than in rural or forest habitats. However, it is also possible that environmental constraints in urban areas are so strong that weather parameters only have a moderate effect on reproductive parameters compared to other factors, such as in house sparrows, where reproductive success was found to be consistently lower in cities, even between years with contrasting weather conditions (Seress et al. 2012).

The first aim of this study was to measure the reproductive success (measured as hatching date, clutch size, hatching rate, nestling number before fledge and fledging rate) of great tits in urban and forest habitats and to characterize each site in terms of pollution and food availability. Secondly, this study aimed to determine weather variations during the breeding period between years and to test if it affects the reproductive success depending on breeding sites. For

this purpose, we followed two different populations of great tits over four years in a city (Strasbourg, France) and a forest (La Wantzenau forest, 20 km away of Strasbourg city center). The great tit is considered an urban adapter and has been the subject of numerous studies concerning the impact of urban environmental factors on population dynamics (Wawrzyniak et al. 2020; Biard et al. 2017; Caizergues et al. 2021). To characterize the habitat at each site, we evaluated vegetal cover, prey availability, and pollution. For this last parameter, we measured different polychlorinated biphenyls, polycyclic aromatic hydrocarbons, and pesticides in the air, and trace metal elements in leaves, prey, and the feathers of birds. We expected a lower level of pollution and a higher vegetal cover and prey availability in the forest site compared to the urban site, and a higher reproductive success in the forest site. For the second aim of this study, concerning the relationship between weather parameters, reproductive success, and site, we evaluated the relationship between rainfall and temperature data and reproductive success. We expected greater differences between sites in years with unfavorable weather conditions (i.e. high precipitation rate and cold temperatures) due to the higher sensitivity of urban birds.

## Material and methods

### Study sites, animal model, and reproduction monitoring

This study was realized on the first broods of two populations of great tit in the Eurometropole of Strasbourg (region Alsace, France) for four years (2015, 2016, 2018, and 2019). The great tit is a relevant biological model because it can easily breed in artificial nest boxes, facilitating the biomonitoring of its reproduction. The studied populations were housed in artificial nest boxes (124 and 60 nest boxes installed within the urban site and the forest site, respectively); however, it is worth noting that the occupancy rate of the nest boxes in urban sites was lower than in forest site (see Appendix A1). The occupancy rate was comprised between 31 and 43% in the urban site whereas it was comprised between 53 and 68% in the forest site. Nest boxes in the urban site (Urban) were installed on urban parks ( $N_{2015}=2$ ,  $N_{2016}=34$ ,  $N_{2018}=78$ ,  $N_{2019}=73$ ) and tree-lined walkways ( $N_{2015-2016}=6$  and  $N_{2018-2019}=12$ ) in the city center of Strasbourg and in a residential area (called “La Robertsau”,  $N_{2015}=20$ ,  $N_{2016}=39$ ,  $N_{2018}=0$  and  $N_{2019}=39$ ; mean DD coordinates: 48.5793°, 7.7677°). See location details in Appendix A2. The forest site (Forest) was located 20 km north of Strasbourg’s city center (mean DD coordinates: 48.6480°; 7.8337°; see location details in Appendix A2) in La Wantzenau.

The reproduction of great tit was monitored at each site from the end of March to the end of May. For each occupied nest box, we monitored the first clutch only: clutch size, hatching date ( $\pm 1$  d), and nestling number (14–16 days old with day 0 considered as the day of hatching of the first chick) with regular visits to the nest boxes. The calculated hatching rate corresponds to the ratio of the number of hatchlings to the clutch size, including nests with desertion at the egg stage where the final clutch size is known. The calculated fledging rate corresponds to the ratio of the nestling number to the number of hatchlings for nests with at least one hatched nestling. The nestling number was estimated for all nests, including nests deserted at the incubation and rearing stages (the nestling number was 0) and was representative of global reproductive success during the first brood at each site. Females usually lay between 5 and 12 eggs per clutch, and the incubation lasted approximately 13 to 14 days. Nestlings usually leave the nest at 18 days of age and become independent after another three weeks. Adults were captured when nestlings were between 8 and 15 days old (to avoid nest desertion before 8 days of age or precocious fledging after 15 days of age). In 2016, for each bird caught, 2–3 breast covering feathers were collected with tweezers for each individual for pollutant analysis. Feathers were kept in a plastic bag and stored at  $-20^{\circ}\text{C}$  until analysis.

### Environmental parameters

#### Vegetation cover and vegetation sampling

The GPS coordinates of each nest box were used to estimate the vegetation cover over a 50 m radius around each nest in 2016 ( $N_{\text{Urban}}=76$  and  $N_{\text{Forest}}=60$ ). This distance was based on the typical home range of a couple of great tit (Demeyrier et al. 2016). Several categories of land usage were determined: no-vegetation surfaces (roads, bare rock, soil, and building), arable lands, high vegetation (forest, isolated trees, groves, and hedges), low vegetation (herbaceous), and water surfaces. For each nest, the percentage of each category was determined using QGIS from land use maps (50 cm resolution) created by the LIVE (Laboratoire Image, Ville, Environnement, UMR 7362 Strasbourg France). In addition, leaf samples were collected several times during the breeding season at each site in 2016. For urban site, leaf samples were collected three times in the city center and two times in the suburban zone of La Robertsau. For forest site three leaf samples were collected during breeding season. Each sample was composed of 10 leaves of different trees among the major tree species observed in both sites. Some of the tree species sampled were the same at both sites, although the choice was more limited in urban areas, where many exotic and ornamental tree species were found.

Tree species common on each sites were *Carpinus betulus*, *Acer pseudoplatanus*, *Fagus sylvaticus*. Tree species sampled only in forest site were *Quercus sp.*, *Fraxinus excelsior* and *Corylus avellana* and tree species sampled only in urban site were *Robinia pseudoacacia*, *Aesculus hippocastanum* and *Ulmus minor*. Samples were frozen at  $-80^{\circ}\text{C}$  until the measurement of pollutants.

### Prey availability

Great tits feed primarily on arthropods during the breeding period, while adults essentially feed their nestlings with caterpillars or spiders (Michalski et al. 2011). To estimate prey availability, invertebrates were sampled at each site three times during the breeding period in 2015 and six times in 2016 using a method modified from (Colas 1948). Invertebrates were collected by vigorously shaking a branch over a large umbrella (91.5 cm radius, that is, an area of  $2.63\text{ m}^2$ ). The operation was repeated under 10 trees of different species (the same tree species used for leaves sampling), randomly chosen on each site for an overall representation of the invertebrate composition of the site. Tree species composition varied slightly between years and between different invertebrate sampling on the same site. Collected invertebrates were classified into three categories: “caterpillars,” “spiders,” and “others,” and counted. Caterpillars and spiders were stored at  $-80^{\circ}\text{C}$  until the measurement of pollutants. Mean prey availability at each site was estimated by taking into account the average high vegetation area within the home range ( $A_{HV\text{mean}}$ ) ( $A_{HV\text{mean\_urban}} = 4779.0\text{ m}^2$ ,  $A_{HV\text{mean\_forest}} = 6901.1\text{ m}^2$ ) and the harvest area ( $A_{U\text{tot}}$ , i.e. ten times the umbrella area,  $2.63 \times 10 = 26.3\text{ m}^2$ ). Calculations were performed for each spider and caterpillar sampling. More precisely, the following equation was used:

$$\text{prey availability}_{(\text{count})} = \text{harvested preys}_{(\text{count})} \times \frac{A_{HV\text{mean}}}{A_{U\text{tot}}}$$

### Measurement of contaminants in biological samples

The concentrations of 15 trace metal elements and metalloids (TME) were analyzed in bird feathers ( $N_{\text{urban}} = 13$  individuals representing 12 nests and  $N_{\text{forest}} = 20$  in 18 different nests), leaves ( $N_{\text{urban}} = 5$  samples and  $N_{\text{forest}} = 3$ ), caterpillars ( $N_{\text{urban}} = 9$  and  $N_{\text{forest}} = 6$ ) and spiders ( $N_{\text{urban}} = 9$  and  $N_{\text{forest}} = 6$ ) collected from both the urban and forest sites in 2015 (invertebrates) and 2016 (feathers, leaves, invertebrates).

Before TME analysis, biological samples were prepared and mineralized. Between 5 and 10 mg of feathers samples were washed three times with NaOH concentrated at  $0.25\text{ mol L}^{-1}$  (3 mL) for 1 min. The feathers were then rinsed

three times with ultrapure water (3 mL) for 1 min. The final wash was performed with water (3 mL) for 1 h. Digestion was performed by heating the samples at  $60^{\circ}\text{C}$  with 65%  $\text{HNO}_3$  (1 mL) for 15 h in capped tubes. Ultrapure water was used to obtain a final volume of 5 mL. For vegetation, 200 mg of samples were subjected to the same digestion protocol without the washing step, and with 2 mL of 65%  $\text{HNO}_3$  with a final volume adjusted to 10 mL. Prey (spiders and caterpillars) were dried overnight at  $80^{\circ}\text{C}$ . The samples were then ground in a mortar, and 200 mg of dried samples were digested with 65%  $\text{HNO}_3$  (2 mL) for 15 h at  $60^{\circ}\text{C}$ . The final volume was adjusted to 10 mL using ultrapure water. For all samples, blanks were prepared and measured in the same manner to control for contamination from reagents and laboratory environment.

The concentrations of the following elements were determined using inductively coupled plasma mass spectrometry (ICP-MS, Agilent 7700): aluminum (Al), arsenic (As), barium (Ba), cadmium (Cd), cerium (Ce), chromium (Cr), cobalt (Co), copper (Cu), lead (Pb), molybdenum (Mo), nickel (Ni), rubidium (Rb), strontium (Sr), vanadium (V), and zinc (Zn). The corresponding concentrations were determined using a calibration curve prepared by the dilution of a multi-element certified standard ( $10\text{ }\mu\text{g mL}^{-1}$ , CPI International). Indium 10 ppb ( $1000\text{ }\mu\text{g mL}^{-1}$ , CPI International) was used as an internal standard (see Appendix B for the operational conditions and instrumental limits of detection of the ICP-MS analysis). The specificity of the analytical methods was evaluated by recovery measurements of the spiked samples. The recovery values were 90–110% for all the elements. Results are expressed in  $\text{mg kg}^{-1}$  of total weight for feathers and vegetation samples and in  $\text{mg kg}^{-1}$  of dry weight for prey.

### Air pollution

The air contaminants were trapped in each site with an XAD-2<sup>®</sup> passive air sampler and renewed every two weeks during the reproduction of birds (end of March to end of May) in 2015 and 2016. Due to the heterogeneity of the urban matrix, two samplers were placed simultaneously: one in the city center and one in the residential area of La Robertsau. For the forest site, only one sampler was placed at a time. It represents three samplings per year in 2015 and 2016 for the forest site and six (2015) or seven (2016) sampling for the urban site. Contaminants were extracted using the methodology developed by Al Dine et al. (2015) and Lévy et al. (2018, 2020). This type of sampler allowed for the detection of four types of pollutants classified into eight categories according to their characteristics and toxicity: polychlorinated biphenyl (PCB) separated in dioxin-like PCBs (DL-PCBs) and non-dioxin-like PCBs (NDL-PCBs), polycyclic aromatic



hydrocarbons (PAHs), organochlorine pesticides (OCCs), and non-organochlorine pesticide components split into insecticides, herbicides, and fungicides (see Appendix C1 for a list of the pollutants in each category). For each sampling, the concentrations of pollutants in the same category were summed. Among the 169 air pollutants (measured in  $\text{ng m}^{-3}$ ) we aimed to identify, 89 had concentrations above their quantification limits (Lévy et al. 2018).

### Weather conditions and temperature

A temperature logger (Thermochron iButton; Embedded Data Systems<sup>®</sup>) was placed under one nest box at the forest site, while two nest boxes were used at the urban site (one in the city center and one in the residential area of La Robertsau), protected from the sun, to measure ambient temperature (1 measure/h) between April and May in 2015 and 2016, but not in 2018 and 2019. Temperatures showed no significant differences between sites during the total reproductive period (LM:  $F = 0.946$ ,  $p = 0.39$ ). Temperature data from each site obtained with loggers were similar to those recorded by the logger of the weather station of Météo-France (station N°67,482,001, 48.5819444°, 8.2688889°DD) in the city (Mann–Whitney–Wilcoxon test: Urban (center),  $W = 4019$  and  $p = 0.21$ ; Urban (residential),  $W = 3417$  and  $p = 0.93$ ; Forest,  $W = 3571$  and  $p = 0.65$ ). Therefore, hourly temperature and hourly precipitation data provided by Météo-France in 2015, 2016, 2018, and 2019 were used for the following analyses. To transform hourly data in daily data, we calculated the mean daily temperature and the daily range of temperature and, for precipitations; we sum up the total daily precipitations. For each occupied nest box, two periods were defined: the incubation period (14 days before hatching) and the rearing period (14 days after hatching, hatching date included). For nest failing before hatching and for which laying date was determined with certitude, the incubation period was calculated as 14 days after the date of laying of the last egg (laying date of 1<sup>st</sup> egg + clutch size). For each period and for each nest, the average temperature ( $T_{\text{mean}}$ , in °C) and average daily temperature range ( $T_{\text{range}}$ , in °C) were calculated. The average daily rainfall rate (RR, in mm) and the number of rainy days (NbRD with a rainy day considered as a day with  $\text{RR} > 0$ ) during each period were also calculated. More details on value of each weather parameter and comparison of loggers and weather station parameters are provided in appendix C.5.

### Statistical analyses

Statistical analyses were performed using R (version 3.6.2) in RStudio (R Development Core Team 2021). The

hatching date was converted in relative days from March 1<sup>st</sup> and scaled for the analyses including this parameter as an explanatory variable. The significance level alpha was set at 0.05. Predated nests or nests with dead adults inside were excluded from the analyses ( $N_{\text{urban}} = 2$  and  $N_{\text{forest}} = 8$ ; see Appendix 1 for more details).

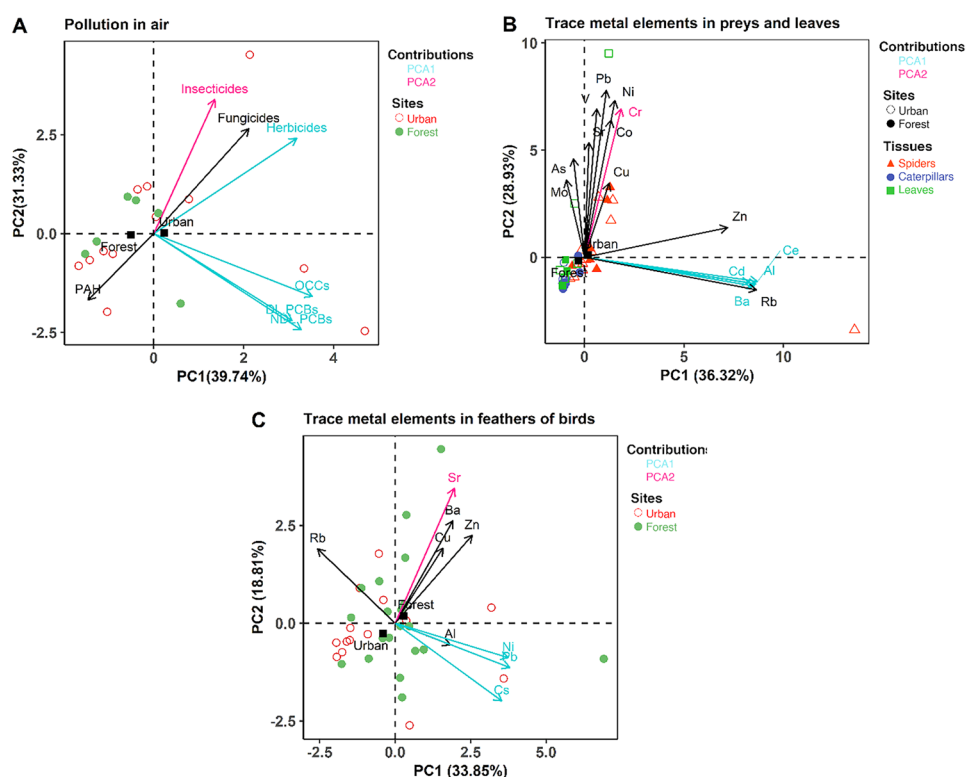
### Differences in environmental parameters between sites

Aerial pollutants, the TME concentrations in the biological tissues (bird feathers leaves and invertebrates), and vegetation cover between urban and forest sites were examined using principal component analyses (PCA) (“FactoMineR” package, Lê et al. 2008). The values were scaled before the analyses. Missing values for feathers (26%), leaves (14%) and prey (9% for spiders and 10% for caterpillars) due to concentrations below the limit of detection (LOD) were imputed by the value of  $\text{LOD}/\sqrt{2}$  (Helsel 2011). Four separate PCAs were performed: (i) air pollution, (ii) feather pollutants, (iii) leaves and invertebrates (caterpillars and spiders) pollutants, and (iv) vegetation cover (see Appendix C for more details). The percentages of variation explained by the first two axes, PC1 and PC2, of the different PCAs were 71.1% for the air pollution PCA (Fig. 1A); 52.7% for the TME concentration in bird feathers PCA (Fig. 1C), 65.3% for the TME concentration in leaves and invertebrates PCA (Fig. 1B), and 64.3% for the vegetation cover PCA (Fig. 2A). Differences between sites along the PCA axes were tested using the Wilcoxon test for aerial pollutants and vegetal cover, and the Kruskal–Wallis rank sum test with Holm correction (function “dunn.test (method = “holm”)” in R) for biological tissues. Differences in prey availability were tested using linear mixed models with the interaction between the type of prey (i.e. caterpillars or spiders) and the site as an explanatory variable, and the sampling ID as a random variable to take into account tree species variation during invertebrate collection. The normality of the residuals was verified using the Kolmogorov–Smirnov test and heteroscedasticity with a Bartlett test. *Post-hoc* differences between sites and between types of preys were tested using Tukey’s test.

### Differences in reproductive outputs between sites

Generalized linear models (GLMs) with the Poisson family (link function: “log”) followed by type III Wald tests were used for clutch size, nestling number before fledge, and hatching date. GLM with the binomial family was used for the hatching and fledging rates (see reproduction monitoring for definition, link function: “logit”). The models included the site, the year and the interaction between site and year as the explanatory variables. Non-significant interactions were excluded from the models if  $p > 0.10$ . The overdispersion of

**Fig. 1** Representation of principal component analyses of pollution signature in **A** air, **B** prey and leaves, and **C** bird feathers in urban and forest sites. The variables contributing the most to each axis ( $\cos^2 > 0.5$  and/or contribution  $> 20\%$ ,  $\cos^2$  corresponds to projection quality of the variable on the given dimension) are shown in different colors, and the mean coordinates of each site are represented by black squares. Details of each variable contribution are provided in Appendix C

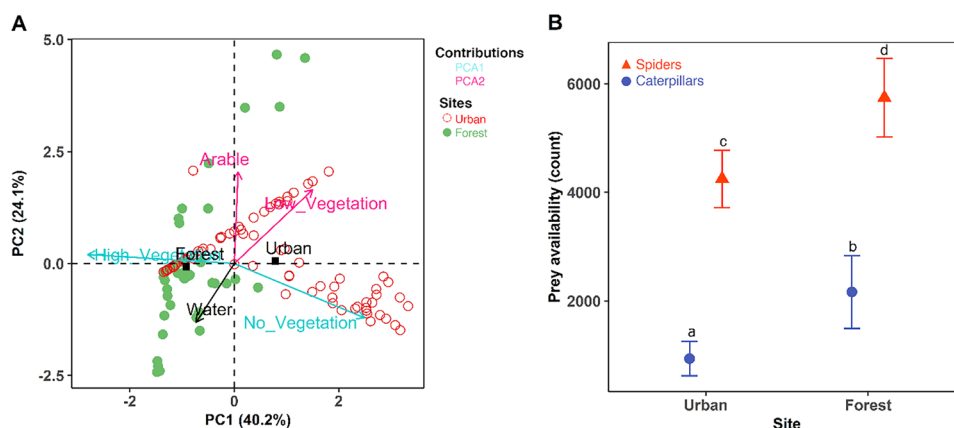


all models was verified (ratio model deviance on model df residual). If data were over-dispersed (ratio  $> 1$ ), we used quasi-binomial or quasi-Poisson families. Some nests were excluded from the models due to missing or imprecise data (two nests excluded for clutch size and six for hatching and fledging rate, nestling number, and hatching date). The hatching date and fledging rate were calculated, excluding nests in which no eggs hatched ( $N=26$ ). The normality of the residuals was verified using the Kolmogorov–Smirnov test and heteroscedasticity with a Bartlett test. *Post-hoc* differences between sites per year and between years per site were tested using Tukey's test.

### Effect of weather on reproduction

Weather parameters calculated for the incubation and rearing period of each nest were probed using PCA ("FactoMineR" package). The values were scaled before the analyses. The first two axes, PC1 and PC2, of weather PCA explained 75.5% of the inter-annual variation. These two components were used as composite variables to describe the weather conditions during reproduction for each nest. Differences between years in PC1 and PC2 were tested using the Kruskal–Wallis rank sum test with Holm correction (function "dunn.test (method = "holm")" in R). These

**Fig. 2** **A** Principal component analysis of vegetal cover in the vital domain of reproductive birds and **B** invertebrate availability (count). See Appendix C4 for details of each variable contribution for A. In B, different letters represent significant differences in post-hoc tests between sites. Results are shown as means and standard errors



components were further used in generalized linear mixed models (Poisson or binomial depending on parameters; see above for more details) followed by type III Wald tests, with reproduction parameters (nestling number, hatching, and fledging rate). For some nests included in the reproduction parameter analysis ( $N=8$ ), the weather parameters could not be calculated because of the unknown hatching date. These nests were therefore excluded from the analyses. The analyses included PC1 and PC2 in interaction with site as explanatory variables, the hatching date as a covariable, and the year as a random effect. For hatching models, only PC1 was included in the models because PC2 was mainly related to temperature during rearing (see Results for more details). Non-significant interactions were removed sequentially from the models if  $p > 0.10$  to show marginal significance if it exist.

## Results

### Environmental parameters in urban and forest sites

For air pollution, the OCCs, herbicides, and PCBs (NDL and DL) were identified as the major contributors to PC1, whereas the insecticides were the main contributors to PC2 (Fig. 1A and Appendix C1). No significant differences were observed between sites in PC1 (Wilcoxon:  $W=34$ ,  $p=0.70$ ) or PC2 (Wilcoxon:  $W=43$ ,  $p=0.77$ ).

For the TME concentrations in the leaves and invertebrates, Cd, Al, Ce and Ba were identified as the major contributors to PC1, whereas Cr was the major contributor to PC2 (Fig. 1B, see also Appendix C2). No significant differences were observed between sites (Wilcoxon for PC1:  $W=183$ ,  $p=0.91$  and PC2:  $W=192$ ,  $p=0.91$ ). However, significant differences were observed between leaves, spiders and caterpillars metal concentrations (Fig. 1B PC1: Kruskal-Wallis,  $\chi^2=22.08$ ,  $p<0.001$  and PC2: Kruskal-Wallis,  $\chi^2=14.37$ ,  $p<0.001$ ). PC1 separated spiders from caterpillars and leaves which contained higher concentration of Cd, Al, Ce and Ba ( $p_{\text{caterpillars-spiders}} < 0.001$  and  $p_{\text{spider-leaves}} = 0.01$  and  $p_{\text{leaves-caterpillars}} = 0.30$ ). The PC2 separated spiders from caterpillars. Concentrations of Cr are higher in spiders than in caterpillars ( $p < 0.01$ ). No difference was observed between spiders and leaves concentrations nor leaves and caterpillars concentrations ( $p_{\text{leaves-spiders}} = 0.41$  and  $p_{\text{caterpillars-leaves}} = 0.06$ ).

For the TME concentrations in bird feathers, Ni, Cs and Pb were identified as the major contributors to PC1, whereas Sr was the major contributors to PC2 (Fig. 1C, see also Appendix C3). There were no significant site effects on either axis (Wilcoxon for PC1,  $W=87$  and  $p=0.07$ ; PC2,  $W=124$  and  $p=0.59$ ).

The vegetation cover differed significantly between sites on both PC1 ( $W=4240.5$ ,  $p<0.01$ ) and PC2 ( $W=2949.5$ ,  $p=0.047$ ). PC1 was negatively related to the high vegetation surfaces and positively related to the non-vegetal surfaces (Fig. 2A, see Appendix C4). The major contributors of PC2 were arable and low vegetation surfaces (Fig. 2A, see Appendix C4). The urban site was mainly characterized by a high proportion of non-vegetal surfaces on PC1 and, to a lesser extent, by a higher proportion of low vegetation and arable surface on PC2. The forest site was mainly characterized by high vegetation.

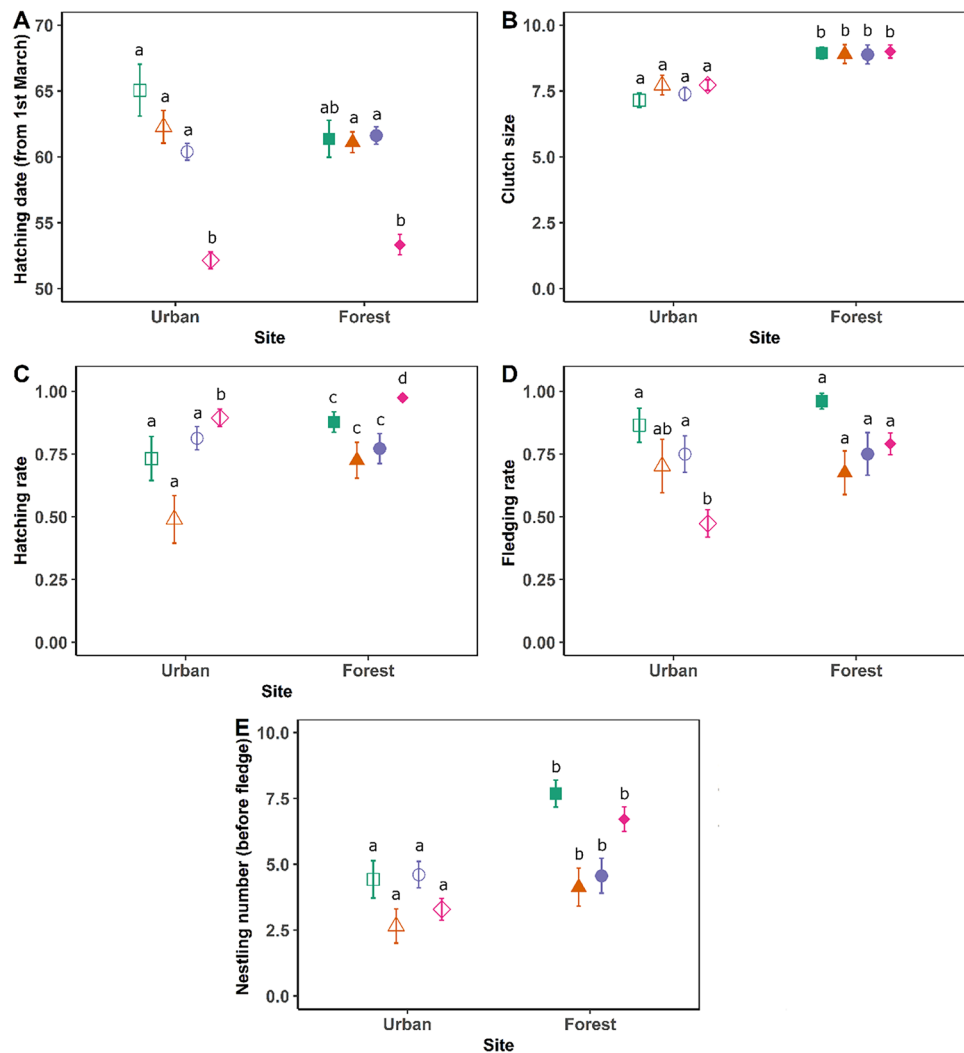
Regarding prey availability, the number of prey was significantly different between the sites (LMM,  $F_{\text{site}}=73.02$ ,  $p<0.001$ , Fig. 2B), and between the type of prey (LMM,  $F_{\text{type}}=35.10$ ,  $p<0.001$ , Fig. 2B). The interaction between the site and type of prey was not significant (LMM,  $F_{\text{site*type}}=0.07$ ,  $p=0.79$ ). The average number of prey was lower at the urban site than at the forest site (Tukey,  $p=0.02$ , Fig. 2B), and the average number of spiders was higher than the average number of caterpillars (Tukey,  $p<0.001$ , Fig. 2B).

### Differences in reproductive outputs between sites and years

The interaction between site and year was significant for the hatching date (Table 1 and Fig. 3A). For a given year, no difference was observed between sites (Tukey, all  $p>0.14$ ) but inter-annual differences varied between sites. Earlier hatching dates were observed in 2019 compared to all other years in urban site (Table 1, Tukey,  $p_{2019\text{-other years}} < 0.001$  and all other  $p>0.62$ ). For forest site, similar differences were observed, except for 2015 (Tukey,  $p_{2019\text{-other years}} < 0.005$  and  $p_{2019-2015} > 0.07$ , Fig. 3A). The clutch size was significantly different between the sites but not between the years (Table 1), with a smaller clutch for urban breeders (Tukey,  $p<0.001$ , Fig. 3B for clutch size).

The site effect was significant for the hatching rate, lower in urban compared to forest site. Hatching rate varied significantly between years: it was higher in 2019 than in other years (Tukey,  $p<0.005$ , Table 1, Fig. 3C). The interaction between site and year was significant for the fledging rate (Table 1). For a given year, the fledging rate was not different between the urban and forest site, except for 2019. A lower fledging rate was observed in the urban site in 2019 compared to urban site in 2015 (Tukey,  $p=0.03$ ) and 2018 (Tukey,  $p=0.03$ ) and compared to the forest site (Tukey,  $p<0.001$ ) whatever the years. A lower nestling number before fledge was observed in urban sites compared to the forest site (Tukey,  $p<0.02$ ) whatever the years.

**Fig. 3** Reproductive parameters for birds at urban and forest sites across the years. For post-hoc tests, we tested differences between years for a given site and also differences between sites for a given year. Different letters illustrate significant differences. Results are shown as means and standard errors. Squares, triangles, circles, and diamonds represent 2015, 2016, 2018, and 2019 respectively



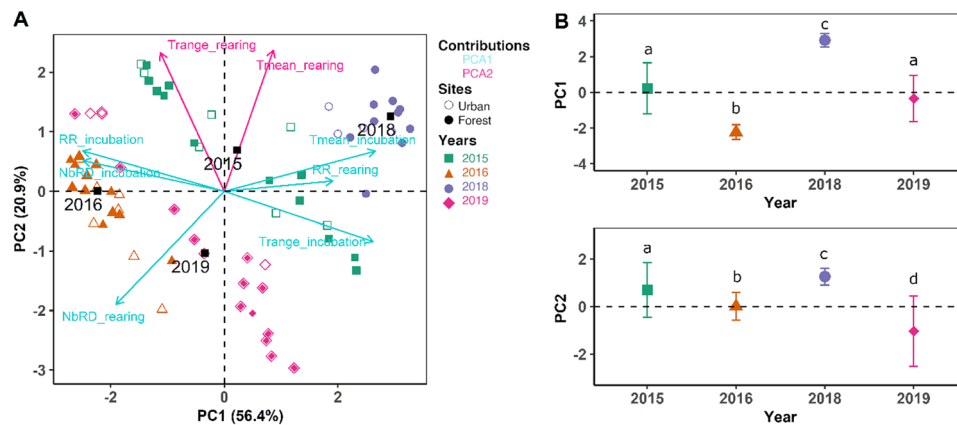
### Relationship between weather and reproduction parameters

First, the weather parameters during the incubation and rearing periods according to years were analyzed using the two axes of the PCA. PC1 was found to be negatively correlated with temperature ( $T_{\text{mean}}$  and  $T_{\text{range}}$ ) during incubation and RR during rearing and positively related to rain (RR during incubation, NbRD during incubation, and NbRD during rearing, Fig. 4A, see Appendix C.5). PC2 was positively correlated with temperature ( $T_{\text{mean}}$  and  $T_{\text{range}}$ ) during rearing. Significant differences between years were revealed for both PC1 and PC2 (Fig. 4B, Kruskal-Wallis for PC1,  $\chi^2 = 160.91$  and  $p < 0.001$ ; Kruskal-Wallis for PC2,  $\chi^2 = 95.81$  and  $p < 0.001$ ). Years were significantly different on PC1, except in 2015 and 2019, which were not different ( $p_{2015-2019} = 0.11$  and all others  $p < 0.001$ ). All years were different for PC2 (all  $p < 0.0053$ ). These results indicate that the year 2015 was characterized by high temperatures during rearing, 2016 by low temperature

during incubation and high precipitation during the reproduction period (incubation and rearing). Year 2018, in opposition to the year 2016 is characterized by high temperatures during reproduction period, low precipitation during the incubation and some occasional rainfall during rearing. Year 2019 is characterized by mild temperatures and rainfall during incubation, and low temperatures during the rearing period.

Next, we analyzed the link between breeding parameters and weather principal components. There was a significant interaction between the site and PC1 for the hatching rate. However, for both sites, correlations between hatching rate and PC1 were not significant ( $p_{\text{urban}} = 0.95$ ,  $p_{\text{forest}} = 0.11$ ). The fledging rate and the nestling number before fledge were not significantly correlated with PC1 (Table 2, see also Appendix E); however, these parameters were significantly correlated with the interaction between PC2 and site (Table 2 and Fig. 5). The fledging rate and the nestling number increased with increasing PC2 (positively correlated to temperature during rearing) in the urban site





**Fig. 4** Representation of **A** PCA of weather parameters during the reproduction of birds and **B** inter-annual differences on PC1 and PC2. See Appendix E for details of each variable contribution for A. Mean coordinates of each site are represented by black squares.  $T_{mean}$  corresponds to average temperatures ( $^{\circ}\text{C}$ ),  $T_{range}$  corresponds to average

daily temperature range ( $^{\circ}\text{C}$ ), RR corresponds to the average daily rainfall rate (in mm) and NbRD the number of rainy days ( $RR > 0$ ) during rearing or incubation. In B, different letters represent significant differences in post-hoc tests. Results are shown as means and standard deviations

(Tukey,  $p = 0.02$  for fledging rate,  $p = 0.01$  for nestling number) but not in the forest site (Tukey,  $p > 0.05$ ).

## Discussion

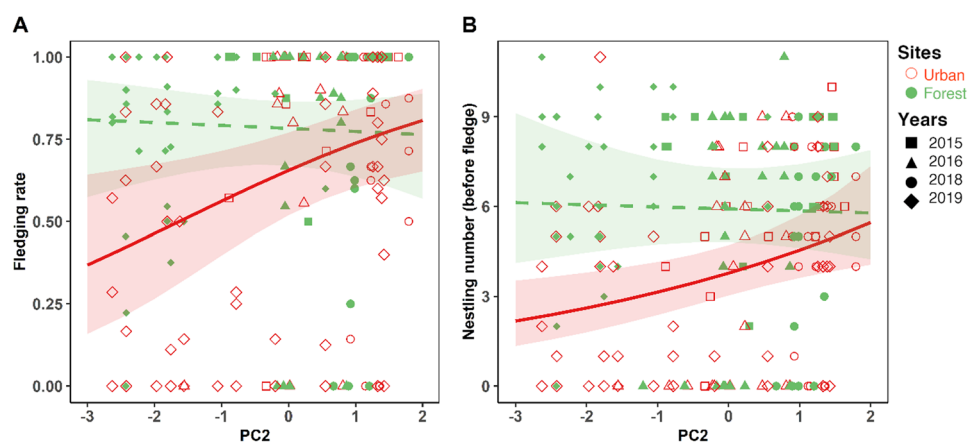
The first aim of this study was to evaluate the differences in reproductive success between urban and forest sites for which multiple environmental parameters were measured, including chemical pollution, vegetation cover and food availability. The second aim was to test the hypothesis of the higher sensitivity of urban birds to harsh weather conditions, leading to year-dependent variations in reproductive success differences between sites.

### Reproductive differences between urban and forest populations: role of environmental parameters

For a given year, our study revealed that the hatching date did not differ between urban and forest site, contrary to

previous studies (Bailly et al. 2016; Charmantier et al. 2017; Wawrzyniak et al. 2015b). Some studies have shown that advanced hatching dates in cities are related to the heat halo associated with concrete surfaces (Chmielewski et al. 2013). However, in the present study, no variation in temperature was observed between the urban and forest sites during reproduction, which could explain the similar hatching date found between sites. The urban heat halo is mitigated by the presence of greenery (Onishi et al. 2010; Price et al. 2015) and most of the nest boxes in our study were placed in urban parks maybe explaining the lack of temperatures differences. Moreover, we only measured temperature during the reproduction. It is possible that the temperature differences between our two sites are more pronounced later in the season in summer or even in winter. The clutch size and hatching rate of urban birds in our study were lower than those of forest birds, regardless of the year and weather parameters, as observed in several other studies on great tits. Some studies have reported on the impact of pollutant exposure on these breeding parameters (Scheuhammer

**Fig. 5** Correlation between PC2 of PCA with weather parameters and **A** fledging rate and **B** nestling number before fledge. Significant slopes are represented in solid lines, while non-significant slopes are represented with dashed lines



**Table 1** Results of statistical analyses of reproduction parameters between urban and forest birds during four different years

|                                 | N     | Site         |                  | Year         |                  | Site*Year   |                  |
|---------------------------------|-------|--------------|------------------|--------------|------------------|-------------|------------------|
|                                 |       | F (df)       | p                | F (df)       | p                | F (df)      | p                |
| Hatching date (From March 1st)  | N=204 | 4.98 (1197)  | <b>0.03</b>      | 37.84(3197)  | <b>&lt;0.001</b> | 3.86 (3193) | <b>0.01</b>      |
| Clutch size                     | N=230 | 45.08 (1227) | <b>&lt;0.001</b> | 0.56 (3227)  | 0.64             |             |                  |
| Hatching rate                   | N=226 | 6.34 (1212)  | <b>0.012</b>     | 12.87 (3212) | <b>&lt;0.001</b> |             |                  |
| Fledging rate                   | N=198 | 2.26 (1191)  | 0.13             | 6.47 (3191)  | <b>&lt;0.001</b> | 5.06 (3191) | <b>&lt;0.001</b> |
| Nestling number (before fledge) | N=224 | 6.45 (1217)  | <b>0.01</b>      | 2.08 (3217)  | 0.10             | 2.53 (3217) | 0.06             |

Significant values are shown in bold

*df* degree of freedom. These results were obtained using generalized linear models followed by the type III ANOVA. See the Methods section for further details

1987; Koivula and Eeva 2010; Hellou et al. 2013). No differences in pollutant concentration was observed between the urban and forest sites, neither for air pollutants nor for TME pollution in leaves, prey, and feathers, contrary to studies that showed a higher concentration of TME in the feathers of urban blackbird (*Turdus merula*) (Scheifler et al. 2006; Meillère et al. 2016) and house sparrow (Bichet et al. 2013) in other cities. However, no pollutant difference between urban site and forest is in line with the result of Chatelain et al (2021a) that has shown little differences in metal concentrations between urban parks and adjacent forests.

Moreover, the concentrations measured in Strasbourg were much lower than those reported in other cities. For example, the Pb feather concentration obtained in Strasbourg (on average 2.53 mg/kg) was much lower than that found in sparrows in other French cities, such as Paris (19.54 mg/kg), Gennevilliers (18.70 mg/kg), or Berk (6.7 mg/kg) (Bichet et al. 2013), suggesting that the city of Strasbourg could be a low metal-polluted site. Exposure to pollutants, therefore, does not appear to be a reason for the reproductive differences observed between urban and forest sites. However, the sample size of this study was small, and further research is required to validate this hypothesis (e.g. by increasing the number of replicates and distinguishing between urban and

suburban areas, for example). Moreover, contaminants are concentrated in new feathers formed during the molting of individuals, which generally occur at the end of the breeding period, which was outside of our study interval, as first brood interval was examined in this study. Therefore, metal concentrations measured in this study reflect pollution levels at adult's previous breeding ground. The possibility that adults may disperse between the two breeding seasons cannot be dismissed even though we have not yet found any individuals banded in the forest and found in town or vice versa. Other environmental constraints, such as noise or light pollution, can cause chronic stress in individuals, leading to the production of reactive oxygen species (Isaksson 2015) and oxidative stress. Chronic exposure to a stressful environment can alter the fertility of individuals, and thus the number of laid eggs for females (Isaksson et al. 2008; Bize et al. 2008; Wawrzyniak et al. 2020) or egg fertilization for males (Vallverdú-Coll et al. 2016; Mora et al. 2017; Bisht et al. 2017). The smaller clutch size and the lower hatching rate could be therefore related to a lower egg quality in the city, as observed in other studies on urbanization (Isaksson et al. 2008; Toledo et al. 2016). Stress constraints could also increase the corticosterone concentration (Meillère et al. 2016; Marasco et al. 2017), reduce parental care (Angelier

**Table 2** Results of statistical analyses of reproduction parameters with PC1 and PC2 of weather parameters PCA

| Variables     | Hatching rate       |             | Fledging rate       |             | Nestling number (before fledge) |                  |
|---------------|---------------------|-------------|---------------------|-------------|---------------------------------|------------------|
|               | N=218               |             | N=198               |             | N=217                           |                  |
|               | X <sup>2</sup> (df) | p           | X <sup>2</sup> (df) | p           | X <sup>2</sup> (df)             | p                |
| Site          | 11.31 (1210)        | <b>0.03</b> | 6.14 (1189)         | <b>0.04</b> | 29.86 (1199)                    | <b>&lt;0.001</b> |
| PC1           | 0.06 (1210)         | 0.80        | 0.04 (1189)         | 0.82        | 0.22 (1199)                     | 0.64             |
| PC2           |                     |             | 6.25 (1189)         | <b>0.01</b> | 8.01 (1199)                     | <b>0.004</b>     |
| Hatching date | 4.02 (1210)         | <b>0.05</b> | 0.32 (1189)         | 0.57        | 0.054 (1199)                    | 0.81             |
| Site*PC1      | 6.25 (1210)         | <b>0.01</b> |                     |             |                                 |                  |
| Site*PC2      |                     |             | 5.57 (1189)         | <b>0.03</b> | 7.37 (1199)                     | <b>0.007</b>     |

Significant values are shown in bold

*df* degree of freedom. These results were obtained using generalized linear models followed by the type III Wald test. See the Methods section for further details

\* Represent variable interactions in models

and Chastel 2009), potentially leading to nest desertion, in favor of parental survival. A lower fecundity due to physiological stress can also be proposed (Bize et al. 2008).

In this study we also highlighted lower prey availability in the city. The urban environment in Strasbourg was mainly characterized by low vegetal and non-vegetal surfaces. Surprisingly, there was also a notable part of arable surfaces, probably due to the presence of fields in the suburban part of Strasbourg (*La Robertsau*). Reduced vegetation cover in cities has a direct impact on invertebrate populations (Thomas et al. 2001; Jones and Leather 2012). The number of preys available for each nest on the urban site in our study was, on average, two times less than that for the forest site. This lack of prey is likely to impose an increased effort on urban adult birds to search for prey. Urban birds have to search over a greater distance (Bonier et al. 2007; Stauss et al. 2005), which increases the time spent searching for preys (Jarrett et al. 2020; Naef-Daenzer and Keller 1999) and increases the energy expenditure associated with foraging (Hinsley et al. 2008). The association between the amount of food during egg laying and clutch size in cities has already been demonstrated in great tits (Wawrzyniak et al. 2020, 2015a) and blue tits (Marciniak et al. 2007). Some studies point to the fact that low food availability leads to a reduction in clutch size due to a suboptimal diet (Wawrzyniak et al. 2015b) or to increased competition for resources in the city (Chamberlain et al. 2009). A study testing reproductive selection in the city showed that birds with larger clutches in city have better fitness which tends to confirm that smaller clutches in city result from food limitations in urban areas (Caizergues et al. 2018). Yet, a smaller clutch size requires less food after hatching, this would allow parents to invest enough to ensure the survival of their young (Martin et al. 2000). Our results showed that while the nestling number before fledge was generally lower at the urban site than at the forest site, the fledging rate did not differ between the two environments (except in 2019). This suggests that the reduced clutch size in urban sites could be an adaptation to environmental constraints (Boyce and Perrins 1987) and that different reproductive strategies exist between urban and forest areas and, more generally, a difference in the pace of life (Charmantier et al. 2017; Sepp et al. 2017). Urban individuals tend to have a slower pace of life and invest more in their own survival than in reproduction, thus laying smaller clutches and rearing fewer chicks than their counterparts in the forest. This hypothesis on the pace of life should be tested by simultaneously measuring several life history traits. This hypothesis could also explain that clutch size is the only reproductive parameter that did not vary between years. Similar results were also observed in

a long-term study of the same species (Wawrzyniak et al. 2020, 2015a).

### **Reproductive differences between urban and forest populations: inter-annual variations and role of weather parameters**

Interestingly, the year 2019 was characterized by an earlier hatching date (except with 2015 in forest) and a higher hatching rate in both sites. The hatching date was, on average, 8–10 days earlier than in other years in urban site and earlier than in 2016 and in 2018 in forest site. The year 2019 seemed to be characterized by higher winter temperatures than the seasonal averages (meteoFrance.fr 2021). Many studies have reported on advances in breeding following a significant increase in temperature in late winter or warmer spring (Charmantier et al. 2008; Schaper et al. 2012). An advance in bird reproduction allows a match or a reduction in the mismatch between the food peak and the period of higher energetic nestling needs. This earlier start of reproduction in 2019 was also associated with a higher hatching rate compared to other years. The good hatching rate in 2019 would therefore probably be linked to favorable weather conditions during incubation (i.e. a combination of mild temperatures and low precipitations), contrary to 2016, which was characterized by cold and wet weather. Cold weather could lead to difficulty in maintaining egg temperatures above the optimal growth temperatures, leading to embryonic growth delays and mortality (Durant et al. 2013; Webb 1987) and increased female energy expenditure during incubation (Bryan & Bryant 1999). This results in a trade-off between self-maintenance and incubation time, leading to nest desertion. However, weather parameters alone do not explain all observed differences, especially between 2019 and 2015, because the two years had comparable weather conditions during incubation. This suggests that other environmental parameters, such as the fluctuation of prey availability that are not dependent on weather parameters, may also influence the hatching rate.

For the fledging rate, our study revealed differences between years and within sites for the same year as in 2019. This result could be directly related to inadequate food availability, as found in several other studies (Seress et al. 2012; Caizergues et al. 2021). Interestingly, contrary to our initial hypothesis that proposed a greater inter-annual variation in the reproductive success of urban birds due to the strongest effect of weather, low inter-annual variations in nestling number before fledge were observed for each site. Nestling number remained constantly lower in urban site whatever the year. Moreover, the mean nestling number before fledge in cities was never above 5 and ranged from a mean of 2.6 to 4.6 nestlings, depending on the years, whereas it ranged

from 4.1 to 7.7 nestlings in the forest site. Considering that the clutch size is lower in the urban site, this result could suggest that urban birds would invest more in their own survival than parental care, as described in the slow pace of life theory. However, both nestling number before fledge and fledging rate were positively correlated with PC2 weather only in urban areas and not in the forest site. The nestling number calculated here represents the reproductive success of breeders, including all failed nests (incubation or rearing), whereas the annual mean fledging rate is representative of nestling mortality during rearing (excluding the deserted nests during incubation). In the present study, high temperatures during the rearing period increased fledging in the city, but also increased their survival. A lower urban fledging rate was observed in 2019, the coldest of the four years (during rearing). However, no difference was observed at the forest site for this parameter. Previous studies have already shown a positive correlation between nestling survival with temperature, and a negative correlation with heavy rains (Dawson et al. 2005; Dawson and Bortolotti 2000; Eeva et al. 2002; Kosicki 2012; Krijgsveld et al. 2003). Low temperatures, especially when chicks are thermo-dependent (Dawson et al. 2005), and the negative impact of heavy rain on prey availability and catching (Avery and Krebs 2008; Dawson and Bortolotti 2000), led to nestlings suffering from hypothermia and/or starvation, increasing the risk of death. Adults may also have more difficulties meeting their own needs (Öberg et al. 2015). Unfavorable climatic conditions can also increase corticosterone concentrations in parents (Citrule et al. 2017; Wingfield 1988) which enhances the probability of desertion (Love et al. 2004; Thierry et al. 2013). The food limitation observed in urban sites and others environmental constraints (e. g. noise and light pollution) in urban areas may contribute to exacerbate effect of unfavorable weather during reproduction, leading to a decrease in urban productivity and higher nestling mortality. To really understand the link between weather parameters, food availability and reproduction it could be interesting to follow the annual variations of prey abundance in both sites.

To conclude, in a medium-sized city, such as Strasbourg, the constraints linked to urbanization seem to be mainly related to the reduction of the vegetation cover, which limits the availability of food for insectivorous passerines, compared to other cities where birds also have to deal with higher levels of chemical pollution. Our results therefore highlight that lower food availability could considerably limit the nestling number, especially during harsh years. The lower nestling numbers and poor inter annual variation in urban environments for this parameter, suggests a threshold of breeding performance that parents cannot exceed. However the lower productivity would lead to a decline in the population of great tits in cities, particularly if one tough year followed another. It is worth

noting that a lower nestling number may be compensated by a higher survival, especially in winter. To determine whether urban populations are sustainable or whether they are maintained due to continuous immigration from rural areas, there is a need to measure the rates of survival, recruitment, and immigration. In addition, our results showed negative impact of cold weather on reproductive success of birds but it also known that warm temperatures and heat wave can have negative consequences on birds reproduction impacting both birds fertility and nestling development (Pipoly et al. 2013; Salaberria et al. 2014; McCowan and Griffith 2021). Long-term studies are therefore necessary to understand all the aspects of the additive effects of weather conditions and the urban environment, especially during the rearing of offspring.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11252-022-01305-9>.

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**Authors' contributions** Conceptualization: S. Massemin; Methodology: A. Boos, M. Millet, S. Zahn, P. Ronot And I. El Masoudi; Validation: A. Saulnier, J. Bleu, A. Boos, M. Millet, S. Zahn, P. Ronot, I. El Masoudi And S. Massemin; Formal Analysis: A. Saulnier, J. Bleu, And S. Massemin, Investigation: A. Saulnier, J. Bleu, A. Boos, M. Millet, P. Uhlrich, E. R. Rojas, P. Ronot, I. El Masoudi, S. Zahn And S. Massemin; Resources: A. Boos, M. Millet, S. Zahn And S. Massemin; Data Curation: A. Saulnier, J. Bleu, P. Uhlrich, E. R. Rojas And S. Massemin; Writing-Original Draft Preparation: A. Saulnier, J. Bleu And S. Massemin; Writing-Review And Editing: A. Saulnier, J. Bleu, A. Boos, M. Millet, S. Zahn, P. Ronot, I. El Masoudi, E. R. Rojas, P. Uhlrich, M. Del Nero And S. Massemin; Visualization: A. Saulnier, J. Bleu And S. Massemin; Supervision: J. Bleu And S. Massemin, Project Administration: S. Massemin; Funding Acquisition: M. Del Nero And S. Massemin.

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**Data availability** All data from this study are part of a long-term project and will be available on demand.

**Code availability** Not applicable.

## Declarations

**Ethics approval** This article does not contain any studies with human participants performed by any of the authors. This work is in accordance with the French legislation concerning the capture and the biological sampling of wildlife. SM, JB and PU received ringing licenses



and authorizations for blood and feather sampling from the CRBPO (National Museum of Natural History) as part of a research program led by SM (PP N°673). The protocol has been approved by the French national ethical committee n°35 and approved by the French ministry of research (project APAFIS# 9160–2017030316182730 v2).

**Consent to participate** Not applicable.

**Consent for publication** All authors have given their consent to the publication of this article.

**Conflicts of interest** The authors declare that they have no conflict of interest.

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